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Spatio-temporal dynamics of soft-bottom macrobenthic communities in a rapidly changing Arctic: a case study of the Northwestern Barents Sea

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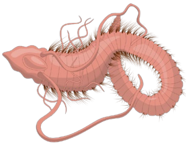
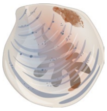
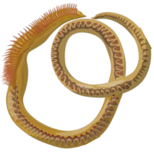
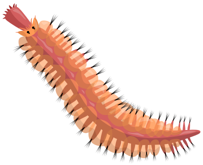



"El vent se desferma
i tot el mar canta.
Mar brava, mar verda, mar escumejanta!
L'onada s'adreça,
venint s'ageganta,
avença i s'acosta
callada que espanta.
L'escuma enlluerna,
el sol l'abrillanta,
l'onada l'esberla
i cau ressonanta.
Mar brava, mar verda, mar escumejanta!"
Joan Maragall




"I know the cure for everything: salt water… in one form or another:
Sweat, Tears or the Sea."
Karen Blixen





Drawings by Èric Jordà Molina

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SUMMARY

The Barents Sea is one of the most productive Arctic seas. Due to a strong pelagic-benthic coupling in the relatively shallow continental shelf, a highly productive seafloor ecosystem is also sustained. Seafloor-associated biomes (benthic communities) have critical ecological roles in the biogeochemistry of marine sediments. They can influence the processes of organic matter burial that sinks to the seafloor through their sediment reworking activites and the remineralization of detritus back into the water column in the form of nutrients, which fuel primary production in the euphotic zone.

In the Barents Sea, macrobenthic communities are highly spatially structured according to prevailing environmental conditions of the overlaying waters and seafloor environment. With increasing impacts of climate change, critically imporant questions arise about the future of benthic structure and function in a warmer Barents Sea. In particular, the northwestern Barents Sea, which is highly influenced by seasonal ice cover and Arctic waters, is experiencing an accelarated rate of warming since the beginning of the 21st century. Increased influx of warm Atlantic waters from the south towards this “Arctic” domain, coupled with a significant retreat in sea ice cover, could alter several sympagic-pelagic-benthic coupling interactions, with consquences for the functioning of the Barents Sea ecosystem.

The aim of the present thesis is to investigate patterns of macrobenthic community structure and function at different spatio-temporal scales in the northwestern Barents Sea. The hypotheses are that: 1) long-term fluctuations of high-Arctic benthos have been driven by warmer waters in recent decades; 2) seasonality of macrobenthic assemblages in the northwestern Barents Sea is pronounced due to a strong pelagic-benthic coupling, making these communities susceptible to water column phenological shifts induced by climate change, and 3) benthic remineralisation will increase with warming and changes in food supply in the near future.

At a decadal scale, a time series in a northern fjord of the Svalbard archipelago revelaed significant fluctuations in macrofaunal community structure most likely caused by the

effects of Atlantic water intrusions into this otherwise “Arctic” cold-water system. The outer parts of the fjord were more impacted by these warming events and, after a recovery phase, some taxa started dominating these locations. In contrast, the inner-most basin was partially isolated by a submarine sill and, although impacts of a strong Atlantic intrusion were also noted, the diverstiy of macrobenthic communities remained more stable afterwards. This indicates that silled inner-basins could act as refugia. At the same time, the seasonal study along the northwestern Barents Sea, surprisingly, revealed little seasonality in macrofauna structure and function, indicating that seafloor communities are highly decoupled from phenological fluctuations of highly seasonal pelagic processes. This relative stability could be due to a “food bank” in surface sediments, which satisfies benthic energetic needs throughout the polar night. In contrast, an experimental study revealed that benthic communities react immediately to increases of fresh food supply, in addition to higher bottom temperatures, by increasing sediment oxygen demand rates. This suggests that a predicted warmer and more productive northern Barents Sea will increase benthic remineralization rates, potentially transforming the seafloor of this Arctic sea from a carbon sink into a carbon source.

Overall, the results of this thesis revealed that macrofauna communities of the northwesern Barents Sea could be resilient to short-term phenological changes of the overlying water column. However, these communities can be (and most likely will be) affected by long-term shifts of sympagic-pelagic-benthic interactions and food avilability, as they are largely spatially constrained by regional environmental conditions over differing water mass domains, productivity regimes, and geomorphological settings. This thesis provides new valuable insights into the spatiol-temporal dynamics of seafloor communities in the northwestern Barents Sea and evidences that these communities are already transitioning into alternative configurations, for which far reaching consequences to the whole Arctic marine ecosystem are still unkown and poorly understood.

SAMMENDRAG PÅ NORSK

Barentshavet er et av de mest produktive hav i Arktis. På grunn av en sterk pelagisk-bentisk kobling på denne relativt grunne kontinentalsokkelen opprettholdes også et veldig produktivt havbunnsøkosystem. Bunndyrsamfunn har kritiske økologiske roller i biogeokjemien til marine sedimenter. De kan påvirke prosessene som graver ned organisk materiale som synker til havbunnen gjennom sin bearbeidingsaktivitet i sedimentene, og påvirker også remineralisering av dødt organisk material tilbake til vannsøylen i form av næringsstoffer som driver primærproduksjonen i den eufotiske sonen.

I Barentshavet er makrobentiske samfunn svært romlig strukturert avhengig av rådende miljøforhold i det overliggende vannet og havbunnsmiljøet. Med økende påtrykk fra klimaendringer reises kritiske spørsmål om fremtiden til bunndyrstruktur og funksjon i et varmere Barentshav. Spesielt det nordvestlige Barentshavet, som er sterkt påvirket av sesongmessig isdekke og arktiske vannmasser, har man sett en akselerert oppvarmingshastighet siden begynnelsen av det 21. århundre. Økt tilstrømning av varmt atlantisk vann fra sør mot dette «arktiske» domenet, kombinert med en betydelig tilbaketrekning i havisdekket, kan endre flere sympagiske-pelagiske-bentiske koblingsinteraksjoner, med konsekvenser for funksjonen til økosystemet i Barentshavet.

Målet med dette arbeidet er å undersøke mønstre og funksjon av makrobentisk samfunnsstruktur på ulike skalaer i rom og tid i det nordvestlige Barentshavet. Hypotesene er at: 1) langsiktige svingninger i høyarktiske bunndyrsamfunn har vært drevet av varmere vannmasser de siste tiårene; 2) sesongvariasjoner av makrobentiske sammensetninger i det nordvestlige Barentshavet er stor på grunn av en sterk pelagisk-bentisk kobling, noe som gjør disse samfunnene mottakelige for fenologiske endringer i vannsøylen indusert av klimaendringer, og 3) remineralisering fra bunndyrsamfunn vil øke med oppvarming og endringer i næringstilgang i nær fremtid.

En tidsserie i en nordlig fjord på Svalbard har avslørt betydelige svingninger i samfunnsstrukturen til makrofauna over en tiårsskala, mest sannsynlig forårsaket av effektene av atlantisk vanninntrenging i dette ellers "arktiske" kaldtvannssystemet. De ytre delene av fjorden ble mer påvirket av disse oppvarmingshendelsene, og etter en gjenopprettingsfase begynte noen arter å dominere i disse områdene. Derimot var det innerste bassenget delvis isolert av en undersjøisk terskel, og selv om påvirkningene av en sterk atlantisk inntrenging også ble sett der, forble mangfoldet av makrobentiske samfunn mer stabilt etterpå. Dette indikerer at terskelisolerte indre bassenger kan fungere som tilfluktssteder. Samtidig avslørte sesongstudiene langs det nordvestlige Barentshavet overraskende nok, lite sesongvariasjoner i makrofaunastruktur og funksjon, noe som indikerer at havbunnssamfunn er sterkt frikoblet fra fenologiske fluktuasjoner i sterkt sesongmessige pelagiske prosesser. Denne relative stabiliteten kan skyldes en "matbank" i overflatesedimenter, som tilfredsstiller bentiske energibehov gjennom hele polarnatten. I motsetning til dette avslørte den eksperimentelle studien at bunnlevende samfunn reagerer umiddelbart på økt tilgang på fersk mat, i tillegg til høyere bunntemperaturer, ved økt behov for oksygen i sedimentene. Dette antyder at et forutsagt varmere og mer produktivt nordlige Barentshav vil øke bentisk remineraliseringshastighet, og potensielt forvandle havbunnen i dette arktiske havet fra et karbonsluk til en karbonkilde.

Samlet sett viste resultatene av denne oppgaven at makrofaunasamfunn i det nordvestlige Barentshavet kan være motstandsdyktige mot kortsiktige fenologiske endringer i den overliggende vannsøylen. Imidlertid kan disse samfunnene bli (og vil mest sannsynlig bli) påvirket av langsiktige endringer av sympagisk-pelagisk-bentiske interaksjoner og næringstilgang, ettersom de i stor grad er romlig begrenset av regionale miljøforhold av forskjellige vannmassedomener, produktivitetsregimer og geomorfologiske tilstander. Denne oppgaven gir ny verdifull innsikt i den romlige og tidsmessige dynamikken til havbunnssamfunnene i det nordvestlige Barentshavet og viser at disse samfunnene allerede er i ferd med å gå over til alternative konfigurasjoner, mens hvor vidtrekkende konsekvenser dette kommer til å få for hele det arktiske marine økosystemet fortsatt er ukjent og dårlig forstått.

1 INTRODUCTION

1.1 Arctic benthic communities

Marine benthic communities comprise invertebrate organisms that live permanently (or part of their life cycle) attached, on top, or embedded in the seafloor. Most benthic organisms tend to present low mobility and some are relatively long-lived, with life spans ranging on the order of years to decades. The community structure and function of benthic communities are determined by a combination of local environmental drivers and faunal interactions over multiple temporal and spatial scales (Griffiths et al., 2017; Ehrnsten et al., 2020). By integrating the variability of these processes into their community structure, benthic assemblages have been proposed as excellent sentinels of environmental change (Renaud et al., 2008; Carroll et al., 2011), and consequently their compositional fluctuations can thus also indicate climate- or other anthropogenically derived impacts (e.g., Kröncke et al., 1998; Larkin et al., 2010; Serrano et al., 2022). In fact, components of marine seafloor communities are widely used as monitoring elements to assess the ecological status and seafloor integrity in marine ecosystems as part of the European Marine Strategy Framework Directive (MSFD) (e.g. Rice et al., 2012). Benthic organisms are usually compartmentalized into different groups according to the mesh sizes that are used to retain them: microfauna (<63µm), meiofauna (63-500µm), macrofauna (500 µm-5cm) and megafauna (>5cm) (Grey and Elliott, 2009). In particular, infaunal macrofauna (benthic organisms that live generally embedded in sediments; **Fig. 1**) are some of the most dominant inhabitants of soft-bottom seafloor sediments (i.e., clay, mud, sand and small gravel). Soft-bottom sediments, in turn, are one of the most common marine habitats in the extensive oceanic continental shelves and deep ocean basins. Most importantly, macrofaunal communities play crucial roles in seafloor biogeochemical processes of the overlying water-sediment interface through their activities (e.g. bioturbation and bioirrigation) which dictate, for instance, pathways of carbon cycling at the seafloor (Snelgrove et al., 2018). It is because of their important ecological roles, together with the suitability to use these assemblages as monitoring subjects of environmental change, that the focus of this thesis revolves around macrofauna community patterns in the context of a rapidly changing Arctic.

Figure 1. *Some of the representative macrobenthic taxa analyzed throughout the present study along the Northern Barents Sea. Photos by Èric Jordà Molina*

The interplay of several ecological and evolutionary processes, acting on multiple spatial and temporal scales, generates and maintains marine benthic biodiversity (Ellingsen, 2002; Renaud et al., 2009; Silberberger et al., 2019). Particularly in the Arctic, the effects of several glaciation and tectonic processes acting over millions of years have determined the observed structure in today's Arctic benthic communities on a pan-Arctic scale (Renaud et al., 2015). One of the most drastic events was the lowering of the Bering land bridge around 3.5 Mya, which enabled the flow of highly diverse benthic communities of the North Pacific benthos (Briggs, 2003) into the Arctic, reaching even into the North Atlantic (Renaud et al., 2015). These exchanges across ocean basins over geological history have led to a marked duality between poorly diverse Atlantic-origin benthos and highly rich ancestral Pacific benthos, while glacial history has originated refugia "pockets" and disjunct distributions contributing to the genetic structure of Arctic benthic populations and communities (Renaud et al., 2015; and references therein). Despite the seemingly minor effects of current climatic drivers when compared to the impacts of geological scale processes on current ecosystem structure, several important abiotic parameters have been identified to constrain macrobenthic community structure and function in the present. Large spatial and temporal variations in community structure of Arctic benthos are driven, amongst others, by water depth, ocean currents and water masses, ocean temperature, overlying water irradiance and primary productivity, seafloor food availability and sediment composition (Gray 2002; Piepenburg 2005; CAFF, 2017). Also, sea ice dynamics can act as a driver of benthic structure by affecting hydrographic conditions and contributing to marked differentiated regimes, affecting for instance primary production (Sejr et al., 2009).

Several knowledge gaps about Arctic benthos still exist today, hampering our ability to project climate change impacts into the future (Renaud et al., 2015). Major observed and expected drivers of change linked to climate change and other anthropogenic effects are sea-ice retreat, increased ocean mixing, bottom-water temperature change, bottom trawling, ocean acidification, freshwater run-off and invasions of non-indigenous species, among others (CAFF, 2017). However, large uncertainties on the spatio-temporal change of some of these drivers, the poorly understood autoecology of several Arctic taxa and the confounding effects from multiple ecological interactions limit the mechanistic understanding by which Arctic seafloor communities will be shaped in the future (Renaud et al., 2015).

National and international efforts to improve the monitoring of Arctic benthic diversity in areas susceptible of change by implementing time series and a network of fixed stations, transects and sampling grids is a first step to filling in some of these gaps (Renaud et al., 2015). At the same time, field studies should investigate multi-stressor impacts and the relationships between environmental drivers and community structure to predict compositional change (Renaud et al., 2015). Moreover, experimental studies investigating the consequences from predicted scenarios of change on community structure and function should be prioritized as they can be of great value for researchers and policy makers in order to study and manage future Arctic ecosystems (Renaud et al., 2015).

Following some of these recommendations, the present thesis investigates the spatio-temporal dynamics of macrobenthic communities in a case study of the northwestern Barents Sea, covering different hydrographic domains, geomorphological environments and extending throughout the open shelf and adjacent coastal fjords, down to the continental slope and into the abyssal depths of the Arctic Ocean.

1.2 The Barents Sea Shelf ecosystem: a seafloor perspective

The Barents Sea, located off the northern coasts of Norway and Russia, presents a relatively shallow continental shelf (with an average depth of ca. 230 m) and covers an area of approximately 1.6 million km^2. Together with the Fram Strait, the Barents Sea is considered as the gateway for Atlantic Water into the European Arctic, between 69° and 81°N (**Fig. 2**). The northwestern Barents Sea and adjacent areas receive warm Atlantic waters from both the south and the north. From the south, Atlantic waters enter through the Barents Sea Opening (BSO). From the north, adjacent to the Nansen Basin, the Svalbard Branch (developing into the Arctic Circumpolar Boundary Current (ACBC)) flows along the slope near the shelf break and is occasionally lifted, protruding into the northern shelf through several troughs at bottom depths (Lundesgaard et al., 2022; Osadchiev et al., 2022). The Svalbard Branch is a continuation of the West Spitsbergen Current (WSC), the latter being an extension of the Norwegian current flowing along the shelf break of the Norwegian and Greenland Seas into the Fram Strait (**Fig. 2**).

The waters of the Barents Sea comprise a transitional hydrographic system between an Atlantic domain in the south (water masses of > 34.7 salinity and > 3°C: Atlantic Water (AW)) and a predominantly Arctic domain in the north (water masses of 34.0-

34.7 salinity and < -1.5°C: Arctic Water (ArW)). These two main water masses meet each other at the Polar Front (**Fig. 2**) (Ingvaldsen and Loeng, 2009), a highly dynamic meso-scale oceanographic feature where water stratification processes play a crucial role for the biology of the ecosystem (see section 1.2.1). Due to ice formation and posterior melting, highly stratified Barents Sea water (also known as intermediate Arctic water) originates and serves as a buffer zone between the Arctic and Atlantic waters of the region (Lind et al., 2018). The influx of nutrient-rich warm Atlantic water from the south into highly stratified colder Arctic waters from the north makes the Barents Sea one of the Arctic seas with highest biolgical productivity (49% of the total pan-Arctic shelf primary production (Sakshaug, 2004)), with an average of 93 g C m^{-2} yr^{-1} over the whole shelf extent (Wassmann et al., 2006).

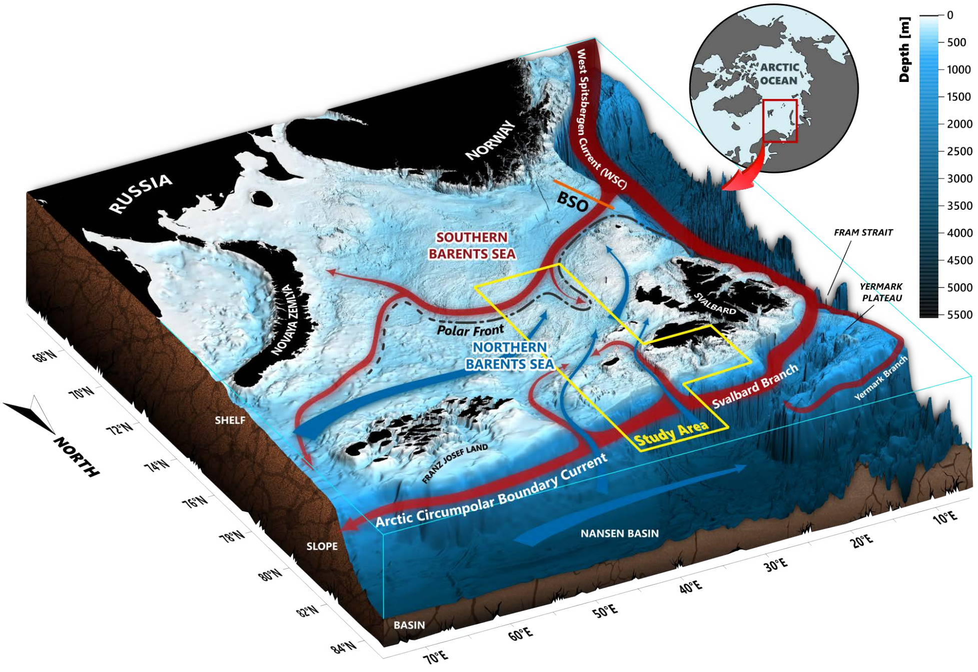


Figure 2. Bathymetric map of the Barents Sea Shelf and adjacent Arctic Ocean. The main domains are indicated: the Southern Barents Sea, with presence of Atlantic Waters indicated with red arrows, and the Northern Barents Sea, with presence of Arctic Waters indicated by blue arrows. Both domains are separated by the Polar Front (black discontinuous line). The yellow frame approximately indicates the study area of the present thesis. Bathymetric data from GEBCO, 2022.

The primary production of the ice-free southern Barents Sea shelf, south of the Polar Front, is roughly twice that of the northern Barents Sea shelf, usually covered with sea ice and comprising the seasonal ice zone (SIZ) (Sakshaug, 1997) (**Fig. 3**). The SIZ is the area in which sea ice originates and melts seasonally from early winter to summer (Carmack and Wassmann, 2006) (**Fig. 3**). This seasonal melting of ice leaves highly stratified waters which are replenished with nutrients during the well mixed winter conditions. Together with the return of light after the polar night period and the shallow mixing depths caused by stratification, these nutrient-rich waters fuel primary production and originate the short-lived but very intense spring bloom (Wassmann et al., 2011; Leu et al., 2015). These blooms support the Arctic marine food-web from large marine mammals to seafloor communities. In turn, these highly productive waters make the Barents Sea one of the most important regions for commercial fisheries in the world.

1.2.1 Sympagic-pelagic-benthic coupling in the Barents Sea

A tight connectivity between the sea ice realm (sympagic), water column (pelagic) and seafloor (benthic) associated communities has traditionally been posited to govern the interactions in marine ecosystems of Arctic shelves (Grebmeier et al., 1988; Wassmann et al., 1991; Graf, 1992; Søreide et al., 2013) through the transfer of organic matter by vertical flux (Renaud et al., 2008; Riser et al., 2008; Wassmann and Reigstad, 2011). Vertical fluxes of organic matter to the seafloor play an important role in modulating food availability and quality for macrobenthic communities, which they rely on to maintain their functions and standing stocks (Ambrose and Renaud, 1995). Therefore, overlaying water column processes in a complex hydrographical setting such as the Barents Sea need to be taken into account, or at least proxies from those, when assessing spatio-temporal dynamics of benthic communities in this region.

Primary production in the surface water of the Barents Sea is mainly bottom-up regulated by physical forcing, including sea-ice cover, stratification and mixing depth, light and nutrients availability (Carmack and Wassmann, 2006) (**Fig. 3**). At the same time, the amount, nature and phenology of primary production in the euphotic zone will condition all posterior interactions with overlaying water processes and impact its fate to the seafloor. For instance, phytoplanktonic blooms prevail in the ice-free southern Barents Sea, and tend to sink slowly due to the dominance of small-sized cells. Conversely, under sea ice-algae blooms, which are usually dominated by large diatom aggregates, tend to sink faster and in short pulses after sea ice melt (Carmack and Wassmann, 2006) (**Fig. 3**). Sinking rates of these organic matter falls throughout the water column will influence their retention times in the pelagic realm, and therefore, the exposure time to the interactions with pelagic organisms. Below the euphotic zone, top-down regulating processes become more important in determining the fate of biogenic carbon (Carmack and Wassmann, 2006). Zooplankton species, for instance, often reproduce and match their phenology with the onset of phytoplankton blooms, presenting high-biomass aggregates just below the euphotic zone to feed on the primary producers (Tamelander et al., 2006; Søreide et al., 2013). High amounts of faecal pellets are produced by these grazing activities, which eventually settle down to the seafloor. However, the retention times of faecal pellets in the water column can be in turn increased through ingestion of pellets (coprophagy), mainly driven by copepods, resulting in further fragmentation (coprorhexy) into smaller, slowly sinking particles (Koski et al., 2017). This facilitates the uptake rates of detritus into the microbial pump, hampering their export to larger depths. Thus, planktonic heterotrophs ultimately determine the extent, degradation and attenuation of vertical fluxes in the water column (Olli et al., 2001; Riser et al., 2001; Carmack and Wassmann, 2006). On average, only 1% of the organic matter produced in the euphotic zone makes it to the deep sea (Suess, 1980). Moreover, laterally advected organic matter by ocean currents and water masses can be deposited at the seafloor far away from its original source in the euphotic zone (Gorsky et al., 2003) (**Fig. 3**).

Because of all these interactions and processes that organic matter is exposed to while descending throughout the water column, food at the seafloor can be found in many different forms and states of degradation. High quality rapidly sinking sea ice algae aggregates can provide a very pulsed, yet highly labile, organic matter source that is readily consumed and assimilated by benthic organisms (McMahon et al., 2006; Boetius et al., 2013; Cautain et al., 2022). Similarly, large phytoplankton blooms can settle quickly into the seafloor in areas of strong pelagic-benthic coupling (Carroll et al., 2008), increasing surface sediment chlorophyll *a* and fatty acid concentrations (Bauerfeind et al., 1997; Sun and Wakeham 1999). This increased seasonal sedimentation of fresh food is usually accompained by increased benthic community respiration rates, and can trigger important physiological processes such as somatic growth, egg production and cold tolerance (Anderson and Pond 2000; Graeve et al., 2005). Consequently, chlorophyll *a* pigments in surface sediments are usually used as a proxy for fresh photoshynthetically derived organic matter at the seafloor (Boon and Duineveld, 1996). Conversely, primary production that has been subjected to high degrees of degradation processes (i.e. through microbial degradation both in the water column and seafloor or highly reworked resuspended material) are usually found in the form of sediment phaeopigments, a degradation product of chloropyll *a* which have longer half-lifes in marine seidments than the more short-lived (about three weeks in polar sediments (Graf et al., 1995; Morata and Renaud, 2008) chlorophyll *a.* Together with other detritus such as faecal pellets, dead zooplankton and marine snow, sediment pigments consititue an important pool of labile material of the total organic matter (TOC) available in the Barents Sea marine sediments. Ultimately, spatio-temporal variation in pelagic-benthic processes will influence the spatio-temporal dynamics of food quality at the seafloor (**Fig. 3**), which will have an impact on the species composition and food-web structure of benthic communities in the Barents Sea shelf (Oleszczuk et al., 2023). In the deep central Arctic ocean, however, pelagic-benthic coupling is weaker than in shelf environments due to more attenuated vertical fluxes and longer exposure times in the water column, with larger water depths. This leads to higher degraded forms of organic matter to reach the abyssal seafloor (Wiedmann et al., 2020). In fact, a mismatch between the calculated carbon demand of deep sea benthos, the carbon supply from insitu primary production in the upper water column and low vertical carbon export to depth, has suggested that alternative food sources such as large sporadic sea ice algae falls, dead zooplankton and big animal carcasses may be important food sources to sustain these deep communities (Wiedmann et al., 2020) (**Fig. 3**), which have shown to display a high level of omnivory (Oleszczuk et al., 2023).

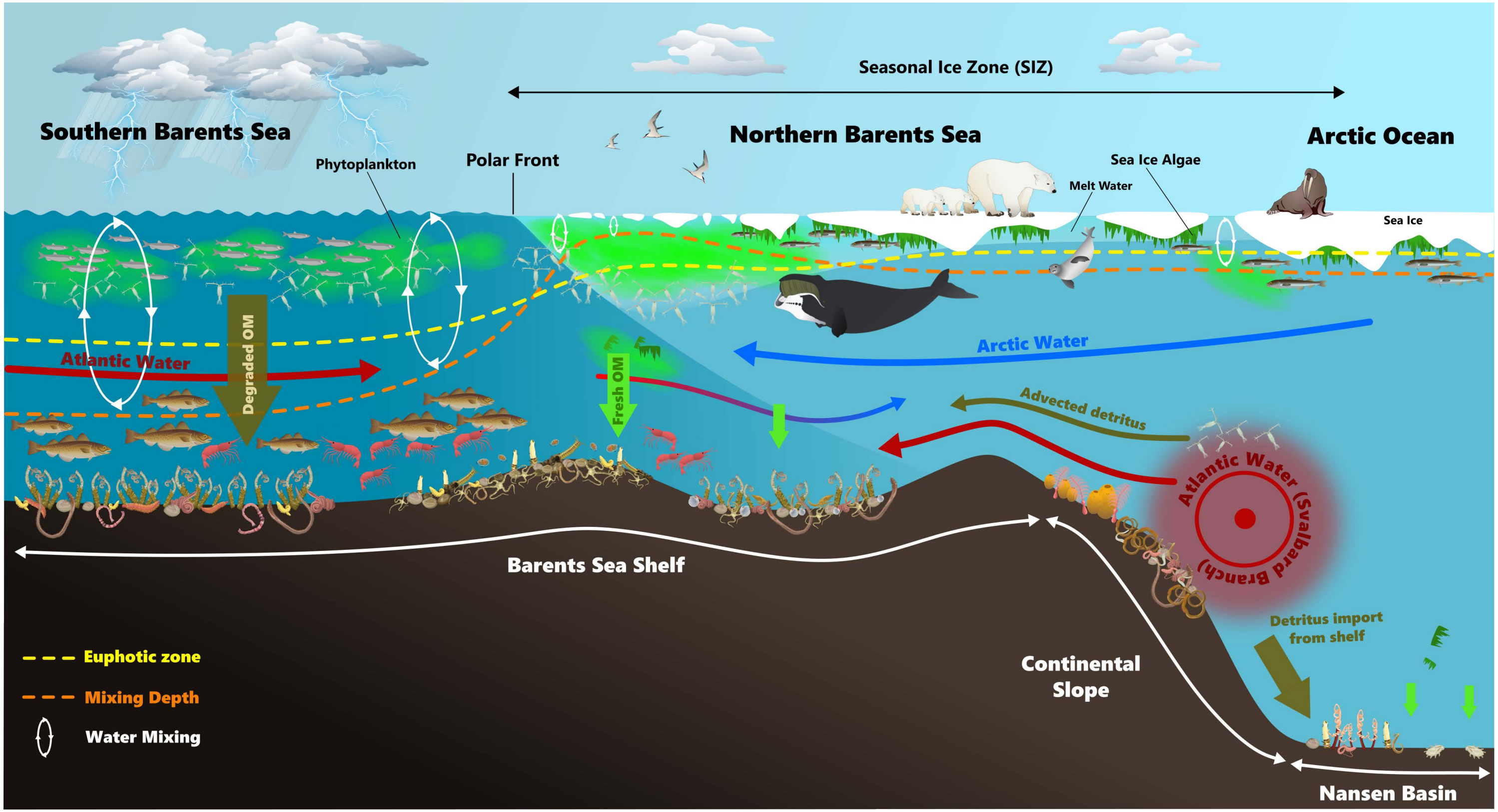


Figure 3 *Graphical representation of the different sympagic-pelagic-benthic coupling processes and interactions occurring in the southern and northern Barents Sea marine ecosystem and adjacent Arctic Ocean. Drawings of all non-seafloor organisms sourced from the Integration and Application Network (ian.umces.edu/media-library) licensed under CC BY-SA 4.0 (Atlantic cod and Arctic cod - Kim Kraeer, Lucy Van Essen-Fishman; copepod, tern, polar bear, walrus and whale – Tracey Saxby, shrimp - Dieter Tracey, Water and Rivers Commission; seal - Joanna Woerner).*

1.2.2 Drivers of macrofauna community structure along the Barents Sea shelf and adjacent deep Arctic Ocean

A multi-variate suit of drivers constrain the structure and distribution of benthic communities in the Barents Sea. Carroll and Ambrose, (2012) described that macrofaunal communities in the northern Barents Sea formed distinct clusters based on water masses characteristics. In particular, macrofauna seems to be constrained by the spatial extent of Atlantic water penetration in bottom waters, which is more stable than the highly seasonal fluctuating surface of the water column (Cochrane et al., 2009). Benthic faunal abundances have been recorded to be 48% higher in the southern Barents Sea than in the north (Cochrane et al., 2009). The northern Arctic macrofaunal biocenosis is dominated in biomass by echinoderms, molluscs and to a lesser extent annelids, while the southern Atlantic assemblages are characterized by more or less equal proportions between molluscs, annelids and echinoderms (Zenkevich, 1963; Cochrane et al., 2009). Overall, benthic biomass in the Barents Sea seems to be higher in the Polar Front region and has been found to be highly variable in the northern Barents Sea, possibly reflecting a high bathymetric and hydrographic heterogeneity (Carroll et al., 2008). Pelagic-benthic coupling seems to be amplified at mesoscales by hydrographic features such as polynyas, fronts and the marginal sea ice zone in the northern Barents Sea (Morata et al., 2011). Sedimentary pigments in Arctic waters are dominated by ice algal detritus, as shown by analysis of isotopic and lipid biomarkers (Renaud et al., 2007; Morata et al., 2008). Episodic pulses of sinking sea-ice algae have been found to constitute an important component of the benthic faunal diet (Sun et al., 2007; Carroll and Ambrose, 2012) as they have been found in benthic consumer tissues (Brown and Belt, 2012; Cautain et al., 2022). Faunal density and diversity have been documented to be higher near the Polar Front in the western Barents Sea (Carroll et al., 2008; Cochrane et al., 2009), indicating that this oceanographic feature might enhance food quality and quantity to the benthos as a result from stronger pelagic-benthic coupling (Piepenburg, 2005).

It has also been observed that highly covered sea-ice areas with low primary production and sediment pigment concentrations (characteristic for the northern Barents Sea) had higher evenness (Simpson's index), while southern areas of the Barents Sea had a higher dominance of specific taxa (e.g. the polychaete *Spiochaetopterus typicus*) (Cochrane et al., 2009). This could be explained by the lack of food resources in the north, which hampers a few species to dominate over others (Ambrose et al., 2009). For polychaetes, for instance, one of the most dominant class of macrofauna in the region, studies have shown that the northern Barents Sea presented 30% higher taxonomic richness than the southern Barents Sea, below the Polar Front (Ambrose et al., 2009).

For parts of the central Arctic Ocean, such as the Nansen and Amundsen basins, infaunal species richness, abundance and biomass decrease along a shelf-basin gradient with water depth (Piepenburg, 2005; Bluhm et al., 2011). Vedenin et al. (2018), concluded that macrobenthos of the Barents Sea slope and the abyssal zones of the Nansen Basin grouped according to water depth from the shelf (~50 m), lower shelf and upper slope (73-577 m), mid-slope (981-1216 m), lower slope (1991-3054 m) and abyssal plain (3236-4381 m). This grouping is associated with a descreasing density and biomass of macrofaunal communities with depth towards the Central Arctic Basin. The communities at those depths are highly food-deprived, and therefore highly constrained by food availability, indicated by lower amounts of phaeopigments (Vedenin et al., 2018) and particle flux (Degen et al., 2015). For a while it was accepted that deep-benthic communities of the central Arctic basins largely relied on organic carbon imported from the adjacent shelves to satisfy their carbon demand (Dunton et al., 2005). In fact, important injections of carbon-rich polar dense water plumes outflowing from the Barents Sea into the Nansen Basin have been documented (Rogge et al., 2023). Nonetheless, it has also been suggested that the communities of these deep areas can be more driven by the sedimentation of fresh organic material than previously thought and that the production in the marginal surface waters of the central Arctic Ocean, although low, can be sufficient to maintain their benthic standing-stocks (Kröncke et al., 2000; Klages et al., 2004). For instance, fresh aggregates of sea ice algae have been found in the central Arctic Ocean at thousands of meters of depth (Boetius et al., 2013) and this sporadic but high quality food source is hypothesized to be enough to feed the local benthic standing stocks for an entire year (Wiedmann et al., 2020).

1.2.3 Functional diversity of macrobenthos

It is clear that macrofauna communities of the Barents Sea are highly influenced by the overlying local pelagic production and vertical fluxes, and ultimately, food availability at the seafloor, which drives their abundances, structure, biomass and species richness (Carroll et al., 2008; Cochrane et al., 2009; Piepenburg et al., 1997; Renaud et al., 2008). Simultaneously, the composition of macrofaunal assemblages reflects the overall different ecological functions that can be displayed by the different organisms themselves. Macrofaunal functional traits can give information about the ecological roles displayed by these communities. For instance, their movement might give insights into their ability to mobilize energy through nutrient cycling and carbon deposition in the sediments; their larval developmental strategies might indicate their dispersal capabilities; or their feeding habits can reflect hydrodynamic conditions and carbon transport in the seafloor (Sutton et al. 2021).

Macrofaunal organisms modify the properties of the sediments through their digging and burrowing activities (bioturbation) (e.g. by excavating galleries, building tubes in muddy environments, crawling and moving in the surface sediments, etc.) (Kristensen, 2000; Kristensen et al., 2012) (**Fig. 4**). At the same time, organisms generate small currents of water inside burrows and galleries through their feeding and movement activities, which transport food particles and oxygen-rich overlaying waters into the otherwise highly vertically stratified anoxic sediment layers (bioirrigation) (Kristensen, 2000) (**Fig. 4**). Bioturbation and bioirrigation from macrobenthic infauna thus, play a crucial role in i.a. structuring the oxygen gradients of sediments (Glud, 2008) (**Fig. 4**). This, in turn, determines chemical reactions, facilitating aerobic metabolic pathways of organic matter degradation (i.e. respiration) or, alternatively, inducing anoxic pathways mainly mediated by sediment microbial communities. All these interplays between seafloor fauna and physico-chemical gradients will mediate and regulate organic matter remineralization rates and pathways in the sediment (**Fig. 4**).

1.2.4 Benthic remineralization and biogeochemical processes in the seafloor sediments

A vital ecosystem function in which soft-bottom benthic communities are involved is the recycling of organic matter at the seafloor (Klages et al., 2004). Sinking organic matter from the overlaying water, when reaching the seafloor, will follow one of the subsequent pathways: it will be 1) remineralized by benthic organisms into CO_2 and nutrients through catalytic degradation processes (i.e. respiration (or oxygen demand)), 2) stored in benthic biomass (incorporated in the seafloor organisms' tissues) or 3) buried in deeper sediments for centuries (Klages et al., 2004; Wlodarska-Kowalczuk et al., 2019) (**Fig. 4**). The first path, the remineralization of organic matter, plays a key role in marine biogeochemical cycles since it closes the carbon cycle, replenishing nutrients (mainly bioavailable phosphorous and nitrogen) back into the system that can be utilized for new primary production in the photic zone (Thamdrup and Canfield, 2000). The second process is what sustains and determines benthic secondary production and standing stocks. The last process, plays a crucial role in climatic stability as it sequestrates atmospoheric carbon deep into the sediments and mitigates effects of climate change.

The extensive Barents Sea shelf is known to act as a carbon sink, taking up approximately $22\pm11\text{x}10^6$ tCyr^{-1} (Kivimäe et al., 2010). In the northern Barents Sea, most of the organic matter reaching the seafloor is rapidly consumed by benthic organisms. As a consequence, aerobic respiration in the northern Barents Sea contributes to >40% of the total seafloor respiration, which is unexpectedly high for shelf sediments that typically range from less than 10% to 17% (Freitas et al., 2020). Arctic shelf sediments exhibit high sediment oxygen demands (10 ± 7.9 mmol O_2 $m^{-2}d^{-1}$)

which is associated with high availability of fresh and highly reactive organic matter at the seafloor (Renaud et al., 2008; Bourgeois et al., 2017). Degradation rates, distributions of organic matter reactivity patterns (determined by bulk distribution and average lifetime) and nutrient fluxes suggest a strong benthic-pelagic coupling in the Barents Sea, which appears to be controlled by the spatial heterogeneity of the seafloor and prevailing water masses, rather than by spatio-temporal (i.e. seasonal) variations in sea ice cover or primary productivity dynamics (Freitas et al., 2020).

Sediment oxygen demand (SOD) rates are concomitantly determined by the intrinsic community composition of the benthic assemblages and their activities (e.g. bioturbation and bioirrigation), which affects the surface-sediment/overlying-water interactions (**Fig. 4**) (Piepenburg et al., 1995; Piepenburg, 2005; Bourgeois et al. 2017). Attempts have been made to partition the SOD contributions from several components of the benthic ecosystem (among micro- meio- macro- and megabenthos) by using several methodological approaches (Piepenburg et al., 1995). In the Bering and Chukchi Seas, the documented SOD rates were significantly positively correlated with macrofaunal biomass (Clough et al., 2005; Grebmeier et al., 2006). For the western Arctic Ocean, macrofaunal biomass explained approximately 74% of the variability in SOD rates (Clough et al., 2005). Additionally, community composition, and more specifically abundances of the most dominant taxonomic groups (i.e. polychaete, molluscs and crustaceans), also helped explain the patterns in SOD (Clough et al., 2005). In fact, macrofaunal communities have been found to be the most important contributors to total sediment respiration in Arctic shelves (Clough et al., 2005; Renaud et al., 2008) and therefore have been shown to be the main contributors to benthic carbon cycling in these regions (Renaud et al., 2007). However, the oxygen demands from bacterial and meiofaunal communities may become more important in deep-sea sediments than macrofaunal ones (Gebmeier et al., 2006; Bourgeois et al., 2017).

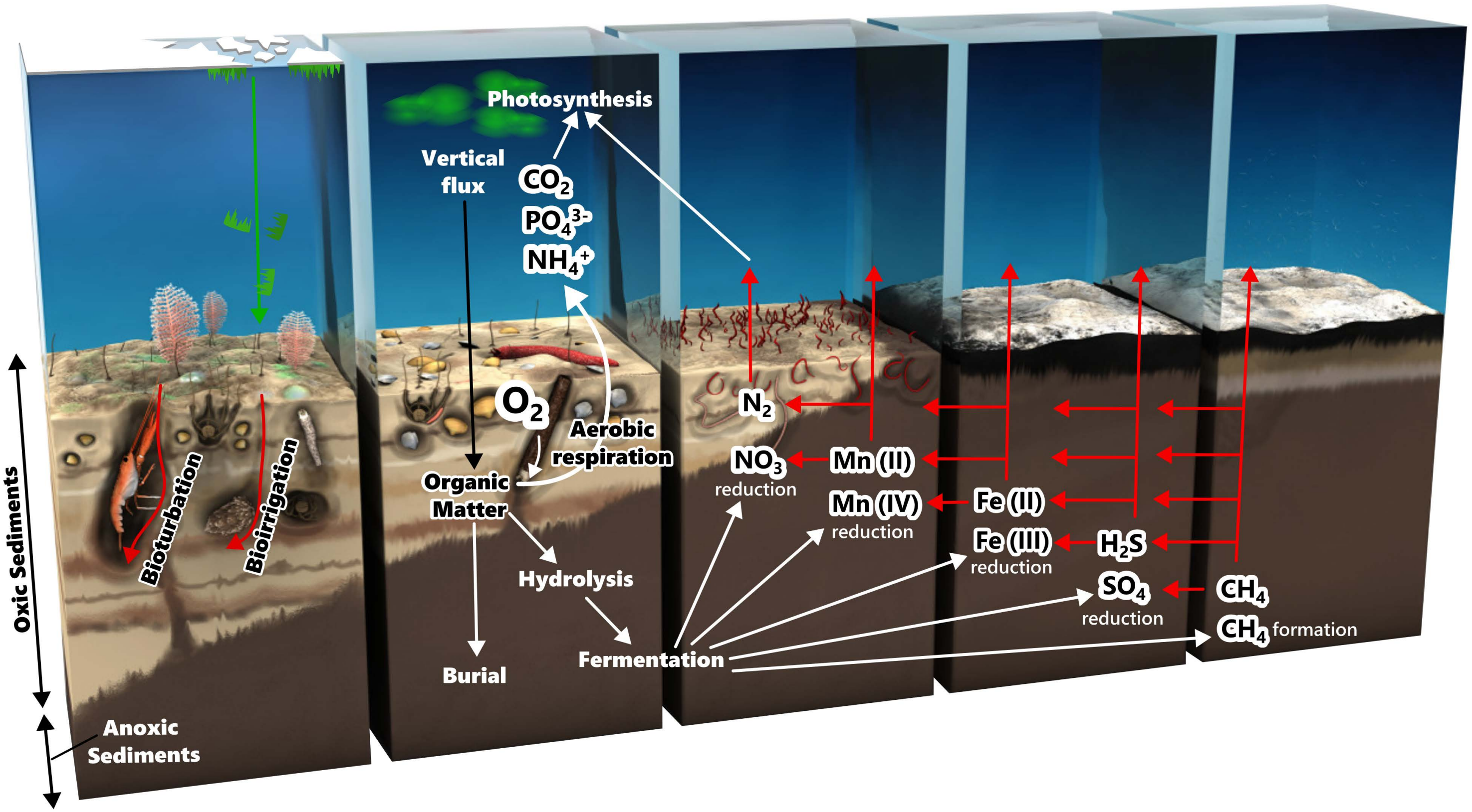


Figure 4. An overview of the different biogeochemical pathways that organic matter can follow once it sinks to the seafloor and the role of macrofauna in defining oxygen gradients in marine sediments. Modified after Middelburg (2018) and Solan et al. (2020), originally redrawn from Pearson and Rosenberg, 1978. The red arrows indicate the fate of "energy-rich" substrates released during anaerobic mineralization.

1.2.5 High-Arctic fjordic macrofaunal communities

Most of the pelagic-benthic coupling relationships and mechanisms that influence function and benthic standing stocks in open-shelf waters also apply in coastal areas. However, fjords are unique geomorphological settings that create very localized conditions of hydrographic, sedimentary and productivity regimes, which may add layers of complexity to these processes.

Fjords are deep coastal estuaries commonly found at high latitudes of both hemispheres (Syvitsky et al., 2012). Around the Barents Sea water, fjords are commonly found in the Svalbard archipelago, in Novaya Zemlya (Russia) and in northern Norway. These marine geomorphological formations originated from the erosion of massive ice caps during the last ice age after their retreat. Fjords are usually regarded as model systems to study patterns and mechanisms of community structure, since extreme gradients in abiotic drivers occur along the relatively short head-to-mouth axis, which results in distinct macrofaunal assemblages (Włodarska-Kowalczuk et al., 2005; Renaud et al., 2007b; Kędra et al., 2010; Jordà-Molina et al., 2019; Udalov et al., 2021).

In high-Arctic fjords around Svalbard waters, macrofauna communities are constrained by several physical parameters (sediment grain size, sedimentation rates and glacial runoff, sea ice cover, bottom water masses, food avilability, etc.) (Holte and Gulliksen, 1998; Włodarska-Kowalczuk et al., 1998; Włodarska-Kowalczuk and Pearson, 2004; Włodarska-Kowalczuk et al., 2005; Jordà Molina et al., 2019; Udalov et al., 2021) and by biological interactions (e.g. species competition, predation) (Kokarev, 2021, Pavlova et al., 2023). However, low connectivity due to dispersal barriers such as sills (i.e. submarine ridges) among basin/fjord systems may lead also to independent macrofauna community assembly (Kokarev, 2021a). Arctic inner-fjord benthic communities, in fact, seem to differ in species composition, species richness, diversity, functional complexity and redundancy from outer shelf communities (Włodarska-Kowalczuk et al., 2012; Kokarev, 2021a; Udalov et al., 2021). The isolation caused by shallow sills in Arctic fjords may protect inner-basin communities from strong fluctuations of abiotic factors occurring in off-shore shelf regions and may act as refugia for certain taxa (Renaud et al., 2007b; Kędra et al., 2010; Węsławski et al., 2011). Consequently, communities of inner-fjord basins could be less resilient to species losses or invasions, and the extent of environmental variation that these communities can tolerate remains unclear in case of extreme disturbance events (Włodarska-Kowalczuk et al., 2012). This implies that community assembly is not solely influenced by fjord-dependent suits of abiotic drivers per-se, but also by the particular evolutionary histories of each system and their interconnectivity. Therefore, monitoring programs of, for instance, macrofauna diversity in sub-Arctic and Arctic fjordic ecosystems cannot rely on a single fjord as proxy for largescale community patterns, but rather should cover several systems to account for fjord to fjord, or even basin to basin, variation.

Fjords located in the western coast of Svalbard have been extensively studied (reviewed in Molis et al., 2019), and significant shifts in ecosystem composition and function of both pelagic and benthic realms have been documented throughout the last decades from increasing fluxes of warm Atlantic waters protruding into the shelf areas of this region (Kedra et al., 2010; Bloshkina et al., 2021). However, little is known about the northernmost fjords of the archipelago, presenting higher influence from Arctic waters and higher drifting sea ice cover from the Arctic Ocean, resembling the conditions of the northern Barents Sea shelf. Evidence suggests, though, that these fjords also started to be more frequently impacted by Atlantic waters during the last decade (Hop et al., 2019).

Although fjordic environments constitute only a 0.1% area of the global ocean, fjords have been recognized as important organic carbon sequestration hotspots, contributing to an 11% share in global carbon burial, hundred times higher than the global ocean average (Smith et al., 2015; Wlodarska-Kowalczuk et al., 2019).

1.3 A rapidly changing Barents Sea and adjacent waters

1.3.1 Climate change in the Arctic

In times of the Anthropocene, global mean surface temperatures increased by 1.1°C from pre-industrial times (1850-1900) compared to the second decade of the 21st century (2011-2020) (IPCC, 2022). Best model predictions suggest that ongoing greenhouse gas emissions will likely lead to a global increase of 1.5°C by 2030-2052, and that it will likely exceed 2°C by the end of the century unless critical reductions in carbon dioxide and other greenhouse gas emissions take place throughout the coming decades (IPCC, 2022). These projected temperature increases will have, and are already having, severe impacts on a global scale for terrestrial, freshwater and ocean marine ecosystems (IPCC, 2022).

In light of this unprecedented rate of ecosystem change, research and monitoring efforts that assess biodiversity, species distributions and ecological shifts in different spatio-temporal scales are urgently needed in order to establish baselines and rates of change. These will be capital to disentangle short-term variation from long-term shifts and will help predict and understand future environmental conditions relevant to ecosystem management efforts.

The effects of climate warming are exacerbated in the polar regions through what is known as polar amplification (Stuecker et al., 2018). This phenomenon is due to surface-albedo feedback processes and atmospheric and oceanic heat transport changes, in which sea ice cover and its retreat plays a crucial role (Goosse et al., 2018). In particular, the air temperature in the Arctic has warmed four times faster than the global average since 1979 (Rantanen et al., 2022). At the same time, some models suggest that the upper 2000 m of the Arctic Ocean are warming at 2.3 times the global mean rate for this depth range throughout the 21st century (Shu et al. 2022). This unprecedented warming rate is having detrimental consequences for the Arctic sea-ice cover, which in September of 2012 reached the lowest minimum extent of about 3.6 million km^2, equivalent to a 50% reduction in area compared to the average of the

1980s and 1990s (Kokhanovsky and Tomasi, 2020). Model predictions, although with high uncertainty, point towards a sea ice free Arctic in September sometime between the 2030s and the 2060s (Wang and Overland, 2012; Vavrus and Holland, 2021).

1.3.2 The Barents Sea as a warming "hotspot"

Highest losses of winter sea ice cover during the last two decades have been observed in areas with important Atlantic water inflow: the Barents Sea, the Kara Sea and the Western Nansen Basin between Svalbard and Franz Joseph Land. Consequently, these regions have been coined the Arctic warming hotspot (Screen and Simmonds, 2010; Lind et al., 2018).

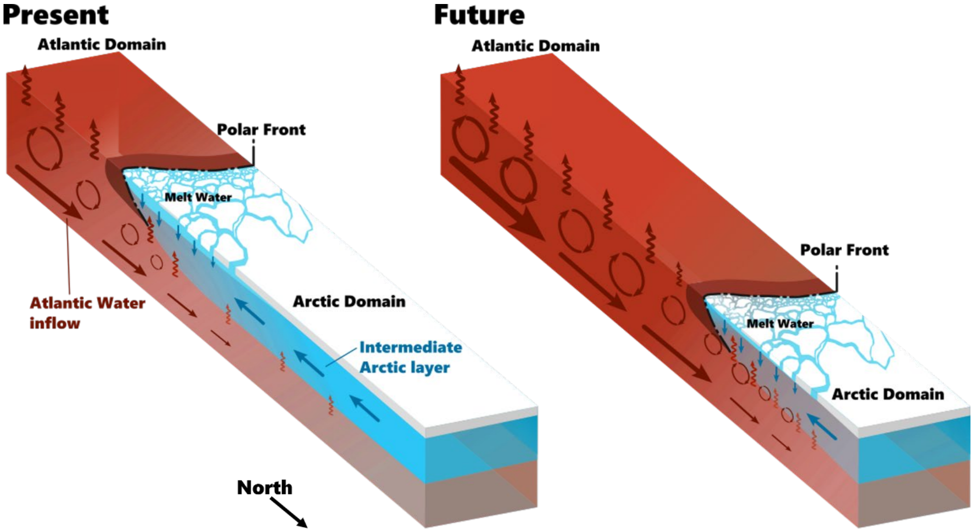


Figure 5. *Hydrographic conditions for the Atlantic domain of the southern Barents Sea and for the Arctic domain of the northern Barents Sea. Diagrams show the present conditions, and the future conditions after increased influx of Atlantic water from the south and sea ice retreat to the north. Based on Polyakov et al., 2017 and Lind et al., 2018.*

The ongoing ocean warming may soon lead to a transition in the northern Barents Sea from a cold and stratified Arctic to a warm and potentially more mixed Atlantic regime, what has been termed as the "Atlantification" of the northern Barents Sea (Lind et al., 2018, Ingvaldsen et al., 2021).

A positive feedback between an increased inflow of warmer, well mixed and saline Atlantic water into the region and a decrease in sea-ice formation in Arctic waters could possibly explain the Atlantification of the Arctic (Ivanov et al. 2016). Since the mid-2000s, the observed increase in ocean temperature and salinity has reduced sea-ice formation which, in turn, releases less freshwater throughout the melting season. The reduced production of seasonal meltwater weakens the permanent halocline between intermediate Arctic and Atlantic water masses, facilitating vertical mixing and thermohaline convection (Polyakov et al., 2017; Polyakov et al. 2018). This loss in stratification results in an increased upward heat flux and heat content in the surface layer that diminishes the thickness of newly formed sea ice or even completely inhibits its formation during winter (Screen and Simmonds, 2010; Ivanov et al., 2016; Lind et al., 2018). Between 1980 and 2010, a retreat of 240 km of the sea ice edge to the north occurred in the Barents Sea accompanied by increases in Atlantic heat transport (Årthun and Eldevik, 2012).

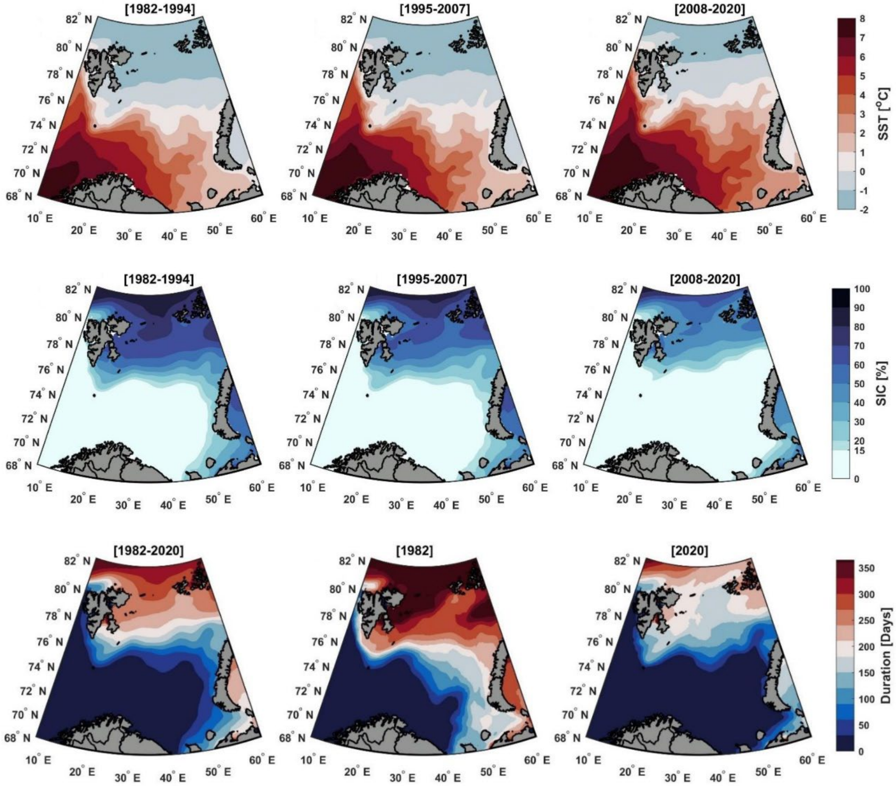


Figure 6. Average sea surface temperature (SST) in °C (top), percentage in sea ice concentration (SIC) (middle), and days of duration of sea ice cover (bottom) for the Barents Sea for the periods 1982-1994, 1995-2007 and 2008-2020 (Mohammed et al., 2022)

1.3.3 Atlantification of the Barents Sea: Increasing heat flux and more frequent marine heatwaves

It is now suggested that decadal variability in climatic trends of the North Atlantic Subpolar Gyre can generate increases in Atlantic water inflow propagating throughout the Norwegian Current, which reaches the Barents Sea with an advective delay of c.a. 5 years (Koul et al., 2022). This means that regional trends of ocean temperature and, consequently sea ice dynamics and linked primary production, could be governed by large-scale climatic patterns originated further south and propagated in an upstream direction with a lag of several years. However, the exact physical mechanisms of these links are still not well understood (Lundesgaard et al., 2022).

The Barents Sea experienced a significant warming in 2004, with consistent increases in ocean temperature and salinity since then (Lind et al., 2018; Mohamed et al., 2022). In western Svalbard, Atlantic water intrusions into the shelf and adjacent fjords have been increasingly frequent throughout the first two decades of the 21st century, particularly after 2011 (Bloshkina et al., 2021). At the same time, the waters of the shelf and shelf-break north of Svalbard showed increased near-surface water temperatures, more ice-free conditions and higher interannual variability in mixing layer depths and in ocean-to-atmosphere heat fluxes compared to prior 2011 (Athanase et al., 2020). In this more recent period, the occurrence of extreme winter conditions with exceptional deep mixing has also been observed (Athanase et al., 2020).

Sustained long-term warming of atmosphere and oceans world-wide have been accompanied by increasing frequency and intensity of extreme temperature events (usually characterized as distinct anomalies over a period of time) (Perkins et al., 2012; Hobday et al., 2016). Marine heatwaves (MHWs) have been defined as temperature anomalies lasting for five or more days and exceeding the 90th percentile based on 30-year historical baseline climatology (Hobday et al., 2016). Between 1982 and 2020, the average MHWs documented in the Arctic have been as strong (or even stronger) as in other ocean basins, and their annual intensity became stronger from the year 2000 onwards with consistent changes in air temperature, sea-ice and cloud cover patterns (Huang et al., 2021). Overall, higher air temperatures and a decreased sea-ice concentration simultaneously mediated by higher ocean temperature and sea ice feedback interactions are thought to have led to increasing observations of MHWs in the Arctic (Huang et al., 2021; Mohamed et al., 2022b). Marine heatwaves have also been detected in adjacent areas of the Barents Sea, for instance in the Fram Strait (Beszczynska-Möller et al., 2012).

1.4 Responses of macrobenthic communities to a changing environment

Water temperature in the Barents Sea can be regarded as a “master parameter”, and its future increase is expected to trigger, either through direct or indirect effects, changes in the structure and functioning of macrofaunal communities (Renaud et al., 2019). Bottom water temperatures in the Barents Sea are expected to increase by up to 6°C between 1979-2008 and 2090-2099, with minor increases in deeper areas (>500 m) of the Arctic and North Atlantic basins (Renaud et al., 2019). Thermal tolerance in marine ectotherm species is a key driver for spatial distribution which, globally and in general terms, follows latitudinal gradients (Sunday et al. 2012). Marine species can adapt to new thermal conditions either by actively following their climatic niches in space (distribution shifts) or time (phenological shifts) (García Molinos et al., 2015). In the Barents Sea, several studies have already documented an increase in the presence of boreal fish, zooplankton and benthic species (Dalpadado et al., 2012; Kortsch et al., 2012; Fossheim et al., 2015; Gordó-Vilaseca et al., 2022). This poleward borealization of communities might come with drastic and long-lasting shifts in the structural and functional organization of the receiving local communities (Kortsch et al., 2012). When not displaced, mass mortality events in benthic assemblages have been documented in temperate and tropical latitudes after periods of warm water anomalies (Hughes et al., 2003; Garrabou et al., 2001, 2009). In parallel, increasing bottom water temperatures will most likely lead to potentially higher metabolic rates in benthic species (Jørgensen et al., 2022), consequently rising their oxygen demands.

A warmer Barents Sea and declining sea ice will also have drastic effects on primary productivity regimes and, ultimately, on food availability to the benthos. However, these shifts will not be uniform across regions. Three different scenarios are predicted for the southern, central and the northern parts of this system. For todays’ southernmost Barents Sea, in the ice free and highly Atlantic influenced sector, higher surface water temperatures are predicted. This new situation is expected to produce smaller cell-sized pelagic autotrophs, which will increase retention times of primary production into the water column and will strengthen the microbial loop (Li et al., 2009, Rokkan et al., 2010, Wassmann and Reigstad, 2011). At the same time, increased thermal stratification will hamper the upward mixing of nutrients originated form remineralization processes (a large part originated from benthic remineralization) that fuels primary production (Wassmann and Reigstad, 2011). Therefore, in some areas of the southern Barents Sea, a decrease in productivity is expected (Wassmann and Reigstad, 2011). However, the role of large-scale advected primary production in this Atlantic gateway could compensate the decrease in local productivity (Wassmann and Reigstad, 2011). In the central and northern Barents Sea it is predicted that the seasonal ice zone (SIZ) will move northwards. The disappearance of sea ice cover in the southernmost areas of today's SIZ will increase the euphotic zone as light might penetrate deeper into the water column. At the same time, higher wind exposure and erosion from storms will increase mixing depths on the upper water column. Therefore, it is expected that primary production will increase in today's northern Barents Sea (Wassmann and Reigstad, 2011). Lastly, the outcomes for primary production changes in the deep Arctic basins are more uncertain. Although primary production in the Arctic Ocean has been observed to increase with sea ice retreat during the last two decades (Arrigo and van Dijken, 2015), evidence in the deep Canadian Basin adjacent to the Chuckchi Sea suggests that a decreased overall pelagic-benthic coupling due to increased water freshening and stratification could occur in some areas of the Beaufort Gyre (Zhulay et al., 2023). This suggests that possible outcomes of primary production and their impacts for the deep-sea benthos will not necessarily apply to all Arctic basins equally and will be region context dependent.

Responses to Atlantification impacts might differ in open shelf systems from more isolated coastal environments (e.g. fjords) or from continental shelves to deep-sea basins. Studying its potential effects in different environmental settings and spatial scales is critical to provide effective tools for management efforts. Long-term monitoring programs of benthic diversity along the axis of semi-enclosed environments such as fjords, can therefore provide invaluable information about whether environmental and biological changes across time follow a uniform pattern from coastal to open shelf environments or if, on the contrary, they follow non-uniform spatial patterns. These can also provide important insights into the mechanistic relationships between abiotic forcing and biological structure and function.

1.4.1 Seasonal variation vs. long-term shifts in macrobenthic communities

Most important environmental drivers of the Barents Sea marine ecosystem are highly seasonal (Walsh, 2008). Extreme light regime shifts occur on an annual basis, from midnight sun periods with 24 hours sunlight in summer to permanent dusk throughout the polar night in winter. Simultaneously, sea ice formation and melting occur across the SIZ annually. Not only are the abiotic components of this system in constant transition, but also primary producers are phenologically tied to these seasonal fluctuations (Wassmann et al., 2011; Leu et al., 2015). Spring blooms of short lived pelagic and sympagic algae characterize the seasonality in Arctic primary production (see above).

Peak abundance and biomass of primary producers and zooplankton communities in the water column typically start around early spring and extend throughout the summer (Hassel, 1986; Wassmann et al., 1999; Weydmann et al., 2013), followed by a sharp decrease in winter, when a lot of zooplankton species enter diapause in deeper waters (Daase et al., 2013; Søreide et al., 2013). Since the Barents Sea is characterized by a strong pelagic-benthic coupling, it was thought until quite recently that seafloor communities also entered a state of torpor and dormancy during the polar night, when little photosynthetic activity is possible and little organic matter is exported to depth. However, recent studies have shown that benthic organisms sustain their activities and reproduce during this time of the year, relying on stored food or detrital and advected sources (Berge et al., 2015; Renaud et al., 2020).

Seasonality of macrobenthic communities in the Barents Sea region have only been studied in few coastal areas. In spite of the strong seasonality in sympagic and pelagic systems, seasonal studies in the western fjords of Svalbard yielded surprisingly constant macrofaunal abundances, food-web structure, size spectra, community composition across seasons and SOD rates (Kędra et al., 2012; Włodarska-Kowalczuk et al., 2016; Mazurkiewicz et al., 2019; Morata et al., 2020). A similar trend has been described for the West Antarctic Peninsula shelf (Smith et al., 2006; Glover et al., 2008). In both cases it was suggested that the constancy in macrofaunal assemblages was due to a “food bank” of fresh organic matter accumulated in the sediments (Mincks et al., 2005; Smith et al., 2012). However, in a highly pelagic-benthic coupled system such as the open Barents Sea shelf, this theory remains to be validated and was, therefore, a focus in this thesis.

Food availability at the seafloor, structure and function of benthic standing stocks and sediment remineralization rates are interlinked processes that are driven by several environmental and biological interactions. However, these processes may or may not show similar temporal variability in their interactions (Klages et al., 2004). Renaud et al. (2008), for instance pointed out that although SOD rates around the northern waters of Svalbard seemed to be dominated by benthic macrofauna, there was no correlation with its biomass, suggesting that studies that have previously linked high SOD values with high macrofaunal biomass might have been observed fortuitously in a period of high deposition of organic material in the seafloor. Thus, secondary production (reflected in biomass) is usually a long-term result in the scale of months to years, while respiration processes could be detected in the scale of hours to weeks (Renaud et al., 2008). Link et al. (2011) concluded that shifts in benthic remineralization, food supply, and biodiversity caused by climate change could be reflected on different time scales, and that their interactive effects may obscure the detection of gradual change, particularly in highly productive and diverse benthic environments.

2 OBJECTIVES AND HYPOTHESES

The overarching goal of this thesis is to investigate Arctic soft-bottom macrobenthic community dynamics, from species composition to functional diversity, across spatial and temporal scales. Spatial gradients include the northwestern Barents Sea shelf comprising its open waters and surrounding coastal fjords and adjacent deep Nansen Basin (**Fig. 7**). Temporal scales investigated range from long-term patterns (decades) to short-term (seasons to days). Further, the thesis aims at identifying important abiotic and biotic environmental drivers that potentially constrain macrobenthic communities over these multiple spatio-temporal scales.

The specific aims for the different chapters of the thesis are to:

Paper I: Investigate long-term trends of macrobenthic community composition throughout the first two decades of the 21st century of a cold-Arctic fjord in northern Svalbard (Rijpfjorden) (**Fig. 7**). The hypothesis was that temperature anomalies, either through direct or indirect temperature effects, have driven fluctuations in macrofauna community structure linked to increased presence of Atlantic water. Further, it was hypothesized that locations close to the mouth of the fjord, more exposed to off-shelf conditions, would be largely affected by ocean temperature anomalies while the inner-most locations, partially isolated by a submarine sill, would be less affected by these temperature fluctuations. This time series provides a first long-term assessment of soft-bottom macrofauna in the understudied northern Svalbard fjords under the context of rapid climate change.

Under the premise of Atlantic water intrusions recorded by a mooring system since 2006, the fjord axis from head to mouth was sampled intermittently to identify the potential effects of temperature anomalies on benthic communities along the entire fjord axis and how isolation by a submarine sill might provide refugia to inner-most communities.

Paper II: Assess the seasonal variation in species composition and functional diversity of macrofaunal communities from the northwestern Barents Sea shelf along a transect ranging from south of the Polar Front up to the adjacent deep Nansen Basin (**Fig. 7**). Several environmental parameters were assessed to understand how these communities are constrained across space and seasons, and to answer the question as to whether seafloor communities follow similar seasonal fluctuations as the pelagic realm in this, a priori, highly coupled system.

The hypothesis investigated was that macrofauna taxonomic and functional structure could show signs of seasonality related to fluctuations in seafloor food availability. The results of this study can indicate whether macrofaunal communities are susceptible to short-term phenological shifts predicted in the near future for pelagic processes. It is also the first study in the Barents Sea open shelf, looking at seasonality of macrobenthic communities, covering the under-sampled polar night period.

Paper III: Assess seafloor remineralization rates of benthic communities in response to predicted scenarios of increased temperature and food availability in the future northwestern Barents Sea. It was hypothesised that both temperature and food increase would generally increase SOD rates, and that Arctic influenced and high sea ice covered stations would show a stronger response than the Atlantic open-water stations. Also, that the largest increases in SOD rates to temperature and food increases (individually and additively) would be in seasons with lower ambient bottom temperatures and lowest food availability (i.e. Polar night and late winter). The results of this study will help to better understand biogeochemical processes of the Barents Sea seafloor driven by climate change and the potential consequences for the carbon cycle.

To do so, sediment incubations are performed to measure sediment oxygen demand (SOD) rates at some of the same stations from **Paper II** and with the same seasonal coverage, to understand how communities may respond to the expected climate driven changes of the future northern Barents Sea (**Fig.7**). The incubation experiments consisted in three treatments: increasing sediment overlaying water temperature by 2-4°C above the in-situ seafloor temperatures, supplying grounded algae powder on the surface sediments, and a combination of both.

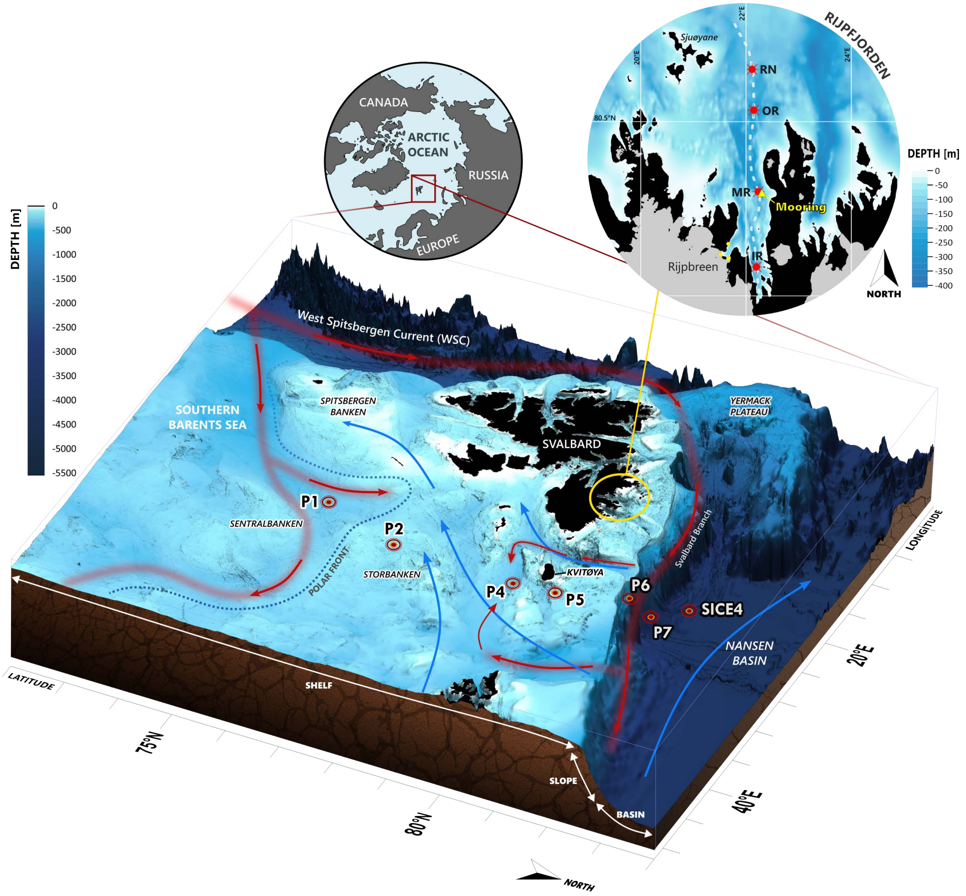


Figure 7. *Sampling locations for the studies of the present thesis in the northwestern Barents Sea region. For the time-series study in Rijpfjorden (indicated with a yellow circle, north of Svalbard), four locations were sampled along the fjord axis (IR=Inner Rijpfjorden; MR=Mid-Rijpfjorden; OR=Outer Rijpfjorden; RN=Rijpfjorden north) in 2003, 2007, 2010, 2013 and 2017. The yellow triangle depicts the location of a long term mooring in the fjord and the yellow small dots in the Rijpbreen marine terminating glacier are the locations from runoff simulations. The sampling location for the macrofauna seasonality study (Paper II) and the experimental study on benthic remineralization rates (Paper III) constitute a transect along the northwestern Barents Sea: P1 (an Atlantic influenced station south of the Polar Front), P2 (a station located near the Polar Front on the Storbanken shallow bank), P4 (located in the northern Barents Sea shelf with high ice cover and Arctic influence), P5 (a shallow station in the northern shelf), P6 (at the continental slope with Atlantic influence from the Svalbard Branch), P7 and SICE4 (in the deep Nansen Basin). Bathymetric from GEBCO Compilation Group, 2022.*

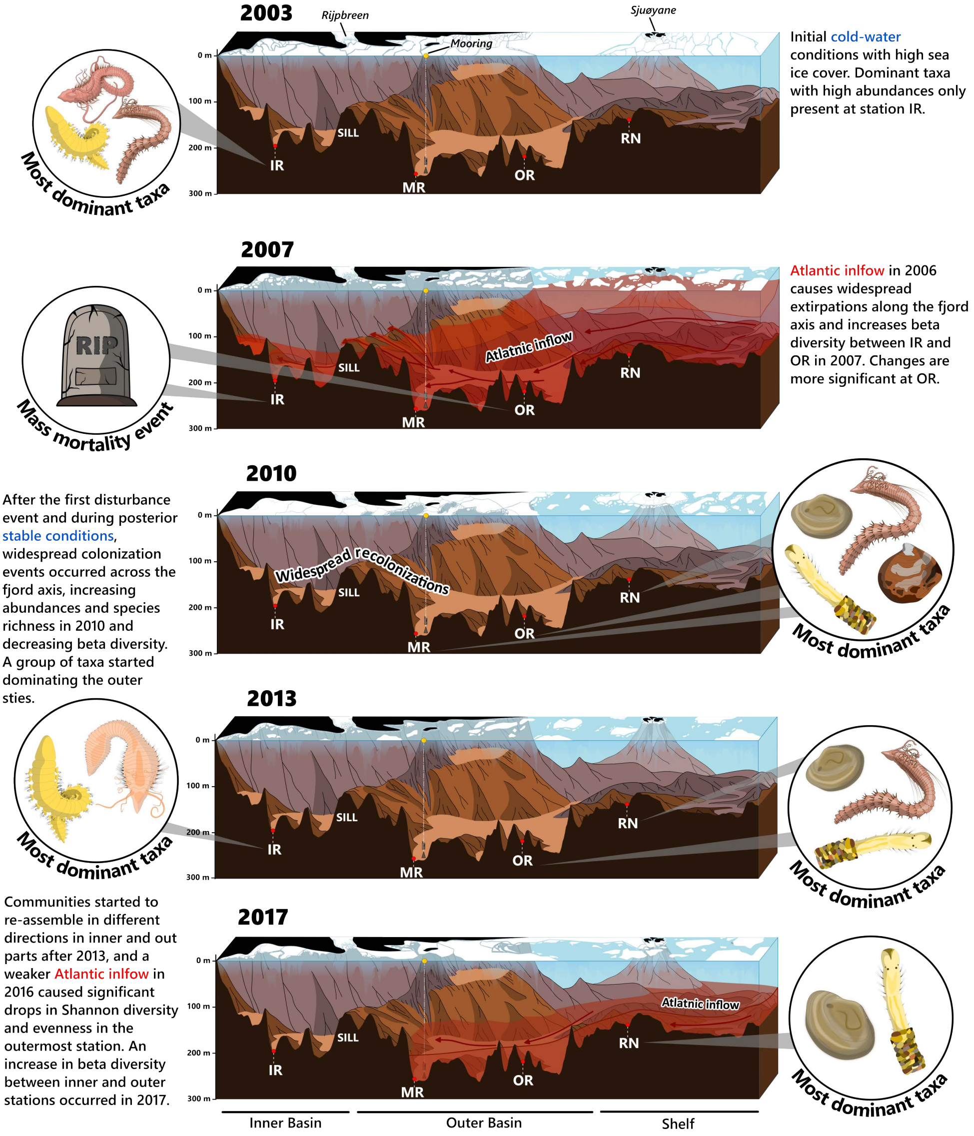
3 MAIN FINDINGS

The north-western Barents Sea is a highly spatially structured ecosystem in both abiotic parameters and benthic community composition, with high inter-annual variability (e.g., extreme events) in parameters such as temperature. The results of this thesis suggest that spatial and temporal patterns of change are not necessarily the same for macrobenthic structure and function (which can vary from year to year) as for physiological responses (which can respond in the timescale of days to seasons). Therefore, predicted shifts in the phenology, intensity and quality of food availability to the seafloor is likely to affect organic matter remineralization at the seafloor, while macrofauna community structure and function is not expected to change immediately due to a decoupling of seasonal processes from the pelagic environment. However, the predicted regime shifts in temperature and primary production, can potentially lead to a re-structuring of macrofauna composition that will not necessarily follow a uniform spatial pattern in the heterogeneous northern Barents Sea seafloor.

3.1 Paper I: Seafloor warm water temperature anomalies created shifts in benthic macrofauna communities of a high-Arctic cold-water fjord

Shifts in macrobenthic communities of Rijpfjorden followed Atlantic water intrusions throughout the first two decades of the 21st century (**Fig. 8**). In 2006, the intrusion of transformed Atlantic Water into the fjord caused a temperature anomaly that led to a series of local extirpations of macrobenthic taxa across the whole fjord axis. This translated into a significant decrease in macrofauna abundance and diversity at the outer stations close to the shelf, and an increase in beta diversity between inner and outer parts of the fjord. This was followed by a period with colder temperatures and more stable sea ice conditions until 2010, when widespread recolonization events of several taxa were observed. At the same time, abundance and species richness increased while beta diversity between inner and outer sites decreased, which resulted in the homogenization of community composition throughout the fjord. However, a significant decline in evenness was also recorded for 2010, indicating that some taxa started dominating the outer parts of the fjord (e.g. the polychaetes *Galathowenia oculata* and *Chaetozone* sp. and the bivalves *Yoldiella* spp. and *Mendicula* sp.). After that, a gradual re-structuring of the community assemblages took place from 2013 to 2017, gradually increasing beta diversity between inner and outer sites. In 2016, another warm temperature anomaly accompanied by the intrusion of Atlantic water into the fjord was recorded, with significant declines in diversity and evenness mainly at the outer most stations only, possibly indicating a minor AW penetration into the fjord than in 2006. Although significant fluctuations in abundance and species richness occurred in the partially isolated innermost basin of the fjord, a more stable Shannon diversity and Pielou evenness was observed here, suggesting that the sill might offer some protection against the impacts of Atlantic water intrusions.

The original hypothesis was confirmed, as macrobenthic fluctuations appeared to be driven either by direct or indirect effects of temperature anomalies associated with intrusions of Atlantic waters into the fjord. Despite evidence of a certain degree of resilience in macrobenthic communities against potential seafloor marine heatwave events, especially at more isolated sites in the inner fjord, it is likely that increased frequency and intensity of extreme anomaly events will impact the macrofauna composition of this northern fjord in the future. Most likely, the macrofauna assemblages of northern Svalbard fjords will gradually resemble those in western Svalbard in the future, which are more exposed to the effects of periodic Atlantic intrusions. This transition could have important consequences for the fjordic ecosystems of these high-Arctic fjords.



Initial cold-water conditions with high sea ice cover. Dominant taxa with high abundances only present at station IR.

Atlantic inlfow in 2006 causes widespread extirpations along the fjord axis and increases beta diversity between IR and OR in 2007. Changes are more significant at OR.

After the first disturbance event and during posterior stable conditions, widespread colonization events occurred across the fjord axis, increasing abundances and species richness in 2010 and decreasing beta diversity. A group of taxa started dominating the outer sties.

Communities started to re-assemble in different directions in inner and out parts after 2013, and a weaker Atlantic inlfow in 2016 caused significant drops in Shannon diversity and evenness in the outermost station. An increase in beta diversity between inner and outer stations occurred in 2017.

Figure 8. *Graphical representation of the main results from Paper I, looking at a time-series of macrofauna communities in Ripfjorden in relation with Atlantic water intrusions. IR: Inner Rijpfjorden; MR: Mid-Rijpfjorden; OR: Outer Rijpfjorden; RN: Rijpfjorden North. For locations in a map see Figure 7.*

3.2 Paper II: Lack of strong seasonality in macrobenthic communities from the northern Barents Sea shelf and Nansen Basin

Macrobenthic communities along the northwestern Barents Sea shelf and adjacent Nansen basin displayed weak signs of seasonality in community composition and functional diversity overall (sampled in August, December, March and May). Surprisingly, most of the environmental variables at the seafloor remained relatively constant, suggesting a potential decoupling from overlying water conditions and pelagic-benthic processes (**Fig. 9**). However, a somewhat higher variability in macrobenthic composition than in most stations was observed at one location close to the polar front (station P2), where also significantly higher diversity (S and H') and evenness (J') was observed in March. Although some variations in food quality were observed at this station, community changes seem to reflect fluctuations in bottom temperature. This suggests that mesoscale features like the Polar Front, which fluctuate seasonally due to water mass and sea ice cover variability, might enhance vertical flux and fuel communities that are very efficient at consuming fresh organic matter exported to the seafloor. Some significant temporal variations were also found in community metrics at the continental slope (station P6) and deep Nansen Basin (P7), but this could rather be a result from spatial heterogeneity in seafloor morphology of the slope or high patchiness and low sampling size at abyssal depths than seasonal fluctuations.

Generally, functional redundancy (Fdis/H') also showed weak seasonal variation, and only varied significantly across seasons at station P2 (Polar Front) and at station P7 (Nansen Basin). Moreover, it was observed that functional redundancy was the highest at P2 and the lowest at P7, suggesting that deep sea macrobenthos of the Nansen Basin would be less resilient to ecosystem changes.

The results showed that 24% of the variation in macrofauna composition in this region of the Barents Sea is explained by the environmental variables and the spatial structure together, while only 1 % of the variation is explained by temporal predictors together with environmental variables. For the functional composition (community weighted means (CWM)), 35% of the macrofauna variation was explained by both the spatial structure and the environmental variables together, while temporal predictors did not explain any variance.

The original hypothesis was partly rejected, as an overall lack of seasonality in macrofaunal composition and functional diversity was observed. Also, it seems that in most regions, macrofaunal community processes are relatively decoupled from overlying water seasonal fluctuations and that food availability is generally constant at the seafloor. This indicates that expected future changes in the phenology of pelagic processes might not strongly affect macrobenthic function and structure, since pelagic-benthic coupling interactions seem to be buffered by a “food bank” of organic matter resources in the sediment.

3.3 Paper III: Benthic remineralization under future Arctic conditions

The results from the respiration incubation treatments (warming and additional food supply) showed a general increase in sediment oxygen demand rates (SOD) compared to baseline rates, consistent with our hypothesis (**Fig. 9**). This increase occurred in at least one season at all stations for at least the combined treatment of increased temperature (2-4°C) plus additional food supply in the form of ground microalgae. Highest increases in SOD (of up to three-fold) were recorded at the deep stations (P6 and P7). Highest SOD responses were usually recorded for both treaments combined, warming and additional food supply, than for each of them separately. Surprisingly, significant responses for most stations were observed in March and May, when ambient bottom temperatures were generally at their warmest.

Therefore, the original hypothesis was partly refuted since, although SOD rates tended to increase with increasing temperature and food supply, signficant responses to both treatments were detected in all stations, independently of water mass, productivity or biotic assemblage domains. Most importantly, the combination of both treatments, warming and increased food supply, increased SOD rates at most stations especially during months with pre- or during pelagic bloom conditions (March-May) and when temperatures were at their warmest. This finding implies that future phenological shifts in primary production and vertical fluxes, coupled with ocean warming, will have implications for the metabolic activities of benthic communities and biogeochemical processes at the seafloor, with consequences for carbon cycling in the northern Barents Sea.

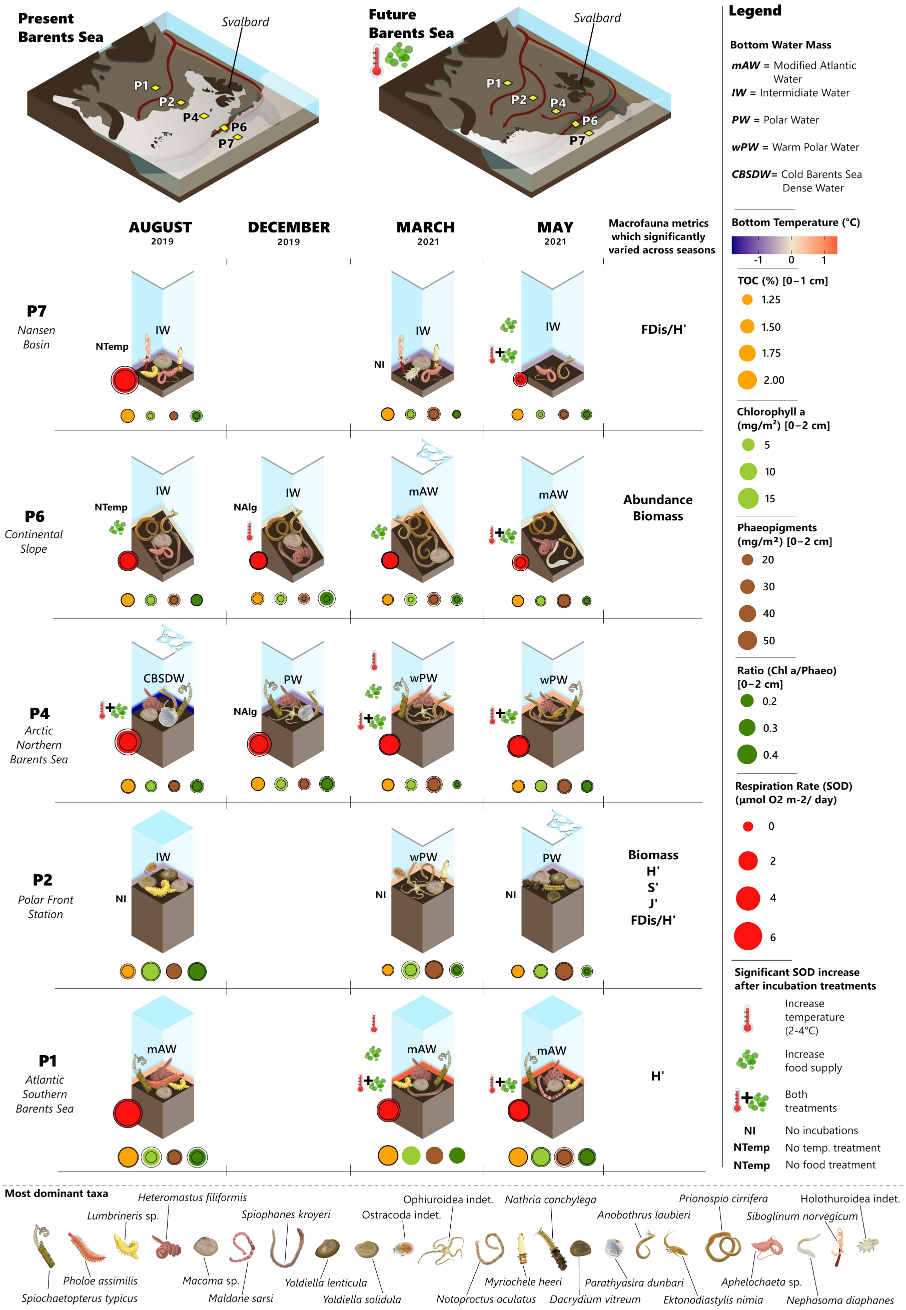


Figure 9. *Summary figure from main results of* ***Papers II*** *and* ***III****. Seasonal patterns in environmental parameters and macrofauna communities are presented. The five-most abundant taxa for each station/season are drawn. Also, the main results of sediment incubation experiments assessing responses in sediment oxygen demand rates (SOD) with predicted scenarios of increased temperatures and increased food availability to the benthos are shown. Black rims in circles indicate standard deviations.*

4 GENERAL DISCUSSION

Although benthic communities in the Barents Sea region have been extensively studied throughout the last four decades, fundamental uncertainties still exist today about how benthic community composition, seafloor biogeochemical processes and ecosystem functioning will respond to the unprecedented ongoing changes in the Arctic (e.g. decreasing sea ice extent and thickness and increasing ocean temperatures) (Macdonald et al., 2015; März et al., 2022). Temporal scales and timing of such responses might be heterogeneous due to the intrinsic dynamics of biological communities. Also, the high spatial heterogeneity of the Barents Sea ecosystem, with complex bathymetric features (local to regional scale) and well defined hydrographic domains (large scale), may play an important role in determining spatially differentiated community responses in the future. Therefore, a wide range of bathymetric and geomorphological environments with differing hydrographic and productivity regimes were investigated in this thesis to gain a better understanding on how abiotic drivers constrain macrofauna communities on different temporal scales. To do so, long-term trends and intra-annual fluctuations in community structure and function were investigated to determine patterns of change. Moreover, changes in rates of organic matter remineralization at the seafloor in response to projected climate change conditions were examined using an experimental approach in order to predict possible outcomes of future shifts in biogeochemical processes of the northern Barents Sea.

The main contributions to scientific knowledge from the thesis are the findings that: 1) significant shifts in macrofauna community composition have occurred during the last two decades in the northern coast of Svalbard due to warm water anomalies, with stronger effects in the open shelf than in semi-isolated inner-fjord basins; 2) that seasonality in macrofauna composition and functional diversity is surprisingly weak in the northwestern Barents Sea shelf and adjacent deep Nansen Basin, despite high intra-annual variability in abiotic drivers and pelagic processes, suggesting a decoupling to some extent between the pelagic system and the benthos; and that 3) projected scenarios of increased primary production and increased water temperatures in the northern Barents Sea are likely to increase remineralization rates of benthic communities.

4.1 Decadal shifts in macrofauna community composition in conjunction with temperature anomalies

The Barents Sea experienced a sharp increase in surface ocean temperature and salinity around the mid-2000s, accompanied by near-bottom temperature increases and increased frequency, length and intensity of marine heatwaves (MHWs) (Lind et al., 2018; Skagseth et al., 2020; Mohammed et al., 2022b). MHWs have been properly defined just recently within the scientific community (Hobday et al., 2016) in order to use a common terminology to study their impacts. This definition is constrained by long-term climatology data (i.e. 30 years), and since a lot of studies in the Arctic have just started to monitor environmental change over the last two decades the term MHW could be misused. Therefore, the term warm water anomaly (WWA) will be used hereafter to refer to anomalously warm water periods over the span of years available for each study referred to in this discussion.

Results from **Paper I** show that a WWA was recorded by the end of 2006 in Rijpfjorden bottom waters , associated with the presence of transformed Atlantic Water (tAW) inside the fjord. Concurrently, between 2004 and 2007, a pronounced WWA was recorded in the Fram Strait (in the HAUSGARTEN observatory, located in the Atlantic gateway to the Arctic at around 79°N off the west coast of Svalbard) (Beszczynska-Möller et al., 2012; Soltwedel et al., 2016). Particularly, in September 2006, temperatures at depths of 250 m exceeded 3°C along the eastern side of the West Spitsbergen Current even during winter, while temperatures in this range were until then restricted to summer months (Soltwedel et al., 2016). Due to this anomaly, several cascading effects were observed in the entire open-ocean of the Fram Strait, from the pelagic to the deep seafloor realm (Soltwedel et al., 2016). The WWA observed in the Fram Strait most likely propagated all the way across the Yermak Plateau and reached the continental shelf north of Svalbard, advected through the Svalbard Branch. Therefore, the processes observed in the HAUSGARTEN observatory throughout the last two decades might bring some valuable insights into the processes observed in Rijpfjorden.

Significant decreases in abundance and species richness in macrofauna across the Rijpfjorden axis were observed during the WWA in 2007 compared to pre-WWA conditions in 2003 (**Paper I**), which could be attributed to a mass mortality event linked to the seafloor WWA documented by the end of 2006. No macrofauna samples from the WWA event are available in HAUSGARTEN (only sampled in 2000, 2010 and 2017; Górska et al., 2022) for comparison with the study of **Paper I**. However, yearly meiofauna samples in HAUSGARTEN from 2000 to 2014 indicate that mean nematode densities significantly decreased in 2004 and 2005 during the WWA compared to previous years, followed by generally increased values in the following years, especially in 2006 (Hoste et al., 2007; Grzelak, 2015; Soltwedel et al., 2016; Soltwedel et al., 2020). These fluctuations in nematode communities were attributed to immediate responses to food quality changes induced by the WWA, which decreased between 2004 and 2006 and shifted from low to higher sediment-bound pigment concentrations from 2006/2007 onwards(Meyer et al., 2013; Soltwedel et al. 2016). A change in overall food availability at the Fram Strait seafloor also translated into substantial decreases in richness of seafloor bacterial communities during the WWA in 2005-2007, bouncing back to similar levels after the WWA in 2008 as before the WWA in 2003 (Jacob et al., 2013). Meiofauna are known to be highly sensitive to environmental changes because of their short generation time and low dispersal capabilities (Schratzberger and Ingels, 2018). However, it is important to keep in mind that macrofauna and megafauna communities might present a more delayed response to the effects of WWA (and associated food availability shifts) than the more short-lived meiofaunal communities, which already showed recovered abundances and highest trophic diversity by the end of the WWA in the Fram Strait. For deep-sea megafauna, a 1 to 1.5 year time lag in community structure responses to food availability changes has been observed (Ruhl, 2007). This could be the reason why, in HAUSGARTEN, Meyer et al. (2013) observed lower megafaunal densities in 2007 compared to 2002 (see also Bergmann et al. 2011), despite the fact that biogenic sediment compounds had already shifted to higher concentrations for that year. This observation is in line with the low macrofauna abundances and species richness observed in Rijpfjorden (Paper I) in 2007, which could point towards a similar lag in macrofauna responses to the WWA of about one year. Overall, and using the HAUSGARTEN area as an analogous system, it seems reasonable to hypothesize that the faunal extirpation event in Rijpfjorden observed in 2007 could be ultimately linked to food availability changes at the seafloor induced by the WWA, rather than just induced by thermal stress from increased bottom temperatures.

The reason behind fluctuating food availability and/or quality might be linked to vertical fluxes influenced by sea ice cover dynamics. In Rijpfjorden, higher frequencies of close to very close drift ice were observed in 2003 and 2008/2009 prior and after the WWA than during the WWA at the outer parts of the fjord, and high frequency of fast ice in the inner parts for those periods (**Paper I**). In the Fram Strait, similar positive anomalies in sea ice cover in the same years were associated with increased flux rates of biogenic particulate silica and zooplankton fecal pellets observed in sediment traps (Lalande et al., 2013), which suggests that sea ice extent in Rijpfjorden might also have determined the quality and sedimentation rates of organic matter to the seafloor with potential effects on the macrofauna communities. In HAUSGARTEN, an abrupt shift from diatom-dominated phytoplankton to pelagic communities dominated by micro- and nanoflagellates was observed during the WWA (Mebrahtom Kidane, 2011; Soltwedel et al., 2016), favoring the development of microbial communities and leading to long retention times of organic matter in the water column (Lalande et al., 2013; Cardozo-Mino et al., 2023). This indicated that sedimentation rates were diminished during the WWA. Similarly, during the seafloor WWA in Rijpfjorden, general declines in sea ice cover were observed, especially in 2006 and 2007, which translated into high dissimilarity in macrofauna species composition for 2007 compared to 2003 and 2010.

Significant increases in abundance and species richness of macrofauna were documented in Rijpfjorden for 2010, some years after the WWA, relative to 2007 (**Paper I**), dominated by species gains and recolonization processes across the whole fjord axis, which made the fjord more homogeneous in species composition. Similarly, higher macrofauna abundances and species richness at the HAUSGARTEN observatory were recorded between 2000 (before the WWA) and 2010 (after the WWA) (Górska et al., 2022). For megabenthos, a significant increase in densities (of almost two-fold) between 2007 and 2012 was found at a HAUSGARTEN site (Meyer et al. 2013). The time series in Rijpfjorden revealed an increase in abundance of certain taxa that started dominating from 2010 onwards, especially in the outer regions of the fjord. Some of these taxa were also found dominating the shelf stations of HAUSGARTEN after the WWA (e.g., *Galathowenia oculata,* an opportunistic arcto-boreal polychaete) (Górska et al., 2022). This indicates that some of these species could have been benefited from the disturbance of the WWA and potentially recolonized parts of the shelf north and west off Svalbard after the extirpation event.

More WWA anomalies have been recorded after the WWA of 2004-2007 around Svalbard waters. In 2014, the strongest and most intense WWA was registered in Isfjorden, a western Svalbard fjord (Bloshkina et al., 2021). Although the WWA from 2004-2007 that was observed both in HAUSGARTEN and in Rijpfjorden was also documented in the outer parts of Isfjorden, in 2014 most of the water column at both outer and inner stations of Isfjorden were occupied by AW (Bloshkina et al., 2021). In Kongsfjorden, a fjord just north of Isfjorden and adjacent to the HAUSGARTEN observatory, AW and Transformed Atlantic Water (tAW) masses also dominated the fjord in 2014, accompanied with sea ice free conditions (Hop et al., 2019b; De Rovere et al., 2022). Interestingly, in Rijpfjorden no tAW at bottom depths for 2014 was detected (**Paper I**). Instead high frequency of very close drift ice was observed for that year, similarly to the situation at the continental slope north of Svalbard (Athanase et al., 2020). In 2014, northerly winds prevailed in the north of Svalbard (Koenig et al., 2017), pushing the drifting sea ice against the coast (Athanase et al., 2020; Lundesgaard et al., 2021), keeping the northern shelf and the coastal areas in a "cold" and "high sea ice cover" state. It seems, therefore, that depending on local wind patterns and prevailing sea-ice drift trajectories the shallowing of the Svalbard Branch can be hampered in the northern Svalbard shelf, mitigating the effects of advected WWAs from further south on shallow waters. Due to this match or mismatch in conditions between the western and northern Svalbard shelves, different scenarios could have taken place between 2013 and 2017 between the northern shelf break (facing Rijpfjorden) and the western shelf break (HAUSGARTEN) of Svalbard, a situation that could have induced divergent outcomes on the respective macrofauna communities. Specifically, a sustained increase of macrofauna abundances and an elevated evenness in 2017 relative to 2010 was observed in HASUGARTEN (Górska et al., 2022). A similar trend was reported by Meyer et al. (2013) for megafauna in HAUSGARTEN from 2010 to 2013. Conversely, we recorded a gradual decrease between 2010 and 2013 in both abundance and evenness in Rijpfjorden, and a sharp decrease in evenness in 2017 (**Paper I**). Gorska et al. (2022) suggested that the higher food input recorded after the first WWA in HAUSGARTEN caused the elevated density and diversity in macrobenthos from 2010 onwards, but that it was not strong enough for opportunistic species to dominate later on in 2017, opposite as to what was observed in Rijpfjorden with a clear dominance of *G. oculate* at the outer sites. In fact, although phytodetritus in sediments increased after the first WWA in HAUSGARTEN, total organic matter in sediments decreased after the warm period, perhaps due to higher microbial degradation or elevated consumption and burial of organic matter by zoobenthos (Górska et al., 2022).

Mesocosm experiments have shown differential responses to single or sequential marine heatwaves at the macrofauna community level, especially in the sessile/infaunal fraction (Pansch et al., 2018). Phenological and functional shifts may produce diverging responses in the community when subjected to episodic versus chronic thermal stress. For instance, after three sequential vs. one single heatwave, macrofauna populations tended to increase in abundance but decrease in biomass, indicating perhaps enhanced recruitment (Pansch et al., 2018). At the same time, detritivore feeding types were reduced after a single heatwave, while suspension feeders declined after three sequential heatwaves (Pansch et al., 2018). Concurrently, acclimation capabilities and indirect responses mediated by shifts in biotic interactions post-disturbance could be responsible for diverging species-specific effects, resulting in diverging outcomes in community structure (Pansch et al., 2018). Some of these could be reasons for the differences in evenness patterns observed between both regions, which although highly speculative, could be behind the different restructuring patterns in macrofauna communities after the sequential heatwaves in 2014 and 2016 in HAUSGARTEN compared to Rijpfjorden (with only one WWA in 2016). For both shelves and adjacent fjords, independently from divergent outcomes after the last WWA events, the first WWA in 2004-2007 triggered cascading effects in the whole marine ecosystem, leading to potential permanent shifts in macrobenthic community structure and seafloor environmental parameters (**Paper I**; Górska et al., 2022), most likely mediated through a shift in pelagic conditions (Soltwedel et al., 2016).

Temperature can exhert both direct metabolic effects as well as indirect effects related to changes in environmental conditions and other drivers constraining macrofauna, especially in coastal ecosystems. Relatively low thermal limits for Arctic taxa have been defined, and changes in suitable habitat for many of these species have been predicted by increases of a few degrees (Renaud et al., 2015; 2019). In fact, it has been observed that small temperature increases (of up to 2°C) can cause significant reorganization of benthic communities (e.g., in the Gulf of Alaska; Anderson and Piatt, 1999). Along this line, a homogenization of macrofauna assemblages was observed in Kongsfjorden between the outer and central parts of the fjord in 2006 compared to the 1990s, during the period with increased Atlantic Water inflow in 2004-2006 (Kędra et al., 2010). A similar homogenization across the fjord occurred in Rijpfjorden (**Paper I**) in 2010 after the WWA, although we saw signs of restructuring of both inner and outer parts in the years after, suggesting some sort of resilience capability. However, the taxa that became dominant at the outer parts of Rijpfjorden in 2010 persisted until (at least) 2017, suggesting a permanent shift in those taxa. The inner parts of fjords, which are more sheltered from offshore conditions, appear to be more resilient to effects of temperature increases, especially when isolated by submarine sills (Renaud et al., 2007b). Several studies have reported the high stability of these inner locations, indicating that Arctic inner fjordic basins may act as refugia for several cold-water taxa during periods of high Atlantic inflow in more exposed sites (Renaud et al., 2007b; Kędra et al., 2010; Drewnik et al., 2016). In these inner sites, however, glacier runoff and inorganic sedimentation can be an important driving force selecting on macrofauna structure and its fluctuations in time (**Paper I**). For example, glacier retreat and changes in runoff patterns could lead to shifts in these inner communities which have lower functional redundancy than outer and shelf locations (Włodarska-Kowalczuk et al., 2012; Udalov et al., 2021).

The effects of WWA on inter-annual community shifts are difficult to disentangle from other effects that can be triggered by increasing temperatures, such as glacial influence, vertical fluxes and food availability at the seafloor, local weather conditions and associated prevailing winds, etc. In fact, Węsławski et al. (2011) suggested that predicted temperature increases for coastal areas around Svalbard would not have such a strong direct effect on benthic communities compared to concomitant changes in other environmental parameters associated with temperature..

Assessing macrofauna community compositional change through time is difficult when sampling is limited to discrete years (as done in most of the long-term studies in this high Arctic region), with gaps of several years in between. With time lags in macrofauna community responses to environmental fluctuations spanning several months to years, a minimum of annual sampling seems to be required in monitoring efforts if the interactive mechanisms by which environmental drivers determine macrofauna communities are to be disentangled and explained. These should be done concomitantly with monitoring of pelagic processes, since the strong pelagic-benthic coupling in the region greatly determines seafloor processes in inter-annual temporal scales.

Until recently, it was believed that the northern coast of Svalbard was less affected by climate change. However, periodic WWA events and concomitant changes in food availability have induced macrofauna community shifts on a large scale on both the western and northern Svalbard shelves and adjacent fjords, suggesting a substantial advective connection between both systems.

4.2 Weak seasonality in benthic macrofauna community structure and functional diversity of the northwestern Barents Sea

In shallow temperate coastal environments, macrofauna communities often undergo significant seasonal fluctuations in abundance and biomass (Beukema, 1974; Zwarts and Wanink, 1993; Coma et al. 2000; Saulnier et al., 2018). An increase in biomass during summer coincides with increasing temperatures, primary production and food availability to the seafloor, which induces increased somatic growth and is accompanied by recruitment pulses (Reiss and Kröncke, 2005; Saulnier et al., 2018). On the contrary, lower food supply during winter can lead to loss of weight and, together with increased predation pressure, increased natural mortality (Saulnier et al., 2018). These seasonal patterns in temperate environments, however, may differ from equatorial or polar regions with little or extreme seasonality in environmental conditions, respectively (Saulnier et al., 2018).

Although for some time Arctic benthic communities were hypothesized to enter a state of dormancy during the polar night, recent studies have demonstrated that benthic organisms do grow and reproduce during this dark period with ceased primary productivity, most likely relying on detrital and advected resources (Berge et al., 2015; Renaud et al., 2020). Exceptions are intertidal mud-flats that constantly freeze at each low tide for months resulting in seasonal defaunation in winter (e.g. in Adventfjorden, a western Svalbard fjord) (Pawłowska et al., 2011). Besides the intertidal, several studies have documented a general lack of strong seasonal variation in macrofauna community structure (i.e. abundance, biomass, species composition, size spectra, food-web structure), and benthic activity, e.g. in Kongsfjorden (northwestern fjord of Svalbard) (Kędra et al. 2012; Berge et al., 2015; Włodarska-Kowalczuk et al., 2016; Mazurkiewicz et al. 2019; Morata et al., 2020). Similarly, no seasonality on trophic dynamics in hyperbenthic Arctic amphipods has been detected in this fjord (Legeżyńska et al., 2012). Our results from **Paper II** are in line with these recent findings, suggesting that macrofauna community composition and functional diversity on the open Barents Sea shelf also remain relatively constant throughout the year.

The general lack of strong seasonality in macrofauna structure and function observed in **Paper II**, together with the relatively constant food availability in surface sediments despite the high seasonality in overlying water parameters, could be supported by the "food bank theory", which was first postulated by Mincks et al. (2005) for the shelf of the West Antarctic Peninsula. There, the authors found a consistent sediment inventory of chlorophyll *a* and enzymatically hydrolysable amino acids in surface sediments, which remained much more constant throughout the year than chlorophyll a flux into near bottom sediment traps (Mincks et al., 2005; Smith et al., 2012). Similarly, although near-bottom chlorophyll a fluxes were overall much higher in May than the rest of the year across the transect from **Paper II** (Bodur et al., 2023, under review), chlorophyll a in the top 2 cm of the sediment remained almost invariable across seasons (**Paper II**). Similar to findings from **Paper II**, no seasonality in macrofauna community structure, together with continuous recruitment pulses throughout the year were documented at the West Antarctic Peninsula (Echeverria and Paiva 2006; Glover et al., 2008). The low temperatures on polar shelves may reduce bacterial degradation rates and preserve labile organic matter contents in sediments year-round (Mincks et al., 2005; Smith et al., 2012), which could sustain macrofauna energy requirements throughout the low productive polar night (Berge et al., 2015). Also, Włodarska-Kowalczuk et al. (2016) attributed the absence of seasonality observed in macro- and meiofauna communities in Kongsfjorden to the presence of a constant phytodetritus pool in the sediments throughout the year.

It is important to notice that the year-round quality of the organic matter available at the seafloor of the northern Barents Sea, including the periods with higher fresh input, is relatively low compared to other much shallower inflow shelves, such as the Chukchi Sea (with chlorophyll a/phaeopigment ratios between 8 and 80 times higher than in our study region) (McTigue et al., 2015; Ziegler et al., 2023). Although relatively highly labile carbon storage (constituting the food bank) might play a crucial role to sustain specific activities year-round for some taxa in the Barents Sea (Oleszczuk et al., 2023), most representatives from the macrofauna communities of **Paper II** were surface or sub-surface deposit feeders, which in shelves and fjords around Svalbard display a high degree of omnivory, sometimes relying on very degraded organic matter (Oleszczuk et al., 2023; Ziegler et al., 2023), or even switching form one feeding mode to another.

Despite being dominated by surface and sub-surface deposit feeders (**Paper II**), which have high bioturbation potential, sediments of the northern Barents Sea exhibit low intensity of sediment mixing and shallow mixed depths (Carroll et al., 2008). At the same time, the ice covered regions of the Barents Sea produce strong bottom currents originating from brine rejection during ice formation (Årthun et al., 2011). The shallow sediment mixing depth together with the strong seasonal bottom currents around early winter could result into a distinct nephloid layer of resuspended detrital material, which can be redistributed across the Barents Sea (e.g. accumulating in the shelf troughs) and even injected into the deeper Arctic Ocean basin (Büttner et al., 2020; Rogge et al., 2023). This could be the reason for the overall (although small) increase in phaeopigments in the sediment surface in March/May (and the consequent decrease in food quality and increase in C:N ratios), after the intensive resuspension period in early winter, making relatively high quality detritus available to partially sustain macrofauna communities throughout the polar night.

At the same time, advected organic matter arrives in the Barents Sea especially during the highest inflow of AW in autumn and winter (Ingvaldsen et al., 2004). This might explain the relatively higher quality of organic matter observed in sediments during periods when local primary production is low (e.g. December) (Ziegler et al., 2023; **Paper II**). Also, late summer blooms may increase food export in form of phaeopigments and other highly degraded organic matter from planktonic grazing activities throughout the summer until late in the year which could also subsidize food sources. All these factors, together with the apparent dietary plasticity of some macrofauna representatives (Ziegler et al., 2023), might dampen the overall seasonality of food web structure, macrofauna community composition and functional diversity in the northern Barents Sea shelf, similar to other highly advective systems such as the West Antarctic Peninsula shelf (Moffat & Meredith, 2018).

The only station that exhibited some evidence of seasonality was station P2, close to the Polar Front, which also displayed the strongest seasonal variability in environmental parameters (**Paper II**). This fact could be attributed to a possible higher pelagic-benthic coupling in that area, located on the shallow Storbanken bank. Pelagic benthic coupling is probably intensified by the fluctuations in hydrographical characteristics, in particular bottom temperature and stratification induced by highly seasonal sea ice of this frontal zone (Wassmann et al., 2006; Carroll et al., 2008; Cochrane et al., 2009). Despite observing highest POC fluxes, highest C:N ratios of sinking organic matter and highest chlorophyll a fluxes also in May in average throughout the whole transect (Bodur et al., 2023, under review), the sediment food quality was relatively the lowest in March/May compared to August/December (**Paper II and III**). Significantly higher macrofauna biomass and species diversity at P2 was found in March/May. Some of the taxa increasing in abundance during the spring bloom were suspension/filter feeders (or facultative of these traits) (e.g. the oweniid polychaete *Myriochele heeri*, representatives of *Ophiuroidea* indet., *Dacrydium vitreum*) (Degen and Faulwetter, 2019). Despite no clear overall seasonality in food-web structure (Ziegler et al., 2023), suspension feeders occupied a lower trophic level in spring than in summer/winter (based on bulk isotopic analysis of $\delta^{13}C$ and $\delta\ ^{15}N$) suggesting a response to uptake of fresh organic matter. Along a similar line, Kokarev et al. (2023) found evidence of fresh phytoplankton consumption by the polychaete *M. heeri* in the Laptev Sea shelf. Filter feeders, therefore, appear to respond quickly to sinking fresh organic matter (chlorophyll *a*) during the spring bloom, intercepting its deposition by effective consumption and hampering its accumulation in surface sediments (Ziegler et al., 2023). Seasonal studies in Kongsfjorden revealed a decrease in oweniid polychaete sizes in May (Włodarska-Kowalczuk et al., 2016), which coincides with maximum larvae occurrences of this polychaete in Arctic waters during spring (Fetzer and Arntz, 2008). It is important to keep in mind that seasonal fluctuations in food availability at the seafloor do not translate instantly into macrofaunal community composition fluctuations over short time-scales, as most recruitment, mortality, and somatic growth processes have longer time lags before they are reflected in the benthic structure for most taxa.

The overall apparent seasonal decoupling of macrofauna community dynamics from seasonal fluctuations of the overlying water column, seems to also apply to reproduction processes and recruitment. A clear mismatch between meroplankton abundance peaks, the larvae of benthic organisms, and phytoplankton bloom was observed in the Barents Sea (Descôteaux et al., 2021). Although most of the larvae observed were planktotrophic, it is suggested that a potential plasticity in diet of these larvae might allow them to feed on other food sources than the dominant bloom diatoms (Cleary et al., 2017). In line with these observations, direct benthic larval development strategies dominated our macrofauna communities (**Paper II**), suggesting that benthic recruits may utilize the constant food supply in the Barents Sea seafloor to sustain successful recruits. Preliminary results of biomass size spectra analysis from the macrofauna communities of our study suggest little seasonality in recruitment pulses (at least for the highest fractions (> 0.5 mm at the community level) (B. Górska, personal communication). This could indicate that continuous successful recruitment may happen throughout the year with differing timing across taxa which would result in relatively stable community structure as observed in our study. However, this is highly speculative and further studies on the poorly studied life-cycles of benthic taxa from this region could help disentangle seasonal processes and their mechanistic relationships with community structure and function of adult populations.

In summary, these results suggest that macrofauna recruitment processes in polar regions might be more complex and dynamic than previously thought and less tightly coupled to the phenology of primary production, at least in advective shelves.

In temperate soft-bottom ecosystems, up to a 50% bias in annual macrobenthic production estimates was attributed to seasonal fluctuations that were not accounted for with a single sampling event throughout the year (Saulnier et al., 2018). These inaccuracies may lead to biased results when assessing inter-annual fluctuations of highly seasonal macrofaunal communities, requiring sampling at different times of the year to produce a more realistic picture of long-term temporal trends. The lack of strong seasonality in community structure and function of the northern Barents Sea validates the approach of discrete yearly sampling in monitoring efforts of the seafloor (which in the Barents Sea region is typically around the spring and summer months) to elucidate long-term temporal trends (e.g. decadal) of macrofauna compositional change (e.g. **Paper I**). This is relevant since most locations are inaccessible (or logistically challenging to sample) during the highly ice covered period of the polar night, which makes this time of the year heavily under-sampled.

4.3 Sediment oxygen demand responses to food quality may provide insights into future benthic remineralization shifts in the Barents Sea

The results from the sediment incubation experiments from **Paper III** suggest that seafloor communities of the northern Barents Sea respond significantly to both increased temperatures and increased food supply. Responses to these factors were the strongest in March and May, prior to and just at the start of the Arctic spring bloom, respectively (Bodur et al., 2023, under review). At this time, ambient sediment oxygen demand rates (SOD) were lower compared to August and December, with the exception of the Arctic shelf station (P4), which showed no significant seasonal variation in ambient SOD rates. A positive correlation has been previously documented between the availability of labile organic matter (chlorophyll *a*) and SOD rates (Boetius and Damm, 1998; Grant et al., 2002; Clough et al., 2005; Grebmeier et al., 2006; Renaud et al., 2008; Link et al., 2011, 2013; Bourgeois et al., 2017). However, no significant correlations were found between sediment pigments and ambient SOD rates in our study (**Paper III**), pointing perhaps towards a lagged accumulation of organic matter sinking to the seafloor into sediments. With a half-life of approximately three weeks in polar sediments (Graf et al., 1995), integrated chlorophyll *a* from overlying waters can persist over several weeks to a few months in surface sediments (Morata and Renaud, 2008). This might explain the lag between highest vertical fluxes of chlorophyll *a* observed in May (Bodur et al., 2023, under review) and the highest food quality in sediments in August, with highest ambient SOD rates detected in the latter month. It is surprising to notice, however, that chlorophyll *a* in sediments remained almost constant throughout all seasons, indicating that if increases in sedimentary chlorophyll *a* throughout the summer months (after the spring bloom and during summer bloom) triggered a rise in ambient SOD, this fresh food was rapidly and efficiently consumed, hampering its detection. Alternatively, the increased mineralization rates after the onset of the spring bloom were sustained by consumption of phaeopigments (Renaud et al., 2007), which decreased in summer and autumn.

Nonetheless, the strongest responses to the increased food supply treatment were detected in March, prior to the spring bloom, and during lowest POC and chlorophyll a fluxes (Bodur et al., 2023, under review) and lowest fresh food availability in sediments (**Paper II**). This indicates that some seafloor organisms respond efficiently to fresh pulses of food input in a short time scale (days) when ambient food quality is relatively lower (i.e. in late winter/pre-bloom conditions). This is in line with findings from

Morata et al. (2015), which showed rapid increases in SOD in sediment incubations when food was added during the polar night in Rijpfjorden. They suggested that the rapid consumption of fresh quality food input in times of scarcity was the main driver of rapid increases in SOD rates. During the incubations of **Paper III**, the ground algae introduced for the food increase treatments was isotopically labelled with carbon 14 (^{14}C). Analysis of carbon uptake rates of these isotopically labelled algae after the increased food supply treatments on selected organisms could provide some evidence for this efficient consumption, and could help disentangle which fraction responds more rapidly and efficiently to these additions (samples not analyzed).

Macrofauna community metrics (i.e. biomass, diversity and abundance) have been observed to explain patterns in SOD rates in Arctic regions (Clough et al., 2005; Grebmeier et al., 2006; Link et al., 2011, 2013). However, no significant correlations were found between abundance and biomass of macrofauna and ambient SOD rates in the study of **Paper III**, which is not surprising given the lack of seasonality in macrofauna composition and functional diversity observed (**Paper II**). This is not strong enough evidence, though, to rule out the potentially important contributions to SOD rates from macrofauna through changes in their behavioral activities (i.e. bioturbation and bioirrigation) driven by fluctuations in food quality/availability (Morata et al., 2015; Solan et al., 2020). Nonetheless, the lack of relationships between macrofauna composition and SOD rates suggests that it could be possible that bacteria and meiofauna would be the ones responding immediately (days) to pulsed food increases by increasing SOD rates in periods when fresh food was scarce in ambient conditions, especially in the deepest stations. This hypothesis is in agreement with the fast responses of bacteria and meiofauna to changes in food availability documented in the HAUSGARTEN observatory during the WWA between 2004 and 2008 (Soltwedel et al., 2016). In fact, direct links between aerobic processes, reactive organic carbon and highest abundances of bacteria and archaea have been found in the uppermost sediment layers of the Barents Sea, seemingly indicating a strong relationship between organic matter degradation and microbial communities (Stevenson et al., 2020).

However, another study in the Barents Sea observed a weak correlation between bacterial abundances and diffusive oxygen uptake (DOU), which mainly accounts for bacterial mediated respiration (Glud et al., 1994), although it was hypothesized that higher DOU rates could be linked to increased cell-specific activity triggered by the availability of chlorophyll pigments (Kiesel et al., 2020). This same study found high fauna-mediated oxygen uptake, which is considered a proxy from macrofauna and meiofauna respiration and which usually correlates well with macrofauna biomass, (Wenzhöfer and Glud, 2002), in stations with high amounts of fresh phytodetritus (Kiesel et al., 2020). These findings support the idea that macrofauna could, potentially, drive an important part of SOD rates in the Barents Sea floor. Further investigations of bacterial and meiofauna samples from the incubations of the experiments from **Paper III** may provide with some valuable insights into the relative roles of each of these components to contributions of SOD rates observed for the treatments (although accurate partitioning of SOD rates into benthic compartments is difficult and usually not precise (Piepenburg et al., 1995)).

Significant SOD responses to increased temperature (4°C for shelf stations and 2°C for deeper stations) were most frequent in March and May, either alone or in combination with the food increase treatment (with almost always additive effects in the latter). One hypothesis from **Paper III** was that strongest responses to temperature increases would be observed in periods when ambient bottom temperatures would be the lowest. Surprisingly, bottom temperatures during March and May were the highest compared to August/December. Since strongest responses to increased temperatures (alone) were recorded in March, coinciding with lowest quality of food in the sediments, it is therefore possible that responses to increased temperature could be linked to food quality limitation at the seafloor (**Paper III**). Perhaps during late winter/early spring, when benthic communities have been relying on the more resuspended organic material throughout the polar night, seafloor organisms might benefit from a pulse of fresh food that cues feeding and burrowing activities preceding the spring and summer blooms (Renaud et al., 2007). At the same time, if bottom temperatures are increased over ambient ones (which for the food-quality-limited late winter are already at their maximum), metabolic rates and bioturbation activities can be increased (Kauppi et al., 2023). Therefore, there seems to be a critical window in late winter, when food quality is low and ambient bottom temperatures are comparatively high, during which sustained increasing temperatures from climate change could have the largest effect on benthic remineralization rates. Thus, changes in phenology of primary production in the near future could affect benthic physiological activities in food-limited shelf regions where low overall primary production but short pulses of fresh food input to the seafloor occur today (northern Barents Sea shelf region) (Morata et al., 2011). However, an increase in the supply of alternative food sources (e.g. detritus of more degraded nature) and higher remineralization rates of organic matter in the water column as a consequence from long-term Atlantification effects could lead to a gradual decoupling of benthic activities from overlying water processes and to a decreased seasonality in physiological responses (Morata et al., 2020).

The outcomes of this experimental investigation, nonetheless, suggest that benthos in the northern Barents Sea is sensitive to fluctuations in food quality which translated into immediate responses in their physiological activities. This does not necessarily invalidate the "food bank" theory discussed in **Paper II**, since benthic communities, and in particular macrofauna, may in fact sustain their year-round standing stocks with the constant storage of relatively labile organic matter in the sediments, translated into the seasonal constancy in community structure observed in **Paper II**. However, it suggests that short pulses of fresh organic matter may be important in triggering activities for some species, perhaps related to feeding or to reproduction, which may be hampered if food supply is too low (Ambrose and Renaud, 1997; Renaud et al., 2007; Morata et al., 2015). Therefore, the decreased food availability during the WWA (2004-2008) in HAUSGARTEN (Soltwedel et al., 2016), and potentially in Rijpfjorden (**Paper II**), could have led to lower macrofaunal recruitment reflected in lower abundances and widespread extirpations in the following years. At the same time, macrofauna communities may have to utilize the more degraded organic matter of sediments during these anomalous warm water events, needing to consume more food to supply their needs and may increase bioturbation activities to access more buried food stored in lower sediment layers (Górska et al., 2022). A higher consumption of lower quality food and increased activities, together with increased benthic metabolic rates induced from warmer temperatures (Jørgensen et al., 2022), can theoretically lead to overall increased oxygen demands and induce depletion of oxygen in sediments, potentially suffocating seafloor communities and leading to a collapse of their standing stocks (Vaquer-Sunyer and Duarte, 2010; Levin and Le Bris, 2015; Górska et al., 2022). Although less clear, thermal stress could also induce detrimental physiological responses (Whiteley and Mackenzie, 2016) if species thermal niches are surpassed (Morley et al., 2019), which could increase mortality (Hobday et al., 2016; Garrabou et al., 2022; **Paper I**). However, these are highly speculative scenarios for the Barents Sea seafloor.

Macrofauna communities in the Barents Sea are highly spatially structured (**Paper II**), supporting the evidence that water mass domains and sea ice cover in part drive the large spatial scale patterns in community structure (Carroll et al., 2008; Cochrane et al., 2009). Given that conditions of increased temperatures and food supply are projected in a context of Atlantification of the northern Barents Sea (i.e. a progression of the Atlantic domain into the Arctic domain), we might expect a gradual restructuring of the communities according to the prevailing drivers operating in each domain (Solan et al., 2020). Therefore, caution should be taken when using the results of the incubation experiments conducted on present day communities to extrapolate long term responses to future conditions from a spatial perspective. However, the lack of significant differences in ambient SOD rates between the Atlantic shelf station (P1) and the Arctic shelf station (P4), plus similar significant responses to increased food and temperature at most stations and at the same time of the year, may indicate that responses could be generalized throughout the Atlantic to Arctic and shelf to basin gradients. Also, it is important to bear in mind that the projected increased primary production in a warmer scenario will not necessarily translate into higher food availability to the seafloor (or at least not necessarily of high quality food), since pelagic communities with higher retention capabilities are also predicted to develop in warmer conditions, especially in Atlantic dominated regions (Wassmann and Reigstad, 2011). Although highly topographically steered, if the Polar Front moves northwards, where local primary production is low in present day highly ice-covered regions, a stronger pelagic-benthic coupling and increased vertical flux could lead to significant increased remineralization rates at the shelfs' seafloor. Similarly, if the seasonal ice edge moves northwards towards the Arctic Ocean basin, a potential increase in sea ice algae production and export to depths during the melting season in this highly food limited region may make these ice algae falls an important food source for deep-sea benthos (Boetius et al., 2013). The lower functional redundancy of macrobenthic communities at the deep Nansen Basin compared to the shelf stations (**Paper II**) could imply a higher sensitivity to changes in food availability in the central Arctic, similar to what was observed by Górska et al. (2022), a situation which could produce functional shifts in these environments.

Svalbard fjords subjected to frequent warm Atlantic water intrusions (e.g., Kongsfjorden) have shown to be more efficient at mineralizing organic matter and to bury less carbon in deeper sediments than fjords with cold Arctic water conditions protected by sills (such as Hornsund) (Zaborska et al., 2018). This difference was attributed to diverging macrofaunal communities and sediment carbon stocks prevailing in each fjord. Specifically, complex and effective food webs are developed in the warmer fjord systems, with a higher state of maturity and more biologically accommodated communities, which utilize and consume carbon sources more efficiently. In contrast, the simpler assemblages in the colder water fjords are less efficient at consuming organic matter at the seafloor, making these colder systems act as carbon sinks to a larger degree than the warmer water systems (Zaborska et al., 2018). The community change observed in Rijpfjorden after the seafloor WWA (**Paper I**) could the start of a similar "maturation" of communities, and in the long run, these fjords may gradually transition from a sink to a carbon source. Total sediment oxygen uptakes have been measured to be up to 50% higher in the warmer Kongsfjorden than in the cold-water Hornsund-fjord (Kotwicki et al., 2018), suggesting a much higher carbon demand for the former. Similarly, baseline SOD rates were generally higher on the warmer Atlantic shelf station than at the stations north of the Polar Front (**Paper III**). Therefore, the increases in remineralization rates and potentially decreasing capabilities of carbon sequestration in the rapidly changing cold Arctic fjords could be extrapolated to the highly ice-covered regions of the northern Barents Sea shelf, which might evolve towards the assemblages of the Atlantic stations following the space-for-time substitution paradigm. However, this transitions may not be so straight forward due to the highly spatially structured Barents Sea, with very local and context-dependent geographical and environmental settings, which may give place to diverging directions of change independent of latitude, hydrographic domain or productivity regimes. Although food availability (and most importantly its quality) is an important driver for future remineralization processes in the Arctic (**Paper III**), biological reorganization in composition and function of benthic assemblages might also play an important role in determining the fate of carbon in the Barents Sea seafloor (Solan et al., 2020).

5 CONCLUSIONS AND FUTURE PERSPECTIVES

Macrofaunal communities in the northwestern Barents Sea, including adjacent fjords, have been affected by climate change throughout the first two decades of the 21st century, and evidence suggests that they will most likely continue to be affected in the coming decades. Although temperature is a master parameter that will likely continue to increase in a future Arctic, many other environmental parameters that constrain macrofauna communities will be altered simultaneously. Consequently, the spatio-temporal extent of these multivariate changes and potential synergistic effects on biological communities may not be uniform or easily predictable.

Constant macrofaunal standing stocks throughout the year appear to indicate resilience of these communities to short-term seasonal fluctuations of the environment, suggesting a certain level of decoupling from the seasonality of overlying water-column processes. Indeed, macrofauna in this region seems to rely quite heavily on degraded forms of organic matter, in part from advected Atlantic-influenced regions, which remains near-constant throughout the year. However, benthic remineralization rates seem to react quickly and efficiently to pulses of fresh organic matter. Therefore, the integrated “food bank” of the Barents Sea sediments and advective inputs appear to satisfy the macrofauna demands throughout periods of low primary production like the polar night. Nevertheless, the sporadic food supply of higher quality seems to be important in triggering physiological activities, such as increased feeding or reproduction. However, lacking signs of pulsed recruitment events of the analyzed fractions (>0.5 mm) and the asynchronicity of meroplankton larval peaks with the spring bloom (Descoteaux et al., 2019), would contradict the theory that reproduction of adult benthic organisms is phenologically tied to the overlying-water primary production. This short-term responses to food quality may simply suggest that benthic communities in this region are food limited for high quality organic matter, and that any pulsed increase in food quality can activate organisms to profit as much from it and in the most efficient way possible, although not necessarily to fuel specific activities (e.g. reproduction). However, it remains uncertain if these responses are mainly mediated by macrofauna, or by other smaller organismal fractions such as bacteria or meiofauna. The partitioning of contributions to remineralization rates of these three benthic components could help better explain this caveat.

In the long term, the Atlantification of the northern Barents Sea (and adjacent fjords), will produce community shifts that may result in profound changes in ecosystem function. For example, the seafloor of northern locations could transition from a sink to a source of carbon, with severe consequences for the Arctic carbon cycle. Extreme events such as warm water anomalies may trigger biological shifts in a more precipitated way than gradual change from Atlantification in the open shelf, while sheltered inner-fjord locations may be more resilient to these events and could act as refugia.

Changes in pelagic ecosystems could also be pivotal to define the fate of seafloor communities and their function in the future, stressing the strong integrated effects of long-term pelagic-benthic interactions of this system, despite the weak influence of its seasonal fluctuations in community structure. While primary production may increase with warmer conditions and long-term sea ice retreat, water columns with longer retention times may develop, hampering the export of higher quality food availability to the benthos. Given the sensitivity of macrofauna activities to food quality, these shifts in vertical flux processes could have far reaching consequences for the benthic ecosystem. Therefore, the pelagic environment (e.g. primary production, grazing communities, vertical fluxes) and the seafloor realm (e.g. megafauna, macrofauna, meiofauna and bacteria) together with abiotic drivers should be sampled jointly to accurately describe the mechanisms of such interactions in the context of rapid climate change.

If benthic remineralization rates and overall ecosystem productivity increase, as predicted for the northern Barents Sea, an increase in fisheries could occur, making this region even more profitable fishing grounds. At the same time, Norway has recently opened the possibility to carry out deep sea mining activities in the deep ocean adjacent to the western Barents Sea (Norwegian Oil and Energy Minister Terje Aasland). Given that deep sea macrofauna communities have lower functional redundancy, and therefore are less resilient than shelf communities, management practices should urgently account for this fact and a precautionary approach should be implemented. Despite efforts from many studies (including the present thesis), the specific mechanisms of change for seafloor communities of the Barents Sea are still poorly understood and the directions in which they will shift remain uncertain depending on location and time-scale. Therefore, governments should continue to prioritize further national efforts (e.g. multidisciplinary projects like the Nansen Legacy) to gain a better understanding into the fate of a rapidly changing Barents Sea marine ecosystem. This knowledge will be critical to implement effective management strategies if anthropogenic activities are meant to develop responsibly in the future.

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Paper I

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Seafloor warm water temperature anomalies impact benthic macrofauna communities of a high-Arctic cold-water fjord

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ABSTRACT

Amid the alarming atmospheric and oceanic warming rates taking place in the Arctic, western fjords around the Svalbard archipelago are experiencing an increased frequency of warm water intrusions in recent decades, causing ecological shifts in their ecosystems. However, hardly anything is known about their potential impacts on the until recently considered stable and colder northern fjords. We analyzed macrobenthic fauna from four locations in Rijpfjorden (a high-Arctic fjord in the north of Svalbard) along its axis, sampled intermittently in the years 2003, 2007, 2010, 2013 and 2017. After a strong seafloor warm water temperature anomaly (SfWWTA) in 2006, the abundance of individuals and species richness dropped significantly across the entire fjord in 2007, together with diversity declines at the outer parts (reflected in Shannon index drops) and increases in beta diversity between inner and outer parts of the fjord. After a period of three years with stable water temperatures and higher sea-ice cover, communities recovered through recolonization processes by 2010, leading to homogenization in community composition across the fjord and less beta diversity. For the last two periods (2010-2013 and 2013-2017), beta diversity between the inner and outer parts gradually increased again, and both the inner and outer sites started to re-assemble in different directions. A few taxa began to dominate the fjord from 2010 onwards at the outer parts, translating into evenness and diversity drops. The inner basin, however, although experiencing strong shifts in abundances, was partially protected by a fjordic sill from impacts of these temperature anomalies and remained comparatively more stable regarding community diversity after the disturbance event. Our results indicate that although shifts in abundances were behind important spatio-temporal community fluctuations, beta diversity variations were also driven by the occurrence-based macrofauna data, suggesting an important role of rare taxa. This is the first multidecadal time series of soft-bottom macrobenthic communities for a high-Arctic fjord, indicating that potential periodic marine heatwaves might drive shifts in community structure, either through direct effects from thermal stress on the communities or through changes in environmental regimes led by temperature fluctuations (i.e. sea ice cover and glacial runoff, which could lead to shifts in primary production and food supply to the benthos). Although high-Arctic macrobenthic communities might be resilient to some extent, sustained warm water anomalies could lead to permanent changes in cold-water fjordic benthic systems.

Abbreviations: SfWWTA, Seafloor Warm Water Temperature Anomaly; MHW, Marine Heatwave; AW, Atlantic Water; ArW, Arctic Water; AO, Arctic Oscillation Index; LCBD, Local Contribution to Betadiversity; AEMs, Assimetric Eigenvector Maps; TBI, Temporal Beta diversity Index.

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1. Introduction

Arctic air temperatures have warmed more than four times faster in the last four decades than in other parts of the globe (Rantanen et al., 2022). In particular, the warming rate for the Northern Barents Sea region is five to seven times the global averages and this exceptional heating is strongly linked to large reductions in sea ice concentration and increased sea surface temperatures in this “warming hotspot” (Isaksen et al., 2022). In light of this rapid change, long-term monitoring programs of the marine Arctic ecosystem are urgently needed in order to establish baselines and rates of environmental change to disentangle short-term variation from long-term shifts, and to predict future scenarios relevant to management efforts. Benthic community structure and function are determined by environmental drivers and faunal interactions over multiple temporal and spatial scales (Griffiths et al., 2017; Ehrnsten et al., 2020). By integrating the variability of these processes into their structure, benthic communities (which are mainly sessile and long-lived) have been proposed as excellent sentinels of environmental change (Renaud et al., 2008; Carroll et al., 2011). Their community fluctuations can thus indicate climate- or other human-driven changes (e.g., Kröncke et al., 1998; Larkin et al., 2010; Serrano et al., 2022).

In shelf and coastal areas, macrobenthic communities play crucial roles in carbon cycling and the remineralization of nutrients (Bourgeois et al., 2017; Solan et al., 2020). Particularly, fjords, which are common geomorphological features in high and mid-latitude regions, are regarded as important carbon sinks on a global scale (Smith et al., 2015; Faust and Knies, 2019; Włodarska-Kowalczuk et al., 2019). These semi-enclosed estuaries experience high seasonality in primary production and strong gradients in abiotic parameters such as salinity, temperature, oxygen concentrations, sedimentation rates, supply of nutrients, and organic matter concentration in the sediments that cause gradients of benthic assemblages along the fjord axis (Holte and Gulliksen, 1998; Włodarska-Kowalczuk et al., 1998; Włodarska-Kowalczuk et al., 2005; Jordà Molina et al., 2019; Udalov et al., 2021).

Isolation caused by fjordic sills in Arctic fjords may protect inner-basin communities from strong fluctuations of abiotic factors occurring in off-shore shelf regions and, therefore, such fjords are assumed to act as refugia (Renaud et al., 2007; Kędra et al., 2010; Wesławski et al., 2011). Consequently, inner-fjord benthic communities are not just subsets of the species pools present in adjacent shelves but, in fact, they rather differ in species composition, species richness, diversity, functional complexity and redundancy (Włodarska-Kowalczuk et al., 2012; Udalov et al., 2021). Therefore, benthic communities from Arctic inner-fjord basins could be less resilient to species losses or invasions, and the extent of environmental variation that these communities can tolerate remains unclear in case of extreme disturbance events (Włodarska-Kowalczuk et al., 2012).

The waters around the Svalbard archipelago comprise a transitional domain from warm and salty Atlantic Waters (AW) dominating the south and west of the archipelago, to colder and less saline Arctic Waters (ArW) mainly present in the northern and eastern regions. In recent decades, a progression of the AW over the ArW domain has been observed, a phenomenon that has been termed Atlantification of the Arctic (Polyakov et al., 2020; Ingvaldsen et al., 2021; Tsubouchi et al., 2021). Periodic intrusions of AW into the western Svalbard shelf and the adjacent fjords have been increasingly frequent in the last two decades, especially after 2011 (Bloshkina et al., 2021). Similarly, a time series in the northern waters of the shelf and shelf-break of Svalbard showed that after 2011, previous stable conditions with high ice cover, below 0 °C water temperatures in the upper 50 m and shallow mixing layer depths shifted towards more open-water conditions, persistent shallow water temperatures above 0 °C and large interannual variations in mixing layer depths and ocean-to-atmosphere heat fluxes (including observations of extreme winter conditions with exceptional deep mixing layer depths) (Athanase et al., 2020). In north-eastern fjords of the archipelago, abundant sea ice cover during the early 2000’s was followed by a decrease in winter sea-ice cover after 2010, with strong links to increased surface air temperatures (Dahlke et al., 2020). In addition, marine heatwaves (MHWs), characterized as prolonged discrete anomalously warm water events (Hobday et al., 2016), have been increasingly recorded in the Barents Sea and in the Fram Strait throughout the last two decades (Beszczynska-Möller et al., 2012; Mohamed et al., 2022).

The impacts of this ongoing Atlantification and extreme warming events of the waters around Svalbard are not limited to hydrography, but also to shifts in the structure and function of their ecosystems (Wassmann et al., 2011; Ingvaldsen et al., 2021). With increased ocean temperatures, the ranges of many boreal species are expected to expand northward (Kraft et al., 2013; Renaud et al., 2015, 2019). In the Barents Sea, several studies have already documented an increase in the presence of boreal fish, zooplankton, and benthic species (Dalpadado et al., 2012; Kortsch et al., 2012; Fossheim et al., 2015). This poleward expansion of boreal species may alter the intrinsic functionality of receiving communities (Kortsch et al., 2012; Węsławski et al., 2017; Renaud et al., 2019; Csapó et al., 2021). Thermal stress induced by unusual warm water temperature events (temperature anomalies such as MHWs) can have detrimental consequences for benthic communities when exceeding species thermal ranges (Dolbeth et al., 2021), inducing mass mortality events in severe cases (Hobday et al., 2016; Garrabou et al., 2022) or shifts in species abundances and/or biomass (Pansch et al., 2018). At the same time, when not lethal, thermal stress may lead to behavioral changes in benthic organisms affecting, for instance, bioturbation activities (Kauppi et al., 2023). However, indirect responses can also be mediated by changes in other biotic interactions “post-disturbance” (Pansch et al., 2018). For instance, ocean temperature fluctuations in Arctic fjords can simultaneously lead to shifts in other important environmental variables that constrain benthic community structure and function (e.g. sea ice cover with consequent shifts in primary production, qualitative and quantitative food availability at the seafloor, water mass properties and glacier runoff and turbidity) (Wesławski et al., 2011). Therefore, the extreme complexity of interactions in the natural environment driven from temperature shifts and its effects on biological communities should be taken into account.

The western and southern fjords of Svalbard have been extensively studied (Molis et al., 2019). Carroll and Ambrose (2012) first reported on macrofaunal patterns on the shelf and fjords of northeastern Svalbard in 2003 in relation to Atlantic and Arctic water masses. Although changes in sea ice and oceanographic regimes have been documented in northern Svalbard during the last two decades (Athanase et al., 2020; Dahlke et al., 2020), no long-term monitoring studies exist of benthic fauna for this area.

Here, we analyze an intermittent time series (from 2003 to 2017) of the soft-bottom macrobenthic communities from Rijpfjorden, a fjord located on the northern coast of the Svalbard archipelago. Although this has historically been considered a fjord with predominantly Arctic conditions, periodic intrusions of warm Atlantic waters from the continental slope have been reported to protrude into the shelf area, affecting the physico-chemical setting and the pelagic ecosystem surrounding this fjord (Hop et al., 2019). Although no significant sustained warming trends have been found throughout the last decades in Rijpfjorden (Cottier et al., 2022), a long-term mooring deployed at the mid-region of the fjord since 2006 provides indications of seafloor warm water temperature anomalies (SfWWTAs) throughout the last decades, which we report in the present article.

Our study investigates how these periodic SfWWTAs in the historically ArW-influenced Rijpfjorden might have affected the temporal dynamics of macrofauna communities. We hypothesize that the species composition in years preceded by SfWWTAs will differ from those preceded by more stable and cold-water periods. We then put the interannual changes in community composition into the spatial context along the fjord axis and hypothesize that outer stations, which are more exposed to the continental shelf and therefore more directly influenced by the effects of potential warm Atlantic inflows from the slope, will show larger inter-annual fluctuations than communities inhabiting the inner silled basin. We also investigate whether bottom temperature fluctuations (i.e. anomalies) by themselves can drive community shifts and if other environmental variables known to be important for benthic community structure in Arctic fjords (which can be simultaneously impacted by temperature, such as sea ice cover and glacier runoff) can also have an impact on macrofauna compositional change. Once again, we hypothesize that at outer stations, fluctuations in temperature will have a stronger influence in determining community composition through time, while more protected inner locations will be less directly influenced by bottom water temperature.

2. Materials and methods

2.1. Study area

Rijpfjorden is located on the northern coast of the Nordaustlandet island, in the north-east of the Svalbard archipelago (Fig. 1a). This fjord is ca. 40 km long and between 7 and 13 km wide. The fjord opens into a wide bay which connects it to the shelf north of Svalbard (100–200 m water depth) which leads to the shelf-break of the Arctic Ocean. The fjord has an inner basin with a maximum water depth of 215 m and an outer basin with 290 m water depth. These two basins are separated by a sill, crossing the fjord diagonally in a northwest-southeast direction, with water depths ranging from ca. 50 m–140 m (Fig. 1d).

Rijpfjorden faces towards the Arctic Ocean and is mainly influenced by comparatively cold and fresh ArW (Hop et al., 2019) with surface temperatures close to the freezing point for most of the year (Wang et al., 2013). AW, however, occasionally penetrates into the shelf area surrounding the fjord (Hop et al., 2019; Wallace et al., 2010). These intrusions are influenced by topographic features of the submarine landscape (troughs and banks along the shelf break) (Bluhm et al., 2020) and also by the wind patterns prevailing in the area (Onarheim et al., 2014; Kolås et al., 2020).

Sea ice usually covers the fjord for up to 9 months a year (Ambrose et al., 2006; Leu et al., 2011) although sea ice extent and volume have been variable during the last decade, with a minimum in 2013 (Hop et al., 2019), and shorter fjord ice seasons have been attributed to reduced sea ice north-east of Svalbard and increased water temperatures (Johansson et al., 2020). Two marine-terminating glaciers are located in the western part of the fjord (Fig. 1c).

2.2. Sampling and macrofauna processing

Sampling took place in 2003, 2007, 2010, 2013 and 2017 with the research vessels *Lance* and *Helmer Hanssen* between late July and early September. Four stations along a transect were studied in the time-series: 'Inner Rijpfjorden' (**IR**) in the inner basin, 'Middle Rijpfjorden' (**MR**) in the outer basin, 'Outer Rijpfjorden' (**OR**) at the fjord mouth located in a depression outside of the outer basin, and 'Rijpfjorden North' (**RN**) just north of the fjord, on the shallow shelf (Table 1; Fig. 1c and d). Stations IR and OR were sampled in all sampled events, station RN in four years and MR in two years (Table 1).

At each station, three Van Veen grab samples of 0.1 m^2 each were retrieved and sediment was sieved over a 0.5 mm mesh. Fauna collected were preserved in a 4% buffered formaldehyde and Rose Bengal stain. In the lab, macrofauna was sorted under the stereomicroscope and identified to the lowest taxonomic level possible. Taxonomic names were checked using the World Register of Marine Species (WoRMS) (Worms Editorial Board, 2022).

2.3. Environmental data

Mean daily water temperatures between 2006 and 2019 from 200 m depth were retrieved from a mooring system located close to station MR (80.3N; 022.3E). From these, the temperature climatology of the bottom water was calculated by averaging data over all the years for each day of the year. Periods of time when mean temperatures exceeded the 90th percentile of the climatology and which lasted for more than five consecutive days were defined as periods with MHWs, following the definition of Marine Heatwaves (MHWs) by Hobday et al. (2016), but with climatology calculated from the 14 years of available mooring data instead of 30 years. Since we calculated climatology based on 14 years of available data in contrast to the recommended 30 years, our MHW definitions should be regarded with caution and just as indicative of temperature anomalies that could potentially be considered MHWs. Therefore, we refer to these as seafloor warm water temperature anomalies (SfWWTAs) in our study.

CTD casts were used to retrieve temperature and salinity profiles close to each station during events of macrofauna sampling. However, for some stations/years some CTD casts were missing, and we retrieved the closest CTD casts in space and time to the sampling points from the UNIS hydrographic database (Skogseth et al., 2019).

Monthly mean Arctic Oscillation indices (AO) were retrieved from the National Weather Service of NOAA,[1] and the average of the year prior to each macrofauna sampling event was calculated to include in constrained analysis of environmental drivers on macrofauna. Some studies suggest that higher inflows of Atlantic water into the Arctic Ocean could be consistent with the positive phase of the AO (Ślubowska et al., 2005), a climate index that describes the patterns in atmospheric circulation over the Arctic. In its negative phase, the polar vortex over the Arctic gets weaker, allowing cold air to escape towards lower latitudes while the westerly winds in the Arctic region fade (Rigor et al., 2002). The opposite occurs during the positive phase, when the polar vortex strengthens and cold air and lower pressures are kept in the Arctic.

In high Arctic fjords, such as Kongsfjorden, it has been postulated that the sedimentation gradient caused by glacial runoff is one of the main drivers of macrofauna composition along the fjordic axis (Włodarska-Kowalczuk et al., 2005; Udalov et al., 2021). Glacial input into Rijpfjorden is not substantial relative to other Svalbard fjords (Santos-Garcia et al., 2022), but may have local influence on the inner fjord station. Therefore, daily glacial runoff simulations ($m^3\ s^{-1}$) based on the simulations by van Pelt et al. (2019) were computed using surface topography and ice thickness to derive the equipotential surface (Torsvik et al., 2019). These data were provided by the Norwegian Polar Institute (Jack Kohler, personal communication) for four locations around the discharge area of the marine-terminating glacier Rijpbreen available from 2006 to 2019 (Fig. 1c). The daily average runoff for all discharge stations was calculated and then the average runoff from the previous year before each macrofauna sampling event was calculated to use as constraining variables for the macrofauna variation partition.

Granulometry analysis and the assessment of Total Organic Carbon content (TOC) in the sediments were conducted for the years 2003 and 2010 taken from an extra grab sample. Granulometry samples were split into coarse (>0.063 mm) and fine fractions (<0.063 mm) by wet sieving and dried at 60 °C and weighted (Carroll and Ambrose, 2012). For TOC content analysis, samples were treated with hydrochloric acid (HCl) to eliminate carbonates and posteriorly, samples were burned at 480 °C in a Leco IR 212 carbon analyzer (Carroll and Ambrose, 2012). Finally, the CO_2 content from the liberated gas was converted to %TOC (Nelson and Sommers, 1996).

A time series of sea ice categories at each station was retrieved from an ice chart repository courtesy of Ice Service at the Norwegian Meteorological Institute, Tromsø, Norway (Nick Hughes, personal communication). The Ice Service classifies sea ice into six categories based on the type of ice and its concentration (out of 10) according to the World

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[1] https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml; accessed the 09.09.2022.

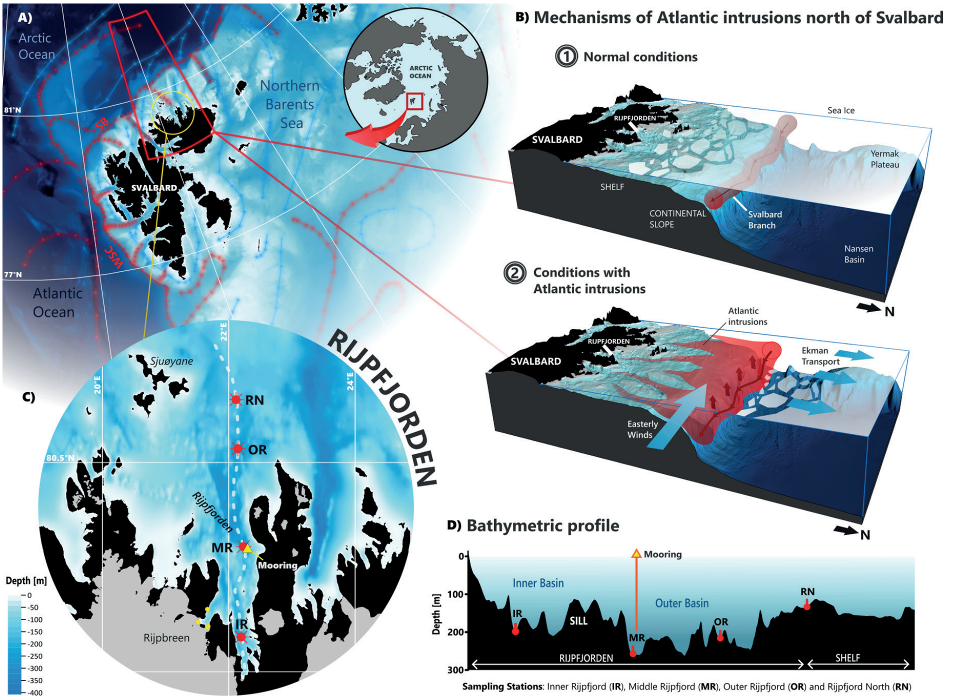

Fig. 1. Study area. **a)** An overview of the Svalbard archipelago with the main currents (red arrows indicate warm Atlantic waters and blue arrows indicate colder Arctic waters; Vihtakari, 2020) and bathymetry. WSC=West Spitsbergen Current; SB=Svalbard Branch. **b)** Mechanisms of Atlantic intrusions in the area north of Svalbard and in the area around Rijpfjorden (red polygon); **1**, during normal conditions without Atlantic instrusions, the Svalbard branch flows along the continental slope and sea ice cover is usually high in the area. **2**, when easterly winds prevail in the area, the Ekman transport generated pushes the drifting sea ice northwards, lifting the Svalbard branch and protruding into the shelf area. **c)** Map of Rijpfjorden (indicated by the yellow circle in map a)) showing the macrofauna sampling locations (IR=Inner Rijpfjorden; MR = Middle Rijpfjorden; OR=Outer Rijpfjorden and RN=Rijpfjorden North) shown with red dots. Yellow triangle indicates the location of the long-term mooring system. Yellow dots indicate the coordinates for glacial runoff simulations of Rijpbreen. Land is indicated in black and glaciers are in grey. **d)** Bathymetric profile along the fjord axis (indicated with white dashed line in map c)), including the location of the four stations with their respective water depths and approximate location of the mooring system. Bathymetry data source: GEBCO Compilation Group (2022)

Table 1
Sampling years, coordinates (latitude and longitude), water depth and average bottom water temperature and salinity over the years sampled from CTD casts (standard deviation (±) and range of minimum and maximum values are indicated). Total organic carbon content (TOC (%)) and grain size fraction <0.063 μm (%) of the 0–2 cm sediment layer only for years 2003 and 2010 are indicated as super index A and B respectively.

Station	Sampled years	Latitude °N	Longitude °E	Depth [m]	Bottom Temperature [°C]	Bottom Salinity	TOC (%)	Grain size fraction <0.063 μm (%)
IR (Inner Rijpfjorden)	*2003, 2007, 2010, 2013, 2017*	80.083	22.195	205	−1.78 ± 0.12 (-1.87; −1.63)	34.74 ± 0.12 (34.61; 34.90)	1.19^{A} 1.35^{B}	91,9^{A} 93^{B}
MR (Middle Rijpfjorden)	*2007, 2010*	80.299	22.233	250	−1.71 ± 0.06 (-1.75; −1.66)	34.68 ± 0.07 (34.63; 34.72)	1.45^{B}	83,3^{B}
OR (Outer Rijpfjorden)	*2003, 2007, 2010, 2013, 2017*	80.533	22.146	230	−1.36 ± 0.54 (-1.82; −0.54)	34.69 ± 0.13 (34.59; 34.90)	1.44^{A} 1.66^{B}	97,6^{A} 94,2^{B}
RN (Rijpfjorden North)	*2007, 2010, 2013, 2017*	80.650	22.115	130	0.37 ± 1.60 (-0.56; 2.75)	34.72 ± 0.15 (34.59; 34.90)	1.48^{B}	90^{B}

Meteorological Organization (WMO) Ice Chart Colour Code Standard (WMO/TD-No. 1215) and Sea Ice Nomenclature (WMO-259): Fast Ice (10/10th), Very Close Drift Ice (9–10/10ths), Close Drift Ice (7–9/10ths), Open Drift Ice (4–7/10ths), Very Open Drift Ice (1–4/10ths) and Open Water (0–1/10ths). Using qGIS (QGIS.org, 2022), the polygons for each ice type was retrieved daily from 2003 to 2018 at each sampling station (Fig. 2f).

2.4. Analysis of inter-annual fluctuations in macrofauna composition

2.4.1. Alpha-diversity

Alpha-diversity indices (species richness (S), Shannon diversity

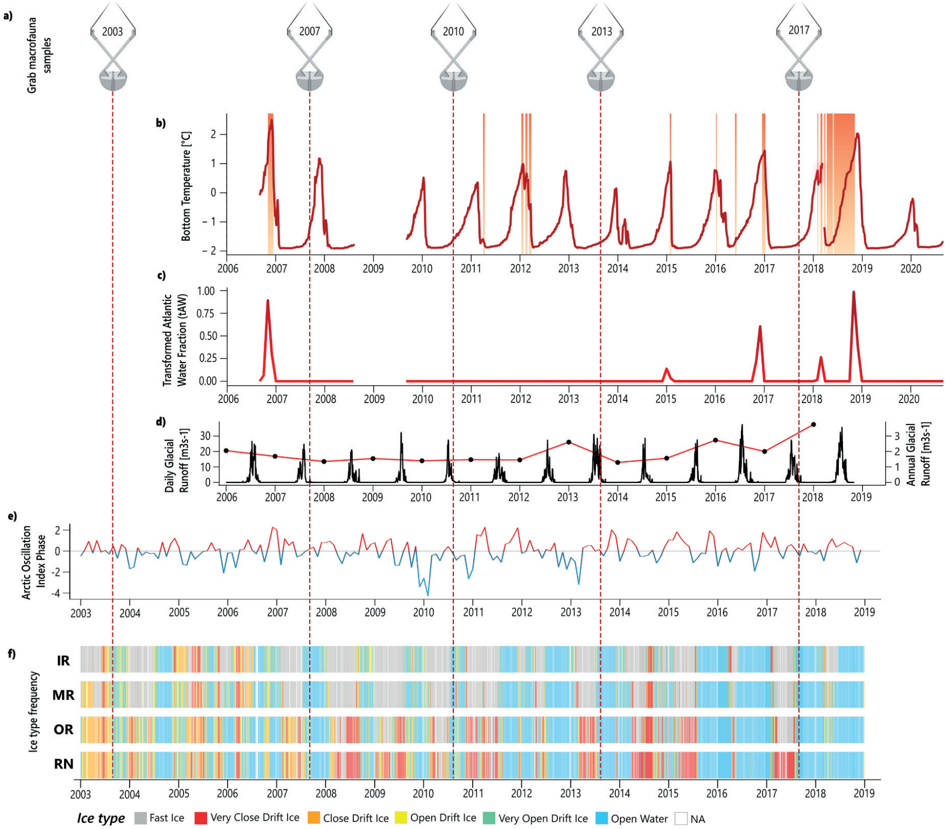

Fig. 2. Environmental variables throughout the study period. **a)** Times at which grab samples for the different years were taken are indicated with red dotted lines across all environmental variables **b)** Daily bottom water temperatures recorded at 200 m depth from the long-term mooring are indicated with a dark red continuous line (for location of mooring see maps Fig. 1). Gaps in the red line indicate non-available data. Periods shaded with orange indicate MHW events where temperatures are above the 90th percentile of the climatology baseline (based on 14 years of data) for more than five consecutive days. **c)** Transformed Atlantic Water (tAW) fraction (as the monthly average) at 200 m depth from the mooring defined as Temperature > 1 °C and Salinity >34.65 and represented by a red continuous line (gaps represent non-available data). **d)** Averaged daily glacial runoff (m^3/s) from four locations outside the discharge area of Rijpbreen (see Fig. 1c for location) based on runoff simulations from 2006 to 2019 (left axis with black line) and annual glacial runoff (m^3/s) from averaged daily runoff (right axis with red line and black dots) (Data courtesy of Jack Kohler, Norwegian Polar Institute (NPI)). **e)** Monthly Arctic Oscillation Index (AO) values from 2003 to 2018. Red lines indicate the positive phase of the AO, while blue lines indicate the negative phase. **f)** Sea-ice type frequencies for the four stations in Rijpfjorden (IR, MR, OR and RN) from 2003 to 2019. Each color band indicates a sea ice type based on the Norwegian Meteorological Institute (Ice Service) classification of ice types. Empty bands in white indicate no available data.

index ($H'_{(\log e)}$) and Pielou's evenness (J')) were calculated for each replicate sample with the "vegan" R package (Oksanen et al., 2020). To test for significant trends in total abundance, S, H′, and J′ over time and across stations, we built *generalized additive models* (GAM) with the "mgcv" package in R (Wood, 2011) for each of these response variables. The sampling years for each station were introduced as the smoothing parameter in the model ($k = 5$) together with the factor station as the predictor variables. For abundance and species richness, negative binomial family distribution was chosen with *log* as link function, whereas for H′ and J′ gaussian family distribution with *identity* link function was selected. Deviation, normality and homoscedasticity of residuals, together with the goodness of fit of observed values against response values were visually inspected with the function "gam.check" to identify violation of assumptions of the models (See Fig. A.2 to A.5).

2.4.2. *Ordination and cluster analysis*

In order to explore grouping patterns in species composition across time and space, non-metric multidimensional scaling (nMDS) analysis was performed with Euclidean distances derived from Hellinger transformed macrofauna abundance and presence-absence dissimilarities with the package "vegan". The Hellinger transformation was chosen to make the data suitable for Euclidean-based methods and to give a low weight to rare species (Legendre and Gallagher, 2001).

A cluster analysis using the UPGMA method was conducted with the R package "clustsig" (Whitaker and Christman, 2014) for the Hellinger transformed abundance data to support the patterns identified by the nMDS. Both nMDS and clustering were carried out with the averaged abundances and species occurrences for the three replicates at each station/year.

2.4.3. *Beta diversity*

The variation in community composition among sites in a region can be evaluated by calculating beta-diversity values (Whittaker, 1972). Changes in beta diversity can also be assessed through time and in the combination of time and space simultaneously (Legendre and Gauthier, 2014; Legendre, 2019).

Hellinger transformation was applied both to the abundance and occurrence data (each averaged over all replicates per station and sampling year) to calculate the beta diversity index (β_{TOTAL}) and the local contribution to beta diversity (LCBD) with the function “beta.div” of “adespatial” package (Dray et al., 2021) using Hellinger dissimilarity coefficients (Legendre and de Cáceres, 2013; Legendre and Borcard, 2018) between all stations and years. LCBD indices represent the degree of uniqueness of the samples in terms of community composition (Legendre and de Cáceres, 2013) and show how much each observation contributes to beta diversity; a sample unit with an LCBD value of 0 would have the species composition of the average centroid for all sites. LCBD values can be tested for statistical significance by random, independent permutations of the species matrix. Adjusted p-values (Holm correction method for multiple testing) for the LCBD values were calculated with 999 permutations, testing the null hypothesis (H_o) that species are randomly distributed and independent of one another across the sites/time (Legendre and de Cáceres, 2013).

When assessing diversity fluctuations in biological communities, it is of interest to disentangle the potential underlying ecological mechanisms by which species compositions change through time and space, i.e. how they disassemble and reassemble (temporal turnover) (Tatsumi et al., 2020). The change in beta diversity ($\Delta\beta_{TOTAL}$) among two or more sites throughout two time points can be either caused by *disappearances* (extirpations, $\Delta\beta_{E}$) or by *increases* (colonizations, $\Delta\beta_{C}$) of species (Olden and Poff, 2003; Tatsumi et al., 2021). Both extirpations and colonizations can lead to homogenization ($\Delta\beta_{E-}$ and $\Delta\beta_{C-}$) of species composition among the sites, i.e., decreasing β_{TOTAL} ($-\Delta\beta_{TOTAL}$), or to heterogenization ($\Delta\beta_{E+}$ and $\Delta\beta_{C+}$) of species composition between sites, i.e., increasing β_{TOTAL} ($+\Delta\beta_{TOTAL}$) (Tatsumi et al., 2021). $\Delta\beta_{E}$ and $\Delta\beta_{C}$ can be further decomposed into two more components (Type 1 or 2) depending on whether the colonization or extirpation of the species in question appear ($\Delta\beta_{C-}$ Type1) or disappear ($\Delta\beta_{E-}$ Type 1) at both sites simultaneously or at just one site ($\Delta\beta_{C-}$ Type2, if incoming species at one site were already initially present at the other; and $\Delta\beta_{E+}$ Type 2, when species disappearing at one site were initially present at both sites) (See Fig. A.1 for a visual description of the colonization-extirpation processes and how they affect the change in beta diversity among sites, adapted and modified after Tatsumi et al. (2021)). The relative contribution of each component can indicate different ecological processes. For instance, contributions of $\Delta\beta_{E-}$ might reflect stochastic extirpations of regionally rare species, while a greater contribution of $\Delta\beta_{E+}$ might be a sign that widespread species are decreasing more in frequency than rare species (Tatsumi et al., 2021). High $\Delta\beta_{C-}$ could reflect the appearance of species with high dispersal capacity, spreading across all sites, or internal dispersion of species to new sites that were once restricted by a dispersal barrier. Finally, $\Delta\beta_{C+}$ can occur when new species are added to unique locations. All four components of contribution to $\Delta\beta_{TOTAL}$ can happen simultaneously, potentially cancelling each other out, which is the reason why decomposing these changes can help to recognize the underlying fluctuations in species composition that are taking place. Beta diversity values (β_{TOTAL}) using the Sørensen index were calculated between IR and OR for each year for the presence-absence transformed macrofauna data. Following that, we calculated $\Delta\beta_{TOTAL}$ and its decomposition into its components of $\Delta\beta_{C}$ and $\Delta\beta_{E}$ (and their respective homogenization and heterogenization components: $\Delta\beta_{E-}$, $\Delta\beta_{C-}$, $\Delta\beta_{E+}$ and $\Delta\beta_{C+}$) for each time period using the “ecopart.pair” function within the “ecopart” R package (Tatsumi, 2022).

To test whether station IR or station OR changed more exceptionally with respect to one or the other in time, and to evaluate if the sill could have played an important role dampening effects of community change at the inner station, the temporal beta diversity index (TBI) was calculated (Legendre, 2019) using the percentage difference index (%diff) for both abundance and occurrence data with the “TBI” function of the R package “adespatial”. TBI indices measure the change in community composition between two time points (T1 and T2) (Legendre, 2019), generating a vector of TBI dissimilarities for each site. A random permutation test (999 permutations) was used to test for significance of the TBI indices and p-values were corrected for multiple testing using the Holm method (Legendre, 2019). Furthermore, the TBI dissimilarities between the two time points at each site were decomposed into contributions from losses (B) and gains (C) of species and abundances (Legendre, 2019).

2.4.4. *Variation partitioning of temporal and environmental drivers on macrofauna composition*

Redundancy analysis (RDA) was used to partition the variation within the macrofaunal data on a set of environmental predictor variables and a second set of temporal predictor variables (see below), for each station individually (Borcard et al., 1992).

All environmental variables (see section 2.4) were included in the set of environmental predictor variables. The sum of frequencies for each type of ice was calculated for each station over the period of one year prior to each sampling event for macrofauna (to account for time lags of possible integrated sea ice cover effects on macrofauna communities) and were used as environmental variables for constrained ordination analysis. Only stations IR, OR and RN for the period between 2007 and 2017 were used for the analysis (due to missing ice data for year 2002). When using the sea ice frequency as a constraining variable for the macrofauna variation, we grouped the frequencies of the categories for open water and very open drift ice under the category of “open water”, and very close drift ice, close drift ice and open drift ice in the category “drift ice”.

Asymmetric Eigenvector Maps (AEMs) were used as temporal predictor variables (Legendre and Gauthier, 2014). AEM is an eigenfunction method suitable to model multivariate directional processes like temporal change of species abundance data. By incorporating AEMs as constraining temporal predictors one can account for temporal autocorrelation (or temporal structure) in the abiotic drivers or in the species matrix itself (Legendre and Gauthier, 2014). AEMs were calculated for the sampling period with complete environmental data sets available (i.e. 2007 – 2017). To account for the irregular intervals between sampling events, dummy sampling events were added in mid-August (15th August) for years when no samples were collected. AEMs were then calculated using the time between neighboring dates as edge weight with the function “aem.time” from R package “adespatial”. In principle, AEMs of time essentially produce n-1 sine waves of decreasing wavelength (n = total number of sampling dates; here $n = 11$ due to dummy variables). Accordingly, the first AEM (AEM_1) describes a one directional change throughout the entire study period, while the last AEM (AEM_{10}) describes alternating changes from year to year (fine temporal scales).

Prior to variation partitioning, both sets of predictor variables were individually subjected to forward selection using a double-stopping criterion (Blanchet et al., 2008) to avoid overestimation of the explained variation. In this approach, variables are added to the model in order of decreasing explanatory power until no variable adds significantly to the explanatory power or until the $R^2_{adjusted}$ exceeds the $R^2_{adjusted}$ of the full model. The variation partition analysis was performed with the “varpart” function of the R package “vegan”.

3. Results

3.1. *Environmental variables*

The highest bottom water temperatures at 200m depth, reaching above 2 °C, were recorded by the end of 2007, coinciding with the first

SfWWTA recorded in Rijpfjorden (Fig. 2b) which lasted for 40 days. A succession of three shorter SfWWTAs (of between 16 and 18 days each) were recorded at the beginning of 2012. Following that, another SfWWTA (of 25 days) with the second highest temperature values since 2006 occurred by the end of 2016. SfWWTAs were recorded for most part of the year in 2018 (Fig. 2b).

At all stations inside the fjord, the averaged bottom water temperatures from all years of the CTD casts was <0 °C, emphasizing the overriding influence of Arctic characteristics in this system, with winter cold bottom water (WCW), while the outer station RN had average temperatures above 0 °C with the highest temperature recorded of 2.75 °C (Table 1). Bottom water salinity values across all stations and years ranged from 34.6 to 34.9.

The monthly Arctic Oscillation Index (AO) (Fig. 2e) showed the most negative values in early 2010 and early 2013. The highest peaks of positive AO values were observed at the end of 2006 and at the beginning and end of 2011. No clear trends were observed, but between 2009 and 2010 the AO index was more negative than other periods of time.

The daily average glacial runoff for the four locations around the Rijpbreen discharge area was seasonal, with high runoff in the summer months. Peak flows were the highest for 2009, 2013 and 2016 (Fig. 2d). Annual average of daily runoff values ranged between 1.29 m^3/s in 2014 and 2.74 m^3/s in 2016 over the study period. Although year 2018 was not included in the macrofauna time series, annual runoff values for that year were the highest of all with 3.75 m^3/s. Annual runoff values appeared to be more variable from 2012 onwards.

The innermost stations (IR and MR) were dominated by local fast ice, while the outer station (OR) and the shelf station (RN) had a higher frequency of drift ice (Fig. 2f). From 2012 onwards, prolonged periods of open water became more frequent at all stations.

3.2. *Macrofauna community fluctuations in time across the fjord axis*

3.2.1. *Abundance and alpha-diversity*

A total of 345 taxa belonging to 104 families and to 11 phyla were identified. The most abundant classes were Polychaeta (71%), followed by Bivalvia (21.6%).

Both abundance and species richness followed similar statistically significant trends across years for all stations with more than 2 sampling events (see Fig. 3 for significance of results and Table A.1 for detailed output of GAM models) (Fig. 3b and c), indicating big fluctuations through time. On average, abundance at IR and OR in 2007 was respectively between 0.2 and 0.8 times that in 2003, and for richness between 0.7 and 0.5 times. After these decreases, both variables followed a strong increase: on average, abundance at IR, OR and RN in 2007 was respectively between 5.4, 12.4 and 7.3 times that in 2003, and

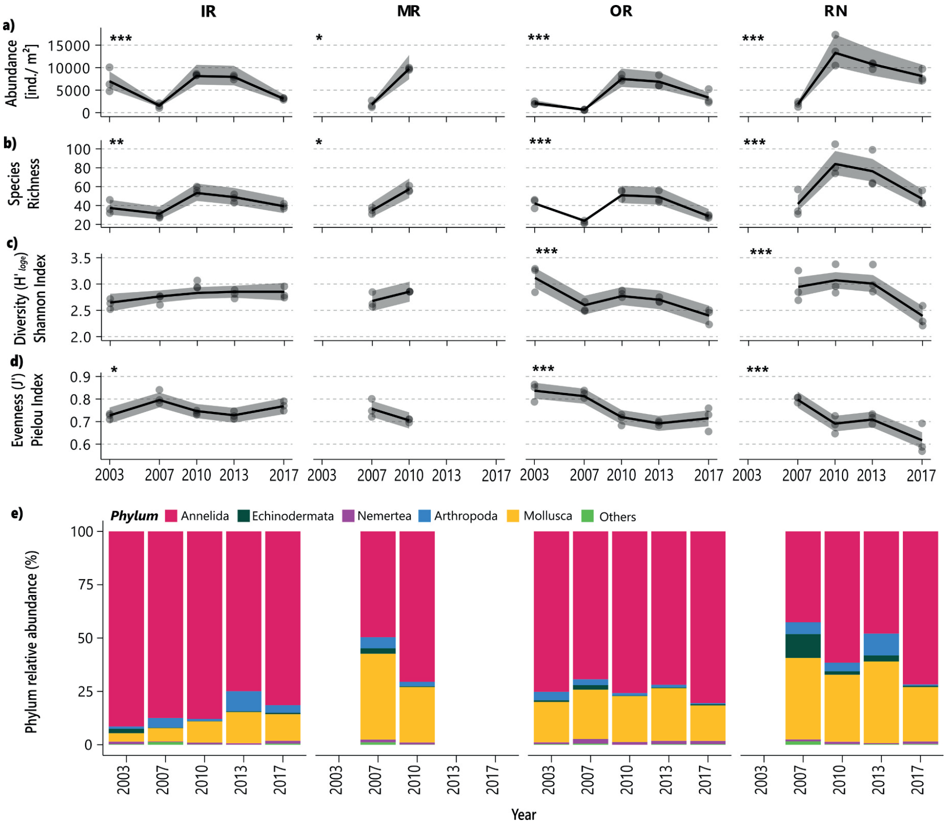

Fig. 3. Macrobenthic community metrics along the Rijpfjorden axis through time. **a)** abundance (ind./m^2), **b)** species richness, **c)** Shannon index (H′), **d)** Pielou's evenness index (J′). Significance of variation across years for each station from the GAM models is indicated with *** = p-value <0.001, ** = p-value 0.001–0.01, * = p-value 0.01–0.05 at the top of each panel. Shading represents the 95% confidence interval. **e)** Relative abundance by phylum for each station across time (averaged for three replicates). Empty data is missing data (no sampling of macrofauna).

for richness between 1.9, 2.3 and 2.1 times. After 2010, both variables decreased again.

H’ showed significant changes through time at stations OR and RN (Fig. 3c), with a significant drop from 2003 to 2007 at OR. Hardly any change in H’ from 2007 until 2013 was observed at both stations, followed by a significant decrease from 2013 to 2017 at OR. Highly significant decreases in J′ occurred at the outer stations (OR and RN), while significant (IR) or non-significant (MR) fluctuations were observed in the inner part of the fjord (Fig. 3d).

In all years, Annelida dominated relative abundances at the inner station (>75%) and at the outer station OR (c.a. 75%) (Fig. 3e). Mollusca were abundant in some years at station MR and RN. At RN, there was an increase in the relative contribution of Annelida to total abundances in the most recent years.

At station IR, most abundant families were Cirratulidae and Lumbrineridae, except for year 2007 (Fig. 4). At station MR, Thyasiridae dominated from 2010 onwards. At station OR, Cirratulidae and Thyasiridae families dominated after 2007, and for station RN, Oweniidae, Thyasiridae and Yoldiidae were the dominant families after that year as well.

3.2.2. *Ordination and cluster analysis*

The community structure of the inner station (IR) was clearly distinct from all other stations in the abundance-based nMDS (Fig. 5a), indicating a spatial differentiation. Additionally, a temporal pattern was observed for stations MR, OR, and RN. These stations grouped together from 2010 onwards, while samples from 2003 to 2007 were more distant from this group. In the occurrence-based nMDS (Fig. 5b), a dominant temporal structure was observed. Samples collected in 2003 and 2010 grouped together, while all samples from 2013 to 2017 were more similar to each other than to other years. Samples from 2007 appeared to group farther apart (with the exception of station IR which grouped

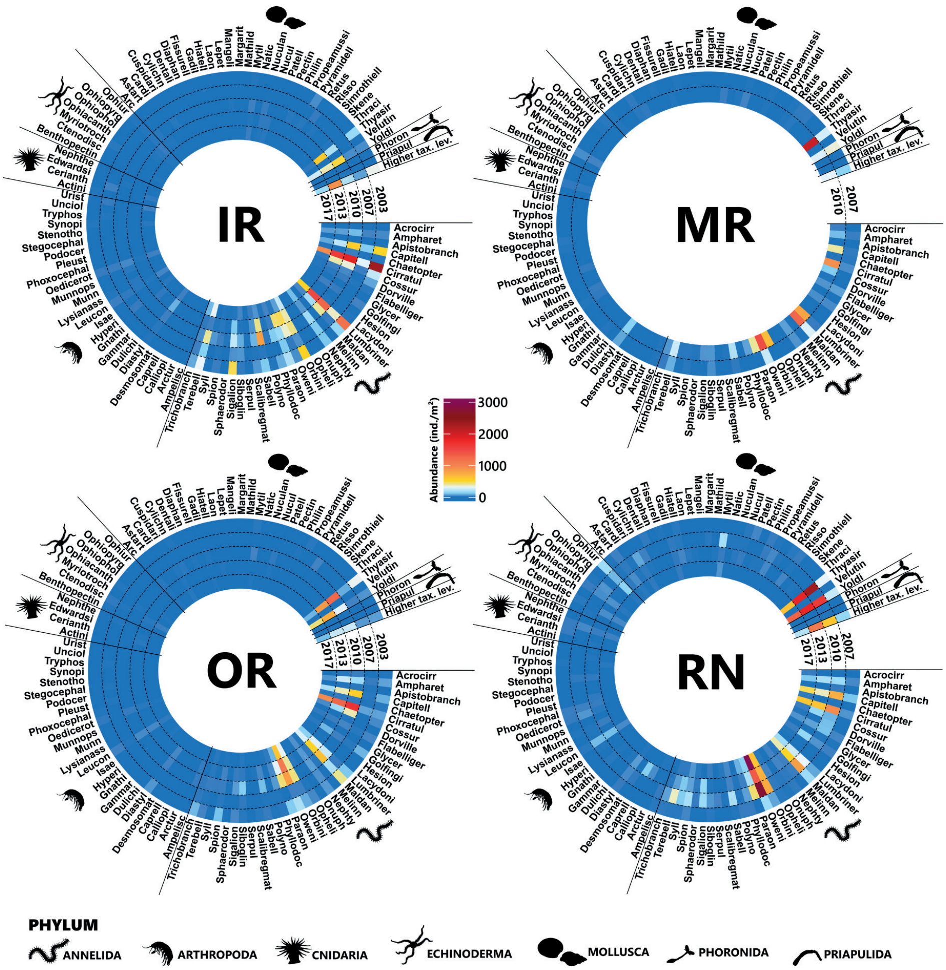

Fig. 4. Heatmaps showing averaged abundances (three replicates) for each Family (note that suffix -idae is missing at the end of each family name for space reasons). Each circle represents one station (IR, MR, OR and RN) and each concentric line represents the different years (2003, 2007, 2010, 2013 and 2017). Families are grouped by phylum (indicated by pictograms at the bottom). The last category belongs to taxa only identified to higher taxonomic level than family. Abundances are given as individuals/m^2 with dark blue representing lowest values and dark red/fuchsia representing highest values (see color scale in the middle). Phylum pictograms modified after Integration and Application Network (IAN) library symbols and PhyloPic.

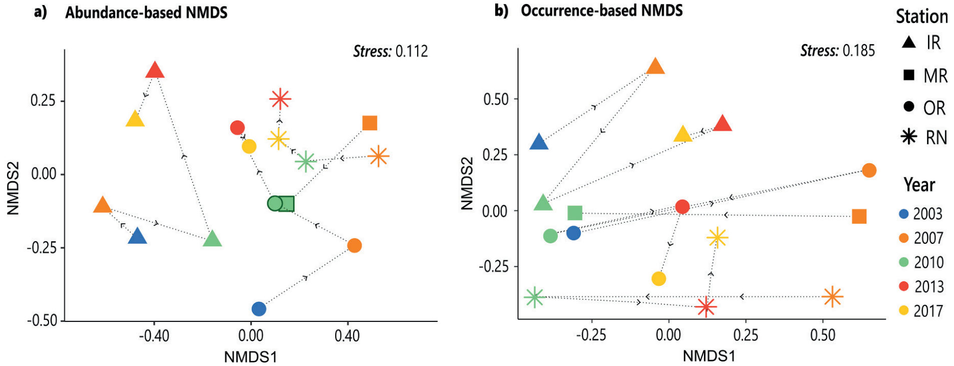

Fig. 5. Two-dimensional nMDS plot of: **a)** Hellinger transformed macrofauna abundance and **b)** Hellinger transformed occurrence data. Colors indicate the year of macrofauna sampling while symbols indicate the four different stations (for station codes and geographical location see Fig. 1). Black dotted lines with arrows track the direction of change at each station from year to year in the ordination space.

closer to the ones from 2013 to 2017).

The UPGMA cluster confirmed the nMDS patterns for the abundance-based dataset (Fig. 6). The most abundant taxa for the IR samples were lumbrinerid (*Lumbrineris mixochaeta, Scoletoma* sp.) and cirratulid polychaetes (*Tharyx* sp., *Aphelochaeta* sp.). Dominant taxa at stations MR, OR and RN included several different polychaetes (*Galathowenia oculata*, *Chaetozone* sp., *Maldane* spp.) and bivalves (*Mendicula* sp., *Yoldiella* spp. – Fig. 6) from 2010 onwards. Other polychaete species such as *Maldane* spp., *Heteromastus filiformis,* and *Leitoscoloplos mammosus* were also abundant at those stations after 2010, but less than the others.

3.2.3. Beta-diversity

The spatio-temporal LCBD values obtained from the abundance-based macrofauna data (Fig. 7a) indicated higher values for all samples from 2003 to 2007, together with most samples in all years at the IR station, indicating a more distinctive species composition at IR than at stations MR, OR and RN and from 2010 onwards (with lower LCBDs). However, no significant differences were detected after the permutation test for any of the station/year. In contrast, for the presence-absence dataset, the LCBD map showed lower values for years 2003 and 2010 than for 2013 and 2017 (Fig. 7b). All samples from 2007 presented the highest values, but only samples from OR and RN stations showed statistically significant uniqueness in species composition after the permutation test.

Beta diversity values between stations IR and OR (Fig. 8a), based on the presence-absence data, showed an increase between 2003 and 2007, and then a large decrease between 2007 and 2010, with the lowest values for 2010. From then onwards, beta diversity increased again gradually.

Temporal changes in beta diversity between IR and OR were mainly driven by colonization. Extirpations of species, in contrast, appeared not to contribute much to beta diversity changes through time ($\Delta\beta_E$ values were close to 0) (Fig. 8b). Nonetheless, when further decomposing its components into attributes of homogenization and heterogenization (Fig. 8c), we found that extirpation contributions had in fact higher values than those of colonization. However, extirpations (both $\Delta\beta_{E-}$ and $\Delta\beta_{E+}$) almost canceled each other out at all time periods. When further decomposing $\Delta\beta_{E+}$ into type 1 and 2, both types equally contributed to $\Delta\beta_{TOTAL}$ during all periods except for 2013–2017, when $\Delta\beta_{E+}$ was dominated by contributions of type 2 (Fig. 8d). Between 2007 and 2010, colonization ($\Delta\beta_C$) of taxa dominated the $\Delta\beta_{TOTAL}$ over extirpations ($\Delta\beta_E$), especially driven by contributions of $\Delta\beta_{C-}$, indicating establishment of widespread species common at both stations. This contribution by $\Delta\beta_{C-}$ was mainly dominated by type 1 colonization, while for the last period 2013–2017 was dominated by type 2 colonization (Fig. 8d). In order to be able to interpret the results from all different components of contributions to change in beta diversity we looked at the number of taxa appearing and disappearing exclusively at each station (IR and OR) and at both stations simultaneously for each consecutive time period (Fig. A.6).

The average dissimilarity at each site (IR and OR) between each period showed a similar pattern for both abundance and occurrence-based data (Fig. 9). On average, the communities at both sites changed more during the first two periods (2003–2007 and 2007–2010), while lower dissimilarities were observed from 2010 onwards. Between 2003-2007 and 2013–2017, changes were on average dominated by losses in species (or abundance), while for 2007–2010 gains dominated at both sites. TBI permutation tests showed that station OR changed more significantly in species composition than IR between 2003 and 2007 for the occurrence dataset. While no significance was reported after p-value correction, station IR changed more than OR between 2010-2013 and 2013–2017 for the abundance-based dataset (with p-values close to significance of 0.06) (Fig. 9 and Table A.2).

3.3. Variation partitioning of environmental and temporal drivers

For station IR, selected environmental drivers of macrofauna community variation were glacial runoff and AO index; for station OR, bottom temperature and glacial runoff; and for RN, bottom temperature, open water frequency and bottom salinity (Fig. 10).

All temporal AEMs generated from the distances between sampling events were also subjected to forward selection at each station. The order of the selected AEMs increased from the shelf station RN (AEMs 5, 3 & 4), toward the outer fjord (OR: AEMs 5 & 9) and further towards the inner basin (IR: AEMs 6 & 9 (Fig. 10).

At station IR, the variation partitioning indicated that throughout 2007, 2010, 2013 and 2017 the selected environmental variables accounted for 12% of the variation in the macrofauna. At the same time, 13% of the variation was also accounted for by the selected temporal predictors, and a total of 27% was explained by the temporal structure of the environmental variables. For station OR, the selected environmental variables only explained 4% of the macrofauna variance, 7% was explained by the temporal AEMs but 38% in combination with the temporal predictors selected. Lastly, for the outer-most station, RN, the environmental variables selected only explained variation in the macrofauna when combined with the selected temporal AEMs (up to 30%).

4. Discussion

Our time series shows that macrofaunal composition fluctuations

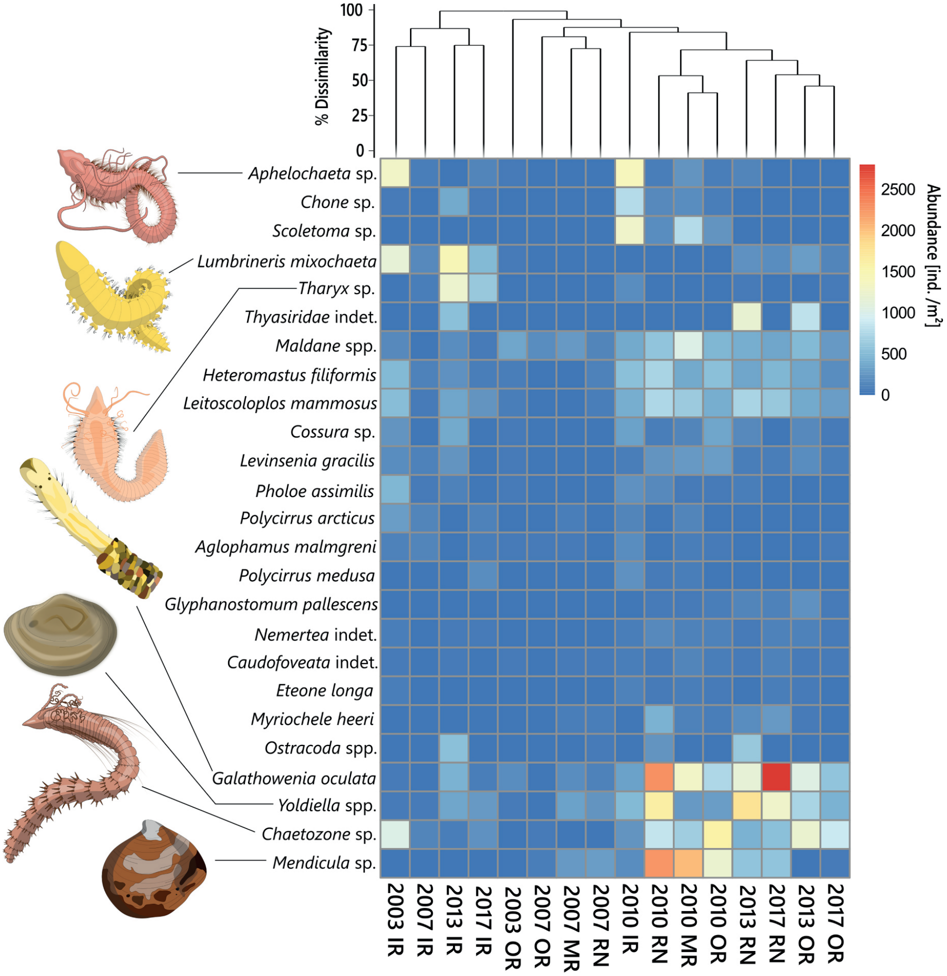

Fig. 6. Cluster derived with the UPGMA method based on Hellinger transformed macrofauna abundances (ind. m^{-2}) of the whole macrofauna community, averaged for the three replicates. The heatmap shows only taxa with more than 500 ind. m^{-2} throughout the whole time series. Color scale indicates raw abundance values (ind./m^2). Drawings for some of the most abundant species are presented (Drawn by: Èric Jordà Molina).

took place in Rijpfjorden during the first two decades of the 21st century, and occurred in conjunction with longer open water periods and times of documented seafloor warm water temperature anomalies (SfWWTAs). We identified three distinct periods of change: a strong disturbance, subsequent recovery, and then a gradual restructuring of macrobenthic communities. We also confirmed that the outer stations were more prone to significant changes in macrofauna species composition through time than the inner silled basin, although this last one also experienced fluctuations.

4.1. 2003–2007: a strong Atlantic inflow in 2006 led to macrofauna extirpations across Rijpfjorden, with less impact in the inner-basin

The mooring at station MR recorded SfWWTAs of up to +2 °C between August and November 2006 (Fig. 2b). Temperature anomalies were also documented in many other western fjords of the archipelago for that year (Bloshkina et al., 2021). At the same time, a significant increase in surface water temperature defined as a warm water anomaly was observed between 2004 and 2008 at the Fram Strait region (Beszczynska-Möller et al., 2012), which translated rapidly into changes in several marine biological components (Soltwedel et al., 2016), from zooplankton communities (Ramondenc et al., 2002) to the seafloor. For instance, studies from the Long-Term Ecological Research HAUSGARTEN observatory, in the deep Fram Strait, revealed that nematode densities between 2000 and 2009 suffered a drop from 2002 to 2005, and bounced back after 2006 (Hoste et al., 2007; Grzelak, 2015; Soltwedel et al., 2016). Our results suggest that this warm water anomaly, reflected as a potential benthic MHW in our mooring data, reached to northern Svalbard fjords and had significant impacts in the macrofauna communities from Rijpfjorden, also reflected as drops in abundance and species richness in 2007 (Fig. 3a and b). The changes in community composition translated into an increase in beta diversity between the inner and outer stations (IR and OR) (Fig. 8a), and although this change was mainly caused by colonizations at one site, further decomposition

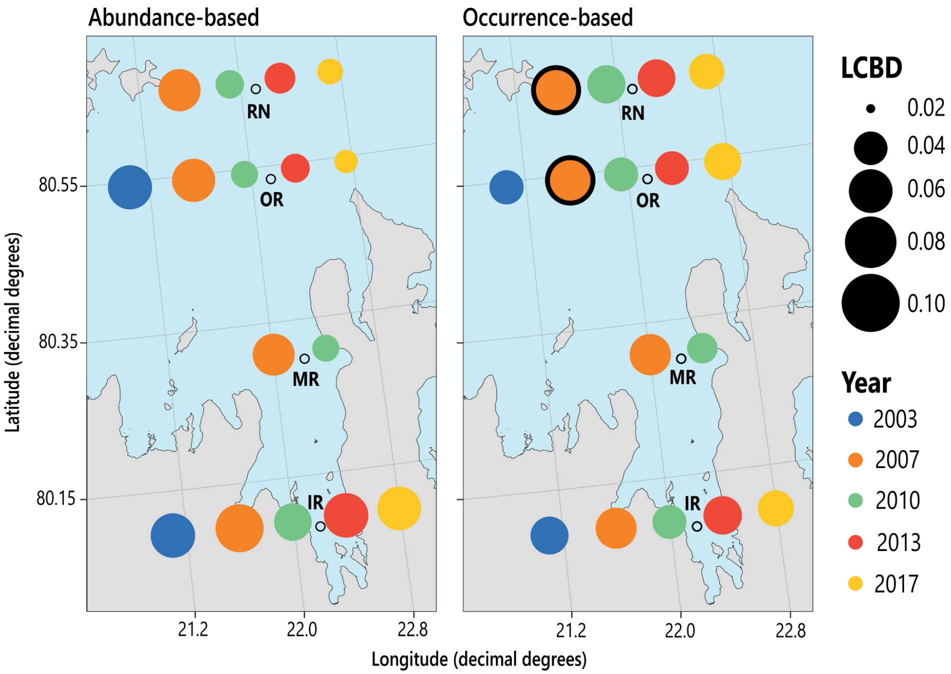

Fig. 7. Local contributions to beta diversity (LCBD) map over time and space for abundance based (left) and occurrence based (right) macrofauna datasets. The size of the bubbles is proportional to the LCBD values and the different colors indicate the year of macrofauna sampling. Black rims around the bubbles indicate LCBD p-values that are significant in the permutation test after the Holm correction (alpha = 0.05).

revealed that important widespread and local extirpations took place (Fig. 8b and c). Mass mortality events (MMEs) among benthic communities have been reported in other marine ecosystems after MHWs. For example, in the Mediterranean Sea, decreases in especially sessile organisms were observed and correlated with the temperature anomalies recorded for the summer of 2003 (Garrabou et al., 2009), while throughout the last decades, five consecutive MMEs associated with more recent MHWs have taken place (Garrabou et al., 2022).

We found supporting evidence for our hypothesis that the macrobenthos of the inner-most silled basin would remain more stable due to dampened fluctuations in environmental conditions compared to the outer sties. Both the nMDS (Fig. 5) and the LCBD indices partially supported this hypothesis, since the magnitude of change at station IR after the SfWWTA of 2006 (2003 vs 2007 years) was smaller than for the outer stations, and LCBD indices were only significant for the outer stations in 2007 (Fig. 7). Both alpha (H′) and beta diversity analyses also supported the possibility of partial protection by the sill. For instance, from the TBI analysis we saw that station OR changed significantly in beta diversity for this period compared to station IR (Fig. 9), and H' plummeted significantly at OR while it remained stable at IR (Fig. 3c). The distinction of macrobenthic communities between inner and outer parts of silled fjords seems to be a common feature in Arctic and sub-Arctic silled fjords (Włodarska-Kowalczuk et al., 2005; Renaud et al., 2007; Kędra et al., 2010; Jordà-Molina et al., 2019; Udalov et al., 2021). The shallow sill of Rijpfjorden, therefore, seems to protect the inner basin from macrofauna fluctuations to certain extent, but not completely as indicated by the widespread non-random extirpation contributions of taxa occurring across the fjord axis during this period, including the inner parts of the fjord, and also indicated by significant drops in abundances at this inner location (Fig. 8c, Fig. A.8).

4.2. *2007–2010: a recovery period with widespread re-colonization resulting in homogeneous fjord macrobenthos*

Our results indicate that the period 2007–2010 was a recovery phase for the macrobenthic communities after the disturbance event of 2006. During this period with prevailing cold water temperatures and longer-lasting sea-ice cover, change in total beta diversity between IR and OR was dominated by contributions of colonizations leading to a decrease in beta diversity, which was mainly driven by widespread species arriving at both sites (from other areas of the fjord not covered in the sampling or from outside the system) (Fig. 8a,b,c). Such a widespread colonization from outside the fjord led to homogenization of benthic communities. Such evidence of homogenization in macrofauna assemblages of previously distinct fjordic regions (mainly in outer and mid-fjord areas) has also been observed in Kongsfjorden (Kędra et al., 2010), which the authors attributed to the increased inflow of AW into the fjord due to a more enhanced West Spitsbergen Current (WSC) transport during the first decade of the 21st century.

The significant increases in abundance and species richness, and moderate increases in H′ reported in most sites across Rijpfjorden between 2007 and 2010 support this recovery scenario through re-colonization (Fig. 3a,b,c). Furthermore, the significant drops in J' for the outer stations indicate that a few taxa already present before the extinction event started dominating the community after 2007 (Fig. 3d). These taxa include *Galathowenia oculata*, *Yoldiella* spp., *Chaetozone* sp., and *Mendicula* sp., followed in lower abundance by *Maldane* spp., *Heteromastus filiformis,* and *Leitoscoloplos mammosus* (Fig. 6). All these species also appeared in the inner station but at much lower abundances. Most of these taxa are opportunists with ranges spanning well into boreal/temperate regions, and capable of strong fluctuations in population size over short periods of time. For example, *G. oculata,* which had

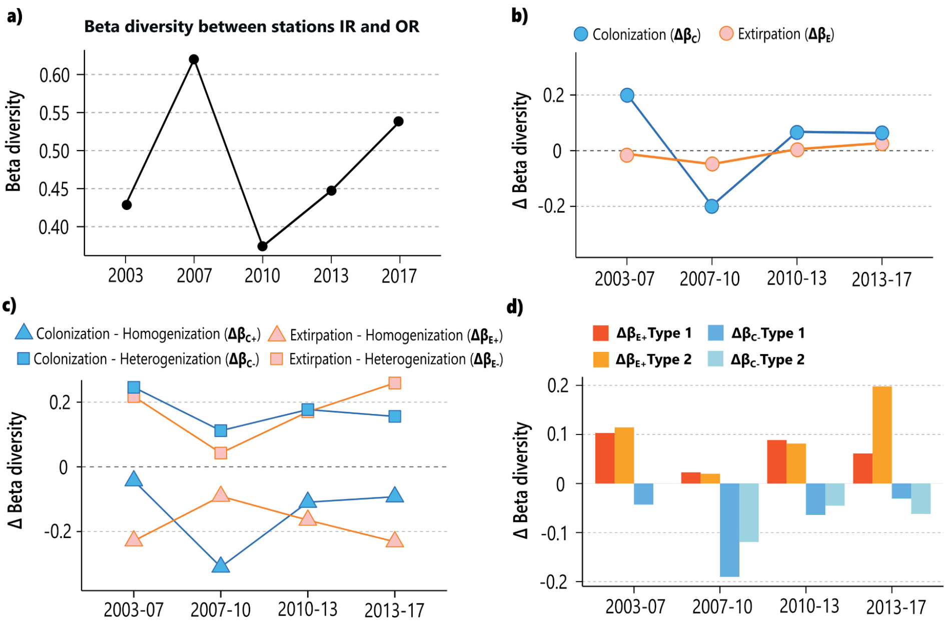

Fig. 8. Changes in beta diversity between stations IR and OR over time. **a)** Sørensen beta diversity values between stations IR and OR for each year for the occurrence macrofauna community data. **b)** Decomposition of temporal change in beta diversity into contributions by colonization ($\Delta\beta_C$) and extirpation ($\Delta\beta_E$) for each consecutive period. **c)** Decomposition of temporal change in beta diversity into contributions by colonization resulting in heterogenization ($\Delta\beta_{C+}$) (blue squares) and homogenization ($\Delta\beta_{C-}$) (blue triangles) and by extirpations leading to heterogenization ($\Delta\beta_{E+}$) (red squares) and homogenization ($\Delta\beta_{E-}$) (red triangles). **d)** Decomposition of $\Delta\beta_{E+}$ into Type 1 (red) and Type 2 (orange) and $\Delta\beta_{C-}$ into Type 1 (dark blue) and Type 2 (light blue). For interpretation of the $\Delta\beta_{E+\ Type\ 1}/\Delta\beta_{E+\ Type\ 2}$ and $\Delta\beta_{C-\ Type\ 1}/\Delta\beta_{C-\ Type\ 2}$ the reader is referred to Fig. A.1 of Appendix.

the highest abundances recorded in the time series, is a surface-deposit feeding tube-building polychaete that has been described as tolerant to environmental stressors such as sedimentation loads or organic enrichment and seems to be facilitated by slight disturbances (Trannum et al., 2022). Although we do not have sediment parameters for all years, TOC values for 2003–2010 (Table 1) for the top 2 cm of the sediment indicate a slight increase in organic carbon content for stations IR and OR (from 1.19 to 1.35% and from 1.44 to 1.66% respectively). This potential increase in food availability, although highly speculative, and the ecological space made available after the massive extinctions seen in 2006 could have contributed to the success of disturbance-tolerant taxa such as *G. oculata, H. filiformis,* and *Chaetozone* sp. Studies comparing macrobenthic samples of the Fram Strait from the year 2000 (before the warm water anomaly recorded in that region) vs. 2010 and 2017 (after the warm water anomaly), revealed significant shifts in macrofauna community composition, with generalized increases in density and diversity across all depths from shelf to basin following a transect at 79°N starting at the shelf off West Spitsbergen (outside of Kongsfjorden) for the latter (Górska et al., 2022). In this case, some of the taxa that experienced highest increases in 2010 at the shelf stations (70–400 m depth) were some of the same representatives that we saw increasing in Rijpfjorden. This was accompanied by increases in food availability (e.g. sediment-bound chloroplastic pigments) at the seafloor from 2007 onwards (Soltwedel et al., 2016). This could indicate that the shift in productivity and food availability at the seafloor recorded in the Fram Strait, could have been observed as well in the northern fjords from Svalbard.

4.3. 2010–2017: the inner and outer areas slowly re-assemble and diverge in structure

For the last two survey periods (2010–2013 and 2013–2017), beta diversity increased gradually between IR and OR (Fig. 8a). We found indications that widespread species that were initially shared at both IR and OR in 2010 disappeared during 2010–2013, contributing to heterogenization between IR and OR. (Fig. A8). However, contributions to change in beta diversity from both widespread and local extirpations cancelled each other out, making contributions of colonizations leading to heterogenization the ones driving the overall beta diversity change. This establishment of new taxa exclusive to each site (especially at station IR (Fig. A8) increased the $\Delta\beta_{TOTAL}$ for this period (Fig. 8a). Although SfWWTAs were detected in early 2012, no tAW was associated with them (Fig. 2b and c). Perhaps this indicates that water from the shelf was advected into the fjord but was heavily mixed with local water, maintaining a higher temperature than the receiving water at that time of the year (late winter). Whether this advective event had any impacts on the recruitment or settlement of benthic larvae is something worth considering, but it seems that this SfWWTA during winter time did not have such a drastic impact as in 2006 on the macrobenthic communities. Interestingly, between 2013 and 2017, the extirpation contributions to $\Delta\beta_{TOTAL}$ (both $\Delta\beta_{E+}$ and $\Delta\beta_{E-}$) (Fig. 8c) had higher values than both components of contributions due to colonization, and most of the heterogenization caused by extirpations was due to the disappearance of species previously common at both sites which disappeared from one of them ($\Delta\beta_{E+}$ Type 2). In fact, although extinctions of taxa exclusive to each site were almost equal (26 and 28 taxa for IR and OR respectively), extirpations at OR from taxa initially shared with IR accounted for 11 taxa, while 6 shared taxa went lost at station IR (Fig. A8). This indicates that the two stations had begun to re-assemble in a divergent manner. It

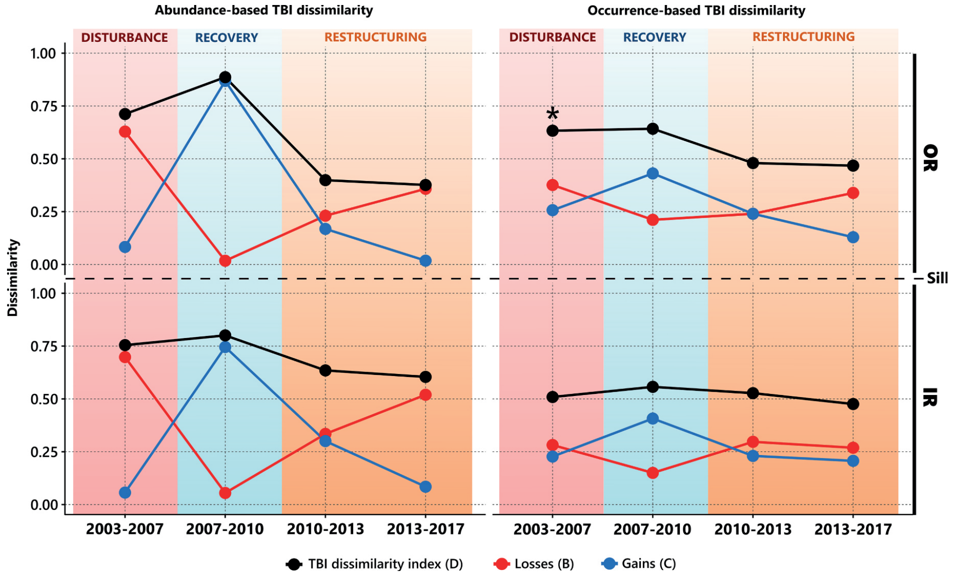

Fig. 9. Temporal beta diversity indices (TBI), calculated with *%diff* dissimilarity index, for the abundance-based (left) and occurrence-based (right) macrofauna and for each station: outer Rijpfjorden (OR, top) and inner Rijpfjorden (IR, bottom) which are physically separated by a sill. The dissimilarity in community composition (abundance or occurrence-based) between years of consecutive intervals at each station is depicted with black dots and lines (that is the total dissimilarity in time (D) which is equivalent to the TBI index). The TBI dissimilarity (D) is then decomposed in abundance or taxa losses (B) represented by red dots and lines, and gains (C) indicated with blue dots and lines. The sum of (B) and (C) is equal to (D). The asterisk (*) at station OR for the period 2003–2007 indicates that this station changed significantly compared to station IR for that time interval (based on the TBI permutation test, with 999 permutations, alpha = 0.05, p-value = 0.04 after Holm correction).

is also possible that the inner station started acting as a refugium for some species present in the outer parts of the fjord during the last AW intrusion, as fewer shared taxa were lost at IR than at OR.

4.4. Spatio-temporal drivers of change in macrofauna communities

The macrofauna communities of the outer stations of Rijpfjorden changed following long temporal patterns, as they were linked with long-term hydrographic trends that we have documented in this fjord potentially reflecting the SfWWTAs. However, the innermost locations followed more stochastic shifts (as indicated by the higher selected AEMs), pointing towards more complex environmental interactions and temporal changes towards the head of the fjord (Fig. 10).

In high Arctic fjords, it is well understood that glacial runoff from adjacent glaciers plays a key role in structuring seafloor communities (Holte and Gulliksen, 1998; Udalov et al., 2021; Włodarska-Kowalczuk et al., 2005; Włodarska-Kowalczuk and Pearson, 2004). This is mainly due to high sedimentation rates of inorganic material that increase towards high glacial activity areas (usually in glacial bays at the head of fjords) diluting food particles at the seafloor and promoting the burial of fauna. Hence, suspension feeders and filter feeders are usually negatively affected by these sedimentary loads, clogging their feeding organs, while relatively motile surface and sub-surface deposit feeders, carnivorous/omnivorous, and predators thrive better in these unstable and stressful conditions (Włodarska-Kowalczuk et al., 1998). This was reflected in the community of the inner-most station of Rijpfjorden, which was dominated by the carnivorous polychaetes *Lumbrineris mixochaeta* and *Scoletoma* sp. as well as surface deposit feeders like the cirratulid polychaetes *Aphelochaeta* sp., *Chaetozone* sp. and *Tharyx* sp. (Fig. 5). Some of these taxa have also been found to be common in inner parts of other silled fjords of Svalbard (i.e. Kongsfjord and van Mijenfjord; (Włodarska-Kowalczuk and Pearson, 2004; Renaud et al., 2007; Kędra et al., 2010). Sedimentation-tolerant nuculanid and thyasirid bivalves have also been reported as co-dominant taxa in inner glacial sites in other Arctic fjords (Udalov et al., 2021), but were only found in low densities in inner Rijpfjorden. Vertical fluxes of organic and inorganic material have been reported to be an order of magnitude higher in Kongsfjorden than in Rijpfjorden (Weydmann-Zwolicka et al., 2021). The relatively low sedimentation in Rijpfjorden might cause carnivore polychaetes to thrive better than the partially infaunal deposit-feeding bivalves (McMahon et al., 2006), perhaps outcompeting the latter. Therefore, it appears to be important to consider the degree of sedimentation impact in high Arctic fjords, as it could give place to unique inner-communities as seen in Rijpfjorden which might react differently to impacts of warming through time.

Although water temperature was not selected at station IR as a macrofauna driver, the fact that the AO index was selected as community fluctuation driver at IR could be linked indirectly to the strength of Atlantic intrusions, the extent of penetration towards the head of the fjord and the effects of prevailing wind patterns in the Rijpfjorden area (Fig. 10). Positive AO phases are positively correlated with inflow anomalies of Atlantic Water in the Barents Sea Opening and onto the shelf areas (Armitage et al., 2018). Wind stress has also been shown to be an important forcing variable in the region (Muilwijk et al., 2018; Smedsrud et al., 2022). When easterly and southerly winds predominate, Ekman transport pushes the pack ice further north and away from the northern coast of Svalbard, leading to shelf-break upwelling which results in the protrusion of Atlantic water onto the shelf (Falk-Petersen et al., 2015, but see Randelhoff and Sundfjord, 2018) (Fig. 1b). Interestingly, in the summer of 2014, exceptional amounts of AW/tW were detected in western Svalbard fjords (Bloshkina et al., 2021; Promińska et al., 2017; Tverberg et al., 2019). In contrast, no signs of tAW presence or warm water anomalies were observed in Rijpfjorden. One possible explanation for this seemingly “intermittent” decoupling between the

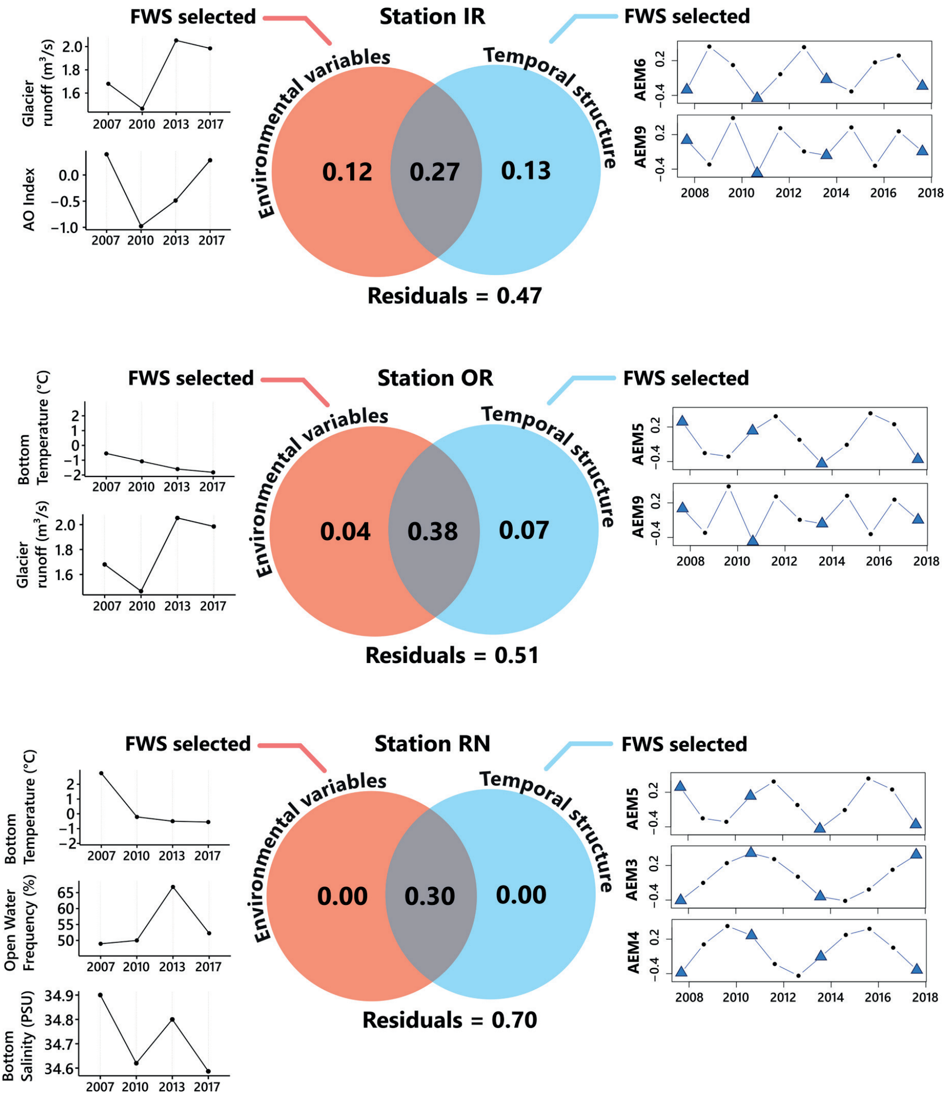

Fig. 10. Venn diagrams of the variation partitioning analysis based on redundancy analysis (RDA) performed with the environmental variables selected after forward selection (pink circle) and the temporal AEMs selected after forward selection (blue circle) at stations IR, Inner Rijpfjorden; OR, Outer Rijpfjorden and RN, Rijpfjorden North, from 2007 to 2017. The numbers in the circles indicate the percentage of variance explained of the macrofauna community (Hellinger transformed) and the circles overlap represents the variance explained by both the environmental variables and the temporal AEMs. Residuals indicate the variance that remains unexplained (either by potential environmental variables not accounted in the time-series or by noise in the data). For each station, the selected environmental variables and the selected AEMs are shown. In the plots from AEMs, blue triangles indicate sampling time of macrofauna events, while the black dots are the dummy variables used to construct the AEMs.

western fjords and the northern fjords could be the local wind patterns prevailing in the north. Nilsen et al., 2021, confirmed that there was a strong correlation between the local wind stress curl pattern over the Yermak Plateau and the seasonal and interannual volume transport anomalies towards the northern shelf of Svalbard. In fact, during summer and autumn of 2014 westerly winds dominated the area (Koenig et al., 2017), pushing the drift ice towards the coast (Lundesgaard et al., 2021) and hampering the lifting of the AW flowing along the continental slope (Svalbard Branch). This stresses the importance to include a northern fjord in monitoring efforts of the archipelagos' fjordic ecosystems, since we cannot rely solely on the processes documented in well studied western fjords to always act as a proxy for northern coastal areas.

The variables selected for OR and RN (bottom temperature, salinity, and open water periods) suggest that the documented SfWWTAs may have played a role in determining macrobenthic structure through time, perhaps inducing thermal stress to the biological communities and promoting species extirpations in periods with high temperatures and recolonizations in periods with low temperatures. However, other processes and factors such as primary production, food availability, and metabolic demands, which were not covered in this study and that can co-vary with water temperature, could play an important role here. Quantification of food supply and organic matter could be consequently of significance for benthic time-series, as responses might range from community level to species level. For instance, growth rates in Arctic cockles in this fjord indicated that food quality and availability were more important than temperature in initiating growth line depositions (Ambrose et al., 2012).

MHVs have been reported to be as strong in the Arctic Ocean and sub-Arctic seas as in other ocean basins, and their annual intensity has increased in strength during the first two decades of the 21st century compared to 1982–2000 (Huang et al., 2021). Such trends have been reported for the Fram Strait, the Bering Sea, the Siberian Arctic Seas and the Barents Sea (Beszczynska-Möller et al., 2012; Carvalho et al., 2021; Golubeva et al., 2021; Mohamed et al., 2022). In our study, we find evidence that potential MHWs recorded in the form of SfWWTAs and AW-like (tAW) intrusions into Rijpfjorden led to changes in macrofauna communities. Interestingly, this response was clear after the heat wave of 2006, but less drastic changes were observed in later SfWWTAs. Further measurements from the mooring in Rijpfjorden recorded an important SfWWTA extending throughout most part of 2018, indicating a much longer anomaly of warm water than in any of the previous years (Fig. 2a). Mesocosm experiments exposing coastal macrofaunal communities to heatwaves have showcased differential responses to single or sequential MHWs at the community level, with a high response in the sessile/infaunal fraction (Pansch et al., 2018). Diverging responses to episodic versus chronic stress may be due to phenological and functional shifts, while acclimation and post-disturbance biotic interactions could also play important roles (Pansch et al., 2018). Some of these mechanisms might be behind the succession of the communities observed in our study. Other studies have reported unexpected resilience of coral reefs against successive MHWs, where despite high mortality rates during the first onset of disturbance events, they lessened over time despite persistent temperature anomaly periods, suggesting that coral communities could adapt to these new warming conditions (Fox et al., 2021). Moreover, a time series assessing the disturbance impacts of climate driven ice-scouring in shallow zoobenthos from Antarctic waters reported surprising short recovery times (within 10 years) to initial conditions prior to high detrimental impact periods, suggesting that typically considered sensitive cold-water communities seem to be more resilient and recover faster than previously thought in polar environments (Zwerschke et al., 2021). From this, the question arises as to whether the heatwaves documented between 2006 and 2017 in Rijpfjorden have conditioned macrobenthic communities to withstand the thermal stress associated with the last warming event of 2018, or, on the contrary, if a large extirpation event took place once again as in 2006.

5. Conclusions

We found strong evidence that Atlantic intrusions into Rijpfjorden, in the form of SfWWTAs and potential MHWs, led to macrobenthic fluctuations observed in the present intermittent time series (i.e. extirpations followed by recovery periods and posterior re-assembling in different directions at different parts of the fjord axis). In general, macrobenthic communities of this high Arctic fjord appeared to be somewhat resilient to these disturbance events, with recovery periods of up to 4 years (2006–2010). Macrofauna diversity was especially more stable at the inner silled basin, suggesting a certain isolation from strong environmental fluctuations outside the fjord (despite strong variations in community abundances). However, a re-structuring in species composition took place after the recovery in abundance and species richness in 2010. This was mainly attributed to newly dominating taxa from that year onwards at the outer part of the fjord.

Stronger and more frequent Atlantic intrusions plus local manifestations of climate change could lead macrobenthic communities from northern fjords to resemble those of western Svalbard today, which are more exposed to the effects of warm water advections from the shelf areas. There is a possibility that with more drastic disturbance events the communities in the innermost locations, partially protected by the sill, could reach a tipping point despite their recovery capabilities, where they could lose their unique characteristics. This could potentially alter ecosystem services such as carbon sequestration or biogeochemical processes within the fjord, with unknown consequences to the whole fjordic ecosystem, and could put these cold-water refugia at stake. Rijpfjorden, therefore, should be regarded as a model for a cold-water high-Arctic coastal system in transition impacted by periodical warming events.

CRediT author statement

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Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2023.106046.

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Paper II

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Lack of strong seasonality in macrobenthic communities from the northern Barents Sea shelf and Nansen Basin

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ABSTRACT

The Barents Sea has been coined 'the Arctic hotspot' of climate change due to the rapidity with which environmental changes are taking place. This transitional domain from Atlantic to Arctic waters is home to highly productive benthic communities. This system strongly fluctuates on a seasonal basis in its sympagic-pelagic-benthic coupling interactions, with potential effects on benthic standing stocks and production. Recent discoveries have questioned the marked seasonality for several high Arctic seafloor communities in coastal waters of Svalbard. Still, the seasonal variability of benthic process in the extensive Barents Sea open shelf remains poorly understood. Therefore, we studied the seasonality of macrofauna communities along a transect in the northwestern Barents Sea comprising two hydrographic domains (Arctic vs. Atlantic Water, across the Polar Front) and three geomorphological settings (shelf, continental slope and abyssal plain). Overall, we did not find strong signs of seasonal variation in taxonomic community structure and functional diversity. However, we found some weak signs of seasonality when examining each station separately, especially at a station close to the Polar Front, with high seasonal fluctuations in abiotic drivers indicating a stronger pelagic-benthic coupling. The lack of seasonality found both at the shelf stations south and north of the Polar Front could be related to organic matter stored in the sediments, reflected in constant levels of total organic carbon in surface sediment across time for all stations. We did observe, as expected, highly spatially structured environmental regimes and macrofauna communities associated to them from shelf to slope and basin locations. Understanding the underlying spatio-temporal mechanisms by which soft-bottom benthic communities are structured along environmental gradients is necessary to predict future impacts of climate change in this area. Our results indicate that short-term climate driven changes in the phenology of pelagic ecosystem components might not be directly reflected in the Arctic benthic system, as seafloor processes seem to be partially decoupled from those in the overlying water.

1. Introduction

The Arctic marine ecosystem is a highly seasonal system (Walsh, 2008). Extreme light regime shifts occur on an annual basis from midnight sun periods with 24 h sunlight in summer to permanent dusk throughout the polar night in winter. This marked transition governs seasonal air temperatures which, in turn and together with ocean–atmosphere interaction processes, drives one of the most characteristic features of this region: the seasonal sea ice. Not only is the abiotic component of this system in constant transition, but also primary producers are phenologically tied to its seasonal fluctuations (Wassmann et al., 2011; Leu et al., 2015). Spring blooms of short lived pelagic and sympagic (ice associated) algae characterize the seasonality in Arctic primary production, which sustains the whole Arctic food-web, including seafloor communities (Sakshaug et al., 2009).

High seasonality characterizes processes occurring in the pelagic realm of marine Arctic environments. For instance, peak abundance and biomass of primary producers and zooplankton communities in the sea

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ice and the water column typically occur around early spring (Hassel, 1986; Wassmann et al., 1999; Weydmann et al., 2013), followed by a sharp decrease in winter, when a lot of zooplankton species enter diapause in deeper waters (Daase et al., 2013). In Arctic shelf seas, such as the Barents Sea, a strong sympagic-pelagic-benthic coupling has traditionally been posited to govern the tight connectivity between the sea ice, water column and seafloor associated communities (Grebmeier et al., 1988; Wassmann et al., 1991; Graf, 1992; Søreide et al., 2013) through the cascading transfer of organic matter (OM) (i.e. vertical flux of particles) (Renaud et al., 2008; Wassmann et al., 2008; Wassmann and Reigstad, 2011). Thus, although expected, seasonal dynamics of macrobenthic communities and seafloor processes in the Arctic have received very little attention, outside of some intertidal (Pawłowska et al., 2011; Naumov, 2013) coastal/fjord studies Kędra et al., 2012; Włodarska-Kowalczuk et al., 2016; Morata et al., 2020) around Svalbard waters. Until recently it was thought that benthic communities entered a state of dormancy during the polar night, when little photosynthetic activity is possible and very little OM is exported to depths (Renaud et al., 2020). Recent studies, however, have demonstrated that benthic organisms do grow and reproduce during this time of the year, most likely relying on stored energy reserves or on detrital and advected resources (Berge et al., 2015).

Renaud et al. (2008) suggested that responses to seasonal food pulses are reflected at variable temporal scales in seafloor communities depending on the process in question. For instance, feeding rates of benthic organisms and sediment oxygen demand (SOD) rates respond within a few hours to weeks to short-term pulses of organic carbon reaching the seafloor. In contrast, responses of biomass and other benthic community metrics fluctuate on longer time-scales of weeks to months in response to seasonal fluctuations in OM input (Carroll et al., 2008; Renaud et al., 2008). However, food supply is not the only factor that can influence seasonality in benthic community processes. Species-specific reproduction strategies, recruitment and settlement of meroplankton larvae, together with post-settlement processes and species interactions, are also factors that can determine the seasonal dynamics of benthic adult populations (Thorson, 1950). Here, benthic functional community composition and its phenological dynamics might provide further insights into the responses of benthic communities to seasonal fluctuations in primary production and abiotic environmental changes.

Soft-bottom benthic communities (mainly dominated by macrofauna representatives) have key roles in biogeochemical processes (Klages et al., 2004; Bourgeois et al., 2017; Snelgrove et al., 2018; Solan et al., 2020) as they are responsible for remineralizing the OM that reaches the seafloor, closing the carbon cycle and replenishing nutrients to the water column which fuel pelagic primary production (Thamdrup and Canfield, 2000). Many macrofaunal traits (i.e., morphological, behavioral and life history traits) can give insights about the ecological roles displayed by these communities (Oug et al., 2012; Degen et al., 2018). For instance, their feeding habits can reflect hydrodynamic conditions and carbon availability at the seafloor (Sutton et al., 2021).

Recent studies have hypothesized that increased effects from climate change, such as ocean warming, sea ice cover retreat and increased primary production and input of OM to the seafloor will cease the seasonality of benthic processes and activities (Morata et al., 2020). This reduction in seasonality might increase the benthos' resilience to intra-annual variability in pelagic primary production, which is expected to shift its phenological timing in high Arctic regions. However, in the long run, it could reduce the communities' functional diversity and redundancy by favoring deposit-feeding taxa over suspension feeders, leading to a decoupling from pelagic-benthic interactions and increasing detrital energy pathways, with unknown tipping points and consequences to the ecosystems' stability (Morata et al., 2020). Therefore, understanding spatio-temporal dynamics of macrobenthic taxonomic and functional community composition is critical to anticipate shifts in seafloor biogeochemical processes that could alter the whole ecosystem function (Degen et al., 2018). Spatio-temporal relationships between macrobenthic taxonomic diversity and functional diversity have yielded diverging results in the Arctic in that some showed a strong link of taxonomic and functional patterns (Kokarev et al., 2017; Włodarska-Kowalczuk et al., 2019) and others a weak link (Cochrane et al., 2012). However, no studies to our knowledge have attempted to assess the dynamics of functional diversity on a seasonal basis and whether it fluctuates in a concomitant temporal scale or not with the community taxonomic structure.

Given the knowledge gaps in seasonality of high Arctic macrobenthic community composition and functional diversity, we conduct here the first seasonal study of macrobenthos in the open northern Barents Sea. We sample a transect with variable influence of sea ice and water masses to gain insight into potential trajectories in system change due to regional warming trends: from the Atlantic-influenced southern, and Arctic-influenced northern Barents Sea, to the continental slope and the adjacent Nansen Basin. The main aims of the study are (i) to assess the seasonality of macrobenthic community composition and functional diversity and (ii) to identify if the temporal dynamics of environmental variables are responsible for the structure of communities in these very distinct hydrographical and ecological settings. We hypothesize that seasonality in environmental variables such as sea ice cover, water mass properties and in OM export to the seafloor will be main drivers of spatio-temporal changes in the taxonomic and functional structure of benthic communities. We hypothesize that macrofauna abundances (and to a lower extent biomass) may reflect to some extent seasonal patterns of productivity in the overlying waters, increasing during the spring bloom, and decreasing during the polar night. Finally, we expect to find different timing in macrofauna seasonality along the transect following the space–time substitution paradigm, which states that bloom phenology is delayed at higher latitudes due to more persistent sea-ice cover (Wassmann et al., 2020), making seasonal patterns along this region site-specific and context dependent.

2. Material and methods

2.1. Study area

The Barents Sea comprises a transitional domain between warm, Atlantic water masses in the south and cold, Arctic water masses in the north, separated by the Polar Front, an oceanographic feature characterized by high biological productivity (Sakshaug et al., 2009). The Barents Sea shelf, with depths ranging from ca. 100 to 300 m, is bathymetrically complex, with several troughs and banks having different granulometric properties, presenting higher clay and silt fractions in the troughs and sandier sediments in the shallower areas (Carroll et al., 2008). To the north, the shelf break leads to a steep continental slope, with a dynamic and small-scale heterogenous geomorphological setting comprising a variety of troughs, furrows, channels, canyons and mouth fans ending with a rugged topography further downslope (Kollsgård et al., 2021). The adjacent Nansen Basin presents an abrupt transition towards the oceanic environment with fine silt and clay types constituting an average of above 90 % of the total sediment (Husum et al., 2015). The West Spitsbergen Current (WSC) flows along the Norwegian shelf break northwards towards the Fram Strait, bringing warm Atlantic Water to the north. Once it crosses the Yermack Plateau, it evolves as the Svalbard Branch, which flows along the continental slope north of Svalbard and occasionally protrudes into the northern Barents Sea shelf (Fig. 1).

The study area comprised a transect of seven stations in the north-western Barents Sea, east of the Svalbard Archipelago ranging from 76.0°N to 81.9°N. Four of these stations were located on the shelf: P1 south of the Polar Front, and P2, P4 and P5 north of it. Station P6 was located on the continental slope, station P7 in the southern Nansen Basin, and station SICE4 in the deep Nansen Basin (Fig. 1 **and** Table 1).

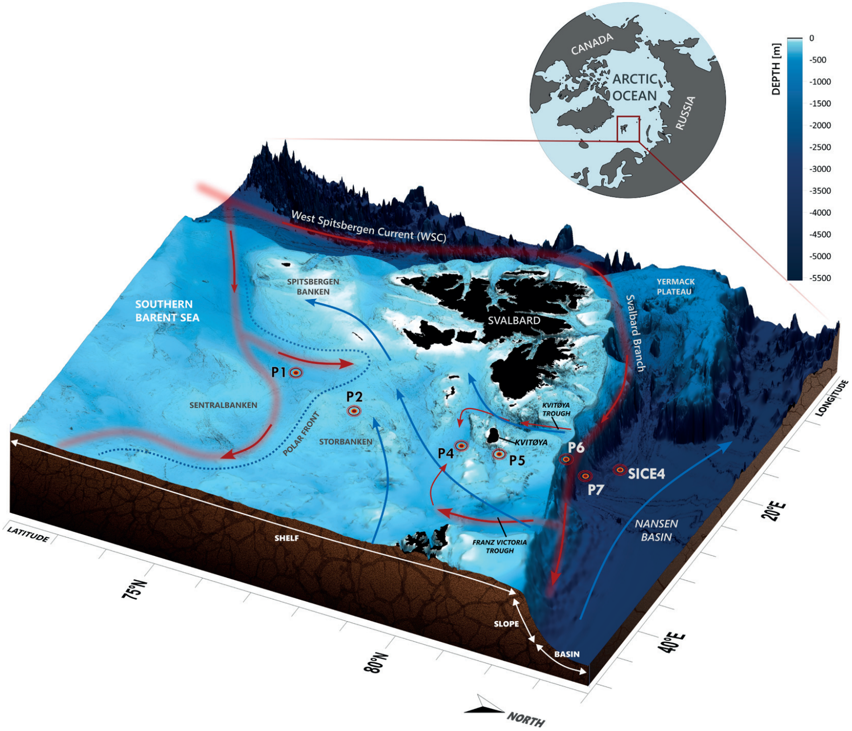

Fig. 1. Map of the northwestern Barents Sea with the location of the sampling stations along the sampling transect (from P1 to SICE4) indicated with red dots. Cold Arctic currents are indicated with blue arrows and warm Atlantic currents are indicated with red arrows. The stippled line indicates the approximate position of the Polar Front. Bathymetric data source. GEBCO Compliation Group, 2022.

2.2. Sampling and sample processing

Sampling was conducted on board of the Norwegian icebreaker R/V *Kronprins Haakon* in August 2019, December 2019, March 2021 and May 2021 (Table 1). Due to the COVID-19 pandemic, the sampling planned for March and May 2020 was deferred to 2021. Therefore, a gap-year exists between the samples from December 2019 and March 2021 in which samples were not available to assess a consecutive annual cycle.

At each station and season, three box core replicates (0.25 m^2) were retrieved (Table 1). Stations P5 and SICE4 were only sampled in August 2019, yet were included in this paper to give a better resolution for the spatial context of the transect. However, since seasonality was the main focus of our study, they were not included in most of the analyses focusing on seasonal variations.

2.2.1. Water masses and sea ice concentration

At each station bottom water temperature and bottom salinity were measured with the ships' conductivity, temperature, depth (CTD) recorder. Following the TEOS-10 convention (IOC, SCOR and IAPSO, 2010) and using the R package "gsw", practical salinity unit (PSU) values were converted to absolute salinity and in-situ temperature values were first calculated to potential temperature prior to obtaining conservative temperature values. Using the same package, potential density was calculated from absolute salinity and in-situ temperature values with sea level pressure as reference. From this, bottom water masses were assigned to each station and for each time of the year (Fig. 2) following the water mass definitions from the Nansen Legacy (Sundfjord et al., 2020).

Daily sea ice concentrations at each station location were retrieved as a 6.25 km gridded product of sea ice concentration from a repository of the University of Bremen based on AMSR-E and AMSR2 passive microwave sensors (https://seaice.uni-bremen.de/sea-ice-concentration/amsre-amsr2/information/) for the years 2019, 2020 and 2021. Sea ice concentration values were extracted for each date of the station/season events (see Table 1 for dates) following the python code from Steer (2022) to use as environmental predictor. Since sea ice concentration was the only environmental parameter for which continuous records were available during the gap year in 2020, we used this environmental data to asses qualitatively if the surface water conditions remained relatively constant or not between the sampled years 2019 and 2021.

2.2.2. Granulometry, total organic carbon (TOC) and sediment pigments

A 5.5 cm in diameter plastic sub-core from each box core replicate (three replicates in total) as described in Ricardo de Freitas et al. (2023, under review this issue) and the core was sliced every centimeter from the surface. Sediment granulometry characteristics (mean grain size, silt content, clay content and sand content) for the 0–2 cm surface sediment layer (average between the 0–1 and 1–2 slices) and total organic carbon content (TOC%) for the 0–1 cm surface sediment layer were determined as described in Ricardo de Freitas et al. (2022a, 2022b, 2022c, 2022d) and Ricardo de Freitas, et al. (2023, under review) and resulting data used as published in Ricardo de Freitas et al. (2022a, 2022b, 2022c, 2022d) and Ricardo de Freitas et al. (2023, under review this issue).

In order to characterize sediment pigments of the surface seafloor (chlorophyll *a* and phaeopigments) one replicate core of 4.7 cm in diameter was retrieved from each of the three box cores replicates. Cores

Table 1
Overview of the sampling conducted in the present study. For each station and season (month) of the year, three box core replicates were deployed (BC-1,2&3). For each box core replicate, the exact coordinates in decimal degrees (°)) and depths (m) are given. At each station/season, five cylindrical core replicates of 11.7 cm diameter (ø) were randomly subsampled from each of the three box core replicates, trying to maximize subsampling from each box core as much as possible. These five core replicates are considered as the macrofauna replicates used for the analyses in this study. For each station/season, the dates in which the three box core replicates were deployed are given. Note that at stations P6 and P7 coordinates and depths differed more than at shelf stations between box core replicates and seasons due to difficulties to maintain the ship's position against strong drifting sea ice conditions.

Station	Month and Year (date of deployment)	Box Core replicate	Number of core Replicates (ø 11.7 cm)	Coordinates (°N,°E)	Depth (m)
P1 (Atlantic Station)	August *(09.08.2019)*	BC-1	2	75.99, 31.22	326.1
		BC-2	2	75.99, 31.22	326.0
		BC-3	1	75.99, 31.22	325.0
	March *(06.03.2021)*	BC-1	2	76.00, 31.21	324.9
		BC-2	2	76.00, 31.21	324.8
		BC-3	1	76.00, 31.22	325.2
	May *(01.05.2021)*	BC-1	2	76.00, 31.22	325.6
		BC-2	1	76.00, 31.22	326.1
		BC-3	2	76.00, 31.22	326.1
P2 (Polar Front Station)	August *(12.08.2019)*	BC-1	2	77.50, 34.00	188.5
		BC-2	1	77.50, 34.00	188.5
		BC-3	2	77.50, 34.00	188.8
	March *(07.03.2021)*	BC-1	3	77.51, 33.70	167.8
		BC-2	1	77.52, 33.65	162.6
		BC-3	1	77.53, 33.60	169.8
	May *(02.05.2021)*	BC-1	3	77.50, 34.00	190.3
		BC-2	2	77.50, 34.00	190.8
		BC-3	-	77.50, 34.00	190.8
P4 (Arctic Station)	August *(14.08.2019)*	BC-1	2	79.75, 34.02	333.8
		BC-2	1	79.74, 34.00	332.7
		BC-3	2	79.75, 34.03	331.1
	December *(09.12.2019)*	BC-1	2	79.76, 34.00	330.0
		BC-2	1	79.75, 34.00	337.0
		BC-3	2	79.74, 34.00	338.0
	March *(11.03.2021)*	BC-1	1	79.77, 33.61	326.9
		BC-2	3	79.77, 33.59	320.5
		BC-3	1	79.76, 33.52	331.9
	May *(06.05.2021)*	BC-1	2	79.75, 34.00	335.3
		BC-2	1	79.76, 33.99	330.1
		BC-3	2	79.76, 34.00	326.8
P5 (Arctic Station shallow)	August *(16.08.2019)*	BC-1	5	80.50, 34.02	160.7
P6 (Continental Slope Station)	August *(19.08.2019)*	BC-1	2	81.55, 30.85	856.6
		BC-2	-	81.53, 30.96	806.3
		BC-3	3	81.54, 30.88	829.1
	December *(05.12.2019)*	BC-1	2	81.54, 30.94	848.0
		BC-2	1	81.55, 30.86	879.0
		BC-3	2	81.55, 30.89	870.0
	March *(15.03.2021)*	BC-1	1	81.55, 30.85	869.1
		BC-2	3	81.55, 30.85	872.3
		BC-3	1	81.55, 30.86	868.3
	May *(11.05.2021)*	BC-1	2	81.54, 30.87	824.2
		BC-2	1	81.56, 30.85	953.8
		BC-3	2	81.56, 30.85	916.7
P7 (Nansen Basin)	August *(22.08.2019)*	BC-1	3	81.73, 28,67	2648.9
		BC-2	2	81.67, 28.79	2349.3
		BC-3	-	81.67, 28.81	2329.0
	March *(18.03.2021)*	BC-1	3	81.73, 28.67	2671.1
		BC-2	2	81.73, 28.67	2668.0
	May *(15.05.2021)*	BC-1	2	81.84, 30.76	3102.6
		BC-2	1	81.81, 30.85	3083.5
		BC-3	2	81.79, 30.95	3065.6
SICE4 (Nansen Basin)	August *(23.08.2019)*	BC-1	1	81.99, 24.53	3603.8
		BC-2	2	81.99, 24.74	3603.8
		BC-3	2	81.99, 24.80	3604.0

were sliced into sections of 0–1 cm and 1–2 cm and stored in whirl-pack bags wrapped in aluminum foil at −20 °C. Pigments were analyzed according to Holm-Hansen et al. (1965). Briefly, sediment samples were thawed in the dark at 4C and pigments were extracted in 100 % acetone in the freezer for 24 h. Samples were centrifuged (6000 rpm for 15 min) and aliquots of the supernatant were measured on a Turner model 10-AU fluorometer before and after acidification with 1 N HCl. Data were standardized to mass per m^2. The sediment pigment data was used as published in Akvaplan-niva (2023a, 2023b, 2023c, 2023d). The two slices (0–1 and 1–2 cm) were then summed together to represent the sediment pigment concentrations of the 0–2 cm surface sediment layer.

2.2.3. *Macrofauna community*

After carefully removing the overlying water from the sediment surface, 11.7 cm diameter plastic cylindrical cores were pushed into the sediment of the box cores. In total, five replicate cores (taken randomly throughout the three box core replicates) were sampled at each station and season for macrofauna community analysis. Samples were sieved over a mesh size of 0.5 mm and preserved in 4 % formaldehyde solution buffered with borax. In the laboratory, organisms were identified to the

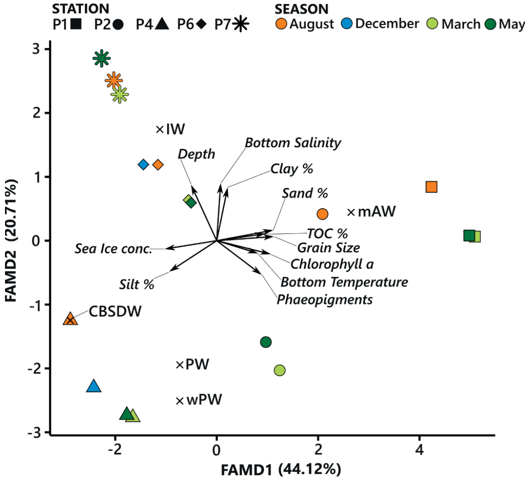

Fig. 2. Factor analysis of mixed data (FAMD) of quantitative (black arrows) and qualitative (water masses as black crosses) environmental variables and sampling stations in the northern Barents Sea across four seasons. The inertia explained by each axis is expressed in percentage. Bottom water-masses are derived from bottom water temperatures and salinities. mAW = modified Atlantic Water; PW = Polar Water; wPW = warm Polar Water; CBSDW = Cold Barents Sea Dense Water; IW = Intermediate Water and PW = Polar Water; based on definitions from Sundfjord et al. (2020).

lowest taxonomic level possible (depending on preservation state of specimens or taxonomic literature available) and counted at the Institute of Oceanology of the Polish Academy of Sciences (IOPAN) labs. Also, the weight (g) of the identified taxa was assessed as wet weight for the lowest taxonomic level possible matching the taxonomic identification. Accepted scientific names were retrieved from the World Register of Marine Species (WoRMS) (December 2021).

2.3. Data analysis

2.3.1. Environmental drivers

In order to explore the seasonality and spatial structure in environmental variables, a factor analysis of mixed data (FAMD) was performed to visualize differences in bottom water-mass properties, sediment parameters and sea ice cover across stations and seasons using the *FAMD* function from the R package “FactoMineR” (Lê et al., 2008). FAMD is a principal component method, similar to Principal Component Analysis, that allows for including both quantitative and qualitative data (Pagès, 2004). Sediment parameters such as grain size and proportions of silt, clay and sand were only available for August 2019 but were assumed to remain constant across seasons given the short amount of time between sampling events.

2.3.2. Macrofauna taxonomic composition and diversity

Univariate alpha diversity indices (species richness (S), Shannon diversity index (H’ (log e)) and Pielou’s evenness (J’)) were calculated for each replicate with the R package “vegan” (Oksanen et al., 2013). In order to test for significant differences of alpha diversity indices across seasons for each station, a Kruskal-Wallis test was performed using the R package “stats” (R Core Team, 2022). After that, a rank sums Conover-Iman test of multiple comparisons with Bonferroni p-adjusted values was performed with the R package “conover.test” (Dinno and Dinno, 2017) to identify which pairs of seasons were significantly different.

A non-Metric Multidimensional Scaling Analysis (nMDS) was performed with both the Hellinger transformed abundance of macrofauna (which allows to work in the Euclidean space) and the square-root transformed biomass for each station and season using the *metaMDS* function from the R package “vegan”. For the Hellinger-transformed abundance-based ordination, Euclidean dissimilarity distances were applied, while for the biomass-based ordination, Bray-Curtis dissimilarity distances were used. Environmental variables were fitted onto the ordination as vectors of correlation with the *envfit* function. A UPGMA cluster analysis of the Hellinger transformed abundance was performed using the *hclust* function from the R package “stats” to validate the grouping patterns from the nMDS. Additionally, a heatmap was used to visualize the most abundant species (individuals with more than 10 individuals for the sum of all samples in the study) below the cluster dendrogram with the R package “pheatmap” (Kolde, 2019). A two-way PERMANOVA analysis was performed with the function *adonis2* from the R package “vegan” to test for significant differences in the multivariate macrofauna community for Hellinger transformed abundances across the different stations and seasons. At the same time, PERMANOVA analysis with 9999 permutations was performed for each station separately to test for significant differences across seasons. Post-hoc pair-wise tests were conducted to search for significantly different pairs, using the Bonferroni method to correct the p-values for multiple testing with the *pairwise.adonis2* function from the R package “pairwiseAdonis” (Martinez Arbizu, 2017). To validate that the differences detected were not affected by heterogeneity of variances across seasons, a test of multivariate homogeneity of groups dispersions was conducted for the Euclidean distance-matrix of Hellinger transformed macrofauna abundance and traits (CWM) for each individual station across the factor seasons with the function *betadisper* from the R package “vegan”. This is a multivariate analogue of Levene’s test for homogeneity of variances in which the distances of each observation to the group centroid (in this case the factor “seasons”) are tested to check whether one group is significantly more variable than the other. The test of significance was performed using the *permutest.betadisper* function from the R package “vegan” with 9999 permutations.

To identify which samples from which seasons were driving the most important betadiversity differences seasonally, local contributions to beta diversity (LCBD) values were calculated with the function *beta.div* of “adespatial” package (Dray et al., 2018) using Hellinger dissimilarity coefficients (Legendre and Borcard, 2018; Legendre and De Cáceres, 2013). LCBD indices represent the degree of uniqueness of the samples in terms of community composition (Legendre and De Cáceres, 2013) and show how much each observation contributes to beta diversity; a sample unit with an LCBD value of 0 would have the species composition of the average centroid for all sites. LCBD values can be tested for statistical significance by random, independent permutations of the species matrix. Adjusted p-values (Holm correction method for multiple testing) for the LCBD values were calculated with 999 permutations, testing the null hypothesis (*Ho*) that species are randomly distributed and independent of one another across seasons (Legendre and De Cáceres, 2013). LCBD values were calculated for each station separately across sampled seasons in order to identify seasons that were significantly unique in taxonomic composition compared to the average community composition of all the seasons.

2.3.3. Biological traits approach (BTA) and functional diversity

For the functional traits analysis, biological traits were retrieved from the Arctic Traits Database (Degen and Faulwetter, 2019). Seven fuzzy coded functional traits were used (size, body form, living habit, adult movement, larval development, feeding habit and environmental position) with a total of 32 categories (**Table S1** in Supplementary material). For each taxon, trait categories were given a value from zero to three, with zero meaning no affinity for that category and three meaning exclusive affinity for that category. For unavailable traits for some of the taxa at the species level, traits were retrieved for the genus or family level. In order to calculate functional diversity indices, fuzzy coded traits were standardized in proportions from 0 to 1 using the function *prep.fuzzy.var* from the R package "ade4" (Dray and Dufour, 2007) and a matrix distance was calculated with the *dist.ktab* function. Using the function *dbFD* from the R package "FD" (Laliberté et al., 2014), functional richness (FRic), functional evenness (FEve), functional dispersion (FDis) and functional redundancy (Fred = FDis/H') were calculated. FRic indicates the amount of functional space occupied by all species in the community and does not take into account the abundance of organisms; FEve accounts for the evenness in the distribution of the abundance of organisms in the functional space; FDis is the mean distance in the trait space of each species to the centroid of all species in the community, which can be weighted by the abundances, shifting the centroid towards the more dominant taxa (Ahmed et al., 2019; Carmona et al., 2016). Functional redundancy (Fred, calculated as the ratio of FDis/H'), indicates to what degree different taxa occupy the same functional space (i.e. display the same traits). Whenever this ratio decreases, functional redundancy increases (van der Linden et al., 2012). Functional diversity indices were tested for significant differences across seasons at each station with a Kruskal-Wallis test followed by a Conover-Iman test of multiple comparisons with Bonferroni p-adjusted values the same way as was done for the alpha-diversity indices.

The community weighted mean (CWM) of functional traits weighted by the Hellinger-transformed abundances was calculated using the function *functcomp* from the package "FD", generating a Stations/Seasons × Traits matrix, where trait categories are expressed in proportions adding up to 1 based on the weight of Hellinger transformed abundance. A Fuzzy Correspondence Analysis (FCA) (Chevene et al., 1994) was performed with the CWM matrix to visualize the contribution of traits and their modalities in differentiating the functional structure among stations and seasons. This was done with the *dudi.fpca* function from the R package "ade4".

For the CWM weighted abundance trait matrix, a two-way PERMANOVA analysis was performed to test for significant differences in trait composition for the different stations and seasons, the same way as for the taxonomic community composition. At the same time, PERMANOVA analysis with 9999 permutations was performed for each station separately to test for significant differences across seasons. Post-hoc par-wise tests were conducted to search for significantly different pairs, using the Bonferroni method to correct the p-values for multiple testing, the same way as for the taxonomic community composition. Also, multivariate heterogeneity of variances were tested the same way as for the abundance dataset (see above).

2.3.4. Variation partition of macrofaunal community with environmental variables

Redundancy analysis (RDA) was used to partition the variation within the Hellinger-transformed abundance and the macrofauna functional composition (CWM Hellinger transformed) datasets on the set of environmental predictor variables, the spatial structure of the sampling stations (spatial-autocorrelation) using Moran Eigenvector Maps (MEMs) and the temporal structure (seasonality, but also other time scale fluctuations) using Asymmetric Eigenvector Maps (AEMs) based on the sampling seasons. MEMs are orthogonal vectors calculated through decomposition of the Moran's I coefficient to maximize spatial autocorrelation. These spatial predictors can then be used in variation partition analysis to explicitly account for spatial structure (Dray et al., 2012). MEMs were calculated based on the geographical coordinates of sampling locations (original targeted coordinates for each station were used instead of the exact coordinates of sampling events, since they generally did not vary significantly between replicates and seasons) (excluding P5 and SICE 4) using the *list.explore()* function from the R package "adespatial". For that we input the coordinates, used "distance" graph type, and after the Euclidean distances between sites were calculated, we defined the weights of the spatial weighting matrix as $1-d/\max(d)$ and finally we obtained the MEMs (the number of which is n-1, where n is the number of sites) by using the standardization style "B", which is the basic binary coding. For all these intermediary steps we used the R packages "sp" and "spdep" (Pebesma and Bivand, 2005; Bivand et al., 2008) (to see the different calculated MEMs the reader is referred to **Fig.S5** from the Supplementary Material). AEM is an eigenfunction method suitable to model multivariate directional processes like temporal change of species abundance data. By incorporating AEMs as constraining temporal predictors one can account for temporal autocorrelation (or temporal structure) in the abiotic drivers or in the species matrix itself (Legendre and Gauthier, 2014). To account for the irregular intervals between sampling events, dummy sampling events were added on the 15th day of every month when no samples were collected, starting the 15th of August and finishing the 15th of May. Based on results from the macrofauna community taxonomic and functional structure (see Results section), which did not show extreme differences between the seasons from 2019 and 2021, we considered seasons as being from consecutive years, instead of taking into account the gap year between 2019 and 2021 (see Discussion section). AEMs were then calculated using the time between neighboring dates as edge weight with the function *aem.time* from R package "adespatial". In principle, AEMs as temporal predictors are essentially n-1 sine waves of decreasing wavelength, where n is the total number of sampling dates; here $n = 10$, including the dummy variables). The smallest AEM, AEM_1 depicts long time scale fluctuations and the biggest AEM, AEM_{10} depicts smaller time-scale variations (**Fig. S6**).

The environmental variables used as community predictors in the RDA analysis were previously standardized. From the granulometric parameters, only the mean grain size was used as surrogate for the silt, clay and sand content variables to avoid high collinearity between environmental predictors (**Fig. S1**). For the sediment pigments and TOC (%) values, the mean between the three replicate samples (or less replicates when not available) from the box core replicates at each station/season event were used as predictor variables (see **Table S2**). For the response variables, the Hellinger transformed macrofauna abundance and functional composition based on Hellinger transformed abundance CWM, the five core replicates (see Table 1) were considered separately.

Prior to variation partitioning, the three sets of environmental, spatial auto-correlation predictors (MEMs) and temporal predictors (AEMs) were individually subjected to forward selection (FWS) for both the abundance and traits (CWM) datasets using a double-stopping criterion (Blanchet et al., 2008) to avoid overestimation of the explained variation. In this approach, variables are added to the model in order of decreasing explanatory power until no variable adds significantly to the explanatory power or until the R^2-adjusted exceeds the R^2-adjusted of the full model (Blanchet et al., 2008). The variation partition analysis was performed with the *varpart* function of the R package "vegan".

Another set of variation partition analyses were performed for each station individually in order to assess the contributions of seasonality (this time without spatial predictors (MEMs)) for both the abundance and traits (CWM) datasets. In this case, depth and sediment grain size parameters were excluded, as they were not expected to vary across seasons. Both AEMs and environmental variables were subjected to forward selection prior to variation partitioning with the same procedure as in the first variation partition sets for the whole transect.

3. Results

3.1. Seasonality and spatial structure in environmental variables

The FAMD analysis revealed clear environmental differences among stations (Fig. 2). For the first axis, which explained most of the variation (44.12 %), the southern stations P1 and P2 correlated positively with bottom water temperature, TOC, grain size, sediment phaeopigments and chlorophyll *a*; while stations from P4 northwards were characterized by higher sea ice concentration and silt fraction. At stations P1, and P4 and P6, but especially at station P4 the August conditions differed from December, March and May conditions along the second axis (which explained 20.71 % of the variation), which was mainly driven by the small variations in bottom water salinity and the different water masses.

Station P2 had the highest seasonality in ice cover, with high cover in March and May, but open water conditions in August. Sea ice concentration at stations P4, P6 and P7 was higher than 80 % for all season, with very small variations in time. Station P1 was free of sea ice during all sampling seasons (Fig. 3, **Table S2**). The qualitative analysis of sea ice concentration during the gap year revealed that the year 2019 had generally higher sea ice cover than the end of 2020 and beginning of 2021, especially on the northern stations P6 and P7.

Bottom water temperatures at stations P1 and P6 were above or close to 0 °C for most of the seasons, while P7 had negative temperatures in all seasons. Stations P2 and P4 had the highest seasonal temperature variations, with values ranging from negative values in December and August to above 0 °C in spring (Fig. 3, **Table S2**). Bottom water salinity was nearly constant at all stations, between ca. 34.7 to 34.9 PSU (**Table S2**). Total organic carbon content in surface sediments (TOC) was highest at station P1 (1.9–2.1 %) compared to all the other stations north of the Polar Front (1.3–1.5 %) (Fig. 3, **Table S2**). No strong seasonal variations were observed at any of the stations (Fig. 3, **Table S2**). Chlorophyll *a* in sediments was mostly constant through seasons at stations P4, P6 and P7 (ranging between 2 and 4.1 mg/m^2 across those stations) (Fig. 3, **Table S2**). Much higher values were observed at stations P1 (12–9.5 mg/m^2) and P2 (11.5–5.9 mg/m^2), with the highest variations at the latter one, where the highest values were noted in August and the lowest in March (Fig. 3, **Table S2**). Sediment phaeopigments had lower values at stations P4, P6 and P7 (14.7–31.2 mg/m^2) compared to stations P1 (29.5–42.4 mg/m^2) and P2 (34.2–43.8 mg/m^2). Seasonal variations were observed in most stations, with lower values in August (and in December at P4 and P6) and highest in March/May (Fig. 3, **Table S2**). This was also reflected in the sediment pigment quality ratios (Chlorophyll *a*/Phaeopigments) indicating an overall lower food quality in March/May than in August/December (Fig. 3).

3.2. Seasonal and spatial patterns in macrofauna taxonomic structure

A total of 272 different taxa belonging to 8 phyla were identified, with Annelida and Mollusca being the most abundant, followed by Arthropoda and Echinodermata. Polychaeta was the most abundant class, contributing to 59 % of the total abundance, followed by Bivalvia (23 %), Malacostraca (7 %) and Ophiuroidea (3 %). Overall, polychaetes (phylum Annelida) dominated numerically at most stations, except at stations P2 and P5, where molluscs were almost equally abundant (Fig. 4**A**). No seasonal differences were found in total abundance at any station except for station P6, where abundance was significantly higher in December than in March and May (Fig. 4**B**). The total abundance at P2 and P5 was higher than for the other shelf stations, and the lowest abundance values were noted in the Nansen Basin (Fig. 4**B**). The only significant seasonal changes in biomass were observed for stations P2 and P6, with a significant increase in biomass from March to May at P2, and significantly higher biomass in August than in May at P6. As with abundance, total macrofauna biomass (Fig. 4**C**) was higher at shelf than slope and basin stations. In general, H' index was higher for shelf and slope stations than for the basin stations (Fig. 4**D**). Significant seasonal differences were only found at P1 (higher values in August compared to March) and P2 (higher values in March than in August and May). Taxon richness followed a similar pattern as abundances across stations, and seasonal significant differences were only found at station P2, with higher values in March compared to August (Fig. 4**E**). J' index values increased gradually with latitude, and seasonal changes were only found at station P2, with significantly higher values in March compared to August and May (Fig. 3**F**).

The cluster analysis revealed relatively stronger seasonal dissimilarities at stations P2, P4 and P6, while almost no dissimilarities were found at the Atlantic station P1 (Fig. 5). In addition, it revealed that the community at station P1 was more similar to P4 than to the neighboring station P2, due to the numerical dominance of the tube-building polychaete *Spiochaetopterus typicus* and high abundances of three other polychaete species: *Heteromastus filiformis*, *Spiophanes kroyeri* and *Anobothrus laubieri*. The two shallowest stations, P2 and P5, clustered together, both being dominated by bivalves such as *Macoma* sp., *Yoldiella solidula* and *Yoldiella lenticula*. At P2 polychaetes *Lumbrineris* sp., *Myriochele heeri* and *Galathowenia oculata* were also relatively numerous. Fauna at station P6 was clearly dominated by the polychaete *Prionospio cirrifera,* while station P7 had relatively high abundance of *Myriochele heeri* and *Siboglinum norvegicum* (Fig. 5 **and Table S3**).

The nMDS based on Hellinger transformed macrofauna abundance revealed a clear separation between the shelf stations (P1, P2, and P4) and the slope and basin stations (P6 and P7). Shelf stations also differed from each other in community composition, with P1 and P4 being more similar to each other than to P2. No clear seasonal differences were observed, as samples taken at different seasons tended to not form distinctive groups for a given sampling station (Fig. 6**A**). A similar pattern was observed for the macrofauna biomass, and in this case stations P1 and P4 stations were grouped even closer (Fig. 6**B**). Environmental variables that correlated best with the community composition of the deeper stations P6 and P7 were sea ice concentration, clay and silt fractions and bottom water salinity. In contrast, the shelf stations were positively correlated with sand fraction and mean grain size, sediment pigments, TOC and bottom water temperature.

LCBD map (Fig. 7) showed that March samples from P2 station had significantly higher LCBD values, indicating that those samples were more unique in community composition than the mean composition of the other seasons. At station P6, significantly higher LCBD values were found for May samples. Although not significant, station P4 had higher LCBD values in March too, while station P7 and P6 had higher values in May. Stations P1 had similar LCBD values for all seasons.

The PERMANOVA analysis based on abundance of macrofaunal community composition (Table 2) revealed significant differences across stations, seasons and the interaction of both. However, the R^2 explained by season (0.05) and the interaction of season and station (0.13) was much lower than for the factor station (0.39), indicating low contribution of the seasonality factor to the variation explained. At P1 significant differences in community composition were found only between August-May and March-May. For P2, P4 and P7 stations, significant differences were found between all pairs of seasons. For station P6, significant seasonal differences were found between all pairs of seasons except between August and December. Both stations P2 and P7 had highest R^2 values for the factor season (0.42 and 0.4 respecitvely). No significant effects for the multivariate heterogeneity of variances were found at any of the stations, indicating homogeneity of variances between seasons (Table 2, **Fig. S2**).

3.3. Seasonal and spatial patterns in functional diversity of macrofauna communities

No significant seasonal differences were observed for functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis). FRic and FDis followed a similar pattern across stations, presenting higher values at the shelf and slope stations compared to the basin stations (Fig. 8**A and C**). FEve increased gradually in variability among replicates for the deep stations (Fig. 8**B**). The functional redundancy at the slope and shallow stations was higher than at the basin stations indicated by low FRed values (Fig. 8**D**). Significant seasonal differences were found at station P2, with significantly higher values in August compared to March and May, and lower values in March than in May, indicating that samples from March had higher functional redundancy. Seasonal differences were also found at station P7, with significantly lower values in March compared to August, indicating again higher functional redundancy in March. Linear regressions between functional diversity (FDis) and H' for all stations and seasons showed significant but not very strong linear relationships (R^2-adjusted = 0.63, p-value= <2e-16 ***) (**Fig. S4**) Relationships were maintained constant

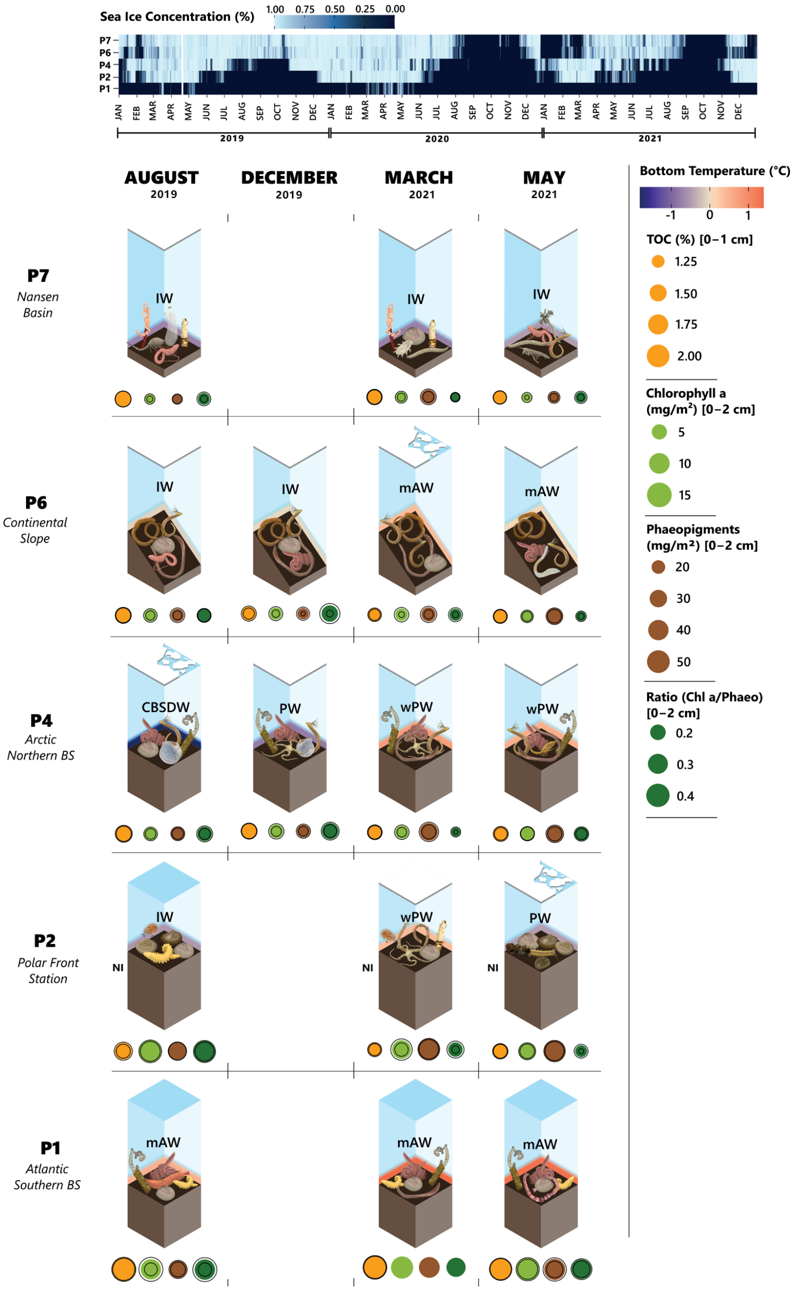

Fig. 3. Overview of some of the most relevant environmental variables varying across stations and seasons. On the top, daily sea ice concentrations from 2019 to 2021 are shown to assess qualitatively the sea ice conditions during the gap year (2020). Bottom water temperatures are shown with color ranging from dark blue to red on top of the seafloor for each station/season (for values see color scale). Bottom water masses are indicated as in Fig. 2. Mean values of sediment pigments (Chlorophyll a and Phaeopigments) and TOC% are shown as colored circles at the bottom of each station/season. Sizes scales represent values and the two black circles around them signify the standard deviation of the mean. Five most abundant taxa for each station/season are shown (for taxa names see Fig. 5 and Table S3).

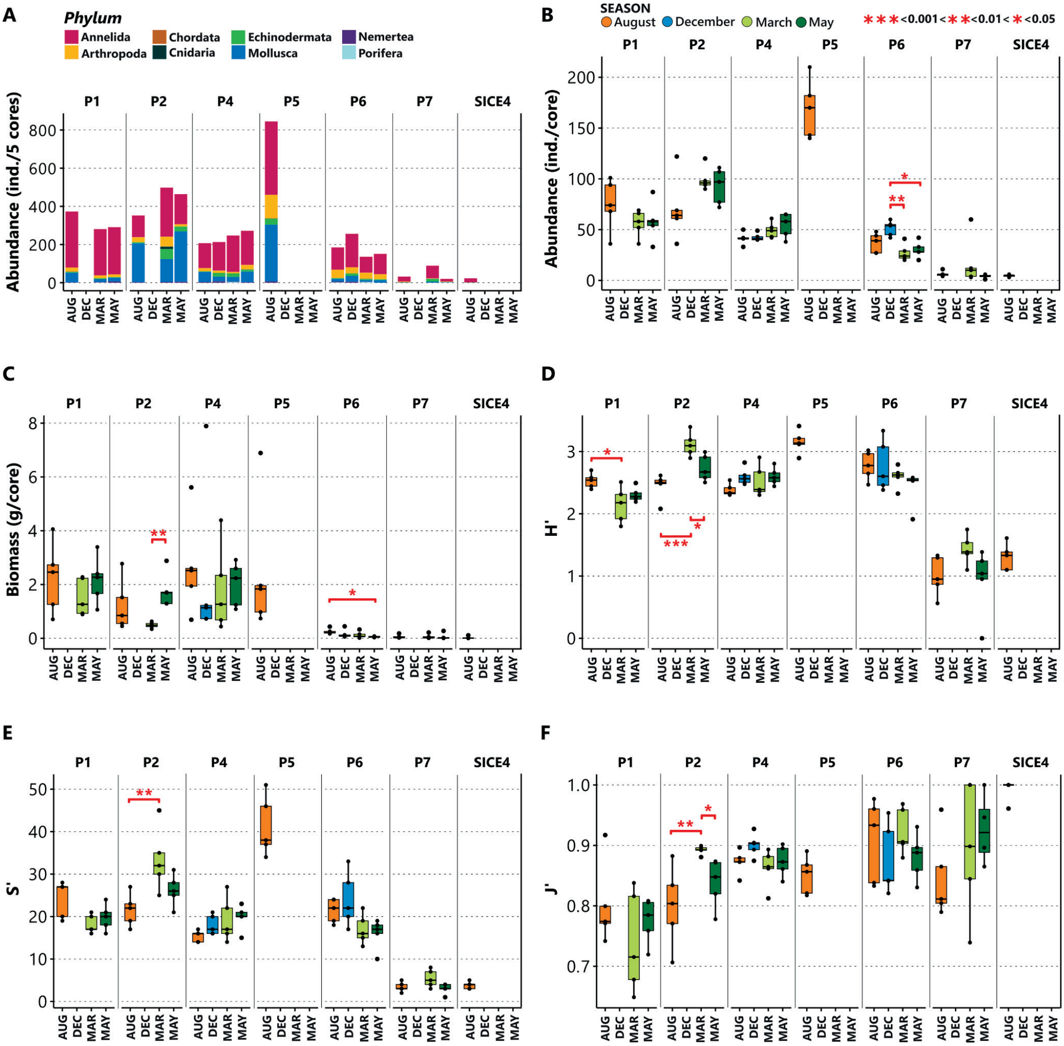

Fig. 4. Macrobenthic community composition and diversity indices from the northern Barents Sea across four seasons from five macrofauna core replicates. A) Stacked bar plots showing abundances of macrobenthos (five replicates pooled) by phylum; B) boxplots for total abundances of macrofauna (significance tests are shown for the square root transformed biomass), C) boxplots for total biomass of macrofauna D) H' (Shannon Index), E) S' (Species richness), F) J' (Pielou Evenness) for each station and season based on abundance. Significant differences in pair-wise comparisons at each station across seasons after the Kruskal-Wallis test and Conover test applying the Bonferroni correction for adjusted p-values are reported in red with asterisks. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. In boxplots, the colored rectangles indicate the interquartile range, which is divided into the upper and lower quartiles by the median (indicated with a black line); whiskers indicate the maximum and minimum values, excluding outliers.

across seasons, except for December due to lack of samples at some stations for that season.

The fuzzy correspondence analysis (FCA) did not show clear groupings across seasons (Fig. 9). Instead, it showed a rather spatial grouping along the first axis (explaining 33.03 % of the variation) differentiating the shelf and slope stations from the P7 station. At the same time, the slope station grouped further apart from the shelf stations along the second axis (which explained 19.56 % of the variation). Trait categories: tube-dwelling (LH3), sessile (MV1), vermiform (BF2), infaunal (EP1), parasite/commensal/symbiotic (FH6) and medium and small/medium (S3 and S2) were positively correlated with samples of P7 along the first axis. In contrast, trait categories for burrower and burrowing (MV2 and LH4), dorso-ventrally and laterally compressed (BF3 and BF4), swimmer and crawler (MV4 and MV3) and small (S1) correlated positively with most shelf station communities, especially at P2. Along the second axis, trait category indicating benthic/direct larval development (LD3) correlated positively with samples of station P6, while pelagic/planktotrophic larval development (LD1) correlated with samples from stations P1 and P2.

The PERMANOVA analysis conducted on the CWM trait matrix

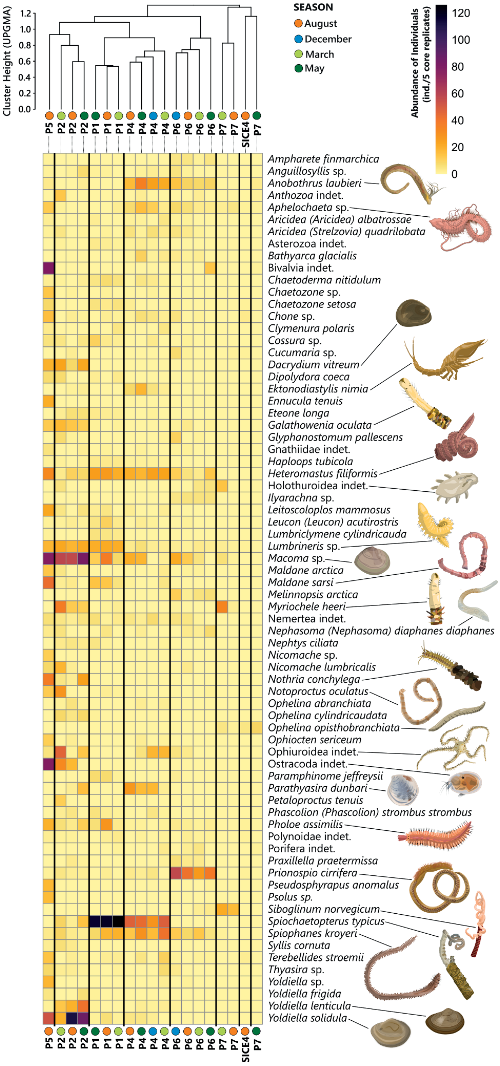

Fig. 5. Cluster dendrogram (UPGMA) based on Euclidean dissimilarity distances calculated from Hellinger transformed macrofauna abundance for the five pooled core replicates for each season (August, December, March and May) and station (P1, P2, P4, P5, P6, P7 and SICE-4). Heatmap shows the raw abundances of the most abundant taxa (>10 individuals in total for all summed samples of the entire study) are shown below the cluster analysis. Macrofauna abundance values are shown for the five pooled core replicates at each station/season (see color scale on the top right). Drawings for some of the most abundant species are presented. *D. vitreum*, *Macoma* sp., *P. dunbari* and *Y. lenticula* are redrawn from images © Amgueddfa Cymru – National Museum Wales using Inkscape. *H. filiformis* is redrawn from image © Fredrik Pleijel using Inkscape. *N. diaphanes* is redrawn from © "Nephasoma diaphanes" - Nephasoma diaphanes (Gerould, 1913) collected in United States of America by Florida Museum of Natural History Invertebrate Zoology (licensed under http://creativecommons.org/licenses/by-nc/4.0/). All drawings made by Èric Jordà Molina with Inkscape 1.3 (0e150ed6c4, 2023–07-21). Drawings are just for illustrative purpose and are not made to taxonomic detail.

considering all stations and seasons (Table 3) identified statistically significant differences between stations ($R^2 = 0.33$), seasons ($R^2 = 0.04$) and the interaction of station and season ($R^2 = 0.12$). When taking each station individually into account, significant seasonal differences were found at station P2 (March samples vs. August and May samples). For station P4, significant differences were found between samples collected in August and March, and August and December. Again, station P2 had the highest R^2 for the factor season ($R^2 = 0.49$). No significant effects for the multivariate heterogeneity of variances were found at any of the stations, indicating homogeneity of variances between seasons (Table 3, **Fig. S2**).

3.4. *Spatio-temporal variation partition of macrofauna with environmental variables*

The variation partition for the macrofauna community composition (Hellinger transformed abundance-based) (Fig. 10**A**) showed that temporal predictors (AEMs 9 and 6, see supplementary material **Fig. S6**) only explained 2 % of the macrofauna variation. Thirty five percent of the variation, in contrast, was explained by the selected environmental variables (in decreasing importance depth, TOC, mean grain size, bottom salinity, bottom temperature, sea ice concentration and sediment phaeopigments) of which 24 % was explained together with the spatial structure (MEM1, 4 and 3). In total, 31 % of variance was explained by the spatial structure.

For the CWM traits dataset (Fig. 10**B**), no AEMs were selected in the forward selection step, and therefore, no variation was attributed to seasonality in macrofauna trait composition. In contrast, environmental variables selected (in decreasing importance: depth, TOC, bottom water salinity, sea ice concentration, mean grain size and bottom temperature) accounted for 29 % of the variation, while the spatial structure (MEM1, 3, 4 and 2) accounted for 26 % of the variation. Of that, 21 % was accounted for by both the environmental variables and spatial structure.

As for the variation partitions at each station (Fig. 11**A,B**), for station P1 the analysis attributed 4 % variation on the abundance based macrofauna dataset to environmental variables (bottom water salinity) and 4 % to the temporal predictors (AEM9). No environmental variables or AEMs were selected for the CWM-based dataset. For station P2, the abundance-based partition attributed 21 % of variation to the environmental variables (bottom water temperature) and 21 % to the selected AEMs (AEM2). For the CWM-based dataset, 39 % of variation was attributed to the environmental variables (bottom water temperature) and 39 % to the temporal predictors (AEM2). For station P4, 12 % of variation was attributed to the environmental variables (chlorophyll *a* and phaeopigments) together with the AEMs selected (AEM4 and 6) for the abundance-based macrofauna, while 6 % of total variation was attributed to the temporal component alone. For the CWM-based dataset, 17 % was attributed to the environmental variables (bottom water salinity) and 18 % to the selected AEMs (AEM4 and 7). At station P6, 8 % and 7 % of variation in the abundance-based macrofauna dataset was attributed to the environmental variables (sediment phaeopigments) and temporal predictors (AEM5) respectively, while no environmental variables were selected for the CWM-based dataset (despite AEM3 being selected after FWS). Lastly, at station P7, 25 % of variation was attributed to environmental variables (bottom water temperature) together with AEMs selected (AEM3 and 1) for the abundance-based dataset, while no variation was explained by either of the explanatory sets alone. No variables were selected for the CWM-based data for that station.

4. Discussion

In shallow temperate coastal environments, macrofauna communities often undergo significant seasonal fluctuations, presenting lower biomass in late winter and an increase in biomass from early summer to early fall (Beukema, 1974; Baird and Ulanowicz, 1989; Zwarts and Wanink, 1993; Coma et al. 2000; Saulnier et al., 2019). This increase in

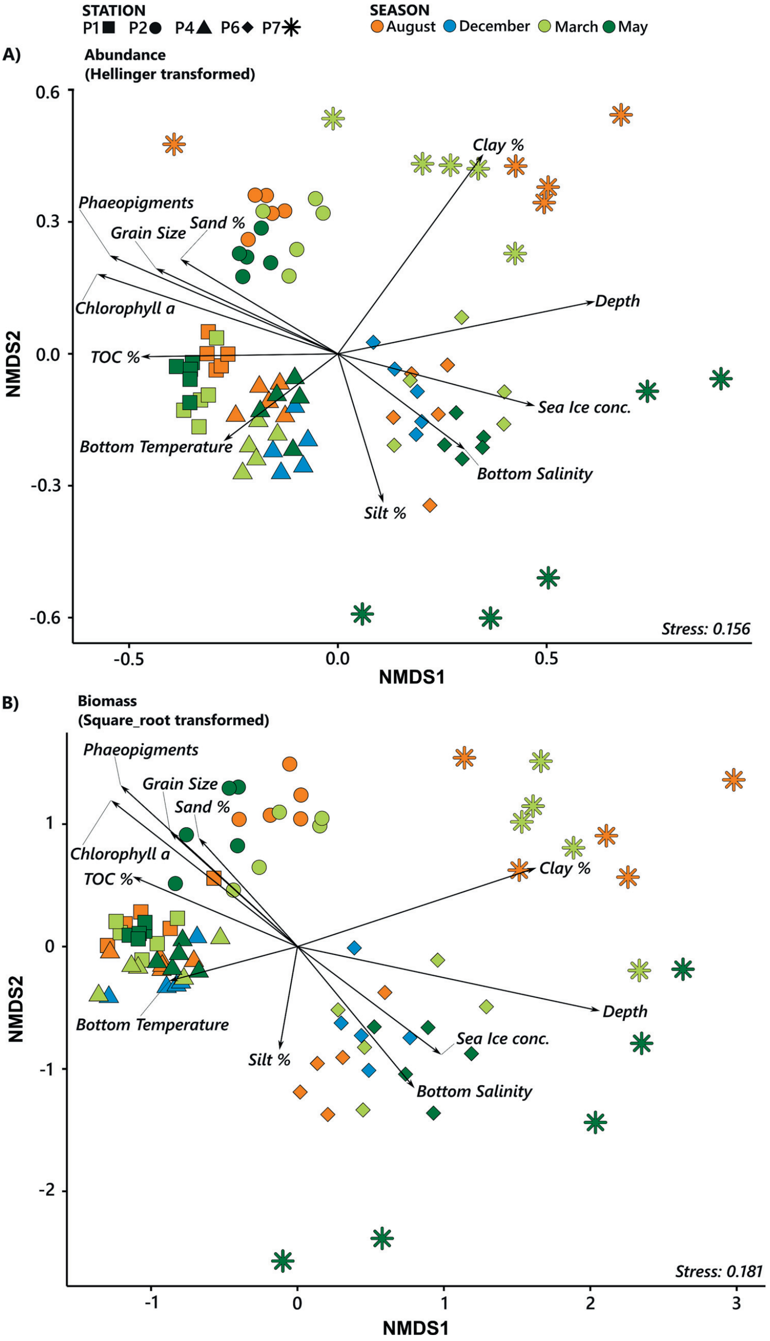

Fig. 6. Non-metric multidimensional ordination (nMDS) showing A) the similarity between sample replicates by season and station of Hellinger-transformed macrofauna abundance data using Euclidean distances, and B) the similarity between replicates by season and station of the square root transformed macrofauna biomass using Bray-Curtis distances from the northern Barents Sea.

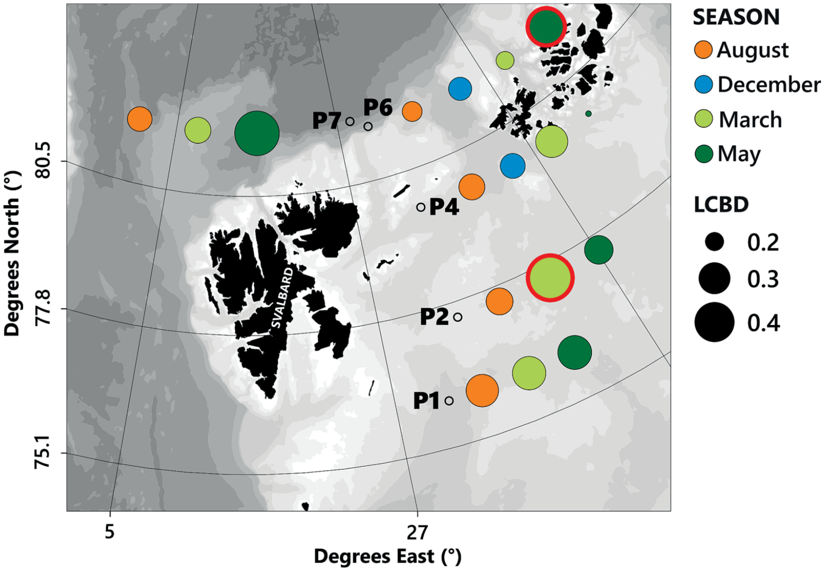

Fig. 7. Map showing the results of the Local contribution to beta diversity (LCBD) for the Hellinger transformed macrofauna abundance in the northern Barents Sea across four seasons. The position of each station is indicated with empty circles. LCBD values for each station across seasons are indicated with colored circles the sizes of which indicate the LCBD value and the color the season. LCBD values are calculated individually for each station comparing seasons and therefore should not be compared between locations. LCBD indices from seasons which are significant are indicated with a red rim (p adjusted-value < 0.05 after applying the Holm correction for multiple testing) indicating seasons that are more unique in community composition than the average composition of the other seasons.

biomass during summer coincides with increasing temperatures, primary production and food availability to the seafloor, which induces an increased somatic growth and is accompanied by recruitment pulses (Reiss and Kröncke, 2005; Saulnier et al., 2019). On the contrary, the lower food supply during winter could be the reason behind weight loss and, together with increased predation pressure, increased natural mortality (Saulnier et al., 2019). These seasonal patterns in temperate environments, however, may differ from equatorial or polar regions with little or extreme seasonality in environmental conditions, respectively (Saulnier et al., 2019).

High Arctic marine ecosystems are characterized by marked seasonal pulses of primary production and fluctuations in abiotic parameters (i.e. seasonal sea ice cover, among others) which constrain the phenology, structure and composition of pelagic communities (Daase et al., 2013; Søreide et al., 2013). Hence, assuming that the Barents Sea is a tightly pelagic-benthic coupled system (Wassmann et al., 2008; Wassmann and Reigstad, 2011), we hypothesized that benthic standing stocks (i.e. macrofauna) might reflect seasonal patterns in their taxonomic and functional composition that mirror those in the overlying water. Conversely, the results of our study indicate a general lack of seasonality in macrobenthic community parameters, and especially, in functional composition (Fig. 10). We found only weak seasonal patterns at some individual stations with respect to the others, indicating that, any seasonality is site-context specific along the northwestern Barents Sea and adjacent Nansen Basin, a region comprising different sea ice, hydrographical and productivity regimes and extending over different geomorphological settings (shelf, slope and deep basin). We also hypothesized that seasonal patterns, if present, might be driven by seasonal fluctuations in sea ice cover, water mass properties and food availability. Although we found seasonal variations in some environmental parameters within stations (in fact environmental variables where highly spatially structured), no pronounced seasonal variations were observed across the whole region for bottom water properties (except at P2 and P4) and food availability, indicating relatively stable seafloor conditions year-round. In particular, total organic carbon in surface sediment (and to some extent sediment pigments) remained seasonally stable at all stations, pointing towards a decoupling of seafloor food availability from seasonal pelagic food export to depth.

Given that no extreme differences were found between seasons from differing years (2019 and 2021) in both taxonomic and functional composition and that most sediment parameters remained relatively stable in most cases, we consider that treating the two years over which the study was conducted as if they were consecutive, reflecting a full annual cycle, is a valid approach to discuss the results of our study.

4.1. Lack of seasonality in macrofauna and similarity in macrofauna on the shelf on either side of the Polar Front

Station P1, south of the Polar Front, did not show strong signs of seasonal variability in either taxonomic or functional composition. This station is Atlantic Water (AW) influenced with year-round presence of modified Atlantic Water (mAW) bottom water masses and consistent open-water conditions. Here, we observed some environmental variability driven mainly by small increases in chlorophyll *a* and phaeopigments in the sediments, and in bottom water temperatures in March and May compared to August, while sediment variables such as TOC remained relatively constant across seasons (Ricardo de Freitas et al., 2023 under review) (Figs. 2 and 3, **Table S2**). Consequently, the environmental variables did not seem to play a major role in driving macrofauna variation across seasons (Fig. 11). Station P4, north of the Polar Front and with high sea ice cover, also lacked seasonal differences in univariate taxonomic and functional metrics, and low variance explained by seasons in species and trait composition despite some significant seasonal differences in community composition (Tables 2 and 3). It is important to bear in mind that the PERMANOVA analyses are taking into account the whole community including the rare species, and

Table 2

PERMANOVA results from the macrofauna community abundance Hellinger-transformed. Results from a two-way model including all stations and all seasons (and interaction) and one-way models for each station separately across the different seasons. Stations with samples in only one season were not included (P5 and SICE-4). P-values from post-hoc pair-wise comparisons were corrected with the Bonferroni method and only significant comparisons are reported. Df = degrees of freedom, Rˆ2 = adjusted Rˆ2, F = F-statistic, Pr(>F) = p-value. The test of homogeneity of multivariate dispersion (Betadisper) is shown for each station for the season factor. Df = degrees of freedom, F = F-statistic and Pr(>F) = p-value from the test are reported.

		Df	Rˆ2	F	Pr(>F)	Pair-wise Comparison (only station by station)
All						
	Station	4	0.39	15.75	**1e-04** ***	
	Season	3	0.05	2.72	**1e-04** ***	
	*Station*Season*	9	0.13	2.35	**1e-04** ***	
	Residuals	68	0.42			
P1						
	Season	2	0.20	1.53	**0.0049** **	August vs May * March vs May *
	Residuals	12	0.80			
	Betadisper	2		0.15	0.860	
P2						
	Season	2	0.42	4.38	**1e-04** ***	August vs March ** August vs May **
	Residuals	12	0.58			March vs May **
	Betadisper	2		0.85	0.447	
P4						
	Season	3	0.34	2.83	**1e-04** ***	August vs December **
	Residuals	16	0.65			August vs March ** August vs May ** December vs March ** December vs May ** March vs May **
	Betadisper	3		0.754	0.531	
P6						
	Season	3	0.25	1.81	**5e-04** ***	August vs May ** December vs March **
	Residuals	16	0.75			December vs May ** March vs May *
	Betadisper	3		2.49	0.100	
P7						
	Season	2	0.40	3.97	**2e-04** ***	August vs March * August vs May **
	Residuals	12	0.60			March vs May **
	Betadisper	2		0.145	0.876	

significant differences could be reflective of sampling size limitations to effectively account for the rare fraction of specimens, yielding significant differences across seasons. Interestingly, this station had similar macrofauna taxonomic composition to station P1 (Figs. 5 and 6**A**). At both stations, the spiochaetopterid polychaete *S. typicus* dominated in abundance. This species has boreal biogeographic affinities (Bhaud, 1998), high tolerance to environmental disturbance and dual surface deposit and filter/suspension feeding modes (Degen and Faulwetter, 2019). This might be an indication that P4 is influenced by AW advective processes, with higher bottom water temperatures and food availability (either in-situ or advected). Lundesgaard et al. (2022) observed intrusions of the Arctic Circumpolar Boundary Current, flowing along the slope, into the northern Barents Sea shelf through the Kvitøya and Franz Victoria Troughs, flowing southwards and converging around our P4 station (Fig. 1). This is supported by the signs of wPW in March and May that we observed in this station, which is likely a product of AW or mAW that has been mixed with PW (Sundfjord et al., 2020). Whether the similarity in faunal assemblages is driven by bottom thermal preferences, larval advection or food availability is difficult to conclude. Benthic communities in the Barents Sea are in fact highly constrained by the spatial extent of bottom water masses, particularly of AW (Carroll et al., 2008; Cochrane et al., 2009). Hence, it appears from our results that AW-influenced bottom water regions along the northwestern Barents Sea shelf displayed the least seasonal fluctuations in macrofauna communities despite presenting spatially distinct sea ice cover and seafloor food availability.

4.2. Weak signs of seasonality in macrofauna at the Polar Front

Macrofauna communities at station P2 showed the strongest seasonal signals in community composition compared to all other stations along the transect, which was also reflected in functional composition (Fig. 11 and Table 2, 3). While fine-scale temporal patterns in macrofauna variation at P2 were not selected to explain any variation on the macrofauna data (Fig. 11 **and S6**; i.e. month to month variability, which do not fit with expected phenological dynamics in the water column), both macrofauna taxonomic and functional fluctuations were partially explained by longer time-scale predictors (i.e. AEM$_2$ Fig. 11), mirroring expected seasonal patterns at these latitudes for water column processes. In general, significant increases in species diversity, richness and evenness were observed from August to March (with more unique taxonomic composition in the latter), followed by general significant decreases in May (Fig. 4). It is well known that in areas with overlaying oceanographical fronts, sea ice edge and polynya areas (such as the Barents Sea Polar Front) macrobenthic species diversity and density is enhanced (Wassmann et al., 2006; Carroll et al., 2008; Cochrane et al., 2009). This was also the case in our study along with the strongest seasonal variations in environmental parameters observed at station P2. For instance, sea ice cover was highly variable together with bottom water masses and, to a certain extent, chlorophyll *a*, phaeopigments and food quality ratios (Fig. 3, **Table S2**). Hence, this station is likely under the influence of the transitional area of the Polar Front, separating both Atlantic and Arctic domains with high seasonal variability in its oceanographic dynamics. This might result in a tighter pelagic-benthic coupling (Carmack and Wassmann, 2006; Cochrane et al., 2009), in which short pulses of high quality food (rather than the overall productivity of the water column) might be of high importance for benthic community structure. However, seasonal differences in macrofaunal taxonomic and functional composition at P2 were better explained by bottom water temperature instead of any food availability proxies. In this station, we found signs of bottom wPW in March, indicating a certain degree of Atlantic advection, but macrofauna community composition was different from the highly Atlantic influenced stations P1 and P4 with surface deposit feeding bivalves (*Macoma* sp. and *Y. solidula*) dominating at P2 (Fig. 5). This distinction in macrofaunal assemblages may arise from the difference in depth and in sediment granulometry between stations, since P1 and P4 were located in troughs with finer sediment grain sizes, while P2 was located in the Storebankken bank, with coarser grain sizes (Fig. 1). This is supported by the similarity in fauna composition of P2 with P5, as the latter was also located in a shallow bank next to Kvitøya, even though we only had data for one season (Fig. 5).

The increase in abundances of several polychaete species (i.e. *Myriochele heeri*, *Nicomache lumbricalis*, *Notoproctus oculatus)* and Ophiuroidea indet. in March at P2 could be due to recruitment into the community (bearing in mind that effects of recruitment in adult populations would be due most likely to recruits from the previous year, since most small recruits would be lost at the mesh sizes that we sieved our samples) (Fig. 5). The life cycles of the polychaeta families these species belong to, oweniids and maldanids, have maximum larval occurrence and posterior recruitments around the spring bloom in Arctic waters (Fetzer and Arntz, 2008), which was also observed by Włodarska-Kowalczuk et al. (2016), who found seasonal differences in the size of oweniid polychaetes in Kongsfjorden.

From our data, however, it is not possible to infer any recruitment

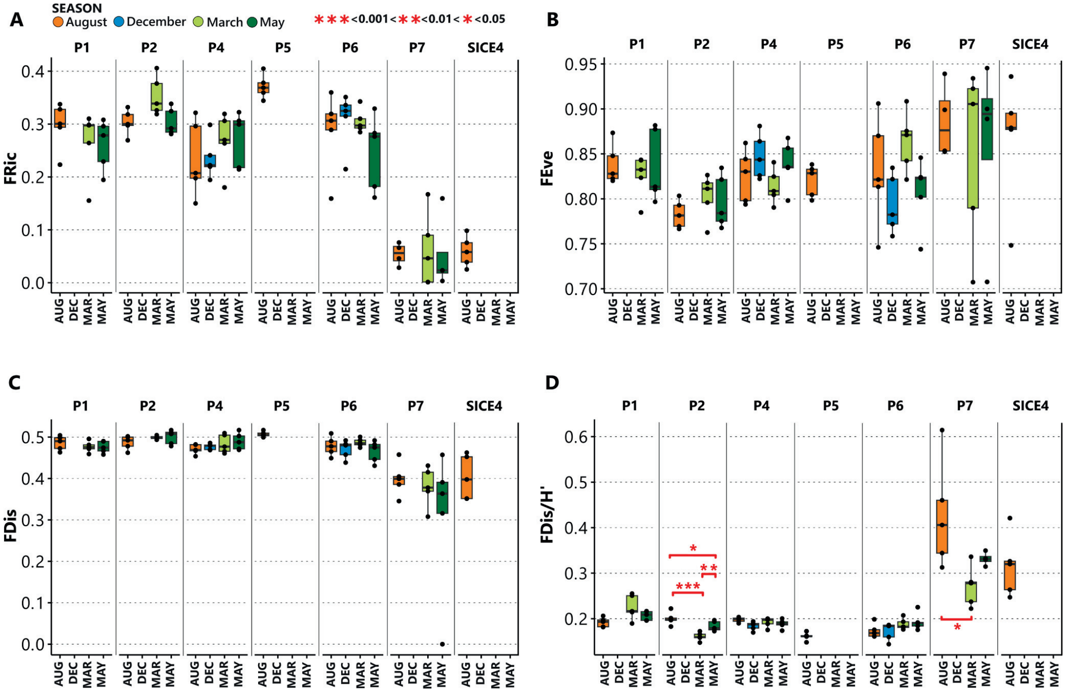

Fig. 8. Boxplots for functional diversity indices of macrofauna traits from Hellinger transformed abundances in the northern Barents Sea across seasons. A) FRic (Functional richness), B) FEve (Functional evenness), C) FDis (Functional dispersion), D) FRed (Functional redundancy ratio = FDis/H', low ratio indicates high functional redundancy). Significant differences in pair-wise comparisons at each station across seasons after the Kruskal-Wallis test and Conover test applying the Bonferroni correction for adjusted p-values are reported in red with asterisks. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. In boxplots, the colored rectangles indicate the interquartile range, which is divided into the upper and lower quartiles by the median (indicated with a black line); whiskers indicate the maximum and minimum values, excluding outliers. Black dots indicate the values of for the different replicates.

patterns, since we did not measure individual sizes and we missed juveniles smaller than our mesh size (0.5 mm) (Mincks and Smith, 2007). However, no distinct recruitment events were evident in our data based on visual observation of macrofauna sizes (e.g. no clear juvenile cohorts were observed in the samples). Also, preliminary results from analysis of biomass size spectra of the macrofauna samples from our study suggest a rather lack of seasonal pulses in the sizes of bigger recruit fractions, only showing relatively stronger variations between seasons at station P2 (Barbara Górska, personal communication in July 2023). Studies from the West Antarctic Peninsula (WAP) have shown that most polychaete species displayed marginally seasonal to non-seasonal patterns of recruitment as indicated by the year-round presence of small juveniles for most macrofaunal taxa (Glover et al., 2008; Mincks and Smith, 2007). Due to this apparent decoupling of recruitment from pelagic processes, direct and lecithotrophic larval development modes seem to be selected rather than the planktotrophic ones in the WAP (Smith et al., 2006). In fact, the dominant larval development in our study was direct benthic larval development, while planktotrophy (LD1) was usually under 40 %. This could support the theory that benthic recruitment processes might be highly decoupled from pelagic bloom phenology in the Barents Sea, and rely mainly on constant food availability to sustain reproduction activities and dispersal/recruitment processes year-round. In a similar line, Descôteaux et al. (2021) identified a clear mismatch between meroplankton bulk abundance peaks and phytoplankton bloom occurrence in the Barents Sea. However, they found that most larvae in the meroplankton bulk were planktotrophic, suggesting that perhaps these larval modes might feed on other sources than the dominant diatoms during the peaks of primary production (Cleary et al., 2017; Descôteaux et al., 2021). Therefore, it is possible that food availability might be an important driver for recruits in this area of the Barents Sea, and that its potential seasonal constancy in the surface sediments might translate into constant pulses of successful recruitments year-round (despite taxon specific differences in timing of reproductive cycles).

4.3. *"Seasonal" differences at the deep stations could be due to spatial heterogeneity or inter-annual changes*

Apart from station P2, the northernmost stations at the continental slope (P6) and in the Nansen Basin (P7) also showed some temporal variations in taxonomic composition (Figs. 7 and 11 **and** Table 2). This could be attributed to the fact that the area around the continental slope and adjacent parts of the Nansen Basin act as a highly dynamic polynya, as the warm circumpolar boundary current flows along the slope north off Svalbard, melting the sea ice (Lundesgaard et al., 2022). This creates zones of frequently open waters with higher seasonal productivity (Falk-Petersen et al., 2015), strong advection processes from further south, and perhaps tighter pelagic-benthic coupling interactions. Dybwad et al. (2022) suggested that vertical fluxes of total particulate matter (TPM) and TOC along the northern slope of Svalbard is higher towards the west where sea ice cover increases gradually and the AW gets mixed along the slope and enters into the Arctic Ocean. However, they observed a greater mismatch between the spring blooms and the grazer communities towards the east of the slope, close to our P6 and P7 stations, indicating more rapid exports of primary production blooms to depth despite their

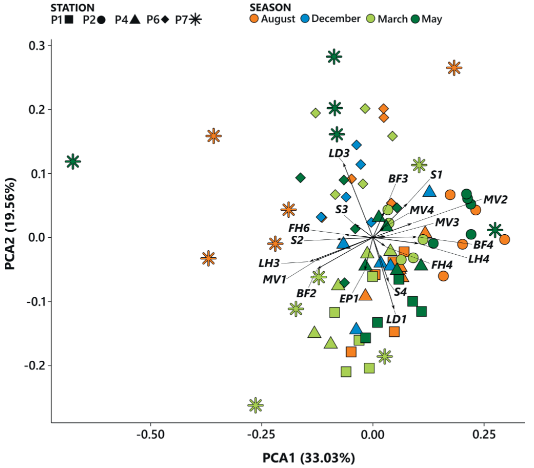

Fig. 9. Fuzzy Correspondence Analysis showing the contribution of trait categories in correlation to the seasonal and spatial (stations) functional structure based on the community weighted means of trait composition of Hellinger transformed abundances. Only trait categories with Pearson correlations higher than 0.5 with either the first or second axis are shown in the vectors. S1 = Small (<10 mm); S2 = Small-medium (10–50 mm); S3 = Medium (50–100 mm); S4 = Medium-large (100–300 mm); BF2 = Vermiform, elongate; BF3 = Dorso-ventral compressed; BF4 = Laterally compressed; LH3 = Tube dwelling; LH4 = Burrowing; MV1 = Sessile/none; MV2 = Burrower; MV3 = Crawler; MV4 = Swimmer (facultative); LD1 = Planktotrophic larval development; LD3 = Direct/benthic larval development; FH4 = Opportunist/Scavenger; FH6 = Parasite/Commensal/Symbiotic; EP1 = Infauna.

lower total bulk.

The sea ice concentration values along the transect from the beginning of 2019 and into 2021, indicated that the polynya around P6 and P7 was of an inter-annual intermittent character, since stations P6 and P7 were generally ice-free around January and February of 2019 and 2021, but were almost completely ice covered in 2020. The fact that no polynya developed in 2020 and that we sampled macrobenthic communities only in 2019 (August and December) and 2021 (March and May) could be one of the reasons why we see more striking differences in the communities (i.e., abundance, biomass and species richness) between these two periods (and perhaps could be more indicative of inter-annual fluctuations). However, the environmental variables at the slope (including sediment pigments and TOC), and in the adjacent basin did not differ substantially across seasons. It is also important to notice that station P6, was at slightly different locations between seasons and the rapid changes in depth due to difficulties to maintain the ship's position in strong sea ice drifting conditions. This might have caused sampling slightly different geomorphological conditions in this heterogeneous environment (Kollsgård et al., 2021), with potentially differing macrofaunal communities associated with it. At P7 the low faunal densities in the deep sea and the resulting high small-scale variability (Gallucci et al., 2009; Rex and Etter, 2010; Vedenin et al., 2016), in combination with relative small sample sizes of our study, might have increased the risk for mistaking small spatial differences for seasonal differences in community structure (compared to the shelf stations). This was reflected in the nMDS, were replicates at the deepest stations were more dissimilar to each other in community composition compared to the replicates from the shelf. Therefore, the "seasonal" differences found for these two stations should be considered with caution. Nevertheless, we want to stress again that all these seasonal differences (although significant in some cases when analyzing each station separately) were small when looking at the whole regional scale of the study area.

Table 3
PERMANOVA results from the community weighted means (CWM) from the macrofauna functional traits weighted by the Hellinger-transformed abundances. Results from a two-way model including all stations and all seasons (and interaction) and one-way models for each station separately across the different seasons. Stations with samples in only one season were not included (P5 and SICE-4). P-values from post-hoc pair-wise comparisons were corrected with the Bonferroni method and only significant comparisons are reported. Df = degrees of freedom, R^2 = adjusted R^2, F = F-statistic, Pr(>F) = p-value. The test of homogeneity of multivariate dispersion (Betadisper) is shown for each station for the season factor. Df = degrees of freedom, F = F-statistic and Pr(>F) = p-value from the test are reported.

		Df	R^2	F	Pr(>F)	Pair-wise Comparison (only station by station)
All						
	Station	4	0.33	10.80	**0.0001** ***	
	Season	3	0.04	1.78	**0.0308** *	
	*Station*Season*	9	0.12	1.79	**0.0016** **	
	Residuals	68	0.51			
P1						
	Season	2	0.22	1.67	0.0635	*March vs May * (p = 0.04)*
	Residuals	12	0.78			
	Betadisper	2		0.20	0.829	
P2						
	Season	2	0.49	5.84	**0.0006** ***	August vs March ** March vs May **
	Residuals	12	0.51			
	Betadisper	2		1.36	0.299	
P4						
	Season	3	0.32	2.56	**0.0024** **	August vs December *
	Residuals	16	0.68			August vs March **
	Betadisper	3		0.35	0.783	
P6						
	Season	3	0.21	1.45	0.145	
	Residuals	16	0.79			
	Betadisper	3		0.60	0.623	
P7						
	Season	2	0.20	1.53	0.161	
	Residuals	12	0.82			
	Betadisper	2		0.60	0.597	

4.4. Lack of macrofauna seasonality through constant food availability (food bank)

Benthic surface sediment pigment concentrations are known to be a good proxy for water column productivity and have been shown to influence benthic community structure and function in Arctic shelves (Ambrose and Renaud, 1995; Piepenburg et al., 1997; Cochrane et al. 2009). Chlorophyll *a* gives an indication of the "freshness" of the organic matter reaching the seafloor, as it is directly derived from pelagic primary production exported to depths (Boon and Duineveld, 1996) having a few-week-long half-life in polar sediments (Renaud et al., 2008). On the other hand, phaeopigments are a result of degradation products from fresher organic matter that have been through degradation processes (such as pelagic grazing), which accumulate in surface sediments over longer temporal scales than chlorophyll *a* (Morata and Renaud, 2008). The pulsed and highly seasonal nature of primary production in the high Arctic would suggest that a similar seasonal pattern should be expected in food availability to the seafloor realm. Of course, the magnitude in the amount of OM reaching the ocean floor through vertical flux will depend, among others, on bacterial degradation and grazing activities by planktonic organisms, but we would expect that the temporal patterns would be similarly translated into the seafloor sediments when it comes to what is available for fueling benthic standing stocks. Nevertheless, pigment concentrations (although displaying spatial differences between stations) remained relatively stable across seasons, especially

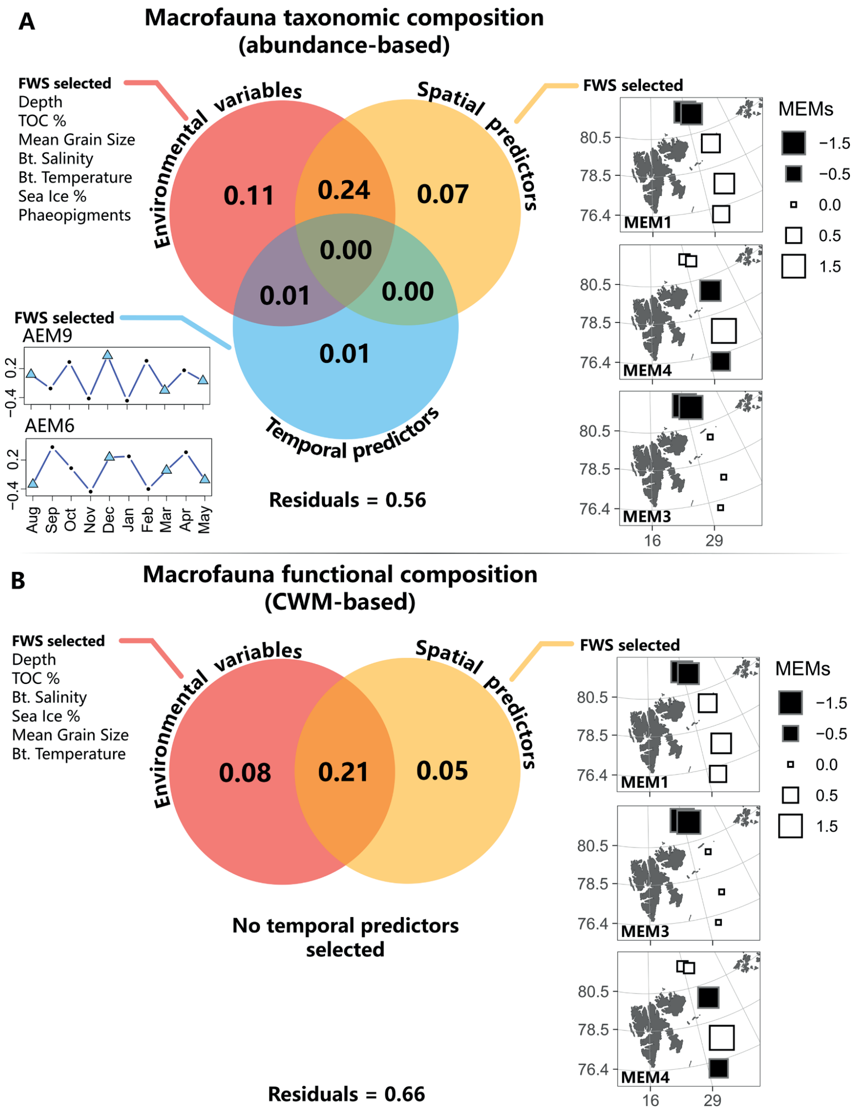

Fig. 10. Venn diagrams showing the variation partition of the temporal structure (Asymmetric Eigenvector Maps. AEMs) (blue circle), environmental variables (pink circle), spatial structure (Mooran Eigenvector Maps. MEMs) (yellow circle) and that contributes to explain the macrofauna taxonomic composition (A) and macrofaunal functional composition (CWM) (B) respectively. stations P5 and SICE4 were excluded. Next to each circle the variables that were selected after forward selection (FWS) are shown. The spatial predictors are shown as Moran eigenvector maps (MEMs) (with axis in degree north latitude and east longitude units) and each square represent a station (P1, P2, P4, P6 and P7 from south to north). Size of the squares are proportional to the scores of the eigenvectors and the color shows the sign of autocorrelation among sites (black, negatively correlated and white, positively correlated). For the temporal predictors, AEMs are shown as decomposed sine waves, with months on the x axis and eigenfunction scores in the y axis. Blue triangles represent sampling dates while black dots are the dummy dates included to construct AEMs due to irregular time intervals of sampling (see methods section for detailed explanation).

for chlorophyll *a*. Also other indicators for high-quality OM such as C:N ratio (Ricardo de Freitas et al., 2023, under review this issue) and, to a lesser extent, phaeopigment content remained relatively constant throughout the seasons (Fig. 3 and **Table S2**). This lack of seasonally fresh OM input to the benthos could be due to intensive grazing activities in the water column, resulting in most of the input to the seafloor being in form of phaeopigments (Morata and Renaud, 2008). In fact, there was quite a strong development of grazing communities around spring and summer in stations north of the Polar Front, as Bodur et al. (2023) (in this issue) measured high amounts of fecal pellet derived carbon with sediment traps down to 200 m, indicating high grazing and degradation of fresh OM during the productive season.

Another possible explanation is that macrobenthic communities from the northern Barents Sea, which are hypothesized to be food-

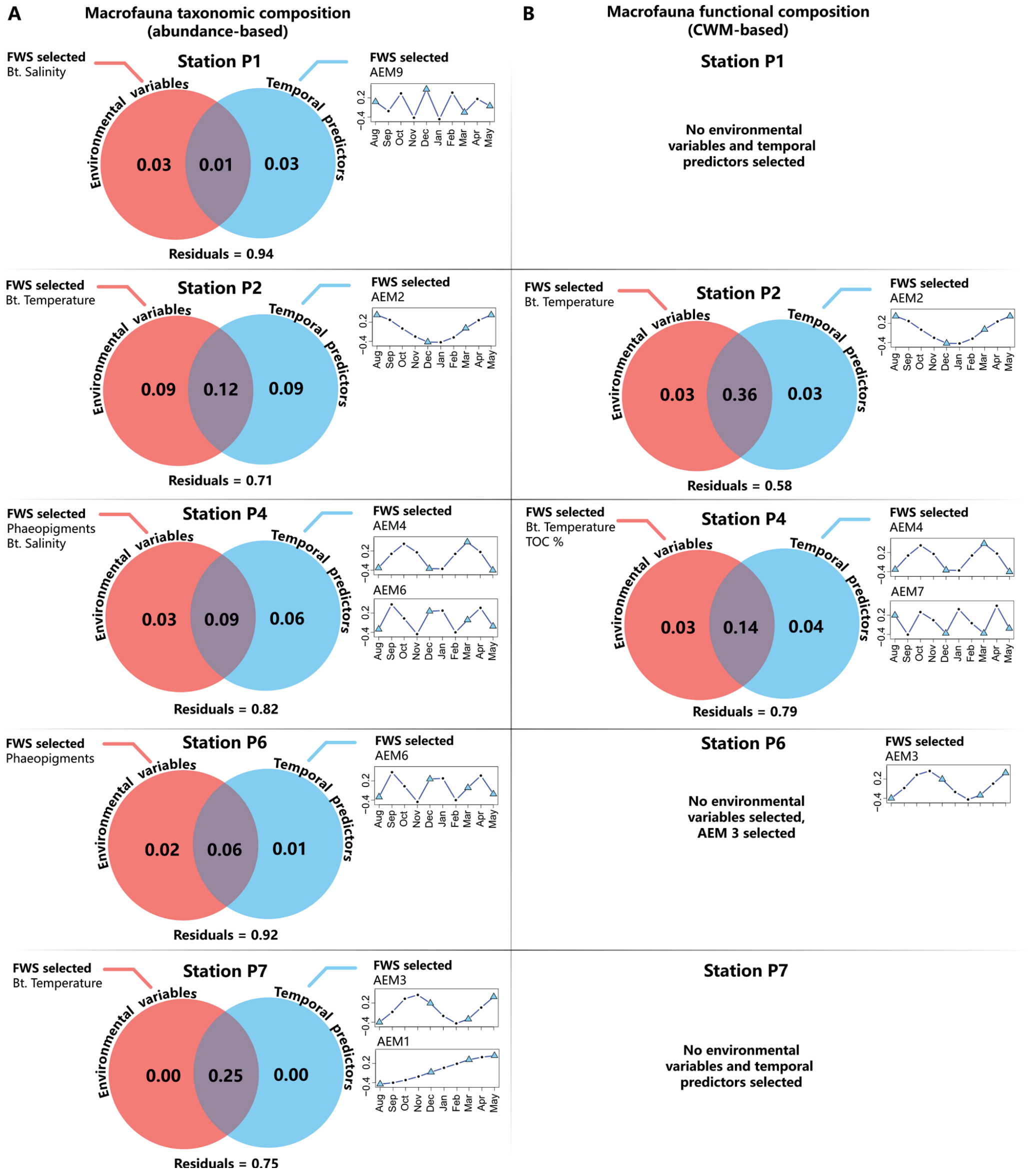

Fig. 11. Venn diagrams showing the variation partition of the temporal structure (Asymmetric Eigenvector Maps. AEMs) (blue circle) and environmental variables (pink circle) and that contribute to explain the macrofauna taxonomic composition and (B) macrofaunal functional composition (CWM) respectively. Variations partitions are conducted for each station individually, and therefore no spatial predictors (Mooran Eigenvector Maps. MEMs) are included. For the temporal predictors, AEMs are shown as decomposed sine waves, with months on the × axis and eigenfunction scores in the y axis. Blue triangles represent sampling dates while black dots are the dummy dates included to construct AEMs due to irregular time intervals of sampling (see methods section for detailed explanation).

limited (Cochrane et al., 2009 and experience lower overall productivity, process and utilize the fresh sporadic pulses of OM reaching the seafloor very efficiently (Morata et al., 2015), hampering its detection in surface sediment. The two most dominant feeding habit modes across the whole transect were sub-surface deposit feeders and suspension/filter feeders, followed, by sub-surface deposit feeder (**Fig.S3**). Carroll et al. (2008) argued that despite the high bioturbation potential of the surface and sub-surface deposit feeding types, the mixing activities of the seafloor fauna in this region of the Barents Sea are much lower compared to those of other continental shelves, and that this leads to low intensity of sediment mixing and shallow mixed depth in the sediments. Ricardo de Freitas et al. (2023, under review this issue) observed almost no variation in TOC across the sediment profiles for the first 5 cm of sediment surface for the same stations of our study, nor seasonal variations for the sediment profiles. Sediment surface OM could therefore be more prone to resuspension, given the occurrence of strong bottom water currents originated by brine rejection in ice-covered areas of the Barents Sea during late autumn (Årthun et al., 2011), which create a distinctive nephloid layer that transports organic matter across the Barents Sea and even injects it into the deeper Arctic Ocean basin (Buettner et al., 2020; Rogge et al., 2023). Therefore, resuspension processes could be another reason why we did not detect high seasonal differences in the concentration of sedimentary phaeopigments. Instead, the constant levels of bulk TOC, which integrates sediment pigments and many other sources of OM, could be the basis for the lack of seasonal patterns observed at this and the other highly advective stations of this region (P1 and P4). This is supported by the lack of variability in food web structure of benthic communities observed in the same locations and seasons by Ziegler et al. (2023), this issue, who found that communities relied consistently on degraded OM, most likely of resuspended origin.

So far, studies on the seasonality of polar benthic communities have yielded diverging results depending on the geographic location, community metrics and responses and spatio-temporal scales under study. For example, studies from the Beaufort Sea documented strong seasonal responses, such as increased SOD rates with increased ice algae standing stocks (Renaud et al., 2007) and a rise in benthic metabolic remineralization with an increase in food availability from spring to summer (Link et al., 2011). On the other hand, observations from the advective system of the European Arctic have supported the lack of pronounced seasonality in benthic community activities (Berge et al., 2015). Studies carried out in Kongsfjorden (West Spitsbergen) showed high resilience of macrofaunal food-web structure to seasonal variability in food quality (Kędra et al.2012) and unchanged size spectra of macro- and meiofauna between summer and winter (Mazurkiewicz et al. 2019). The seasonal stability in size spectra, food-web structure, abundance and biomass (Włodarska-Kowalczuk et al., 2016) and sediment oxygen demand (SOD) rates (Morata et al., 2020) of macrofaunal communities, in the same fjord, were attributed to the existence of a 'food bank' of detrital organic material stored year-round in sediments. The 'food bank' theory was first proposed as an explanation of the quasi-constant abundance patterns and the lack of seasonality in recruitment pulses in both macro- and megafauna and little seasonality in SOD rates observed on the shelf of the West Antarctic Peninsula (Smith et al., 2006; Glover et al., 2008). This apparent seasonal decoupling of benthic dynamics from pelagic processes had been only documented in Svalbard fjords. The fact that we observed so little seasonality in the taxonomic and functional composition of macrofauna community in our study could suggest that the northwestern Barents Sea shelf and adjacent basin present similar seafloor dynamics as that of the West Antarctic Peninsula shelf, which is also an advective system (Moffat & Meredith, 2018). This is supported by recent findings of moderate seasonality in SOD rates for the same study locations and seasons (Sen et al. unpublished data) and little variation in benthic food web structure (Ziegler et al., 2023). Thus, the 'food bank' theory could provide an explanation for analogous mechanism between advective polar environments of both hemispheres to sustain constant benthic communities year-round. Low bottom water temperatures in polar regions are hypothesized to be responsible for the relatively high preservation of food sources at the seafloor by hampering efficient bacterial remineralization (Smith et al., 2012 and references therein). Therefore, predicted increased bottom temperatures for the Barents Sea of up to 6 °C by the end of the 21st century (Renaud et al., 2019), could put the stability of this 'food bank' at risk (Smith et al., 2012 and references therein).

5. Conclusion

Our study revealed only weak signs of seasonality in macrofauna taxonomic composition and no seasonal variations in the analyzed metrics of functional composition in the northwestern Barents Sea. The constant total organic carbon in the sediments across seasons, in line with the non-seasonal community dynamics, might point towards the reliance of macrobenthos on the long-term accumulated food sources in the seafloor of this advective gateway, similarly as to what has been observed in other polar shelves such as the West Antarctic Peninsula.

Although no strong seasonal taxonomic variation was observed in macrofauna communities along the transect, functional composition remained much more constant across seasons. The relationship between functional diversity and taxonomic diversity for the whole transect, including all seasons, showed a significant, but not very strong linear relationship, indicating that the communities of the northwestern Barents Sea show a certain degree of functional resilience throughout all seasons (Kokarev et al., 2021). However, functional resilience was spatially heterogeneous, being much lower at the deep basin (P7 and SICE4) than communities on the shelf stations, most likely resulting from the very low taxonomic richness in these abyssal depths. This is in concordance with other studies showing that deep-sea macrofaunal assemblages from the eastern Fram Strait had lower functional redundancy than the shallower shelf (Górska et al., 2022). Therefore, the lack of seasonality that we observed in trait composition in our study might result from the relatively high functional resilience of the system, especially in the shelf, to slight fluctuations in species composition through time (seasons). This is consistent with the relatively constant benthic food-web structures found by Ziegler et al. (2023) for the same locations and across the same seasons.

It is anticipated that the timing of seasonal primary production will be affected by sea ice retreat and ocean warming driven by climate change. Therefore, fluctuations in the phenology of food export to the seafloor are to be expected. However, the year-round "food bank" on which macrobenthic communities may rely on, might buffer these shifts in the near future, making benthic communities resilient to changes in overlying waters. Nevertheless, regime shifts in productivity and abiotic drivers might cause integrated changes on longer time scales which might affect the stability of the sediment food bank, and thus, food availability. This could have implications for the ecological function and structure of macrobenthic communities in this region.

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CRediT authorship contribution statement

Èric Jordà-Molina: Investigation, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Arunima Sen:** Investigation, Data curation, Writing – review & editing, Supervision. **Bodil A. Bluhm:** Investigation, Data curation, Resources, Writing – review & editing, Supervision. **Paul E. Renaud:** Conceptualization, Resources, Writing – review & editing, Supervision. **Maria Włodarska-Kowalczuk:** Resources, Writing – review & editing. **Joanna Legeżyńska:** Investigation, Writing – review & editing. **Barbara Oleszczuk:** Investigation, Writing – review & editing. **Henning Reiss:** Supervision, Resources, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made publicly available from 2024 on the Global Biodiversity Information Facility (GBIF) and will be accessible through the Svalbard Integrated Arctic Earth Observing System (SIOS).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2023.103150.

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The seafloor of the Barents Sea shelf hosts one of the most productive benthic assemblages of the Arctic seas. In particular, macrofaunal organisms (e.g. annelid worms, crustaceans, molluscs and others) that live in and on marine sediments have critical roles in the recycling of organic matter that sinks from the overlying waters to the seafloor. At the same time, the biological composition of these communities is highly spatially structured by environmental parameters and processes of the overlying waters and the seafloor environment. Hence, unprecedented rates of ocean warming and sea ice retreat driven by climate change are expected to cause significant biological shifts in the northwestern Barents Sea ecosystem in the coming decades, potentially leading to a re-organization of macrofaunal communities. After investigating the dynamics and patterns of macrofaunal communities of this region at different spatio-temporal scales, the results of the present thesis have documented that significant fluctuations occurred in macrofaunal composition throughout the first two decades of the 21st century in conjunction with warm water anomalies caused by increased frequency of Atlantic water inflow in Arctic domains of the Barents Sea. Also, macrofauna communities of this region are highly decoupled from short-term variations of phenological processes occurring in the overlying water column, suggested by little seasonality in the composition and function of benthic assemblages. However, an experimental approach corroborated that benthic remineralization rates will most likely increase in a predicted warmer and more productive Barents Sea, leading to changes in carbon cycling and biogeochemical processes. This thesis contributes to a better understanding of the temporal and spatial dynamics of benthic ecosystems in the Arctic and provides extensive new knowledge relevant to the effective management of the Barents Sea ecosystem, a system heavily impacted by the effects of ongoing climate change.

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