Functioning of Arctic and sub-Arctic shallow benthic ecosystems in highly-stratified coastal systems

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Par
Guillaume BRIDIER

« Functioning of Arctic and sub-Arctic shallow benthic ecosystems in highly-stratified coastal systems »

« Fonctionnement des écosystèmes benthiques peu profonds Arctiques et sub-Arctiques en système côtier hautement stratifié »

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Unité de recherche : Laboratoire des sciences de l'environnement marin (UMR 6539)

Rapporteurs avant soutenance :

Paul RENAUD	Senior researcher, Akvaplan-Niva/UNIS Tromsø/Longyearbyen, Norway
Christine MICHEL	Senior researcher, Fisheries and Oceans Winnipeg, Manitoba, Canada

Composition du Jury :

Paul RENAUD	Senior researcher, Akvaplan-Niva/UNIS *Rapporteur*
Christine MICHEL	Senior researcher, Fisheries and Oceans *Rapportrice*
Erik BONSDORFF	Professor, Åbo Akademi University *Examinateur*
Aude LEYNAERT	Directrice de recherche, CNRS *Examinatrice et présidente du jury*
Laurent CHAUVAUD	Directeur de recherche, CNRS *Directeur de thèse*
Jacques GRALL	Ingénieur de recherche, UBO *Co-encadrant scientifique, invité*
Frédéric OLIVIER	Professeur, MNHN *Co-encadrant scientifique, invité*
Tarik MEZIANE	Professeur, MNHN *Invité*

À ma famille,

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Scientific communications

Scientific articles

Published

Bridier G, Meziane T, Grall J, Chauvaud L, Ser MK, Menneteau S, Olivier F (2019) Coastal waters freshening and extreme seasonality affect organic matter sources, quality, and transfers in a High Arctic fjord (Young Sound, Greenland). *Marine Ecology Progress Series*, 610: 15-31.

In review

Bridier G, Meziane T, Grall J, Chauvaud L, Donnet S, Lazure P, Olivier F (*minor revisions*) Sources, quality and transfers of organic matter in a highly-stratified sub-Arctic coastal system (Saint-Pierre-et-Miquelon, NW Atlantic). *Progress in Oceanography*.

Bridier G, Olivier F, Chauvaud L, Sejr MK, Grall J (*minor revisions*) Food source diversity, trophic plasticity, and omnivory enhance the stability of a shallow benthic food web from a high-Arctic fjord exposed to freshwater inputs. *Limnology and Oceanography*.

In preparation

Bridier G, Olivier F, Chauvaud L, Le Garrec V, Droual G, Grall J (*in preparation*) Thermal stratification does not change the food web structure and functioning of a shallow benthic ecosystem from a sub-Arctic archipelago.

Bridier G, Olivier F, Jourde J, Chauvaud L, Sejr MK, Burel T, Grall J (*in preparation*) Diversity and spatial variability of shallow benthic macrofaunal assemblages in a high Arctic fjord (Young Sound, North-East Greenland). [Research note]

Scientific communications

International conferences

Bridier G, Meziane T, Grall J, Chauvaud L, Sejr MK, Olivier F (2018) Contribution of a trophic multimarker approach to benthic food web studies: example from a High-Arctic fjord (Young Sound, NE Greenland). *World Conference in Marine Biodiversity*, Montréal, Canada. [Oral presentation]

Bridier G, Meziane T, Grall J, Chauvaud L, Sejr MK, Olivier F (2018) Coastal waters freshening and extreme seasonality affect the quality and sources of organic matter in a High-Arctic fjord. *Lipids in the ocean: Structure, function, ecological role and applications*, Brest, France. [Poster presentation]

Bridier G, Olivier F, Chauvaud L, Serj MK, Grall J (2019) Benthic food-web structures exposed to freshwater inputs: insights from intra- and inter-fjord comparisons. *ArcticNet 2019 Annual Scientic Meeting*, Halifax, Canada. [Oral presentation]

National conferences

Bridier G, Meziane T, Grall J, Olivier F, Sejr MK, Chauvaud L (2018) Young Sound, Groenland : Résultats prélimaires de l'étude du fonctionnement trophique d'un fjord Haut-Arctique sous fortes contraintes physiques et saisonnières. *Journées inaugurales du LIA BeBEST*, Brest, France. [Oral presentation]

Local meetings

Bridier G, Meziane T, Grall J, Chauvaud L, Lazure P, Olivier F (2019) Sources et qualité de la matière organique particulaire le long de la radiale Est de Miquelon en début et fin de période estivale. *Université de Bretagne Occidentale (UBO)*, Brest, France. [Oral presentation]

Bridier G, Olivier F, Meziane T, Chauvaud L, Sejr MK, Tremblay R, Menneteau S, Grall J (2020) Fonctionnement des écosystèmes benthiques exposés à des entrées d'eaux douces en zone côtière. *Université du Québec à Rimouski (UQAR)*, Rimouski, Canada. [Oral presentation, 40 mn]

Bridier G, Olivier F, Chauvaud L, Serj MK, Grall J (2020) Benthic food-web structures exposed to freshwater inputs: insights from intra- and inter-fjord comparisons. *Université de Bretagne Occidentale*, Brest, France. [Poster presentation]

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Introduction

Characteristics and functioning of benthic ecosystems

General information

Benthic ecosystems include all living organisms (macrophytes and animals) dwelling in marine and aquatic environments that are directly linked to the seabed. Because the ocean covers 70.8% of the earth's surface, marine benthic ecosystems are the second most widespread habitat on earth after the water column (Gray and Elliott 2009). Benthic ecosystems cover very different depths, from the high intertidal zone (submerged by the highest tides) to abyssal trenches (exceeding 10,000 m). With an average ocean depth of 3680 m (Charrette and Smith 2010), most benthic ecosystems are deprived of light and local autotrophic primary production. These “dark” ecosystems, with the exception of ecosystems based on chemosynthesis, thus relate exclusively on the vertical transfer of organic matter produced in the euphotic zone to the bottom (i.e. pelagic-benthic coupling, Graf 1989, Ambrose and Renaud 1995). Therefore, although coastal ecosystems (i.e. < 200 m) represent 7% of the total surface area of the ocean seabed, the related marine ecosystems constitute the most active part from a biogeochemical point of view, benefiting from both local primary production and/or tight pelagic-benthic coupling (Gattuso et al. 1998). Moreover, because they directly receive large inputs of terrestrial nutrients, coastal ecosystems are among the most productive on earth (Costanza et al. 1993, Cloern et al. 2014), providing 14-30% of global ocean primary production and accounting for 90% of fisheries catches (Gattuso et al. 1998).

Benthic organisms are generally classified into different groups or categories, depending on their size and/or habitat. Benthic species can be classified in different categories according to their position relative to the seabed: suprabenthos (living the first cm above the substratum), epibenthos (living directly on the substratum) and endobenthos (within the sediment) (Gray and Elliott 2009). Benthic fauna can also be classified according to the size of organisms: microfauna (< 63 µm), meiofauna (63 µm - 1 mm), macrofauna (1 mm - 5 cm) and megafauna (> 5 cm). The present PhD focuses only on coastal benthic macro and megafauna since they usually constitute the highest biomasses in benthic ecosystems (Gray and Elliott 2009).

Processes influencing benthic community structures

Benthic ecosystems generally harbor a wide diversity of taxa, mainly dominated by invertebrates (e.g. polychaetes, crustaceans, echinoderms, mollusks; Snelgrove 1999, Bertness et al. 2001). However, the structure of benthic communities (i.e. species composition) varies substantially at both spatial (ranging from a few meters to hundreds of kilometers) and temporal scales (from weeks/months to several decades and more) according to variations in abiotic and biotic environmental factors (Gray and Elliott 2009). Biotic factors include a variety of species interactions such as predation, competition or facilitation that may modify the community structure (Gray and Elliott 2009). For example, engineer species (e.g. reef-building polychaetes, maerl beds) can substantially change the structure of benthic communities by transforming the original physical habitat (e.g. bare sediment) into a complex three-dimensional structure allowing the colonization by new species (e.g. Jones et al. 1994, Rigolet et al. 2014, Boyé et al. 2019). Among abiotic factors, the substrate type (e.g. rock/sediment, size distribution of sedimentary particles) is one of the most structuring constraint for benthic communities (Gray, 1974). Other abiotic factors such as depth, temperature, salinity, oxygen concentration, water temperature or food availability also play an important role (McArthur et al. 2010, Roy et al. 2014). Because of their low mobility, benthic organisms are subjected to environmental constraints occurring in their immediate environment. Therefore, based on their long lifespan and low motility, benthic invertebrates offer an interesting tool for monitoring environmental variations (e.g. catastrophic events, climate variability (Glémarec 1979, Kröncke et al. 1998, Grebmeier et al. 2015).

Significance of benthic organisms to study the functioning of marine ecosystems

Benthic ecosystems do not function separately from the marine systems and play an essential role in ecosystem functioning by controlling carbon and nutrient fluxes. Carbon reaching the seabed is known to have three potential outcomes: it can be (1) buried in marine sediments, (2) remineralized into CO_2 or (3) converted into biomass by benthic organisms (Klages et al. 2004). Burying part of the carbon reaching the seabed or produced locally (e.g. kelp forest in shallow habitats) can play a crucial role in climate regulation by providing a carbon sink for CO_2 from the atmosphere (Klages et al. 2004, Duarte et al. 2005, Fourqurean et al. 2012). A significant proportion of carbon can also be converted into biomass and provide a large source of organic matter for higher trophic levels (Snelgrove 1999). Part of these biomasses can also be ultimately redirected towards the pelagic ecosystems (e.g. through pelagic predation on benthic fauna) and thus partially compensate the energy loss occurring by organic matter sedimentation (Kopp et al. 2015, Griffiths et al. 2017).

Benthic ecosystems also play a key role in other biogeochemical cycles. The benthic fauna facilitates the resuspension and oxygenation of sediments (via bioturbation), which favors aerobic bacterial degradation of sedimentary organic matter and the recycling of nutrients in the water column (Glud et al. 1998). This mineralization is particularly important in shallow coastal areas where part of the recycled nutrients supports pelagic and benthic primary production (Nielsen and Hansen 1995, Rysgaard et al. 1999, Glud et al. 2008). Possible changes in the trophic structure of benthic communities (e.g. biomass increase in suspension-feeders) can thus impact the functioning of marine ecosystems by modifying the benthic top-down control (i.e. grazing) on phytoplankton biomass or by controlling nutrient fluxes between the sediment and the water column (Chauvaud et al. 2000, Grall and Chauvaud 2002).

Characteristics and functioning of Arctic benthic ecosystems

High seasonality

Around the globe, Arctic and sub-Arctic marine ecosystems rank among the most seasonal environments. While temperate and tropical latitudes experience small to moderate seasonal changes in solar radiation, subarctic and arctic latitudes experience a significant limitation or even absence of light for a substantial part of the year (up to 6 months at 90°N, Berge et al. 2015). In addition, marine organisms often experience long periods of very low light or darkness due to the persistence of both thick snow and sea ice cover preventing light penetration into the water column (Sejr et al. 2009, Berge et al. 2015). In response to these high seasonal variations in light, Arctic marine ecosystems are generally characterized by a very short period of primary production, sometimes restricted to less than 2-3 months in the High-Arctic (Rysgaard et al. 1999, Leu et al. 2011).

Functioning of Arctic benthic ecosystems

Arctic benthic ecosystems are relatively shallow compared to other oceans since continental shelves account for more than 50% of the total seabed areas (Jakobsson et al. 2004). This proportion of continental shelves contrasts markedly with the global average, where the combined area of continental shelves and slopes are estimated at 15.3% of the world ocean seabed surface (Menard and Smith 1966). Arctic shelves generally display high faunal abundances and biomasses (e.g. Grebmeier et al. 1988, Ambrose and Renaud 1995, Sejr et al. 2000, Iken et al. 2010) which may appear paradoxical in view of the low productivity of the Arctic Ocean (Piepenburg 2005). These high biomasses are in fact the result of several factors: (1) very tight pelagic-benthic coupling on the continental shelves (e.g. Ambrose and Renaud 1995, Wassmann et al. 2006, Cochrane et al. 2009, Olivier et al. 2020), generally attributed to a mismatch between abundances of phytoplankton and zooplankton, (2) a slow remineralization of the organic matter by microbial communities and (3) a rapid sedimentation of ice-algae (Renaud et al. 2008, Boetius et al. 2013, Kędra et al. 2015).

The origin of carbon sources fueling Arctic benthic communities varies according to the latitude and depth of the ecosystems. High Arctic communities exposed to ice cover for a large part of the year benefit from high sympagic (i.e. ice algae) and limited pelagic primary production (Søreide et al. 2013, Leu et al. 2011, Kędra et al. 2015). However, few exceptions exist such as the High Arctic site of Young Sound (NE Greenland) displaying a long ice cover period but a very low sympagic production (e.g. Rysgaard et al. 2001, Leu et al. 2015, Limoges et al. 2018). By contrast, other Arctic/subArctic communities mainly relate on pelagic production (Wassmann and Reigstad 2011, Kędra et al. 2015). In addition, benthic communities within (or close to) the euphotic zone benefit from local benthic primary production or its export through erosion macroalgae thalli or microphytobenthic production (Glud and Rysgaard 2007, Renaud et al. 2015, Gaillard et al. 2017).

The high biomasses of benthic primary consumers in Arctic coastal ecosystems constitute a fundamental link between primary producers and iconic higher trophic levels such as walruses, eiders or grey whales (see Figure 1, Born et al. 2003, Grebmeier 2012). Some large predators feed directly and intensively on benthic stocks from shallow habitats, such as walrus, which ingests a daily average of 63 kg of fresh meat from the bivalve *Mya truncata* (Born et al. 2003). Empirical models also have shown that both common and kind eiders control half of the benthic secondary production in some fjords in the vicinity of large bird colonies (Blicher et al. 2011). Such results reflect the crucial dependence of these predators on benthos, where variations in benthic biomass might have serious consequences on predator populations (Grebmeier 2012). Humans are not excluded from Arctic food webs because local human populations are highly dependent on benthic biomass, as any change in benthic stocks may have deep impacts on marine mammal populations, and thus on hunting catches (Grebmeier et al. 2006, Darnis et al. 2012). In addition, Arctic coastal benthic habitats are feeding grounds for many key fish species in sub-Arctic/Arctic ecosystems (e.g. Arctic cod, sculpins, eelpouts, flatfish) where they find suitable nursery conditions for the feeding and growth of their juveniles (e.g. Logerwell et al. 2015).

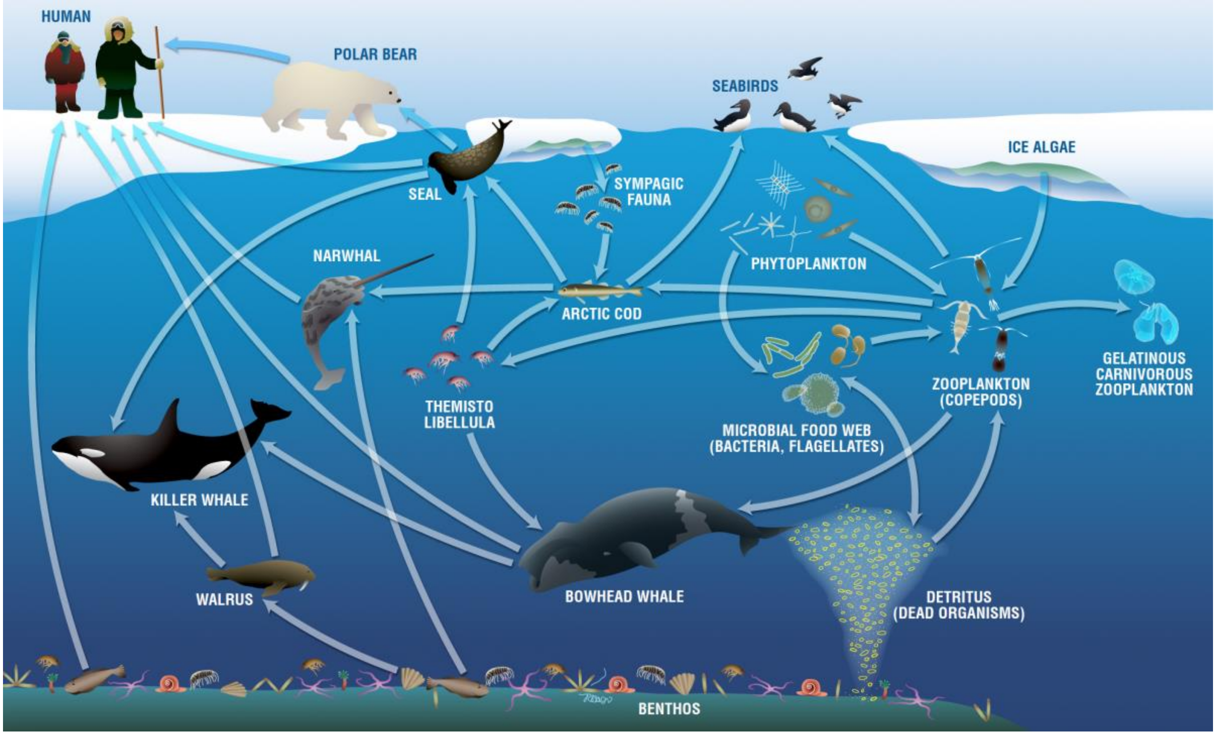

Figure 1: Schematic representation of Arctic marine food webs highlighting the importance of the benthic compartment in the flow of organic matter between primary producers and higher trophic levels (e.g. walrus, Danis et al. 2012).

Species diversity in Arctic benthic ecosystems

Benthic species diversity is still poorly documented in the Arctic compared to temperate and tropical ecosystems. Although benthic Arctic fauna species richness has been often considered to be poor (Know and Lowry 1977, Piepenburg 2005), there is now growing evidence that it is largely underestimated (Bluhm et al. 2011, Piepenburg et al. 2011, Josefson et al. 2013). Recent inventories currently list more than 4600 species and estimate that several thousand species remain to be described from these areas (Bluhm et al. 2011, Josefson et al. 2013). The most diverse phylums are arthropods, polychaetes and mollusks (see Figure 2, Jørgensen et al. 2017), the first two phylum accounting for more than half of the benthic species richness on Arctic continental shelves (Piepenburg et al. 2011). Moreover, echinoderms and mollusks (e.g. Piepenburg and Schmid 1996, Roy et al. 2014) essentially dominate the benthic biomass of Arctic shelves. Records for species richness at the scale of the Arctic show very strong regional disparities. While the Chukchi and Barents Seas have been relatively well studied, large knowledge gaps still exist in north-eastern Greenland, north-eastern Siberia, the Canadian Arctic Archipelago, the Lincoln Sea, and the Central Arctic Ocean (Piepenburg et al. 2011, Jørgensen et al. 2017). Despite the relatively scarce knowledge of Arctic biodiversity, studies have shown that Arctic benthic communities are not characterized by endemism, unlike the Antarctic (e.g. Griffiths et al. 2009) and that the majority of Arctic benthic species observed in the Arctic are wide-ranging boreal species (Piepenburg 2005).

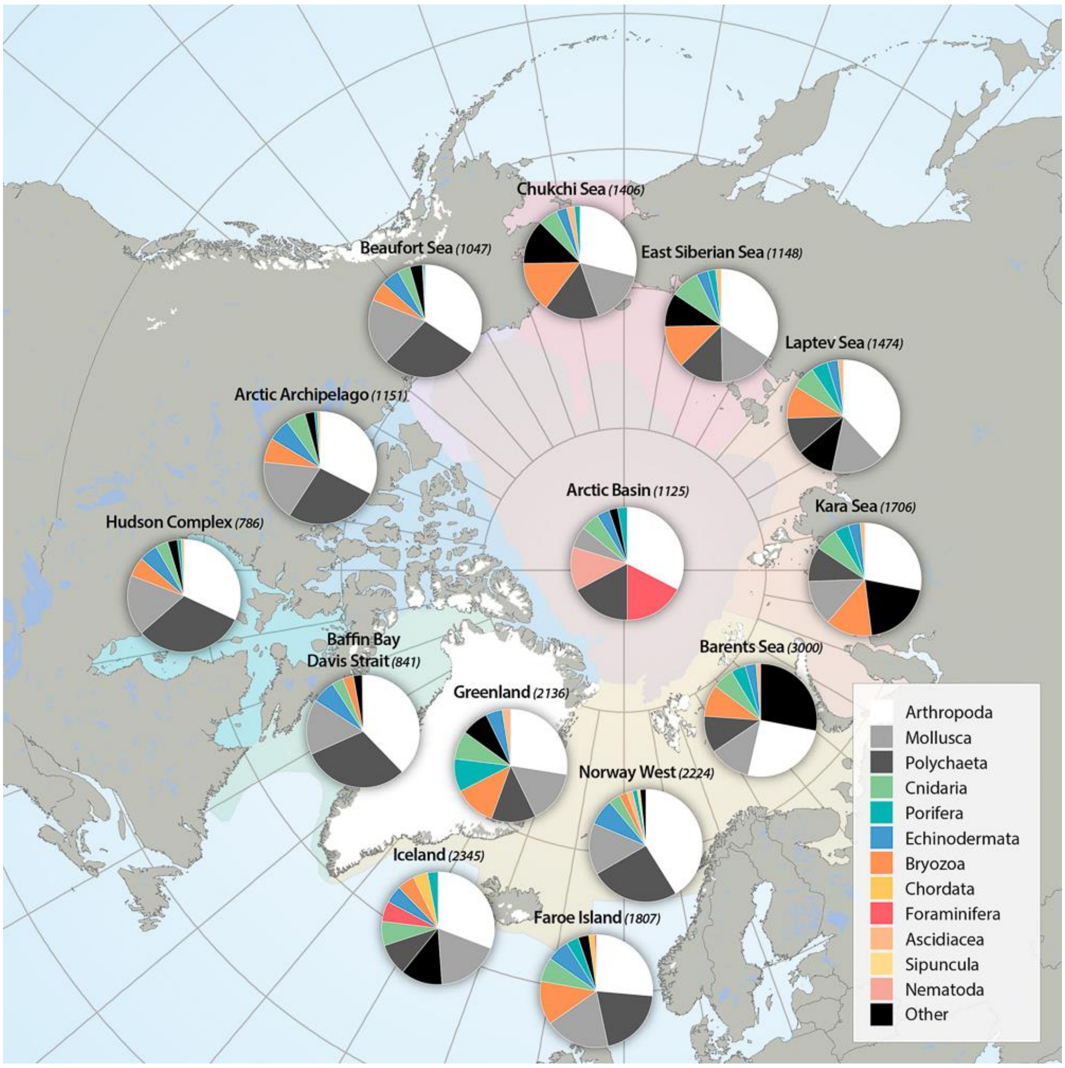

Figure 2: Pan-Arctic view of species/taxon richness (in brackets) per Arctic regions (from Jørgensen et al. 2017). Relative proportions of specific taxa in species richness in each Arctic region are represented by pie charts. Data sources and sampling gears are listed in Jørgensen et al. (2017).

Vulnerability of benthic ecosystems subjected to environmental changes

The life-cycle of Arctic benthic organisms has been scarcely studied. It has long been assumed that high-latitude benthic invertebrates do not have pelagic larval stages (i.e. Thorson's rule, Thorson 1936, Thorson 1950) but this assumption was later refuted by studies showing that many Arctic species also have bentho-pelagic life cycles (Clarke 1992). Kuklinski et al. (2013) and Brandner et al. (2017) showed that the seasonal dynamic of bivalve pelagic larvae is strongly positively synchronized with primary production. Such tight coupling between bivalve pelagic larvae and phytoplankton or ice-algae blooms suggests that future changes in the phenology of primary production is likely to have drastic impacts on benthic communities (e.g. Renaud et al. 2007a, Kuklinski et al. 2013, Stübner et al. 2016). Such sensitivity has already been highlighted for zooplankton larvae such as *Calanus glacialis*, where a mismatch/asynchronisation between ice-algae/phytoplankton blooms and pelagic larvae production led to low recruitment events (Fortier et al. 2002, Søreide et al. 2010, Leu et al. 2011).

In addition, polar benthic ecosystems are generally dominated by species with slow growth rates relative to species from lower latitudes (e.g. Dunton et al. 1982, Al-Habahbeh et al. 2020). This difference in growth is mainly due to the strong trophic constraint in polar environments where low food availability might directly limit growth of benthic invertebrates (Ambrose et al. 2006, Sejr et al. 2009, Blicher et al. 2010). Because of such low growth rates, benthic communities in the Arctic are in turn often characterized by slow resilience from major environmental disturbances (Al-Habahbeh et al. 2020). These findings on the ecology of arctic benthic invertebrates show that any changes in the environmental conditions and seasonality in the Arctic and sub-Arctic seas could potentially have drastic consequences on the benthic compartment and in turn the functioning of the ecosystems.

Arctic benthic ecosystems under a changing climate

General information

During the last decades, sub-Arctic and Arctic latitudes have experienced major warming, 2-3 fold higher than the global average (AMAP 2017). Such temperature increase has led to a sharp decrease in the extent and thickness of the summer sea ice (September), decreasing by > 40 % and 65 % since the 1970s, respectively (Figure 3, Ardyna and Arrigo 2020). Similarly, glaciers are experiencing accelerated melting as observed for the Greenland Ice sheet where mass loss has increased by six-fold since the 1980s (Mouginot et al. 2019). Permafrost is also concerned: since the mid-1980s, a warming of 0.4-1°C per decade has been reported while models predict about 10 to 60 % of its loss under RCP2.1 and RCP8.5 scenarios, respectively (AMAP 2017). All these environmental changes have subsequent impacts on marine ecosystems by increasing coastal erosion (Lantuit et al. 2012) and river flow (Prowse et al. 2015) or reducing sea surface salinity and enhancing water column stratification (Prowse et al. 2015, Nummelin et al. 2016).

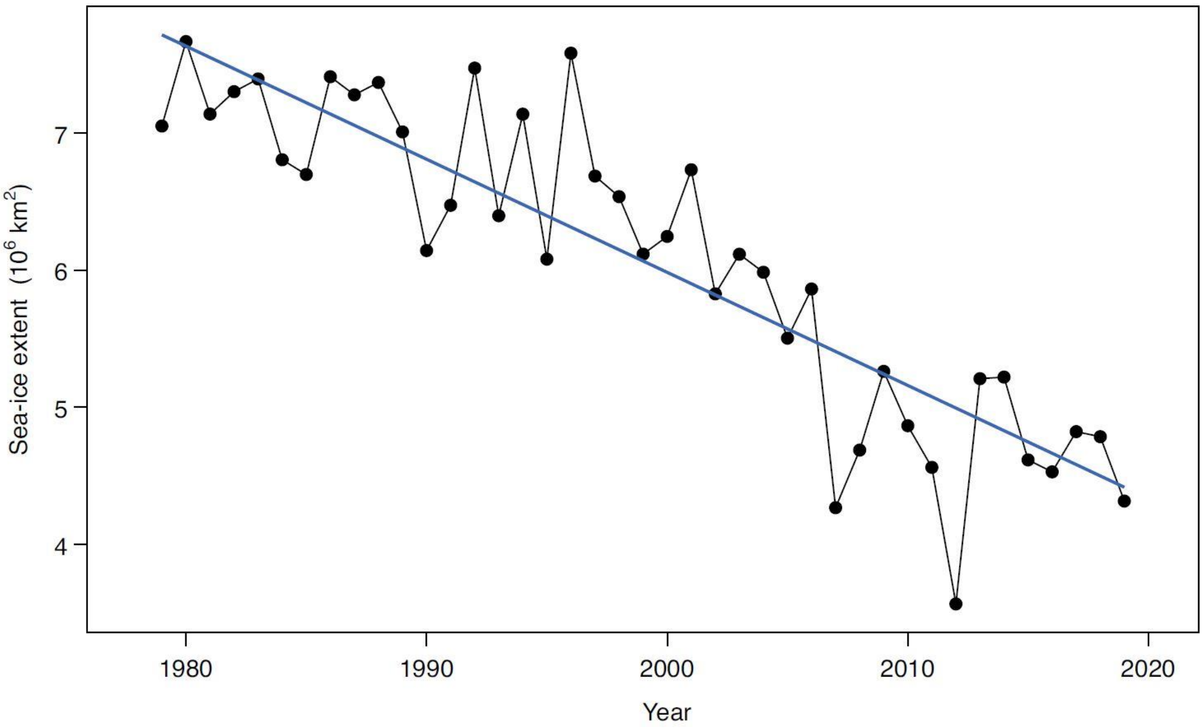

Figure 3: Annual variations in minimum summer sea ice extent (September) over the 1979-2019 period (data from Perovich et al. 2020, figure from Ardyna and Arrigo 2020).

Impact of climate change on Arctic ecosystems: regional scale

Considerable work has been achieved over the last decades to better understand the consequences of climate change on the functioning of sub-Arctic/Arctic marine ecosystems (Wassmann and Reigstad 2011, Kędra et al. 2015). Recent studies have shown that the ecological effects of climate change are complex and variable across the Arctic (e.g. Michel et al. 2015, Ardyna and Arrigo 2020). For instance, although the overall sub-Arctic/Arctic primary production increased over the last decades (Arrigo et al. 2008, Pabi et al. 2008), recent studies revealed that such trend masks heterogeneous responses at regional scale (Arrigo and van Dijken 2015, Slagstad et al. 2015, Lewis et al. 2020, Ardyna and Arrigo 2020). These regionally contrasted trends result from complex interactions between factors that control primary production. For instance, while increased light availability, vertical mixing or nutrient horizontal advection under climate change tend to enhance pelagic primary production, increased turbidity and water column stratification would have opposite effects (see Figure 4a).

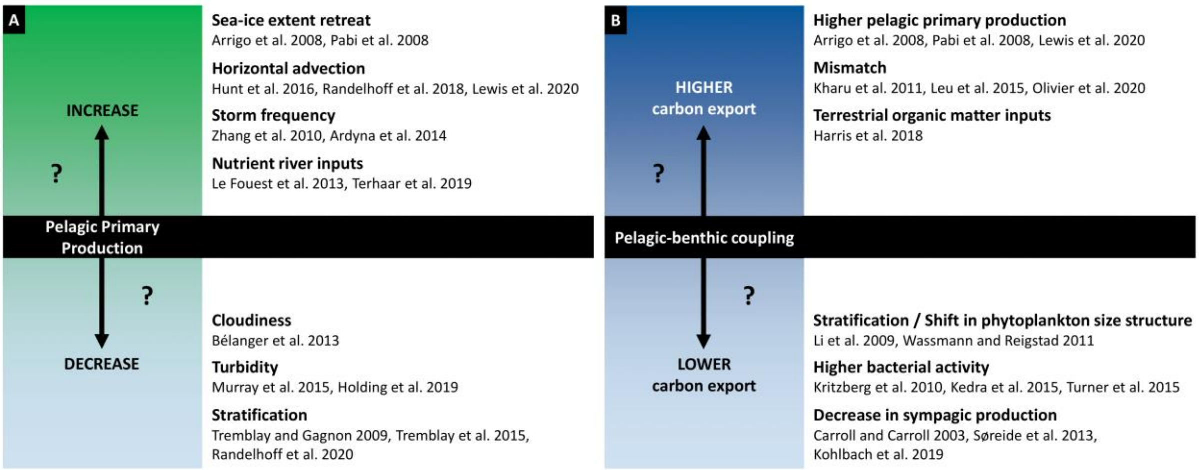

Figure 4: Conceptual diagram representing positive and negative influences of climate change on pelagic primary production (A) and pelagic-benthic coupling (B).

The evolution of pelagic-benthic coupling under climate change is not always clearly understood (Figure 4b). Increased pelagic primary production in arctic open sea areas was expected to strengthen the pelagic-benthic coupling by providing a higher export of pelagic materials toward seabed (e.g. Ambrose et al. 2006, Cochrane et al. 2009). However, several studies also showed opposite trends with a simultaneous decrease of sea ice extent and benthic biomass during the last decades that was attributed to a weakened pelagic-benthic coupling (e.g. Grebmeier et al. 2006). Primary production could shifted from episodic ice algae pulses to more continuous phytoplankton blooms more efficiently directed through pelagic-food webs and resulting in reduced carbon export to benthic communities (“sea-ice algae – benthos” vs “phytoplankton – zooplankton” paradigm, Piepenburg et al. 2005, Grebmeier et al. 2006, Wassmann and Reigstad 2011). These contrasted responses reflect the complexity of the pelagic-benthic coupling that is controlled by numerous factors (e.g. bathymetry, sea-ice extent, riverine inputs) and involves various mechanisms (e.g. zooplankton grazing) that are generally highly variable among Arctic regions (Roy et al. 2014, Stasko et al. 2018).

Assessing specific effects of each environmental factor on ecosystem functioning

Climate change can thus have contrasted effects on the functioning of Arctic marine ecosystems (e.g. primary production, pelagic-benthic coupling) depending on environmental conditions at the regional scale (Michel et al. 2015, Tremblay et al. 2015, Williams and Carmack 2015, Ardyna and Arrigo 2020). Understanding the impacts of climate change on marine ecosystems on a pan-Arctic scale therefore requires (1) identifying the local environmental factors likely to influence the response of marine ecosystems to climate change, (2) assessing the specific roles of each environmental factor on the ecosystem and (3) understanding the interplay of multiple environmental factors and their impacts on ecosystems at regional scale.

Despite a considerable attention devoted to study the potential effects of declined sea ice extent on the functioning of marine ecosystems over the past decades (e.g. Carroll and Carroll 2003, Grebmeier et al. 2006, Søreide et al. 2013), other environmental factors (e.g. stratification, storminess, freshwater inputs, see Figure 4, see Figure 4 in Ardyna and Arrigo 2020) have been considerably less investigated. However, stratification is undergoing profound changes worldwide due to global changes in salinity and/or sea surface temperatures (Belkin et al. 2009, Nummelin et al. 2016, Prowse et al. 2015, Carmack et al. 2016), particularly in the Arctic (Capotondi et al. 2012). It seems therefore crucial to better understand the role of stratification on the functioning of Arctic benthic ecosystems and how increases in stratification may alter their future functioning.

Impacts of stratification on primary production and pelagic-benthic coupling

General information

The vertical structure of the oceans is based on vertical density gradients between surface and bottom waters where lighter water masses overhang heavier water masses. This vertical structure remains stable in the absence of any physical forcings (tide, wind-driven upwellings, deep water formation) inducing vertical miwing of the water column. This vertical density gradient between surface and bottom waters can be either caused by vertical variations in temperature (temperature-based stratification, i.e. typically surface waters are warmer than bottom waters*) or vertical variations in salinity (haline-based stratification, i.e. surface waters are fresher than bottom waters). Therefore, the transition between surface and subsurface water masses usually induces drastic changes in temperature and salinity (and by extension, density) over a thin layer of few meters, commonly thermed the thermocline and halocline (and pycnocline), respectively (Figure 5).

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*Some exceptions exist for low-salinity waters: the density decreases when the water temperature falls below the maximum density temperature. Maximum density temperature is reached at 3.98°C for freshwater. This temperature threshold gradually decreased when seawater salinity increase. At salinities higher than 24.70, the freezing point is always the temperature of maximum density.

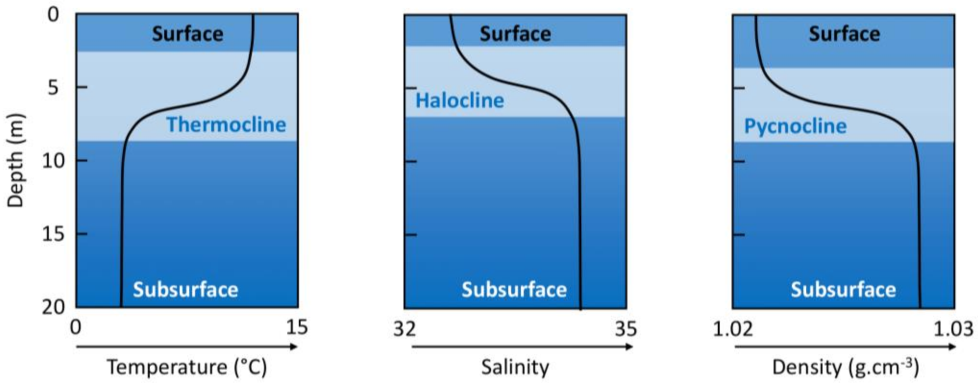

Figure 5: Conceptual diagram representing thermal, haline and density variation along vertical profiles.

Because the strength of stratification is inversely correlated to the turbulent diffusion between two water masses, sharp stratification generally strongly limits vertical nutrient fluxes (e.g. Randelhoff et al. 2020). In the absence of horizontal nutrient inputs (e.g. from rivers), stratification can therefore decrease the pelagic primary production (Tremblay and Gagnon 2009, Randelhoff et al. 2020) or modify the structure of phytoplankton communities (Margalef 1978, Li et al. 2009). Stratification can also have additional consequences on vertical oxygen fluxes between surface and bottom waters, which can even lead to hypoxia of bottom waters (Holte et al. 2005, Rabalais et al. 2009).

Impacts of stratification in tropical/temperate and Arctic/sub-Arctic oceans

Contrary to sub-Arctic/Arctic latitudes, the impacts of increased stratification on primary production have been studied extensively in tropical and temperate open oceans (≈ 45°S – 45°N) and are relatively well understood. For instance, during the last decades, several remote sensing studies pointed to a concomitant increase of sea surface temperatures with a decrease of primary production (Behrenfeld et al. 2006, Boyce et al. 2010). These observations have been attributed to a decrease of surface/subsurface nutrient exchanges and vertical mixing due to enhanced thermal stratification (Behrenfeld et al. 2006, Boyce et al. 2010, D'Alelio et al. 2020). In addition, increased stratification can induce a shift in the phytoplankton size structure from large cells (e.g. diatoms) to smaller cells (e.g. dinoflagellates) which may have subsequent impact on the organic matter transfer toward the seabed (Bopp et al. 2005, Falkowski and Oliver 2007, Turner et al. 2015).

Although high latitudes are expected to experience the largest increases in vertical density gradients (Capotondi et al. 2012), the effects of enhanced stratification on primary production and pelagic-benthic coupling remain still unclear. Some authors suggest that an enhanced stratification and concomitant decrease in mixing layer depth may enhance primary production in a light-limited arctic by retaining more phytoplankton in sunlit waters (Doney 2006, Riebesell et al. 2009). However, Tremblay and Gagnon (2009) evidenced that some Arctic regions may also be nutrient-limited and would not necessarily benefit from increase of light. The future evolution of primary production with simultaneous decrease of sea-ice extent and increase of stratification may actually be different among arctic regions according to their local trophic status (Ardyna et al. 2011, Tremblay and Gagon 2009, Arrigo and van Dijken 2015). Eutrophic regions receiving vertical (e.g. polynya) or horizontal (e.g. interior shelves) supplies of nutrients may benefit from higher light input with enhanced stratification increasing primary production (Figure 6a) while oligotrophic regions (e.g. outflow shelves) may experience an opposite trend (Figure 6b, Arrigo and van Dijken 2015). However, additional factors such as increase in storm frequency at high latitudes with climate change (Ardyna et al. 2014) or the ability of phytoplankton to adapt to low light intensity at or near the pycnocline (Martin et al. 2010) also need to be taken into account. Considering the multiple processes that influence local nutrient supply within surface waters (e.g. upwelling, horizontal advection, wind-driven turbulence, freshwater input, mineralization), accurately predicting the impact of changes in stratification on primary production at the pan-arctic scale remains a challenge (Randelhoff et al. 2020).

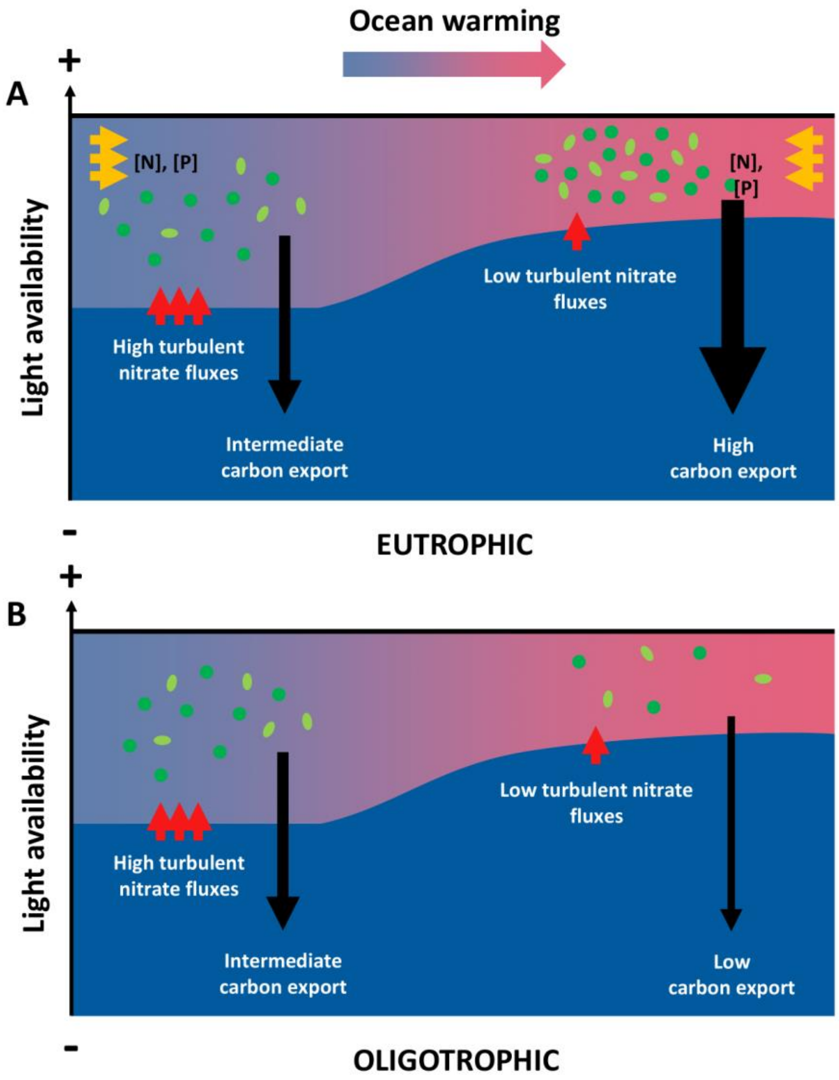

Figure 6: Conceptual diagram showing the potential contrasted evolution of Arctic eutrophic (A) and oligotrophic (B) environment under enhanced stratification (inspired from Riebesell et al. 2009). Nutrient fluxes through the pycnocline are represented by red arrows, horizontal advection of nutrient are depicted by yellow arrows and vertical carbon export are shown by black arrows.

Potential interactions in shallow coastal ecosystems

The fate of primary production and pelagic-benthic coupling is probably even harder to predict in highly-stratified coastal systems where additional interactions can enhance or compensate the effects of stratification on the pelagic compartment. Freshwater input which increases stratification in coastal areas, can induce additional environmental changes in coastal ecosystems with cascading effects on pelagic primary production and export. For example, potentially negative effects of stratification on pelagic primary production may be accentuated when freshwater inflows are coupled with increased turbidity (Holding et al. 2019, Hopwood et al. 2020). Moreover, the impact of haline stratification could also be related to nutrient concentrations in freshwater flows. For instance, haline-based stratification might have a strong impact on coastal pelagic primary production when freshwater flows are nutrient-depleted or imbalanced in nutrient ratios (Holding et al. 2019, Randelhoff et al. 2020) while no effects might be observed when freshwater inputs bring enough nutrients to compensate the low vertical nutrient fluxes. All these local features in coastal domains highlights the difficulty to predict the impact of enhanced stratification in these ecosystems.

On the importance to consider unique features of shallow coastal ecosystems

Predominance of shallow coastal ecosystems in the Arctic

Arctic coastal ecosystems sensu stricto (i.e. continental shelves) cover 52.8% of the Arctic ocean surface, representing 25% of the total surface of world's coastal ecosystems (Carroll and Carroll 2003, Jakobsson et al. 2008). Among them, shallow ecosystems (i.e. above the euphotic zone) represent ≈ 25% of the Arctic continental shelves (i.e. ≈ 12.5% of the Arctic ocean surface, Gattuso et al. 2006). In addition, Arctic and sub-Arctic coastlines represent 35% of the global coastlines (Lantuit et al. 2012). Despite such importance at the world ocean scale, shallow coastal ecosystems have usually been understudied in the Arctic compared to deeper continental shelves and deep basins from which they differ greatly (see below). This is why Arctic coastal studies integrating multiple physical and ecological situations are strongly needed to better predict how these ecosystems may evolve under strengthened stratification conditions under climate change.

Influences of freshwater inputs in shallow coastal ecosystems

Because of their vicinity from the seashore, shallow coastal ecosystems are highly influenced by seasonal variations occurring in terrestrial habitats. Land and tidewater glacier melting, land erosion and increase of river flows during summer strongly influence marine ecosystems by increasing seawater turbidity (Murray et al. 2015), modifying water column stratification and primary productivity (Meire et al. 2017) or increasing sedimentation of terrestrial materials towards the seabed (D’Angelo et al. 2018). Such terrestrial inputs strongly alter marine coastal ecosystems, decreasing benthic communities specific and functional richness in some cases

(Sejr et al. 2010, Włodarska-Kowalczuk et al. 2019), shaping size-primary and secondary producer distributions from pelagic communities (e.g. Arendt et al. 2016, Middelbo et al. 2018) and fueling food webs with carbon of terrestrial origin (Feder et al. 2011, Harris et al. 2018, McGovern et al. 2020). Terrestrial influences on shallow coastal areas may locally be exacerbated within confined areas (e.g. silled-fjords) where freshwater input limits/prevents exchanges between inner and outer fjord or surface and bottom water masses, with potential impacts on primary productivity (Boone et al. 2018, Hopwood et al. 2020).

Primary production in shallow benthic ecosystems

Contrary to offshore systems, shallow habitats have the potential to support both pelagic (i.e. phytoplankton) and benthic (i.e. microphytobenthos and macroalgae) photosynthetic primary production. Benthic primary producers contribute significantly to the carbon budget of Arctic coastal waters (Glud and Rysgaard 2007, Attard et al. 2016) and their productivity usually far exceeds those of phytoplankton at depth below 20 m (Krause-Jensen et al. 2007). As an example, microphytobenthic production can be 1.4 to 7 times higher than the pelagic production at depth below 30 m (Glud et al. 2002, Attard et al. 2014, Attard et al. 2016). This trend is probably exacerbated toward high and oligotrophic latitudes: nutrient concentrations often balance the relative importance of benthic *vs* pelagic primary production because phytoplankton is usually primarily controlled by nutrient availability while benthic primary producers are rather limited by light (Duarte 1995, MacIntyre et al. 1996). Thus, low pelagic primary production in high-latitude areas associated with low nutrient concentrations probably increase light availability for benthic primary producers and thus enhances their relative productivity. This is especially the case for benthic microalgae which have a direct access to nutrients released from the sediment (Glud et al. 2009).

Importance of benthic primary producters in shallow benthic ecosystems

Although benthic communities in shelf or bathyal environments are presumed to be very sensitive to changes in pelagic-benthic coupling, this would be not necessarily the case in coastal environments where both pelagic and benthic organic matter sources supply benthic food webs. Several studies highlighted such point by revealing the large contribution of benthic primary producers to shallow benthic food-webs (e.g. Dunton and Schell 1987, Fredriksen 2003, Gaillard et al. 2017, McTigue and Dunton 2017). There are even some evidences that such contribution of benthic produced carbon would not strictly be limited to shallow habitats. Indeed, studies from the Svalbard and Patagonia fjords have highlighted downward transport of macroalgae (probably facilitated by the steep fjord bathymetries) fueling benthic communities down to 410 m (Sokołowski et al. 2014, Renaud et al. 2015, Cari et al. 2020).

In addition to their locally important contribution to the ecosystem productivity, marine macrophytes have also key ecological roles in sub-Arctic/Arctic coastal ecosystems. Several engineer species such as kelp (e.g. *Agarum clathratum*, *Alaria esculenta*, *Laminaria solidungula*, *Saccharina latissima*), eelgrass (*Zostera marina*) or coralline algae (e.g. *Clathromorphum compactum*, *Lithothmnion glaciale*) are common members of coastal arctic systems (Olesen et al. 2015; Jørgensbye and Halfar 2017, Filbee-Dexter et al. 2019). By forming complex 3-dimensional structures, these species enhance habitat heterogeneity and thus faunal biodiversity (Jones et al. 1994). Kelp forests provide refuges for a wide variety of taxa (fishes, brittle stars, polychaetes; e.g. Gutiérrez et al. 2011, Ronowicz et al. 2018) together with substrata for additional benthic primary producers (i.e. microphytobenthos on coralline algae, red algae on kelp thallus, Grall et al. 2006, Leclerc et al. 2013) or sessile organisms (e.g. Shunatova et al. 2018). In addition, kelp forests protect shoreline from erosion (Gutiérrez et al. 2011) and may retain suspended particles from the water column and thus increasing pelagic food sources availability for primary consumers (Paar et al. 2019). Considering the key structuring role of these ecosystem engineers on benthic communities, predictions of future changes in the functioning of shallow coastal ecosystems need to consider the future expansion of these benthic primary producers with sea-ice retreat (Krause-Jensen et al. 2012, Krause-Jensen and Duarte 2014).

Objectives of the PhD

Although considerable studies have attempted to predict the consequences of climate change on sub-Arctic/Arctic marine ecosystems, we still do not clearly understand the impacts it has on major ecological functions such as primary production or pelagic-benthic coupling (e.g. Arrigo and van Dijken 2015, Ardyna and Arrigo 2020). Studies disentangling the effects of various factors controlling primary production and pelagic-benthic coupling in sub-Arctic/Arctic seas may help in better understand ecosystem responses to increases in stratification. While some of these factors received a considerable interest over the last decades (e.g. decrease in sea ice extent, Rysgaard et al. 1999,Carroll and Carroll 2003, Grebmeier et al. 2006, Kędra et al. 2015), others processes remain little studied (e.g. stratification, wind speed and storminess, freshwater inputs in coastal areas, aerosol deposition). For instance, the impact of stratification has been poorly investigated although sub-Arctic/Arctic seas are expected to experience significant strengthening in vertical density gradients in the forthcoming years (Belkin et al. 2009, Carmack et al. 2016, Nummelin et al. 2016). The effects of strenghtened stratification appear to be particularly difficult to predict in coastal areas where numerous local features may amplify (e.g. high turbidity, Murray et al. 2015) or counteract (e.g. nutrient input, Tremblay et al. 2015) and, consequently, its impacts on primary production and pelagic-benthic coupling. Considering the predominance of coastal areas at sub-Arctic/Arctic latitudes (Lantuit et al. 2012) and the importance of coastal benthic food webs in Arctic marine ecosystems (e.g. Grebmeier et al. 2006), it is crucial to understand how coastal areas will cope with enhanced stratification and associated changed in primary production/pelagic-benthic coupling.

In this context, this thesis aims at investigating how future changes of stratification conditions in Arctic and sub-Arctic regions are likely to influence the functioning of shallow coastal ecosystems. This work focuses principally on two ecosystems characterized by strong seasonal variation in stratification: 1) Saint-Pierre-et-Miquelon (SPM), a sub-Arctic archipelago at the south of Newfoundland with a temperature-based stratification and 2) Young Sound, a high arctic fjord from NE Greenland with a haline-based stratification (Figure 7). In fact, large seasonal variations in sea surface temperatures are well known in SPM, ranging from 0°C in March-April to 18°C in August-September, while bottom waters temperature remain low and very stable all year-round (Lazure et al. 2018, Poitevin et al. 2018). In east Greenland, Young Sound fjord experiences large variations of sea surface salinity during June-September due to strong freshwater inputs that induce a freshening of surficial inner waters, varying from 8 in the innermost to 30 in the outer parts of the fjord (Bendtsen et al. 2007). In addition to high seasonal stratifications, both locations have other specific interests:

(1) Based on actual climate projections, such study sites are likely to be among the most sensitive marine regions to stratification’s intensification. The Newfoundland Shelf has experienced one of the largest warming in sea surface temperatures over the last decades (i.e. 1°C between 1982 and 2006, Belkin et al. 2009) while North-East Greenland has been exposed to a major freshening (Sejr et al. 2017, Perner et al. 2019). Both of these environment changes are expected to lead to major modifications in stratification (Capotondi et al. 2012).

(2) Both study sites are strongly exposed to marine currents from two major outflow shelves (East Greenland Shelf and Canadian Arctic Archipelago). Limitation of nutrient vertical exchanges under conditions of enhanced stratification may have thus considerable

impact on the local dynamics of primary production: horizontal advection is expected to bring less nutrients in the future because of upstream nutrient consumption by phytoplankton in ice-free inflow/interior shelves (Arrigo and van Dijken 2015, Michel et al. 2015, Lewis et al. 2020).

(3) Finally, we provide information on the functioning and biodiversity of the scarcely studied benthic compartment of both sites. These new data will complement baseline knowledge on their functioning, that are presumed to change fast over the forthcoming decades.

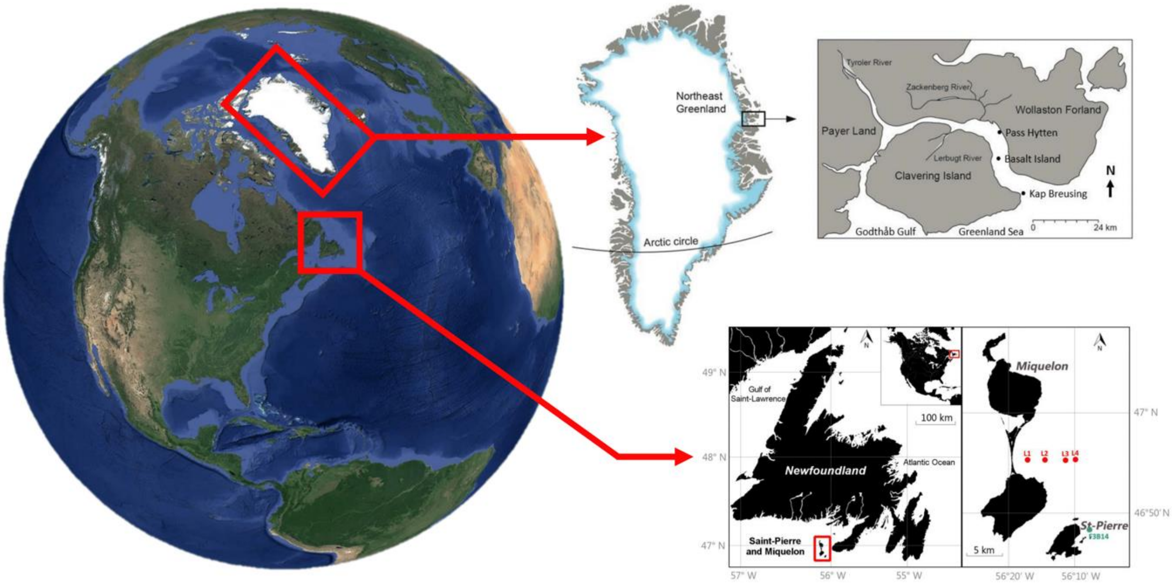

Figure 7: Earth map indicating the locations of Young Sound (top right) and Saint-Pierre and Miquelon (bottom right) study sites with their related sampling stations.

Impacts of enhanced stratification on the functioning of coastal benthic ecosystems was investigated using two different approaches.

Firstly, we examine how stratification impacts the trophic environment (i.e. defined here as the quality, diversity and quantity of the organic matter available in an ecosystem) of the target ecosystems and trophic links between primary producers and primary consumers (**Part I**). Organic matter biochemical composition provides valuable information on the diversity and quality of organic matter sources in ecosystems (e.g. Gaillard et al. 2017, Liénart et al. 2017), but also on the seasonality of primary production (Mayzaud et al. 2013, Connelly et al. 2016) or land/sea interactions (e.g. inputs of terrestrial materials, Connelly et al. 2015). All these factors are important drivers of marine ecosystems functioning (e.g. Campanyà-Llovet et al.

2017). To this end, we studied along a spatial gradient how combined effect of stratification related to surface freshwater inputs and its associated constraints (high turbidity and sedimentation) could influence sources and composition of the organic matter as well as its transfer to two primary consumers (i.e. *Astarte moerchi* and *Mya truncata*) in a high-arctic fjord (**Chapter I**). We also studied how thermal stratification within a subarctic site could impact sources and quality of organic matter when freshwater and terrestrial inputs no more occur (**Chapter II**).

Secondly, we assess how impacts of stratification on the trophic environment may have subsequent effects on the structure and stability of benthic food webs (**Part II**). The structure of benthic food webs provides insights into the functioning of marine ecosystems by revealing organic matter flows from primary producers to secondary consumers (e.g. Roy et al. 2015, Renaud et al. 2015, Harris et al. 2018). It also allows to assess the strength of pelagic-benthic coupling in marine ecosystems (e.g. Iken et al. 2010, Søreide et al. 2013, Stasko et al. 2018). To this aim, we investigated the intra-fjord food-web variability (inner station – assumed to be highly exposed to stratification constraints *vs* outer station – assumed to be less exposed to stratification) of a high-arctic fjord and identified some resilience factors when facing increased freshwater inputs and stratification scenario (**Chapter III**). We then investigated how thermal stratification may impact differently benthic food webs over stratified and unstratified areas from a sub-Arctic archipelago (**Chapter IV**).

In addition to these four studies, we present in the appendix a short note on the diversity and spatial variability of shallow benthic macrofaunal assemblages from Young Sound, as a complement of an earlier inventory by Sejr et al. (2000) (**Chapter V**).

The integration of these five individual studies lead us to propose conceptual models describing the functioning of Arctic/sub-Arctic shallow coastal ecosystems under high stratification constraint. Through these conceptual models, we highlight the importance of considering the local features of these ecosystems in order to predict their response to global change. Finally, we propose research avenue to improve our understanding of the future functioning of coastal Arctic and sub-Arctic ecosystems.

Chapter I

Coastal waters freshening and extreme seasonality affect organic matter sources, quality, and transfers in a High Arctic fjord (Young Sound, Greenland)

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Abstract

Arctic benthic ecosystems are expected to experience strong modifications in the dynamics of primary producers and/or benthic-pelagic coupling under climate change. However, a lack of knowledge about the influence of physical constraints (e.g., ice-melting associated gradients) on organic matter sources, quality, and transfers in systems such as fjords can impede predictions of the evolution of benthic-pelagic coupling in response to global warming. Here, sources and quality of pelagic organic matter (POM) and sedimentary organic matter (SOM) were characterized along an inner-outer gradient in a High Artic fjord (Young Sound, NE Greenland) exposed to extreme seasonal and physical constraints (ice-melting associated gradients). The influence of the seasonal variability of food sources on two dominant filter-feeding bivalves (*Astarte moerchi* and *Mya truncata*) was also investigated. The results revealed the critical impact of long sea ice/snow cover conditions prevailing in Young Sound corresponding to a period of extremely poor and degraded POM and SOM. Freshwater inputs had a very local impact during summer, with relatively more degraded POM at the surface compared to bottom waters that were less nutritionally depleted but more heterogeneous among the sampled stations. Terrestrial inputs contributed to the SOM composition but showed a large variability along the fjord. Finally, diet analyses underlined the contrasted nutritional conditions, showing much higher lipid reserves in *A. moerchi* than in *M. truncata* during winter. Under a scenario with increased freshwater input, such results suggest a decline in organic matter quality and production in Young Sound, with subsequent impacts on benthic food webs.

Key words

Arctic ecosystems • benthic-pelagic coupling • Organic matter • Climate change • Fatty acids • Stable isotopes • Young Sound

Introduction

The Arctic has been subjected to atmospheric warming in recent decades at a rate that exceeds the global average by a factor of 2–3 (AMAP 2017). This warming induces major modifications in the Arctic marine environment, e.g., a decrease in sea-ice cover (extent and thickness) and an increase in freshwater discharge (AMAP 2017, Kwok and Rothrock 2009, McPhee et al. 2009, Ohashi et al. 2016). The Greenland Ice Sheet annual net loss is currently estimated at 186 Gt.yr^{-1}, which is double the melting rate observed for 1983–2003 (Bamber et al. 2012, Kjeldsen et al. 2015). Such changes are expected to impact marine systems through shifts in the spatial distribution of species (Falk-Petersen et al. 2007) and altered food web dynamics via modified quantity, quality, and seasonal timing of primary productivity (Iken et al. 2010, Leu et al. 2011, Ardyna et al. 2014, Arrigo and van Dijken 2015). Moreover, changes in the phenology of primary producers may create mismatches between peak algal blooms and faunal reproductive phases, with major effects on the benthic-pelagic coupling (Søreide et al. 2010, Moran et al. 2012).

Several authors have modeled the evolution of food webs and marine wildlife within a changing Arctic (e.g. Wassmann 2011, Kędra et al. 2015). However, recent studies indicate a regionally variable Arctic ecosystem response to global warming depending on specific habitat characteristics (e.g. water depth, exposure to terrestrial runoff; Carmack et al. 2015, De Cesare et al. 2017, Gaillard et al. 2017). For instance, although the generally accepted paradigm states an increase in primary production in the Arctic Ocean, the opposite trend could occur in coastal areas (which represent 35% of the world's coastline) such as fjord systems, due to the increase in freshwater inputs and turbidity (Carmack et al. 2015, Middelbo et al. 2018). Terrestrial runoff from melting snow and ice increases water column turbidity and diminishes light availability, in turn decreasing primary productivity (Murray et al. 2015, Arimitsu et al. 2016). Freshwater inputs also reduce primary productivity in some fjords due to increased stratification, causing nutrient depletion in surface waters (Piquet et al. 2014, Meire et al. 2016, Middelbo et al. 2018). In addition, freshwater inputs from glacier melting may provide labile organic carbon, which may be a source of bioavailable carbon in low-productivity ecosystems (Lawson et al. 2014). The impact of increased freshwater loads on the quality of organic matter and transfers in Arctic fjords remains poorly understood.

We conducted a sampling program during August 2016 and May 2017 in a High Arctic fjord (Young Sound, NE Greenland) to study how seasonal and physical constraints drive the sources and qualitatively change the organic matter available for dominant benthic primary consumers: the abundant filter-feeding bivalves *Astarte moerchi* and *Mya truncata* (Sejr et al. 2000, Born et al. 2003). Potential bivalve food sources and body tissues were analyzed for fatty acid (FA) and stable isotope (SI) composition. FA analysis can be used to trace the origin of organic matter within an environment, since primary producers often show contrasting FA profiles according to their taxonomic group (e.g. diatoms, dinoflagellates, macroalgae; Meziane and Tsuchiya 2000, Dalsgaard et al. 2003, Kelly and Scheibling 2012). Moreover, biosynthesis of specific FAs, such as polyunsaturated FAs (PUFAs), is usually limited in marine bivalves. This enables the use of FA trophic markers to study diet (Kelly and Scheibling 2012, Thyrring et al. 2017). SI analysis may also help to characterize the trophic diet of organisms (Fry 2006, Gaillard et al. 2017) and to investigate environmental processes occurring within an ecosystem, such as inputs of terrestrial carbon (Calleja et al. 2017), organic matter degradation (McTigue et al. 2015), or the dynamics of blooms (Tamelander et al. 2009).

The main goals of this study were to (1) understand how seasonal and physical constraints in Young Sound may influence the sources and quality of pelagic organic matter (POM) and sedimentary organic matter (SOM), (2) assess the seasonal patterns (ice/snow cover in May *vs*. open sea in August) of organic matter transfers within this fjord, and (3) investigate the response of two dominating bivalve species (*A. moerchi* and *M. truncata*) to such seasonality in food availability.

Materials and methods

Study site and sampling

The study was conducted in Young Sound (74°N 20°W, Fig. 1), a High Arctic Greenland fjord characterized by a long sea-ice duration of 9–10 months (Glud et al. 2007). The fjord is approximately 90 km long and 2–7 km wide. The maximum depth is 330 m, but exchange with coastal waters is limited by a shallow sill with a depth of 45 m at the mouth of the fjord (Bendtsen et al. 2007). During land-glacier and snow melting, the surface waters become more turbid and brackish due to freshwater inputs, especially in the inner part of the fjord (Ribeiro et al. 2017). Generally, such freshwater inputs generate a bilayer estuarine water circulation with low-salinity surface flows from the inner to the outer fjord and inflows occurring close to the seabed (Bendtsen et al. 2014). Young Sound has the typical surface current circulation in fjords affected by the Coriolis effect, with the southern part (Clavering Island side) more exposed to freshwater outflow than the northern part (Wolloston Forland side; Bendtsen et al. 2007).

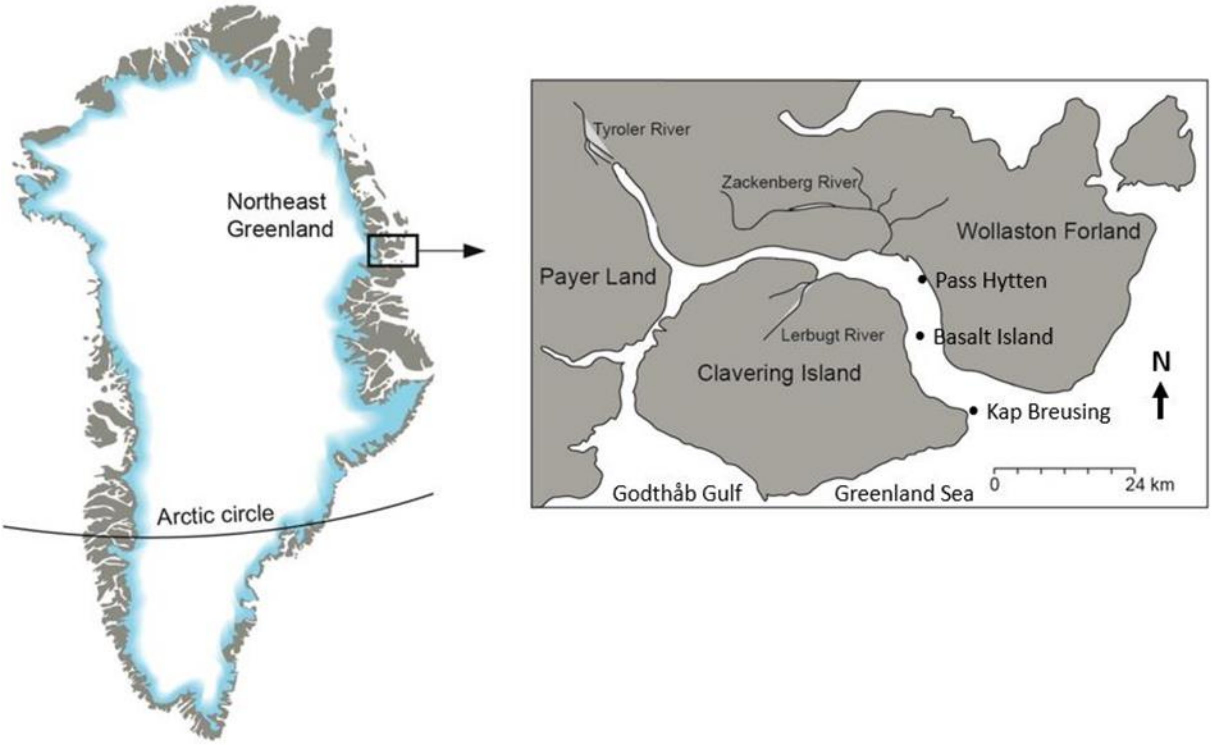

Figure 1: Location of the Young Sound's fjord (NE Greenland) and the three sampled stations: Pass Hytten, Basalt Island, and Kap Breusing (modified from Ribeiro et al. 2017).

Sampling was conducted in August 2016 (open water, early productive period; De Cesare et al. 2017) and May 2017 (ice cover, expected "unproductive" period). We sampled three stations in 2016 (Figure 1), i.e., Pass Hytten (depth = 18 m, 74.41°N 20.33°W), Basalt Island (depth = 21.5 m, 74.33°N 20.36°W), and Kap Breusing (depth = 20 m, 74.21°N 20.11°W), but only Pass Hytten and Basalt Island during 2017 for logistical reasons. At each station, ten liters of seawater were collected at two depths corresponding to the surface (s-POM, 1 m below the surface) or bottom (b-POM, 1 m above the seabed), using two 5l Niskin bottles per sample. In parallel, SOM samples were collected at the sediment surface (≈ 625 cm^2) by scuba divers using a 450 ml syringe. Also, several individuals of *A. moerchi* and *M. truncata* were harvested either by scuba diving or using a triangular biological dredge (KC Denmark A/S) during both seasons. In addition, three macroalgae species (*Desmarestia aculeata*, *Fucus* sp., and *Saccharina latissima*) were harvested during summer in order to assess their potential contribution to the bivalves' diet. Statistical analyses were performed on our own results as well as some raw data previously published in De Cesare (2016) and De Cesare et al. (2017) relating summer samples of *A. moerchi* (SI signatures and FA profiles) and macroalgae (SI signatures).

Analyses of samples

Preliminary treatments

POM samples were obtained by filtering collected water on precombusted GF/F Whatman® microfiber filters (diameter: 47 mm, pore size: 0.7 µm) until clogging when possible (mean filtered volume = 7.9 ± 1.9 l, range: 4–8 l). Because syringe-collected samples comprise a mixture of SOM, inorganic particles, and seawater, we let the samples settle for one hour prior to filtering the supernatants until clogging on GF/F filters (mean volume = 0.260 ± 0.100 ml, range: 100–450 ml) in order to remove most of inorganic sedimentary particles. In the field, all samples were directly frozen at -80°C and transferred to the lab for further analyses. Once in the lab, all samples (i.e., POM and SOM filters as well as digestive glands and muscles) were freeze-dried at -50°C for at least 5 hours (30 hours for animal tissues) and directly weighed. The POM and SOM filters were cut in two parts to perform both FA and SI analyses on the same sample. Each half-filter was weighed and the quantity of organic matter for the FA and SI analysis was calculated by the following equation:

$$M(X) = \frac{W_{Half\ filter}}{W_{Whole\ filter}}\ X\ (W_{Whole\ filter} - W_{Precombusted\ filter})$$

Where M (X) is the mass (mg) of POM or SOM used for the FA or SI analysis and W is the dried weight of the half, whole, or precombusted filters.

Fatty acids analysis

The method used for the FA extraction largely follows the Bligh and Dyer method (1959) as adjusted in Meziane and Tsuchiya (2002). To quantify the FA concentrations, a known volume of a commercial standard (23:0, concentration of 5 mg/ml) was introduced in each sample. Half-filters for POM and SOM analyses were diluted in a distilled water-chloroform-methanol solution (1:1:2, v:v:v) and sonicated for 20 minutes for the FA extraction. The samples were then completed by a distilled water-chloroform solution (1:1, v:v) and centrifuged (3000 rpm, 5 minutes). Lipid phases were transferred to separate tubes, completed by a distilled water-chloroform solution (1:1, v:v), and sonicated again for 20 minutes to maximize the extraction. Then, samples were evaporated under a dinitrogen (N_2) flux, diluted a second time in a mixture of methanol and sodium hydroxide (2:1, v:v; [NaOH] = 2 mol.l^{-1}), and heated at 90°C for 90 minutes for FA saponification. Finally, FAs were converted into FA methyl esters after incubation for ten minutes at 90°C in a methanolic boron trifluoride solution (BF3-CH3OH 14%, 1 ml). At the end of the reaction, the chloroform phase containing FAs was retrieved and stored at -20°C.

The FAs were quantified by gas chromatography (Varian CP-3800 equipped with a Supelco® Omegawax® Capillary GC 320 column [length = 30 m, inside diameter = 0.32 mm, film thickness = 0.25 µm], He as carrier gas). FA pics were identified by comparing with those from an analytical standard (Supelco® 37 Component FAME Mix) and confirmed by mass spectrometry (Varian 220-MS coupled to a Varian 450-GC, He as carrier gas). FA nomenclature is defined as X:YωZ, where X is the number of carbon atoms, Y is the number of double bonds, and Z is the position of the last double bond from the methyl group. The 23:0 standard allowed converting each FA methyl esters area into a concentration using the following equation (Schomburg 1987):

$$C_{FA} = \left(\frac{A_{FA}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

where C_{FA} is the FA concentration (µg/g), A_{FA} is the FA peak area, A_{C23} is the 23:0 peak area, C_{23} is the 23:0 quantity (µg) added to each sample, and M_f is the mass of matter deposited on the analyzed half-filter.

The analytical precision for the samples was generally less than 5% for the total amounts and major components of FA (Meziane pers. com.). Table 1 compiles all the FAs used as organic matter tracers in this study and their related biomarker information.

Table 1: Fatty acids (FAs) used in this study as markers to describe the origin and quality of organic matter.

Descriptor of	Fatty acids (FAs)	References
Organic matter origin		
Diatoms	16:1ω7, 16:4ω1, 20:5ω3	Reuss and Poulsen (2002), Dalsgaard et al. (2003), Kelly and Scheibling (2012)
Dinoflagellates	18:4ω3, 22:6ω3	Napolitano et al. (1997), Kelly and Scheibling (2012)
Macroalgae (Phaeophyceae)	18:2ω6, 18:3ω3, 18:4ω3, 20:5ω3	Kelly and Scheibling (2012), De Cesare et al. (2017), Gaillard et al. (2017)
Organic matter quality		
Degraded organic matter	Dominance of SFA (e.g., 14:0, 16:0, 18:0)	Rhead et al. (1971), Connelly et al. (2015), Connelly et al. (2016)
Labile and nutritionally rich organic matter	Dominance of PUFA and EFA (here, sum of 20:4ω6, 20:5ω3, and 22:6ω3)	Soudant et al. (1996), Parrish et al. (2005), Parrish (2009)

Stable isotope analysis

SI analysis was performed on the second half of each POM and SOM filter and on *A. moerchi* and *M. truncata* tissues. Half-filters were fumigated for at least four hours with 35% HCl to remove inorganic carbon (Lorrain et al. 2003). The surface layer, including filtered POM (or SOM), was scraped and 10–30 mg of material was placed in tin capsules. Due to the small amounts of inorganic carbon in digestive glands and muscles, no acidification was performed with these tissues (Jacob et al. 2005, Søreide et al. 2006). The animal tissues were ground and approximately 1 mg was placed in a single tin capsule for each sample. Macroalgae were ground and separated into two subsamples (De Cesare et al. 2017): one subsample was acidified (1M HCl) to remove inorganic carbon and placed in silver capsules for δ^{13}C analysis, while the second subsample was directly placed in tin capsules (without prior acidification) for δ^{15}N analysis.

All samples were analyzed at the University of California Davis Stable Isotope Facility (Department of Plant Sciences, UC Davis, Davis, California) by continuous flow isotope ratio mass spectrometry (CF-IRMS). The equipment consisted of an elemental analyzer (PDZ Europa ANCA-GSL [Sercon Ltd., Cheschire, UK] and Elementar Vario EL Cube elemental analyzer [Elementar Analysensysteme GmbH, Hanau, Germany] for animal tissue and filter analysis, respectively) interfaced to an isotope ratio mass spectrometer (PDZ Europa 20-20, Sercon Ltd., Cheschire, UK). Several replicates of laboratory standards, compositionally similar to analyzed samples and calibrated against NIST Standard Reference Materials (IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65), were inserted between some of the filter and animal samples to correct deviations occurring during the analysis. The standard deviation of the stable isotope measurements was estimated to ±0.2‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$ (UC Davis Stable Isotope facility pers. com.). Carbon and nitrogen isotopic ratios were expressed in per mill (‰) and calculated from international standards (Vienna Pee Dee Belemnite and Air, respectively) by the following equation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

Where δX is $\delta^{13}C$ or $\delta^{15}N$, and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio (Peterson and Fry 1987).

Data analyses

Since pelagic and benthic components usually show different organic matter sources and qualities (e.g., Magen et al. 2010, Kuliński et al. 2014), we chose to separate the SOM and POM samples for statistical analyses. Because our design was not balanced between the two seasons (two stations sampled in winter *vs* three in summer), we used two-way PERMANOVAs for each season to study the effects of depth (surface or bottom waters) and station factors on the FA profiles of POM. Since PERMANOVAs are not affected by small differences in dispersion, especially with a balanced design, the PERMDISP test was performed to ensure that data dispersion, possibly highly heterogeneous, would not disturb the interpretation of our analysis (Anderson et al. 2008, Anderson and Walsh 2013).

Seasonal differences in FA concentrations were tested by one-way ANOVA, whereas depth and station effects were tested by two-way ANOVA for each season. FA concentrations were log-transformed prior each analysis to validate normality and homoscedasticity assumptions. When significant effects were detected, pairwise Tukey tests were used to determine if the differences were observed among all groups. Similar analyses were performed on carbon and nitrogen isotopic ratios, with either 2 two-way ANOVAs (depth and stations as factors) or 1 one-way ANOVA (season as factor), as well as with pairwise tests if needed.

Regarding FA data in animal tissues, homoscedasticity and normality were rarely observed between the two factors (e.g., digestive glands from May *vs* muscles from August). As data transformation is not recommended for percentage values not derived from count data (as percentage of lipids), we thus performed a one-way PERMANOVA to test each factor separately (e.g. season was tested for each tissue from a single species). Data from the SI analysis on animal tissue were treated similarly with one-way ANOVAs. All statistical analyses were performed using R software (R Core Team 2017).

Results

Fatty acid profiles from POM and SOM samples

Particulate Organic Matter (POM)

Sixty-five FAs were identified in POM and SOM samples (44 FAs in August and 47 in May). Only FA percentages higher than 0.2% in at least one sample are shown in Table 2. Strong seasonal differences were observed in the FA profiles of the POM samples. For example, apart from s-POM from Basalt Island, the total percentage of PUFAs was between 9.7% and 22.1% in August and was always less than 1.5% in May. Concomitantly, the sum of saturated FAs (Σ SFA) shows opposite seasonal variations, with higher values in May (range: 82.5% – 93.1%) compared to August (range: 49.5% – 69.3%).

Table 2: Fatty acid (FA) composition of particulate organic matter (POM) and sedimentary organic matter (SOM) from summer and winter seasons. s-POM: surface POM, b-POM: bottom POM, SFA: saturated FA, MUFA: monounsaturated FA, PUFA: polyunsaturated FA, BrFA: branched FA, EFA: essential FA (sum of 20:4ω6, 20:5ω3, and 22:6ω3 proportions), nd: not detected, tr: trace (FA percentage <0.2%). Standard deviations are represented within brackets. FA percentages lower than 0.2% in all samples were not included in this table.

	August							May				
	Pass Hytten		Basalt Island		Kap Breusing		SOM	Pass Hytten		Basalt Island		SOM
	s-POM	b-POM	s-POM	b-POM	s-POM	b-POM		s-POM	b-POM	s-POM	b-POM	
	N = 5	N = 5	N = 5	N = 4	N = 5	N = 4	N = 10	N = 4	N = 4	N = 5	N = 5	N = 9
12:0	nd	nd	nd	nd	nd	nd	nd	1.6 (0.7)	3.7 (1.3)	6.6 (4.8)	2.4 (0.6)	1.6 (1.1)
13:0	nd	nd	nd	nd	nd	nd	nd	tr	0.3 (0.2)	tr	tr	0.3 (0.1)
14:0	17.8 (6.2)	7.1 (1.6)	19.9 (7)	8.5 (1.6)	12.9 (3.6)	8.4 (0.8)	9.7 (3.7)	7.5 (0.3)	7.4 (0.9)	13.2 (2.7)	9 (1)	6.3 (1.7)
15:0	1.3 (0.3)	1.8 (0.3)	1.5 (0.3)	2.1 (0.5)	1.3 (0.3)	1.3 (0.2)	1 (0.3)	2.7 (0.3)	2.3 (0.4)	2.5 (0.4)	2.8 (0.5)	1.7 (0.3)
16:0	35.3 (9.8)	32.9 (4.9)	45.1 (8.7)	36 (7.9)	31.5 (3.3)	27.1 (4.8)	34.2 (6.4)	43 (0.8)	41.1 (1.7)	38.6 (5.3)	39.5 (6.3)	46 (3)
17:0	0.8 (0.2)	1.1 (0.2)	1.1 (0.5)	1.5 (0.6)	0.8 (0.2)	0.8 (0.2)	0.6 (0.6)	1.6 (0.1)	1.3 (0.1)	1.3 (0.2)	1.6 (0.3)	1.3 (0.2)
18:0	7.5 (2.8)	20.1 (4.2)	13.5 (4.8)	17.6 (3.4)	8.7 (1.3)	9.8 (2)	9 (7.7)	31.8 (3)	30.5 (6.4)	21.6 (3.7)	22.5 (3.4)	30.5 (4.2)
19:0	0.5 (0.2)	0.3 (0.2)	0.7 (0.2)	0.9 (0.5)	0.5 (0.1)	0.3 (0.2)	0.5 (0.5)	nd	nd	tr	nd	nd
20:0	0.3 (0.1)	0.9 (0.1)	0.5 (0.4)	0.8 (0.2)	0.5 (0.2)	0.5 (0.1)	0.4 (0.4)	1.6 (0.0)	1.3 (0.1)	1.1 (0.2)	1.2 (0.1)	1.4 (0.1)
21:0	0.3 (0.3)	0.2 (0.1)	0.6 (0.4)	0.3 (0.3)	0.4 (0.5)	tr	0.3 (0.4)	tr	0.2 (0.2)	0.3 (0.2)	0.3 (0)	tr
22:0	0.5 (0.2)	0.8 (0.1)	0.8 (0.3)	0.6 (0.2)	0.5 (0.1)	0.5 (0.1)	0.5 (0.4)	1.2 (0.1)	1.0 (0.1)	1 (0.3)	1.2 (0.3)	1.2 (0.1)
24:0	0.3 (0)	0.7 (0.3)	0.5 (0.2)	0.9 (0.2)	0.4 (0.2)	0.6 (0.1)	0.7 (0.5)	1.7 (0.1)	1.1 (0.3)	1.5 (0.4)	1.5 (0.3)	1.5 (0.3)
25:0	nd	nd	nd	nd	nd	nd	nd	0.3 (0.0)	0.2 (0.0)	0.2 (0.1)	0.3 (0.1)	0.8 (1.3)
Σ SFA	64.5 (15.2)	65.8 (9.5)	84.4 (14.2)	69.3 (14.2)	57.4 (6.7)	49.5 (6.9)	56.9 (15.7)	93.1 (2.6)	90.4 (5.4)	88.4 (10.1)	82.5 (11.3)	92.8 (2.6)
14:1ω5	nd	nd	nd	nd	nd	nd	nd	tr	0.2 (0.2)	0.2 (0.1)	tr	0.2 (0.2)
15:1ω1	nd	nd	nd	nd	nd	nd	nd	0.3 (0.7)	1.0 (1.4)	1.1 (0.6)	0.6 (0.5)	0.7 (0.8)
16:1ω5	1.1 (0.5)	0.6 (0.3)	0.3 (0.3)	0.4 (0.2)	1.2 (0.2)	0.8 (0.1)	0.3 (0.2)	nd	nd	nd	nd	nd
16:1ω7	7.8 (3.3)	6.9 (1.6)	4 (5.4)	6.6 (4.6)	9.4 (1.6)	12 (1.2)	18.3 (7.8)	0.4 (0.3)	0.4 (0.4)	0.6 (0.7)	0.9 (0.6)	tr
16:1ω9	0.7 (0.2)	1.7 (0.5)	0.4 (0.5)	1.9 (1.2)	0.9 (0.1)	1.2 (0.4)	0.9 (0.5)	0.3 (0.1)	0.3 (0.1)	0.6 (0.9)	1.2 (1)	0.3 (0.2)
17:1ω7	0.2 (0.1)	0.2 (0.1)	tr	0.2 (0.2)	0.2 (0.1)	0.2 (0.1)	tr	nd	nd	tr	nd	nd
17:1ω9	tr	tr	tr	tr	tr	tr	tr	tr	0.2 (0.1)	0.2 (0.1)	tr	tr
18:1ω5	tr	0.3 (0.2)	0.2 (0.2)	0.3 (0.1)	0.2 (0)	0.3 (0.1)	tr	tr	tr	tr	0.3 (0.2)	tr
18:1ω7	1.9 (0.7)	2.2 (0.6)	1 (1.3)	1.4 (0.7)	3 (1.1)	2.5 (0.9)	2.4 (1)	0.2 (0.2)	0.4 (0.3)	0.5 (0.6)	1.1 (0.4)	0.3 (0.5)
18:1ω9	7.1 (2.7)	6.7 (2)	1.9 (2.7)	6.2 (4.1)	9.7 (2.2)	6.4 (0.9)	6 (2.1)	0.7 (0.8)	2.9 (4.8)	3.2 (6.2)	7.3 (8)	0.5 (1)
20:1ω7	0.3 (0.3)	tr	tr	0.2 (0.1)	0.5 (0.3)	0.8 (0.6)	tr	tr	0.4 (0.4)	0.3 (0.2)	0.5 (0.2)	nd
20:1ω9	0.3 (0.2)	0.2 (0.1)	nd	tr	tr	0.2 (0.1)	tr	0.8 (1.4)	0.5 (0.8)	0.2 (0.3)	0.2 (0.2)	0.2 (0.3)
22:1ω9	tr	tr	tr	tr	tr	0.3 (0.1)	tr	nd	nd	tr	tr	nd
22:1ω11	0.4 (0.3)	tr	tr	tr	0.4 (0.3)	0.7 (0.5)	tr	nd	nd	0.5 (0.8)	0.2 (0.1)	nd
Σ MUFA	20.1 (7)	19.4 (4.9)	8 (10.9)	17.9 (10.3)	26 (4.4)	25.6 (1.6)	28.6 (10.7)	3.2 (1.4)	6.2 (5.2)	8 (8.5)	13.1 (10.3)	2.8 (2.3)
16:2ω4	tr	tr	tr	tr	tr	0.4 (0.1)	0.3 (0.2)	nd	nd	nd	nd	nd
16:2ω6	tr	tr	tr	tr	tr	tr	0.2 (0.3)	nd	nd	nd	nd	nd
16:3ω3	tr	tr	nd	tr	nd	0.3 (0.2)	0.2 (0.2)	nd	nd	nd	nd	nd
16:4ω1	tr	0.2 (0.1)	tr	0.4 (0.2)	tr	1.1 (0.5)	0.6 (0.3)	nd	nd	nd	nd	nd
16:4ω3	0.6 (0.3)	0.4 (0.2)	0.2 (0.2)	0.4 (0.1)	0.6 (0.1)	0.7 (0.2)	0.4 (0.3)	nd	nd	nd	nd	nd
18:2ω6	1.3 (0.8)	1.9 (0.7)	0.5 (0.8)	2.8 (1.4)	1.9 (0.4)	2.6 (0.3)	2 (0.9)	tr	0.3 (0.4)	0.5 (0.9)	1.1 (1.3)	tr
18:3ω3	0.9 (0.7)	0.6 (0.2)	0.3 (0.5)	0.7 (0.2)	1.2 (0.3)	0.8 (0.1)	0.5 (0.3)	tr	tr	0.2 (0.1)	0.2 (0.1)	tr
18:4ω3	1.7 (1.4)	1.3 (0.4)	0.3 (0.5)	0.7 (0.3)	1.9 (0.6)	2.4 (0.2)	0.5 (0.4)	nd	nd	tr	nd	nd
20:4ω6	tr	tr	nd	tr	nd	tr	0.2 (0.2)	nd	nd	tr	nd	nd
20:5ω3	2.6 (2.2)	3.7 (2.1)	0.7 (1)	2.7 (2.5)	2.7 (1)	9 (4.9)	6.2 (3.3)	nd	nd	tr	nd	nd
22:2ω9	tr	tr	0.4 (0.5)	0.3 (0.3)	tr	0.2 (0.1)	0.5 (0.4)	nd	nd	nd	nd	nd
22:5ω3	tr	0.3 (0.2)	nd	0.5 (0.2)	tr	0.4 (0.1)	0.3 (0.6)	nd	nd	tr	nd	nd
22:6ω3	3.7 (3.5)	2.4 (1.3)	0.6 (0.9)	0.9 (0.6)	4 (1.4)	3.6 (0.9)	0.8 (0.7)	tr	nd	tr	tr	tr
Σ PUFA	11.6 (9.2)	11.4 (5)	3.1 (4)	9.7 (5.1)	13 (3.9)	22.1 (6.7)	12.9 (5.9)	0.2 (0.1)	0.3 (0.4)	1.1 (1.6)	1.5 (1.5)	tr
Σ BrFA	3.8 (0.7)	3.4 (0.4)	4.5 (0.6)	3.2 (0.9)	3.6 (0.5)	2.8 (0.6)	1.6 (0.5)	3.5 (1.9)	3.1 (1.2)	2.5 (0.2)	2.9 (0.9)	4.2 (1)
Σ PUFA/Σ SFA	0.2 (0.3)	0.2 (0.1)	0.0 (0.1)	0.2 (0.1)	0.2 (0.1)	0.5 (0.2)	0.3 (0.2)	tr	tr	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Σ EFA	6.4 (5.7)	6.2 (3.4)	1.2 (1.9)	3.6 (3.1)	6.8 (2.4)	12.7 (5.8)	7.2 (3.9)	tr	nd	tr	tr	tr
16:1ω7/16:0	0.3 (0.2)	0.2 (0.1)	0.1 (0.2)	0.2 (0.2)	0.3 (0.1)	0.5 (0.1)	0.6 (0.3)	tr	tr	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
[FA] (mg/g)	8.0 (2.1)	9.5 (5.0)	2.6 (0.9)	11.3 (4.4)	9.4 (2.3)	7.2 (5.7)	0.7 (0.4)	3.9 (0.5)	4.9 (2.5)	5.8 (2.4)	8.4 (4.4)	0.2 (0.0)

In August, the FA profiles of the POM samples differed significantly depending on site and depth ($p\text{-value} < 0.01$) and without any interaction between these factors (Table 3). The depth variations in the POM FA profiles were not similar between stations. In fact, the FA profiles of s-POM and b-POM samples from Pass Hytten were rather similar (similarity = 73.1%), but those from Basalt Island differed more with depth (e.g. 18:1ω9 = 1.9% and 6.2% for s-POM and b-POM, respectively; Table 2). In samples from Kap Breusing, the FA profiles strongly differed between surface and bottom waters (similarity = 64.2%) with 20:5ω3 percentages higher in b-POM than in s-POM (9% *vs* 2.7%, respectively, Table 2). Considering spatial variability, FA profiles related to the s-POM from Basalt Island in August (Table 2) revealed much more degraded organic matter compared to those from other stations, with a higher sum of SFAs (84.4%), a lower sum of PUFAs (3.1%), and a much lower FA concentration (2.6 mg.g^{-1}) than in Pass Hytten and Kap Breusing (8.0 and 9.4 mg.g^{-1} respectively; pairwise test: $p\text{-value} < 0.001$). In contrast, the b-POM samples were rather similar between Basalt Island and Pass Hytten, while those from Kap Breusing had a distinct FA composition, with high PUFA and monounsaturated FA (MUFA) proportions (22.1% and 25.6% respectively, Table 2). This was particularly clear with FAs 20:5ω3 and 16:1ω7 reaching 9% and 12% in Kap Breusing, respectively, whereas they were less than 3.7% and 6.9% at the other two sites, respectively (Table 2). However, we did not observe any difference in FA concentration among stations ($p\text{-value} > 0.05$).

Table 3: Result of the two-way permutational multivariate analysis of variance (PERMANOVA) realized on the FA composition of summer and winter POM samples based the Bray Curtis dissimilarity matrix. Site (S) and depth (D) are tested as fixed factors. Significant p-values are displayed in bold.

Source of variation			POM - Summer		
	df	MeanSqs	F Model	R²	p-value
Site (S)	2	0.1360	5.7102	0.2809	**0.0014**
Depth (D)	1	0.1327	5.5725	0.1371	**0.0052**
S x D	2	0.0198	0.8324	0.0410	0.5088
Residuals	22	0.0238		0.5411	
			POM - Winter		
	df	MeanSqs	F Model	R²	p-value
Site (S)	1	0.0494	4.7766	0.2137	**0.0014**
Depth (D)	1	0.0251	2.4328	0.1088	**0.0494**
S x D	1	0.0222	2.1470	0.0960	0.0766
Residuals	13	0.0103		0.5815	

In May, the FA profiles differed significantly according to both site and depth ($p\text{-value} < 0.05$; Table 2) without any interaction between these two factors ($p\text{-value} = 0.077$). At both stations, POM appeared to be slightly more degraded in surface *vs* bottom waters, as shown by the higher proportion of SFAs in s-POM (Table 2). Considering spatial variability, a higher proportion of Σ SFA was observed in Pass Hytten than in Basalt Island (93.1 vs. 88.4 for s-POM and 90.4 vs. 82.5 for b-POM, respectively; Table 2). However, such depth and station differences were relatively weak, as attested by the strong similarity between the s-POM and b-POM (84.7% similarity) as well as the Basalt Island and Pass Hytten samples (81.7% similarity).

Sedimentary Organic Matter (SOM)

SOM exhibited strong seasonal differences with much higher proportions of SFAs in May; yet, these FAs represented only the half of the summer composition (Σ SFA = 92.2% vs. 56.9% for winter and summer, respectively). Similarly, only some traces of PUFAs were detected in May while their proportion reached 12.9% in August (Table 2). Summer PUFA and MUFA proportions were mainly linked to 20:5ω3 and 16:1ω7 contributions (18.3% and 6.2%, respectively; Table 2). Strong seasonal differences were also observed in the FA concentrations, which were three-fold more abundant during August (0.7 vs. 0.2 for August and May, respectively, Table 2). In contrast with the POM samples, no differences among stations were observed in SOM during August ($p\text{-value} = 0.066$) and May ($p\text{-value} = 0.168$).

Stable isotopes of POM and SOM samples

In August, depth appeared to be the first discriminating factor in $\delta^{13}C$ and $\delta^{15}N$ values among the POM samples. At each station, these $\delta^{13}C$ and $\delta^{15}N$ values differed significantly between surface and bottom waters ($p\text{-value} < 0.0001$), with overall more enriched values by 1‰ for $\delta^{13}C$ and 2‰ for $\delta^{15}N$ in b-POM (Figure 2). Globally, the isotopic signatures were closer between samples for the surface compared to the bottom stations. Moreover, no significant differences were observed between s-POM samples from Kap Breusing and Pass Hytten (for both $\delta^{13}C$ and $\delta^{15}N$ values) and between b-POM samples from Pass Hytten and Kap Breusing (only for $\delta^{15}N$ values, $p\text{-value} > 0.05$).

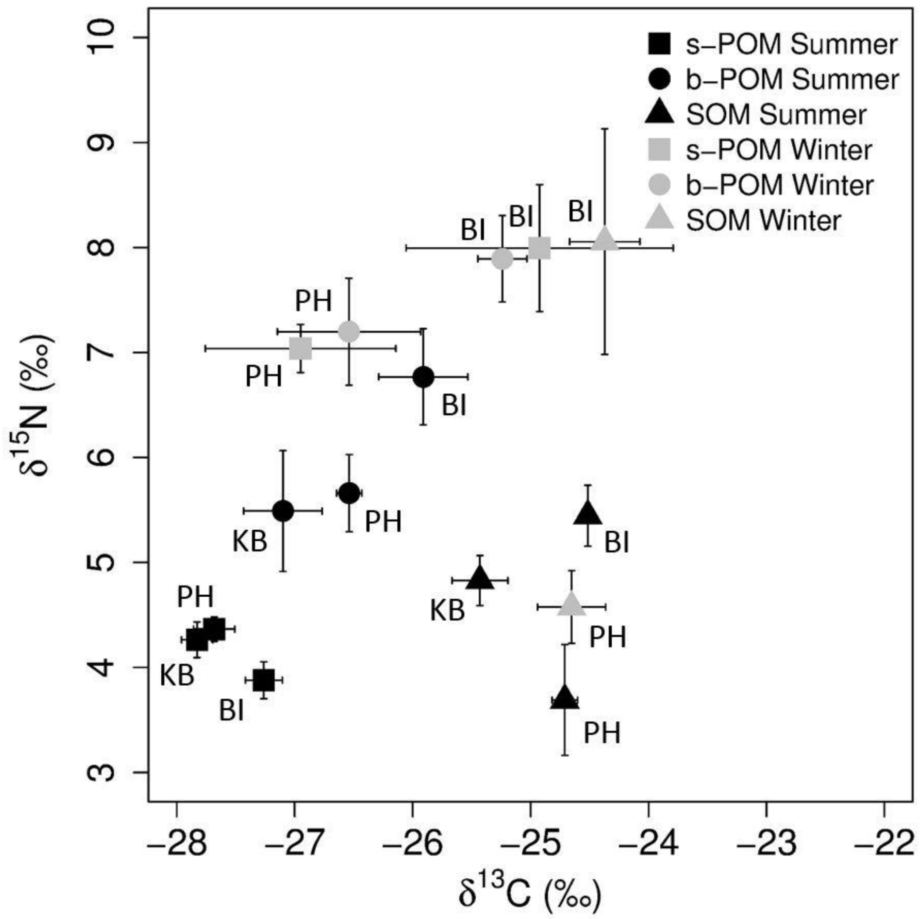

Figure 2: Mean δ13C and δ15N values of surface particulate organic matter (s-POM), bottom POM (b-POM), and sedimentary organic matter (SOM) from Pass Hytten (PH), Basalt Island (BI), and Kap Breusing (KB) collected during summer and winter.

In contrast, all isotopic ratios associated with the May samples increased an average of 1.2‰ and 2.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. These ratios did not vary significantly with depth within each station (p-value > 0.05, Figure 2), but for both s-POM and b-POM, they differed significantly between stations (p-value < 0.05, Fig. 2).

During summer, mean SOM $\delta^{13}C$ levels were more enriched, by 2.7‰ and 1.6‰, when compared to s-POM and b-POM, respectively (Figure 2). Spatial differences were also observed during this season, but they were not significant between Pass Hytten and Basalt Island for $\delta^{13}C$ values and between Basalt Island and Kap Breusing for $\delta^{15}N$ values (pairwise test: p-value > 0.05). During May, the $\delta^{13}C$ level did not differ between Pass Hytten and Basalt Island (p-value = 0.197), and this level was also similar to that from August (-24.7‰ in average for SOM from Pass Hytten and Basalt Island during both seasons, p-value > 0.05, Figure 2).

$\delta^{15}N$ values differed significantly between Pass Hytten and Basalt Island (p-value < 0.001) and increased when compared to August levels by 0.9‰ and 2.6‰ for Pass Hytten and Basalt Island, respectively (Figure 2).

Fatty acids profiles and isotopes values of bivalves

Fatty acids

FA signatures associated with the muscle and digestive gland samples of *M. truncata* differed between seasons (p-value < 0.01, Tables 4 and 5). For the muscle samples, such differences were mainly attributable to essential FA (EFA: here, the sum of 20:4ω6, 20:5ω3, and 22:6ω3) variations (41.7% *vs* 35.1% for August and May, respectively; Table 4). Temporal differences in the digestive gland data were especially obvious for the 20:5ω3/22:6ω3 ratio (14.5 *vs* 1.3 in August and May, respectively; Table 4) and for 16:1ω7 (22.5% *vs* 3.4% in August and May, respectively; Table 4). Interestingly, although FA profiles of muscles differed from those of digestives glands during August (p-value < 0.01, Table 5), they were not statistically different during May (p-value $= 0.322$, Table 5).

Table 4: Fatty acid (FA) composition of digestive gland (DG) and muscle (MU) tissues of Astarte moerchi and Mya truncata collected from Basalt Island and Daneborg during summer and winter. SFA: saturated FA, MUFA: monounsaturated FA, PUFA: polyunsaturated FA, BrFA: branched FA, EFA: essential FA (sum of 20:4ω6, 20:5ω3, and 22:6ω3 proportions), EPA/DHA: 20:5ω3/22:6ω3, nd: not detected, tr: trace (FA percentage <0.2%). Standard deviations are represented within brackets. FA percentages lower than 1% in all samples are not included in this table. Summer FA compositions of digestive glands and muscles from A. moerchi originated from De Cesare (2016) and De Cesare et al. (2017).

	Mya truncata				*Astarte moerchi*			
	August		May		August		May	
	Basalt Island				Daneborg		Basalt Island	
	DG	MU	DG	MU	DG	MU	DG	MU
	N = 5	N = 5	N = 4	N = 5	N = 10	N = 6	N = 5	N = 4
14:0	2.7 (0.6)	0.9 (0.1)	1.1 (0.4)	1.2 (0.1)	2.5 (0.7)	1.7 (0.7)	2.4 (0.4)	0.7 (0.2)
16:0	14.7 (0.5)	13.5 (1.1)	12.1 (2.9)	13.7 (1.2)	10.4 (0.4)	21.9 (5.8)	11.5 (1.3)	16.1 (1.5)
17:0	0.3 (0)	0.5 (0)	0.6 (0.1)	0.6 (0.1)	0.3 (0.1)	1.2 (0.4)	0.5 (0.1)	1.3 (0.1)
18:0	2.3 (0.5)	5.9 (1)	6.1 (1.7)	6.6 (1.7)	1.2 (0.4)	15.6 (11.2)	1.7 (0.6)	4.7 (0.5)
Σ SFA	20.3 (0.7)	21.3 (1.3)	20.7 (3.3)	22.8 (2.7)	14.6 (0.5)	42 (18.8)	16.6 (1.8)	23.3 (2.3)
16:1ω5	0.4 (0)	tr	tr	tr	1.6 (0.4)	1.1 (0.3)	1.2 (0.2)	0.3 (0)
16:1ω7	22.5 (4.3)	5.4 (0.8)	3.4 (1)	4.5 (0.8)	22.6 (5.5)	11.9 (4.5)	12.7 (3.2)	3.6 (0.8)
18:1ω5	0.5 (0.1)	0.3 (0)	0.4 (0)	0.3 (0.1)	4.5 (0.5)	5.5 (1.9)	4.6 (0.6)	5.7 (0.5)
18:1ω7	6.9 (0.7)	2.5 (0.2)	2 (0.6)	2.1 (0.4)	6.9 (1)	5.3 (1.8)	5.6 (0.5)	3.7 (0.5)
18:1ω9	0.8 (0.3)	2.6 (0.4)	2.6 (1.3)	2.9 (0.3)	1.3 (0.1)	2.9 (0.8)	2 (0.3)	2.3 (0.2)
20:1	1.7 (0.7)	6.9 (0.4)	nd	nd	1.3 (0.4)	1 (0.8)	nd	nd
20:1ω11	nd	nd	2.2 (0.4)	2.2 (0.4)	1.5 (0.8)	1 (0.7)	2.3 (0.6)	2.2 (0.2)
20:1ω7	1.7 (0.8)	3.5 (0.4)	5.1 (0.9)	4.1 (0.3)	2.9 (0.9)	3 (1.2)	3 (0.4)	3.7 (0.3)
20:1ω9	nd	nd	2.8 (0.4)	4.9 (0.8)	0.4 (0.2)	0.2 (0.2)	0.7 (0.2)	0.4 (0.1)
22:1ω9	nd	nd	2.3 (3.7)	0.4 (0.5)	tr	nd	0.4 (0.2)	0.3 (0.2)
Σ MUFA	35 (3.9)	21.5 (1.3)	22.1 (5.8)	23.3 (0.7)	43.6 (2.4)	32.2 (9.7)	33.2 (2.2)	22.6 (1.8)
18:4ω3	1.4 (0.2)	0.8 (0.4)	2.7 (1.2)	2.8 (1.2)	1.4 (0.3)	0.6 (0.6)	1.2 (0.1)	0.7 (0.4)
20:2 NMI	1 (0.7)	5.9 (0.8)	8.8 (3)	7.5 (2.7)	0.3 (0.1)	tr	0.2 (0.1)	tr
20:2ω9	nd	nd	nd	nd	1.1 (0.6)	1.1 (0.6)	1.3 (0.4)	2.5 (0.8)
20:4ω6	0.7 (0.2)	2.7 (0.2)	3.5 (0.5)	2.9 (0.2)	1.2 (0.9)	1.9 (1.1)	1.8 (0.3)	5.8 (0.5)
20:5ω3	32 (2.2)	22.4 (1)	17.8 (6.9)	17 (2.8)	25.9 (1.1)	12.5 (6.1)	29.5 (1.9)	17.8 (1.6)
21:5ω3	0.8 (0.2)	1.2 (0.2)	0.9 (0.6)	1.2 (0.3)	0.6 (0)	0.4 (0.4)	0.7 (0.1)	1 (0.1)
22:2ω6	tr	0.4 (0.1)	tr	tr	1.2 (0.5)	0.7 (0.6)	1.4 (0.4)	1.8 (0.2)
22:2ω9	tr	0.6 (0.1)	0.2 (0.3)	0.3 (0.2)	0.7 (0.4)	0.5 (0.4)	1 (0.3)	1.2 (0.3)
22:4ω6	tr	1.5 (0.3)	3.5 (1.6)	2.1 (0.3)	nd	nd	0.3 (0.1)	0.4 (0.1)
22:5ω3	tr	2 (1.1)	2.2 (0.6)	2.9 (0.5)	0.6 (0.4)	0.7 (0.9)	1 (0.2)	4.1 (0.7)
22:5ω6	tr	0.4 (0.1)	0.9 (0.5)	0.8 (0.5)	tr	1 (1.3)	0.3 (0.1)	0.8 (0.4)
22:6ω3	3.4 (2.4)	16.6 (1.3)	13.8 (2.6)	13.8 (1.5)	3.2 (0.5)	2.8 (2)	6.7 (1.6)	14.5 (1.9)
Σ PUFA	44.5 (4.1)	56.2 (1.6)	55.9 (6.6)	52.7 (3.2)	41.1 (2.4)	24.1 (11.3)	49.3 (1.1)	52.7 (3.9)
Σ BrFA	0.3 (0.1)	1 (0.1)	1.3 (0.5)	1.1 (0.3)	0.6 (0.2)	1.7 (1.1)	0.9 (0.2)	1.4 (0.2)
Σ EFA	36.1 (4)	41.7 (2.2)	35.1 (8.4)	33.8 (2.7)	30.3 (1.4)	17.2 (8.7)	38 (0.6)	38 (3.2)
Σ PUFA/Σ SFA	2.2 (0.2)	2.7 (0.2)	2.8 (0.6)	2.4 (0.5)	2.8 (0.2)	0.8 (0.6)	3 (0.3)	2.3 (0.4)
EPA/DHA	14.5 (10.9)	1.4 (0.1)	1.3 (0.4)	1.3 (0.3)	8.4 (1.4)	5 (1.2)	4.7 (1.7)	1.2 (0.2)
[FA] mg/g	NA	NA	21.9 (21.1)	4.5 (2.4)	123.4 (48.3)	19.9 (7.5)	51.8 (24.5)	3.9 (0.4)

Table 5: Result of the one-way permutational multivariate analyses of variance (PERMANOVA). The upper part relates to the FA composition of digestive gland (DG) and muscle (MU) tissues of Astarte moerchi and Mya truncata, with season as a fixed factor. The lower part relates to the FA composition of A. moerchi and M. truncata from summer (Sum.) and winter (Win.) seasons, with tissue as a fixed factor.

Tested group			Season as fixed factor		
	df	MeanSqs	F Model	R^2	p-value
M. truncata DG	1	0.4866	36.8920	0.8405	**0.0062**
M. truncata MU	1	0.0931	20.9360	0.7235	**0.0074**
A. moerchi DG	2	0.1092	16.6220	0.6129	**0.0001**
A. moerchi MU	2	0.2220	7.2209	0.4593	**0.0005**
			Tissue as fixed factor		
	df	MeanSqs	F Model	R^2	p-value
M. truncata May.	1	0.0166	1.175	0.1437	0.3220
M. truncata Aug.	1	0.3589	99.035	0.9253	**0.0084**
A. moerchi May.	1	0.3243	48.958	0.7776	**0.0001**
A. moerchi Aug.	1	0.4510	19.831	0.5862	**0.0001**

For *A. moerchi* tissues, both muscles and digestive glands had distinct FA profiles between seasons (p-value < 0.001, Table 5). The highest PUFA and EFA percentages for digestive glands were found in May (Table 4). In contrast, MUFAs were dominant during August, mainly due to twice higher values of 16:1ω7 compared to May (Table 4). A similar trend was observed for muscle FA profiles, with May contributions of EFA and PUFA double those of August (e.g., fivefold higher in May for 22:6ω3 = 14.5% vs. 2.8%, Table 4).

Isotopes

Although isotopic signatures of the digestive glands of *A. moerchi* ($\delta^{13}C$ = -24.2‰ and $\delta^{15}N$ = 6.5‰) and *M. truncata* ($\delta^{13}C$ = -24.7‰ and $\delta^{15}N$ = 6.2‰) were similar during August, they were more distinct in May (Fig. 3). In fact, seasonal differences for $\delta^{13}C$ and $\delta^{15}N$ were observed in *M. truncata* (+3‰ and +1.5‰ between August and May for $\delta^{13}C$ and $\delta^{15}N$ [p-value < 0.05], respectively, Fig. 3) but not in *A. moerchi* (+0.4‰ and -0.2‰ between August and May for $\delta^{13}C$ and $\delta^{15}N$ [p-value > 0.05], respectively, Fig. 3). Regarding muscle tissues, no seasonal variations of $\delta^{13}C$ and $\delta^{15}N$ were observed in either species (Figure 3), and no inter-specific variations were observed during each season (p-value > 0.05).

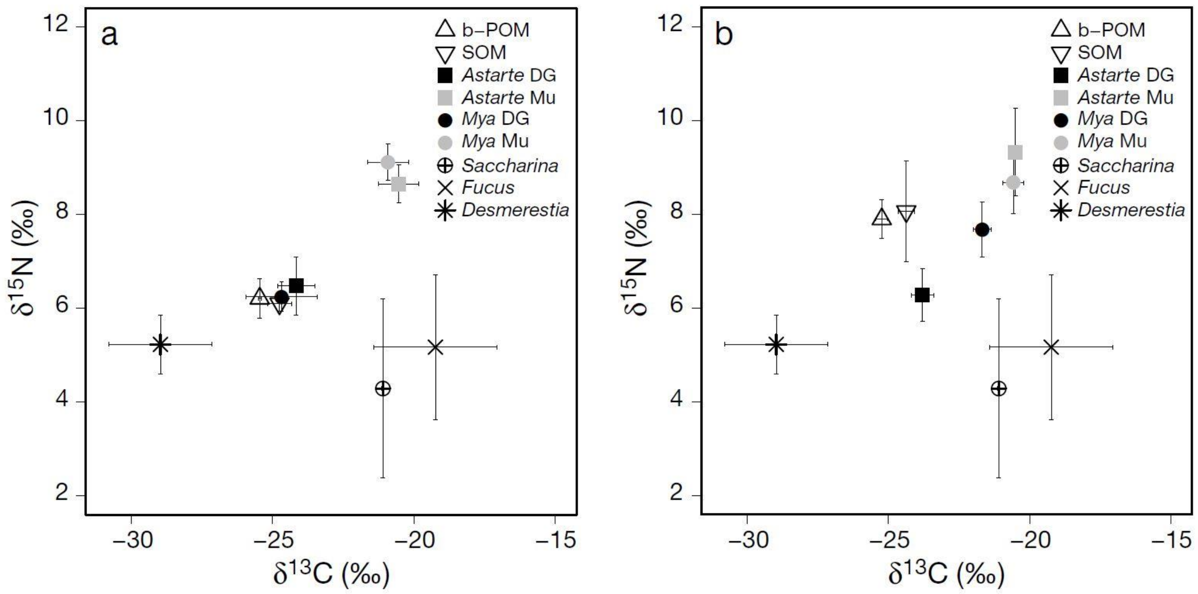

Figure 3: Mean δ13C and δ15N values of Astarte moerchi and Mya truncata tissues and their potential food sources during (A) summer and (B) winter. b-POM: bottom-particulate organic matter, SOM: sedimentary organic matter, DG: digestive gland, MU: muscle. Errors bars represent the standard deviation. Stable isotope values from macroalgae and b-POM, SOM, and Astarte's tissues from wintertime originated from De Cesare (2016) and De Cesare et al. (2017).

In May, carbon and nitrogen isotopic values of s-POM, b-POM, and macroalgae samples clearly differed from those of digestive gland and muscle tissues in both bivalves (Figure 3b). In contrast, isotopic values of A. moerchi and M. truncata became closer in summertime to POM and SOM values (Figure 3a).

Discussion

Influences of season and spatial constraints on the POM and SOM patterns

Seasonal patterns

There have been few studies of the seasonal variability between ice cover and open sea periods in the main pelagic and benthic food sources of bivalves in High Arctic coastal areas (but see Connelly et al. 2015, Connelly et al. 2016). This work constitutes the first contribution for the Young Sound fjord. During the productive summer period, FA composition of the POM in bottom waters revealed the dominant contribution of several photosynthetic producers, such as diatoms (16:1ω7, 20:5ω3), dinoflagellates (18:4ω3, 22:6ω3), and macroalgae (18:2ω6, 18:3ω3, 18:4ω3, 20:5ω3). Moreover, relative high summer abundances of essential FAs (e.g. 20:5ω3, 22:6ω3, 18:4ω3) in animals and bivalves contrast with the winter situation. In winter, with the absence of *in situ* primary production, POM was highly degraded; this was reflected by the large proportion of total SFA (Rhead et al. 1971, Connelly et al. 2015, Connelly et al. 2016). Very low levels of total PUFAs during May (i.e. <1.5%) indicate that the extended duration of ice and snow cover in Young Sound is paired to the absence of fresh organic matter for primary consumers compared to other Arctic fjords (e.g. Σ PUFA = 14.3%–39.8% in Kongsfjorden, 13.4% in Rijpfjorden; Leu et al. 2006, Leu et al. 2011). In fact, in May after 4–5 months in darkness, the POM lipid concentrations measured in Young Sound (2.6–11.3 mg/g) are much lower than in any other Arctic fjord (for example, 95.4–98.6 mg/g in Kobbefjord; Gaillard et al. 2017). In May, despite 24-hour daylight, the presence of snow on the sea ice prevents the transmission of light (Glud et al. 2007), and primary production does not start before mid-July when melt-water ponds that form on the sea ice intensifies light transmission. This in turn triggers a short algal bloom (Rysgaard et al. 1999). PAR sensors fixed at 1 m depth below the sea ice revealed no available PAR for primary producers in May (Mikael Sejr, unpublished data). For SOM, seasonal changes in FA composition show the same trends as in May POM, as shown by low FA and total PUFA concentrations. In contrast, diatoms dominate the SOM during the summer, as revealed by higher relative proportions of 16:1ω7 and 20:5ω3, whereas dinoflagellates (18:4ω3, 22:6ω3) and macroalgae markers (18:2ω6, 18:3ω3, 20:4ω6, 20:5ω3) suggest additional contributions of these primary sources to the pool of organic matter.

The absence of significant primary production in May is confirmed by a general increase in δ^{15}N in both POM and SOM. Indeed, food webs from sea ice–covered ecosystems switch to heterotrophy during the polar night due to the development of protozoans and/or microbial planktonic communities (Berge et al. 2015). As heterotrophic microorganisms may be consumers of organic matter, their isotopic signatures should be enriched in $\delta^{15}N$ when compared to autotrophic algae (Hoch et al. 1996, Tamelander et al. 2009). Hence, such $\delta^{15}N$ enrichment could explain the seasonal increase of the $\delta^{15}N$ in POM during winter (Tamelander et al. 2009, Kędra et al. 2012), but it also may reflect the increased contribution of animal detritus and fecal pellets (Sampei et al. 2012) and diagenesis (Schulz and Zabel 2006).

Spatial patterns

The Marine Basis monitoring program has conducted annual surveys in August since 2003 that documented the strong influence of terrestrial runoff on the water column, especially in surface waters (above 10 m depth), as attested by lower salinity and higher turbidity measurements (Citterio et al. 2017, Middelbo et al. 2018). This influence of direct freshwater inputs is confirmed by s-POM $\delta^{15}N$ values (4.2 ± 0.3‰), which are almost identical with riverine $\delta^{15}N$ values (4.3 ± 0.3‰, Zackenberg River, Rysgaard and Sejr 2007). Poorer organic matter quality in s-POM compared to b-POM (as expressed by the high levels of Σ SFA and low levels of Σ PUFA) suggests an increase in the relative proportion of detrital particles compared to living cells in surface waters (Leu et al. 2006, Mayzaud et al. 2013). Such observations are likely explained by the inflow of nutrient-depleted freshwater (confined to surface waters), which may both discharge a huge amount of terrestrial detrital particles and decrease primary productivity (Mayzaud et al. 2013, Meire et al. 2016, Meire et al. 2017). This hypothesis is consistent with previous findings in Young Sound, which showed lower chlorophyll-a concentrations in the most runoff-exposed parts of the fjord (Meire et al. 2016, Arendt et al. 2016, Middelbo et al. 2018).

Overall, POM from Young Sound bottom waters was nutritionally richer than that from surface waters, as reflected by higher proportions of EFA. However, the related $\delta^{13}C$ and $\delta^{15}N$ values were highly variable among the stations, and we hypothesize that this could be attributable to their differential exposure to freshwater inputs. Thus, higher $\delta^{13}C$ and $\delta^{15}N$ found in b-POM in Pass Hytten and Basalt Island could be explained by greater exposure of inner fjord waters to nutrient-depleted and CO_2-desaturated freshwater inputs (Tamelander et al. 2009, Meire et al. 2015, Meire et al. 2016). It also possibly indicates more degraded organic matter at the inner stations due to higher bacterial activity (McTigue et al. 2015). These spatial SI discrepancies may also reflect different bloom dynamics (duration, kinetics) among stations, since isotopic signatures generally show an enrichment during a bloom (Savoye et al. 2003, Tamelander et al.

2009). In addition, the higher percentages of diatom and dinoflagellate markers (see above details) in Kap Breusing may reflect local primary productivity that is higher in the outer than in the inner part of the fjord. Accordingly, Meire et al. (2016) showed that upwelling of nitrate and phosphate-rich waters around the fjord's mouth sustains a high phytoplankton biomass throughout the summer.

Identifying and quantifying the sources of organic matter in superficial marine sediments is a difficult task, as terrestrial inputs, benthic primary producers (including microphytobenthos and macroalgae), and sedimentation of POM may all be present. For instance, SOM quality and quantity may be affected by benthic organisms through bioturbation, burrowing, use of organic matter, and excretion (e.g. Glud et al. 2000). Although FA analysis results show an input of macroalgae to the SOM, their contributions should be rather limited. Indeed, previous compound-specific isotopic analyses excluded the contribution of *Desmarestia aculeata* to the pelagic and benthic pool of organic matter (De Cesare et al. 2017, Bridier's unpublished data). In addition, the *Fucus* sp. and *Saccharina latissima* contributions seem relatively weak, as $\delta^{13}C$ values of both species (19.2 ± 2.2‰ and -21.1 ± 0.0‰, respectively) strongly differ from the SOM $\delta^{13}C$ value (-24.9 ± 0.6‰). According to published $\delta^{13}C$ signatures of Arctic microphytobenthos (from -23.9‰ to -20.0‰; Oxtoby et al. 2016), riverine POM (-25.6 ± 0.1‰, Zackenberg River; Rysgaard and Sejr 2007), and b-POM measured in the present study (-26.5 ± 0.6‰), the SOM $\delta^{13}C$ values probably reflect either (1) a strong contribution of terrestrial organic matter associated with a minor contribution of microphytobenthos, or (2) an equal contribution of marine b-POM and microphytobenthos to SOM. According to the C/N ratios calculated from the Young Sound (18.3 ± 1.7, 10.3 ± 0.2, and 9.1 ± 0.2 for the SOM of Pass Hytten, Basalt Island, and Kap Breusing, respectively) and riverine data ($10 < C/N$ ratio < 40, Zackenberg river; Rysgaard and Sejr 2007), the FA composition of Kap Breusing sediment should be less influenced by terrestrial inputs than the other two sites. Moreover, FA profiles of Kap Breusing and Basalt Island sediments display the highest percentages of diatom markers (16:1ω7, 16:4ω1, and 20:5ω3), strongly suggesting that the associated SOM originates from both microphytobenthos and sedimented phytoplankton (second scenario). In contrast, sediments from Pass Hytten should receive organic matter from dominant terrestrial inputs with a low contribution from marine primary producers (first scenario).

Comparing marine and riverine POM and SOM $\delta^{13}C$ values, Rysgaard and Sejr (2007) estimated that half of the Young Sound's sediment organic carbon came from terrestrial sources. However, the marine POM $\delta^{13}C$ value (-21.6 ± 0.3‰) used for their estimate originates from a study conducted by Hobson and Welch (1992) in Barrow Strait (NE Canada) that differs from those found here (-26.5 ± 0.6‰, present study; -25.5 ± 0.1‰; De Cesare et al. 2017). Although Young Sound's POM $\delta^{13}C$ isotopic ratios may vary across years, multiannual values relative to a site close to Ny-Ålesund (Kongsfjorden, Svalbard) during May vary slightly between 2007, 2012, and 2013 (-21.6 ± 0.2‰, -22.7‰, and -23.1 ± 0.4‰, respectively; Renaud et al. 2011, De Cesare 2016, Calleja et al. 2017). We therefore suggest that differences in POM $\delta^{13}C$ values between Young Sound and Barrow Strait do not depend on temporal variations, and that future work on the contribution of terrestrial organic matter to SOM should be based on local POM $\delta^{13}C$ values.

Diet of *Astarte moerchi* and *Mya truncata*

Since sampling of bivalves was conducted over two different years, the seasonal comparison of FA profiles and SI signatures probably reflects both seasonal and interannual variabilities of their food sources. However, as the FA profiles of arctic bivalves are usually more sensitive to seasonality than interannual variability (e.g. Birkely et al. 2003), we are confident that the FA profiles from a specific origin and season will be quite stable between years. Moreover, because of the huge seasonality of the Young Sound's physical environment and carbon transport (Rysgaard et al. 2003), the bivalves' food sources should also display much higher seasonal than interannual variations. In contrast, it is more difficult to distinguish seasonal from interannual variability in bivalves' SI signatures, since they vary minimally between seasons and years (Renaud et al. 2011, Kędra et al. 2012, McTigue and Dunton 2014, Gaillard et al. 2017). Thus, seasonal differences in bivalves' SI signatures should be interpreted with caution.

Usually, FA associated with neutral lipids (used as energy storage) is directly mobilized from the diet, while polar FA (cell membrane components) is subjected to strong physiological regulation (Jezyk and Penicnak 1966, Napolitano and Ackman 1992, Pazos et al. 2003, Gaillard et al. 2015). Since the digestive gland has a lipid storage function, this tissue displays high levels of neutral compared to polar lipids. In contrast, muscle tissue contains low levels of neutral and thus higher proportions of polar lipids (Napolitano and Ackman 1992, Pazos et al. 2003). For that reason, digestive glands usually have a higher lipid turnover rate and diet sensitivity, whereas muscles are more sensitive to physiological regulation (Napolitano and Ackman 1992, Napolitano et al. 1997, Nérot et al. 2015). Such inter-tissue differences were also evident in the present study; unlike digestive glands for which high levels of 20:5ω3 and

22:6ω3 are always associated with high levels of diatoms or dinoflagellates dietary FA markers, these two FAs were not associated with high levels of their dietary FA markers in muscle. Therefore, the selective retention of 20:5ω3 and 22:6ω3, which are two EFAs (Soudant et al. 1996, Parrish 2009), confirms that muscle and digestive glands may constitute real proxies of bivalves' diet and physiological conditions, respectively.

During summer, the FA compositions and isotopic signatures of the digestive glands of *A. moerchi* and *M. truncata* were very similar. This suggests that both bivalves have the same diet dominated by diatoms, as shown by the high proportions of 16:1ω7 and 20:5ω3, which are also found in POM and SOM during summer (De Cesare et al. 2017). Such strong similarities in FA profiles between bivalves and their food sources indicate tight benthic-pelagic coupling as well as an efficient organic matter transfer from primary producers to primary consumers in the Young Sound food web. If we consider the summer FA composition of muscles, both species exhibit rather good physiological states as indicated by high levels of EFAs, as these are essential for somatic growth, reproduction, and the maintenance of cell membrane fluidity (Soudant et al. 1996, Parrish 2009).

During winter, $\delta^{13}C$ values associated with POM, SOM, and macroalgae sources were too distinct from those of digestive glands and muscles, thus these sources were unlikely to contribute to the bivalves' diet. Although macroalgae $\delta^{13}C$ values may slightly fluctuate between seasons (Vizzini and Mazzola 2003), the lack of macroalgal FA markers in bivalve tissues provides evidence that macroalgae were not consumed during winter. We thus suggest that poor trophic environmental winter conditions, evidenced by highly degraded organic matter sources, induce a drastic decrease and more likely an interruption in the feeding activity of both bivalves. Such winter quiescence has previously been observed in bivalves (Pernet et al. 2007, Comeau et al. 2012) but contrasts with numerous studies reporting the persistence of long-term "food banks" in polar benthic ecosystems (e.g., Mincks et al. 2005) that fuel many organisms by labile detritus (McClintock 1994, Mincks et al. 2008, McMeans et al. 2015, Silberberger et al. 2018). This is not the case in Young Sound fjord, where the survival of *A. moerchi* and *M. truncata* individuals relates to their reliance on energetic reserves under a poor trophic winter environment. Moreover, each species displays a distinct pattern in its ability to use these lipids. Hence, the similar FA profiles observed during winter between digestive glands and muscle tissues of *M. truncata* may reflect a depletion of its lipid reserves. This phenomenon will induce a decrease in the concentration of neutral lipids (constituent of the lipid reserves in digestive glands) and will mechanically increase the proportion of polar lipids in this tissue (i.e., there will be a higher proportion of polar lipids in winter for a similar concentration between the two seasons). Hence, the similar lipid class composition between digestive glands and muscles may increase the similarity in their lipid profiles. The seasonal increase of digestive gland $\delta^{13}C$ values may strengthen this hypothesis, since lipids are more depleted in $\delta^{13}C$ than in other compounds (Lorrain et al. 2002). The increase in $\delta^{13}C$ and $\delta^{15}N$ may also reflect the impact of starvation on *M. truncata* metabolism (Hertz et al. 2015, Doi et al. 2017). A simultaneous percentage decrease in 20:5ω3 and 22:6ω3 with a percentage increase in 20:2 NMI (non-methylene-interrupted) FA also confirms the poor physiological state of *M. truncata* during winter. In fact, NMI biosynthesis should be critical for this species for maintaining both structure and fluidity of their cell membranes in the face of a decrease in PUFA levels (Pernet et al. 2007, Gaillard et al. 2015). The lipid reserves were less depleted in winter for *A. moerchi* than *M. truncata*. In fact, the winter FA concentration in digestive glands for *A. moerchi* was twice as high as for *M. truncata*, and the proportions of EFA and FA trophic markers remain high compared to those in summer. Such species-specific seasonal patterns of lipid reserves could be explained by (1) differential lipid mobilization during winter, or (2) the differential ability to build lipid reserves during the rise in primary production. Data from the present study do not support one hypothesis over the other. For instance, the first hypothesis may reflect the bivalves' ability to reduce their metabolic rate or their reproduction investment. However, both species show a similar decrease in their ω3/ω6 ratio during winter, which may indicate that they devote similar efforts to reproduction (Leroy et al. 2013, De Cesare 2016). Likewise, little information is available about their ability to reduce their metabolic rate during starvation or any other physiological stress (e.g. Abele-Oeschger and Oeschger 1995, Camus et al. 2003). Hence, further studies, such as in situ measurements of bivalve metabolic rate or clearance rates during winter or observations about their ability to store lipid during a short food supply (e.g. as for *Yoldia hyperborea*; Stead et al. 2013), will be thus helpful to better explore such hypotheses.

Finally, about 30% of Young Sound's seafloor is below 100 m depth (Rysgaard et al. 2003), and the link between filter feeders and primary producers in deeper basins may differ from our results from shallow areas. Although vertical carbon fluxes at both shallow and deeper depths have not been quantified in this fjord, the very low abundance of benthic macrofauna at 85 m depth (Glud et al. 2000, Sejr et al. 2000) suggests a decrease in carbon transfer to deeper areas via pelagic-benthic coupling (Ambrose and Renaud 1995). However, because similar C/N ratios were found at 20 and 163 m depth (Glud et al. 2000), we hypothesize that organic matter transfer from the surface to deeper basins would be fast enough to fuel benthic filter-feeding species with relatively fresh organic matter (i.e., similar to that in shallow waters). Such tight pelagic-benthic coupling has previously been reported up to 600 m depth in the High Arctic Canadian archipelago for the filter-feeding bivalve Bathyarca glacialis (Gaillard et al. 2015).

Conclusion and outlooks

Extremely long sea-ice cover deprives Young Sound of fresh primary production during most of the year, while freshwater inputs strongly degrade the quality of organic matter in surface waters and seems to control the primary production dynamics within bottom waters during summer. However, distinct adaptations are observed among filter-feeding bivalves to cope with the long winter conditions: *A. moerchi* seems to be best adapted to live on stored energy reserves, whereas the depletion of *M. truncata's* lipid reserves during May suggest it has less energetic margin to survive the winter.

In the face of climate change, Young Sound will be exposed to a continued freshening of its surface water masses, preventing the renewal of deeper basin water masses in the inner fjord (e.g. Sejr et al. 2017, Boone et al. 2018). Numerous studies have highlighted the effect of such a freshening on the Young Sound's primary productivity through a decrease in light (Murray et al. 2015) and nutrient availability (Meire et al. 2016). Results from our study suggest that this decrease in primary productivity may be amplified by a decrease in organic matter quality in the inner parts of this fjord. In contrast, the outer part of Young Sound may be less affected by this freshening due to its sill, which allows nutrient replenishment through vertical mixing (Meire et al. 2016). However, such impoverishment of the trophic environment in the inner fjord may weaken the ability of some primary consumers (e.g. *Mya truncata*) to accumulate enough lipid reserves during summer to cope with winter conditions, and this might have cascading effects on their survival and renewal potential. Considering the key functional role of such filter-feeding bivalves for the transfer of organic matter toward higher trophic levels, such a shift could impact the entire benthic food web from primary producers to mammals, especially walrus that can consume up to 57 kg of fresh *Mya truncata* per day (Born et al. 2003).

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Chapter II

Sources, quality and transfers of organic matter in a highly-stratified sub-Arctic coastal system (Saint-Pierre-et-Miquelon, NW Atlantic)

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Abstract

In response to ongoing global climate change, marine ecosystems in the northwest Atlantic are experiencing one of the most drastic increases in sea surface temperatures in the world. This warming can increase water column stratification and decrease surface nutrient concentrations, in turn impacting primary productivity and phytoplankton assemblages. However, the impacts of these changes on sources and quality of organic matter as well as its transfer to the benthic compartment remain uncertain. This survey characterized organic matter sources and quality within a highly-stratified sub-Arctic coastal system (Saint-Pierre and Miquelon) and described its transfer towards a dominant primary consumer, the sand dollar *Echinarachnius parma*. This study analyzed fatty acid and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) composition of surface and bottom Particulate Organic Matter (s-POM and b-POM, respectively), Sedimentary Organic Matter (SOM) and sand dollar tissue along a nearshore to offshore gradient during two contrasting seasons associated either with sharp or weak water column stratification (i.e. High *vs* Low Stratification Periods). Results revealed high relative abundances of polyunsaturated fatty acids (notably macro- and microalgae markers) in POM during the Low Stratification Period while the High Stratification Period was characterized by elevated relative abundance of saturated fatty acids indicating a higher organic matter degradation state. In addition, strong seasonal differences were also observed in food availability with four-fold higher concentrations in total suspended solids during Low *vs* High Stratification Periods. These results suggested thus multiple negative effects of stratification on pelagic-benthic coupling and POM quality. Lower nutrient repletion of surface waters during period of sharp stratification diminishes pelagic-benthic coupling by reducing food availability, POM quality and vertical transfer of organic matter. By contrast, the sediment-based diet of *E. parma* showed a low spatiotemporal variability reflecting the homogenous composition of the SOM. This study suggests that intensified water column stratification due to increasing sea surface temperatures may modify the pelagic-benthic coupling and future quality and composition of POM pools.

Key words

Pelagic-benthic coupling • Seasonal stratification • Organic matter • Fatty acids • Stable isotopes • Subarctic ecosystems • Saint-Pierre et Miquelon archipelago • Newfoundland Shelf

Introduction

Coastal benthic ecosystems are highly productive areas (e.g. Clavier et al. 2014) that provide essential ecosystem services such as seafood production and carbon sequestration (Barbier et al. 2011, Pendleton et al. 2012). However, their functioning and services can strongly depend on the quality and quantity of organic matter made available in the ecosystem through processes like bioturbation, nutrient cycling and secondary production (Müller-Navarra et al. 2004, Wieking and Kröncke 2005, Snelgrove et al. 2014, Campanyà-Llovet et al. 2017). Decreases in the Particulate Organic Matter (POM) quality and quantity for example can reduce the efficiency of organic matter transfers to higher trophic levels. Benthic food webs may suffer subsequent impacts (i.e. shift from fresh organic matter-based to detritus-based food webs) including a decline in benthic secondary/tertiary production (e.g. Iken et al. 2010). The dependency of benthic ecosystems on organic matter quality and quantity suggests that perturbations to organic matter sources and fluxes induced by rising sea surface temperatures may also perturb pelagic-benthic coupling (defined here as the vertical flow of organic matter from the surface to the seafloor) (Campanyà-Llovet et al. 2017, Griffiths et al. 2017).

Previous studies have investigated how pelagic-benthic coupling may evolve with declining surface water nutrient concentrations expected from rising sea surface temperatures and enhanced water column stratification (e.g. Wassmann & Reigstad 2011, Harrison et al. 2013, Randelhoff et al. 2020). A decrease in surface water nutrient concentrations may lead to a drop in phytoplankton production (Riebesell et al. 2009, Turner et al. 2015, D'Alelio et al. 2020) associated with pronounced shifts in the composition of phytoplankton communities (from large diatoms to smaller cells as flagellates; Kiørboe 1993, Finkel et al. 2010). In addition, warmer surface temperatures in thermally-stratified waters can enhance POM degradation by increasing heterotrophic bacteria metabolic activity (Piontek et al. 2009, Wohlers et al. 2009). These reduce carbon fluxes towards bottom waters (Bopp et al. 2005, Turner et al. 2015, Griffiths et al. 2017). In contrast, the impacts of increased stratification on the quality and composition of the organic matter exported towards the seafloor as well as their consequences on the benthic food webs remain unknown.

This research investigated the quality and sources of organic matter (i.e. surface and bottom Particulate Organic Matter, or s-POM and b-POM, respectively, and Sedimentary Organic Matter, or SOM) and their transfers towards a dominant secondary producer, the sand dollar *Echinarachnius parma* in a highly stratified coastal marine ecosystem of the sub-Arctic archipelago Saint-Pierre and Miquelon (SPM) in the NW Atlantic. SPM is an ideal study area due to an exceptionally sharp vertical water column stratification in late-August/mid-September, when temperatures drop abruptly from 18°C at the surface to 0-2°C at 80 m depth (Lazure et al. 2018, Poitevin et al. 2018). Climate change is expected to intensify this stratification. The Newfoundland-Labrador continental shelf is experiencing one of the highest increases in sea surface temperature in the world (i.e. + 1°C between 1982 and 2006, Belkin et al. 2009). A recent study also detected diurnal internal waves along SPM's shallow continental shelf (30 – 60 m depth) during the stratified season (Lazure et al. 2018). Although these waves remain poorly studied, they play a critical role in near shore ecosystem functioning by stimulating nutrient replenishment and primary production in surface waters through increased turbulence and mixing through the pycnocline (Wang et al. 2007, Jantzen et al. 2013, Woodson 2018). Increased stratification can make the thermocline less responsive to perturbations generated by internal waves (i.e. less turbulence and thermocline vertical motion, Woodson 2018). Given these oceanographic factors, climate change is likely to modify the quality and sources of organic matter available around SPM through increased stratification, with potentially cascading effects on benthic food-webs.

In order to better understand these impacts, we conducted two sampling surveys around SPM during periods of either pronounced (August 2017) or weak (July 2018) stratification along a nearshore to offshore gradient (i.e. pelagic-benthic coupling strength gradient; four stations). Quality, sources and transfers of organic matter were assessed through fatty acid and stable isotope analyses since these tools can identify the origin and quality of organic matter at different trophic levels in aquatic ecosystems (e.g. Søreide et al. 2013, Connelly et al. 2015, Mathieu-Resuge et al. 2019). The main goals of this study were to (1) describe spatial variability and seasonality (i.e. periods of strong *vs* weak stratification) in POM and SOM from a poorly studied sub-Arctic ecosystem, (2) assess the potential impact of seasonal sea surface temperature increases on quality and sources of POM and SOM, and their transfer to a dominant primary consumer (i.e. *E. parma*).

Materials and Methods

Study site

The study was conducted in SPM (46°50’N, 56°20’W), a sub-Arctic archipelago located about 20 km south of Newfoundland (Figure 1). Sea surface temperatures usually show large seasonal variations (from sub-zero temperatures in March – April to 18°C in August – September) while bottom water temperatures (i.e. below 80 m) remain stable throughout the year (0 to 2°C; Lazure et al. 2018, Poitevin et al. 2018). The annual primary production occurs mainly during the phytoplankton bloom in April (Harrison et al. 2013, Pepin et al. 2017). Aqua MODIS satellite data (OCI algorithm) over the last two decades have revealed inter-annual variations in which a second phytoplankton bloom may occur in September/October (Appendix, Figure S1). SPM is a costal oligotrophic environment deprived of major surface nutrient inputs from local rivers (C. Jauzein pers. com., Doré et al. 2020). Although the Saint-Lawrence River is a major source of freshwater for the NW Atlantic, its outflows are deflected toward the western part of Cabot Strait and do not influence SPM waters (e.g. Wu et al. 2012). The absence of river influence on SPM environments has been further confirmed by two recent paleoecology studies using primary production proxies (Poitevin et al. 2019, Doré et al. 2020).

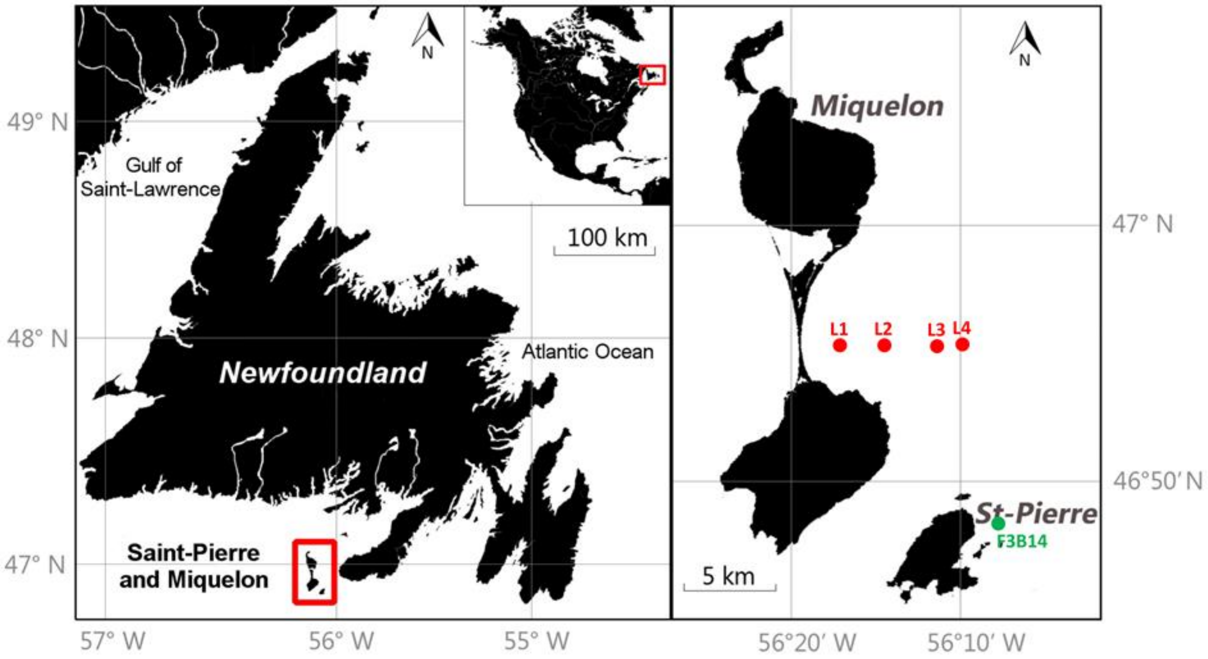

Figure 1: Map of the Saint-Pierre and Miquelon’s archipelago (SPM) showing station F3B14 and the four Langlade’s stations (L1, L2, L3 and L4; modified from Poitevin et al. 2018).

Considering the physical characteristics, SPM is located within the contiguous part of the coastal branch of the Labrador Current flowing through the Avalon channel towards the NW, south of Newfoundland (De Young and Hay 1987, White and Hay 1994, Wu et al., 2012, Lazure et al., 2018). This current speed varies seasonally (strongest in fall/winter, weakest in summer; Wu et al., 2012) with an annual mean value of 10 cm s^{-1} in the middle of Saint-Pierre's Channel (Hay and De Young, 1989). Although mean currents were not measured within our study area, they are probably weaker than average due to higher bottom friction in shallow water areas. Sedimentation rates have not been estimated for SPM but global estimates (usually ranging from 1 to 150 m d^{-1}, Turner et al. 2015) suggest POM sedimentation time is much shorter than one season (e.g. minimum estimates of 1 m d^{-1} implying that POM would settle in 80 days at the deepest station).

Lazure et al. (2018) reported remarkably large near-daily oscillations of near-bottom temperatures around SPM. During the stratification period (July-September), the interaction of surface tides with local bathymetric features generates diurnal internal waves, which propagate around the archipelago guided by bathymetry. The large amplitude of these internal waves (40 – 60 m) and the sharp thermocline can generate temperature gradients along the seafloor of as much as 11°C over a period of hours in mid-September. The 15-25 m depth of the thermocline and internal wave amplitudes lead to strong perturbations between 30 to 60 m depth (respective depths of thermocline elevations and depressions). Water column zones above 30 m and below 60 m do not appear to experience the direct effects of these internal waves.

Sampling strategy

Sampling was conducted in late August 2017 and early July 2018. These timeframes respectively correspond to a “High Stratification Period” and a “Low Stratification Period” observed for the study area (see Lazure et al. 2018). During both sampling campaigns, four stations were sampled along a bathymetric gradient labeled L1 (10 m) to L4 (80 m) and spanning contrasted zones of pelagic-benthic coupling (Figure 1, Table 1). At each station, 10 liters of seawater per replicate were collected by Niskin bottles at one meter below the surface for surface POM samples (s-POM) and one meter above the seafloor for bottom POM samples (b-POM). CTD probes (Seabird 911plus, coupled to a Wetlab ECO FL chlorophyll-a fluorescence sensor in 2017; RBR *concerto* in 2018) were deployed during sampling at each station to record depth profiles of temperature, salinity and fluorescence. Salinity was not measured from station L4 in July 2018 due to logistical reasons and fluorescence was not measured in July 2018 due to the absence of a fluorescence sensor. An oceanographic mooring (composed of 28 TidbiT® temperature sensors ranging from 15 m below the surface to 120 m) was deployed from May 2017 to May 2018 to assess water circulation as well as water column stratification seasonality and short-term variability around SPM (i.e. down to hourly timescales). Temperature profiles sampled at 10 min intervals were then averaged on a weekly basis for the first week of July and the last week of August 2017. The mooring was deployed to the northeast of Saint-Pierre island at 125 m depth (F3B14 in Figure 1). Scuba divers collected SOM samples at stations L1 and L2 in 2017 and only at L2 in 2018 (Table 1). SOM was collected using a 450 ml syringe sucking the upper millimeters of the sediment surface (i.e. 0-3 mm, surface area ≈ 625 cm²). The upper few millimeters of the sediment are expected to be highly-responsive to particle fluxes (e.g. Danovaro et al. 1999) and are more likely to be resuspended and thus assimilated by benthic invertebrates than deeper sediment layers. In order to track organic matter transfers to primary consumers, several sand dollar individuals (i.e. 3 – 9) were collected at each station by either scuba divers or using a “Rallier du Baty” dredge. *E. parma* was selected in our study as a model species for two reasons: (1) *E. parma* is a biomass-dominant species in SPM benthic habitat (i.e. this species has therefore a preponderant role on the organic matter flowing through the benthic food web) and (2) *E. parma* was the only species found at every stations from 10 to 80 m (J. Grall per. obs.). Five macroalgae species (*Agarum clathratum*, *Desmarestia viridis*, *Halosiphon tomentosus*, *Porphyra* spp., *Saccharina latissima*) were also collected in 2017 to assess their potential contribution to POM, SOM and sand dollar diet (Table 1). These five palatable macroalgae represent a major part of the seaweed biomass around SPM and are known to be potentially major food sources for benthic invertebrates (Perez et al. 2013, Renaud et al. 2015, Gaillard et al. 2017).

Table 1: Site coordinates, date and biological material sampled in August 2017 and July 2018 around Saint-Pierre and Miquelon.

Station	Latitude	Longitude	Sampling dates	Depth (m)	Biological material / Physical parameters
L1	46°55.514' N	56°17.279' W	29/08/2017 & 04/07/2018	11	s-POM, b-POM, SOM (only in 2017), *E. parma*, macroalgae, CTD
L2	46°55.678' N	56°14.654' W	30/08/2017 & 02/07/2018	25	s-POM, b-POM, SOM, *E. parma*, macroalgae, CTD
L3	46°55.468' N	56°11.549' W	28/08/2017 & 05/07/2018	60	s-POM, b-POM, *E. parma* (only in 2018), CTD
L4	46°55.909' N	56°09.936' W	28/08/2017 & 07/07/2018	88	s-POM, b-POM, *E. parma* (only in 2017), CTD (only in 2017)
F3B14	46°48' N	56°05' W	01/07/2017 to 31/08/2017	125	CTD

Sample analyses

Preliminary information

We decided to investigate seasonal variations in quality, composition and transfers of organic matter between High and Low Stratification Periods by analyzing fatty acid and stable isotope composition of *E. parma* as well as various sources of organic matter (i.e. POM, SOM and macroalgae). Fatty acids have been shown to constitute powerful tools to identify the origin of the organic matter in aquatic ecosystems (e.g. Meziane & Tsuchiya 2000) since fatty acid profiles (i.e. the list and relative contributions [%] of all fatty acids contained in one lipid sample) of primary producers are usually characteristics of specific taxonomic groups (see Table 2). Moreover, some fatty acids as PolyUnsaturated Fatty Acids (PUFAs) can be used to describe the diet of secondary consumers since they are generally transferred conservatively (Dalsgaard et al. 2003, Gaillard et al. 2017, Thyrring et al. 2017). Stable isotopes are a useful complementary tools to study organic matter transfers in secondary producers (Fry 2006, Perez et al. 2013, De Cesare et al. 2017, Gaillard et al. 2017). Their high sensitivity to biological and physical processes allow also to distinguish organic matter sources according to their compartment (pelagic *vs* benthic), freshness (fresh *vs* refractory) or origin (phytoplankton, microphytobenthos, macroalgae, seagrass, Kharlamenko et al. 2001, McTigue et al. 2015, Mathieu-Resuge et al. 2019). Although POM and SOM pools are inherently highly variable and relate on environmental variations occurring in the ecosystem (e.g. variations in primary production or river inputs), fatty acid and stable isotope analyses are generally adapted to track high temporal variations within 1-2 weeks (Riera and Richard 1997, Lorrain et al. 2002, Leu et al. 2006, Mayzaud et al. 2013). Similarly, turnover rates of animal organs (e.g. digestive gland, stomach) are usually sufficiently high to identify monthly variations of diets of benthic invertebrates (e.g. Pazos et al. 2003, Paulet et al. 2006). Therefore, such a high response of organic matter fatty acid profiles and stable isotope signatures to environmental fluctuations should allow us to track high-frequency variations in organic matter quality and composition related to seasonal changes in stratification conditions. Conversely, the short temporal resolution of these trophic markers eliminates any influences of the spring phytoplankton bloom on our results (occurring usually in April; Pepin et al. 2017, Maillet et al. 2019).

Table 2: List of fatty acids used in this study as tracer and descriptor of the organic matter origin and quality (modified from Bridier et al. 2019). SFA, PUFA and EFA refer to Saturated, PolyUnsaturated and Essential Fatty Acid, respectively.

Descriptor of	Fatty acids (FAs)	References
Organic matter origin		
Diatoms	16:1ω7, 16:4ω1, 20:5ω3	Reuss and Poulsen (2002), Dalsgaard et al. (2003), Kelly and Scheibling (2012)
Dinoflagellates	18:4ω3, 22:6ω3	Napolitano et al. (1997), Kelly and Scheibling (2012)
Macroalgae (Phaeophyceae)	18:2ω6, 18:3ω3, 18:4ω3, 20:5ω3	Kelly and Scheibling (2012), De Cesare et al. (2017), Gaillard et al. (2017)
Organic matter quality		
Degraded organic matter	Dominance of SFA (e.g., 14:0, 16:0, 18:0)	Rhead et al. (1971), Connelly et al. (2015), Connelly et al. (2016)
Labile and nutritionally rich organic matter	Dominance of PUFA and EFA (here, sum of 20:4ω6, 20:5ω3, and 22:6ω3)	Soudant et al. (1996), Parrish et al. (2005), Parrish (2009)

Preliminary treatments

We decided to investigate seasonal variations in quality, composition and transfers of organic matter between High and Low Stratification Periods by analyzing fatty acid and stable isotope composition of *E. parma* as well as various sources of organic matter (i.e. POM, SOM and macroalgae). Fatty acids have been shown to constitute powerful tools to identify the origin of the organic matter in aquatic ecosystems (e.g. Meziane & Tsuchiya 2000) since fatty acid profiles (i.e. the list and relative contributions [%] of all fatty acids contained in one lipid sample) of primary producers are usually characteristics of specific taxonomic groups (see Table 2). Moreover, some fatty acids as PolyUnsaturated Fatty Acids (PUFAs) can be used to describe the diet of secondary consumers since they are generally transferred conservatively (Dalsgaard et al. 2003, Gaillard et al. 2017, Thyrring et al. 2017). Stable isotopes are a useful complementary tools to study organic matter transfers in secondary producers (Fry 2006, Perez et al. 2013, De Cesare et al. 2017, Gaillard et al. 2017). Their high sensitivity to biological and physical processes allow also to distinguish organic matter sources according to their compartment (pelagic *vs* benthic), freshness (fresh *vs* refractory) or origin (phytoplankton, microphytobenthos, macroalgae, seagrass, Kharlamenko et al. 2001, McTigue et al. 2015, Mathieu-Resuge et al. 2019). Although POM and SOM pools are inherently highly variable and relate on environmental variations occurring in the ecosystem (e.g. variations in primary production or river inputs), fatty acid and stable isotope analyses are generally adapted to track high temporal variations within 1-2 weeks (Riera and Richard 1997, Lorrain et al. 2002, Leu et al. 2006, Mayzaud et al. 2013). Similarly, turnover rates of animal organs (e.g. digestive gland, stomach) are usually sufficiently high to identify monthly variations of diets of benthic invertebrates (e.g. Pazos et al. 2003, Paulet et al. 2006). Therefore, such a high response of organic matter fatty acid profiles and stable isotope signatures to environmental fluctuations should allow us to track high-frequency variations in organic matter quality and composition related to seasonal changes in stratification conditions. Conversely, the short temporal resolution of these trophic markers eliminates any influences of the spring phytoplankton bloom on our results (occurring usually in April; Pepin et al. 2017, Maillet et al. 2019).

$$(X) = \frac{W_{Half\ filter}}{W_{Whole\ filter}}\ X\ \left(W_{Whole\ filter} - W_{Precombusted\ filter}\right)$$

Where M (X) is the mass (mg) of POM or SOM used for the fatty acid or stable isotope analysis, and W is the dry weight of half, whole or precombusted filters.

Fatty acid analyses

Fatty acid extraction followed the Bligh and Dyer method (1959) as modified in Meziane & Tsuchiya (2002). Samples were sonicated in a distilled water-chloroform-methanol solution (1:1:2, v:v:v) for 20 minutes. After this extraction, samples were dissolved in a 1:1 (v:v) distilled water-chloroform solution and then centrifuged (1409 X g, 5 min). After this physical separation, the solution containing lipid phases (i.e. 2 ml) was transferred into separate tubes, and subjected to additional rounds of phase transfer, sonication and centrifugation. Lipid were then dried under a dinitrogen (N2), diluted in a sodium hydroxide-methanol solution (1:2, v:v, [NaOH] = 2 mol.l-1) and heated at 90°C for 90 min for fatty acid saponification. This reaction was stopped by the addition of 500 µl of hydrochloric acid (37 %). Lipid fractions were then dissolved in 3 ml chloroform, transferred in separate tubes and dried under a dinitrogen (N_2) gas. Finally, lipid extracts were heated at 90°C for 10 min with 1 ml of a methanolic boron trifluoride solution (BF_3-CH_3OH, 14%) in order to convert fatty acids into Fatty Acid Methyl Esters (FAMEs). At the end of the reaction, lipids were retrieved in 2 ml of chloroform and stored at – 20 °C.

Fatty acid quantification was performed using a Varian CP-3800 gas chromatograph equipped with a Supelco® Omegawax® Capillary GC 320 column and He carrier gas. Fatty acid identifications were validated using retention times and mass spectra measured from a commercial reference standard (Supelco® 37 Component FAME Mix). Mass spectra were measured with a Varian 220-MS coupled to a Varian 450-GC using a He carrier gas. Fatty acid nomenclature is defined as X:YωZ where X is the number of carbon atoms, Y the number of double bonds and Z the position of the last double bond relative to the methyl group. Concentration of each fatty acid peak was determined using an internal commercial standard (23:0, 5 mg.l^{-1}) and the equation given in Schomburg et al. (1987):

$$C_{FA} = \left(\frac{A_{FA}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

Where CFA is the fatty acid concentration (µg.g^{-1}), AFA is the fatty acid peak area, AC23 is the 23:0 peak area, C23 is the 23:0 quantity (µg) added to each sample and Mf is the mass of organic matter measured from the half-filter.

Stable isotope analyses

Half-filters and sand dollar guts were fumigated over 4 and 48 h, respectively, with 37% HCl to remove inorganic carbon (Lorrain et al. 2003, Søreide et al. 2006). The surface layer of POM and SOM filters were scraped into 10-30 mg fragments which were then transferred to tin capsules. Macroalgae and gut samples were first ground into a fine powder using a ball mill. Fractions of about 1 mg were then transferred to tin capsules.

Samples were analyzed at the University of California Davis Stable Isotope Facility (UC Davis SIF) using two different elemental analyzers (PDZ Europa ANCA-GSL, Sercon macroalgae/animal tissues and an Elementar Vario EL Cube elemental analyzer for filters) interfaced with an isotope ratio mass spectrometer (PDZ Europa 20-20, Sercon). Isotopic ratios are expressed using δ notation corresponding to deviation (‰) in 13C/12C and 15N/14N ratios from the international standards (Vienna PeeDee Belemnite and Air, respectively). The δ notation from Peterson & Fry (1987) is as follows:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000$$

Where δX is δ^{13}C or δ^{15}N and R is the corresponding 13C/12C or 15N/14N ratio.

Statistical analyses

Detecting meaningful covariation in the different datasets collected required the application of PERMANOVA statistical tests frequently used in marine ecological surveys. Statistical analyses were performed using the R software (R Core Team 2017) and “vegan” package (Oksanen et al. 2019). In contrast to ANOVAs, well designed PERMANOVA analyses do not depend on assumptions of normality and homoscedasticity (Anderson & Walsh 2013). Three-factor PERMANOVA was not appropriate given strong interactions among factors. We applied one-way PERMANOVA to test the seasonal variability of POM fatty acid profiles. A two-way PERMANOVA procedure was applied to test the effects of station and depth on POM fatty acid profiles for both seasons. We also used pairwise PERMANOVA to test for interactions between station and depth factors for both seasons. The effect of season on SOM fatty acid profiles could not be tested due to the low number of replicates (i.e. only 2 replicates in July 2018). Spatial variability of SOM fatty profiles was tested through one one-way PERMANOVA. Similar to fatty acid profiles, effects of seasons and stations-depth on POM stable isotope signatures were tested by one-way and two-way PERMANOVAs, respectively. Station effects on SOM stable isotope signatures during the High Stratification Period and station-depth effects influencing stable isotope signatures from sand dollars were also tested by one-way and two-ways PERMANOVAs, respectively.

Finally, one Principal Component Analysis (PCA) was computed on the entire POM fatty acid data set to identify POM seasonal variation. In addition, two others PCAs were realized separately on POM fatty acid profiles from High and Low Stratification Periods in order to highlight spatial and depth variations. The PCA procedure used a Hellinger similarity matrix in order to reduce the influence of rare fatty acids in the ordination (Legendre and Gallagher 2001).

Results

Environmental measurements

During the High Stratification Period, CTD profiles showed pronounced water column stratification characterized by temperatures above 16 °C in surface waters and below 4°C in bottom waters (i.e. below 50 m, Figure 2A). The thermocline occurred at around 15 – 25 m, where temperature decreases from 15°C to 9°C. This zone also exhibits a peak in fluorescence (Figure 2A). During the Low Stratification Period, datasets showed more gradual declines in temperature. These decreased continuously from about 10 °C or less at the surface to 4 °C at the bottom (Figure 2B). Figure 2 shows averaged temperature profiles for the first week of July and the last week of August 2017 (Fig. 2C and 2D, respectively). These profiles show a clear increase in stratification in which the temperature gradient increases from about 5°C to 10°C between 15 and 60 m. This shift matches that observed in CTD profiles taken during Low and High Stratification Periods. Consistency across sampled years (2017-2018) suggests that inter-annual variation is negligible compared to seasonal variation in terms of their relative influence on water column stratification.

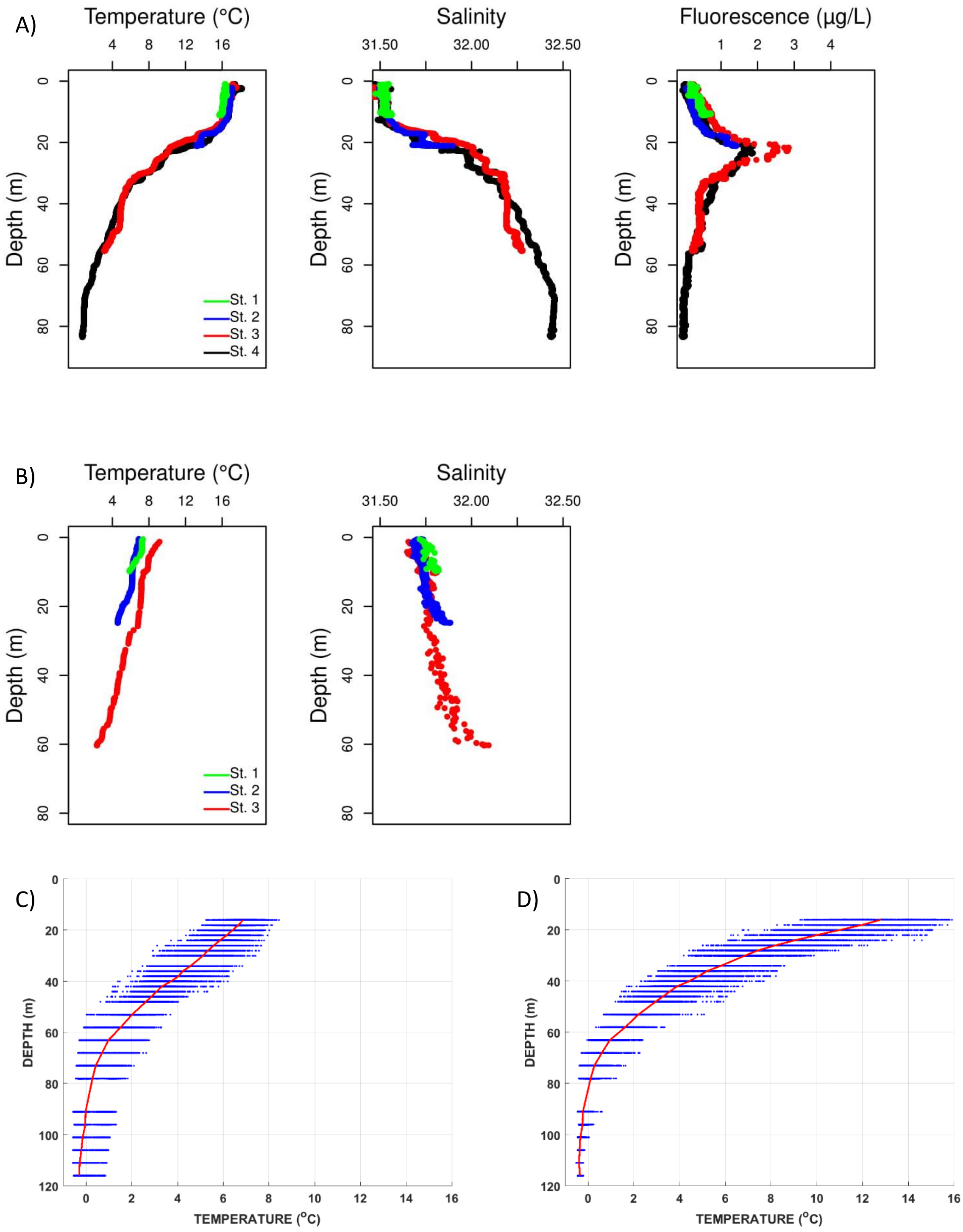

Figure 2: Temperature (°C), Salinity and Fluorescence (µg.l^{-1}) depth profiles at sample stations in either August 2017 (L1 to L4, A) or July 2018 (L1 to L3, B). Averaged (red lines) and raw temperatures (blue dots) at station F3B14 from 1 to 7th July 2017 (C) and from 25th to 31th August 2017 (D).

Fatty acids profiles from POM and SOM samples

Particulate Organic Matter

Sixty fatty acids were identified in POM and SOM samples (51 and 52 fatty acids during High and Low Stratification Periods, respectively). Only fatty acids with a relative abundance higher than 0.2 % in all samples were represented in Table S1 (Supplementary material). POM fatty acid profiles varied considerably between High and Low Stratification Periods ($p < 0.001$, Table S1). Seasonal differences in POM composition were mainly observed for PUFAs. Relative to those collected during the High Stratification Period, samples collected during the Low Stratification Period contained higher levels of PUFAs, especially 18:2ω6, 18:3ω3, 18:4ω3 and 20:5ω3 (Figure 3a, b, Σ PUFA range = 5.3 – 36.7 % and 3.0 – 19.7 % for Low and High Stratification Periods, respectively). Samples collected during the High Stratification Period contained larger levels of saturated Fatty Acids (SFA) relative to those collected during the Low Stratification Period (Σ SFA range = 53.7 – 80.6 % and 38.2 – 61.5 % for High and Low Stratification Periods, respectively). POM quantity showed strong temporal variation with four-fold higher concentrations of total suspended solids (TSS) during the Low Stratification Period (mean [TSS] = 4.0 ± 1.0 mg l^{-1}) compared to the High Stratification Period (mean [TSS] = 1.5 ± 1.1 mg l^{-1}). TSS samples exhibited similar fatty acid concentrations for both seasons (mean [FA] = 4.4 ± 2.8 µg mg^{-1} TSS for High Stratification vs 5.0 ± 4.0 µg mg^{-1} TSS for Low Stratification Period).

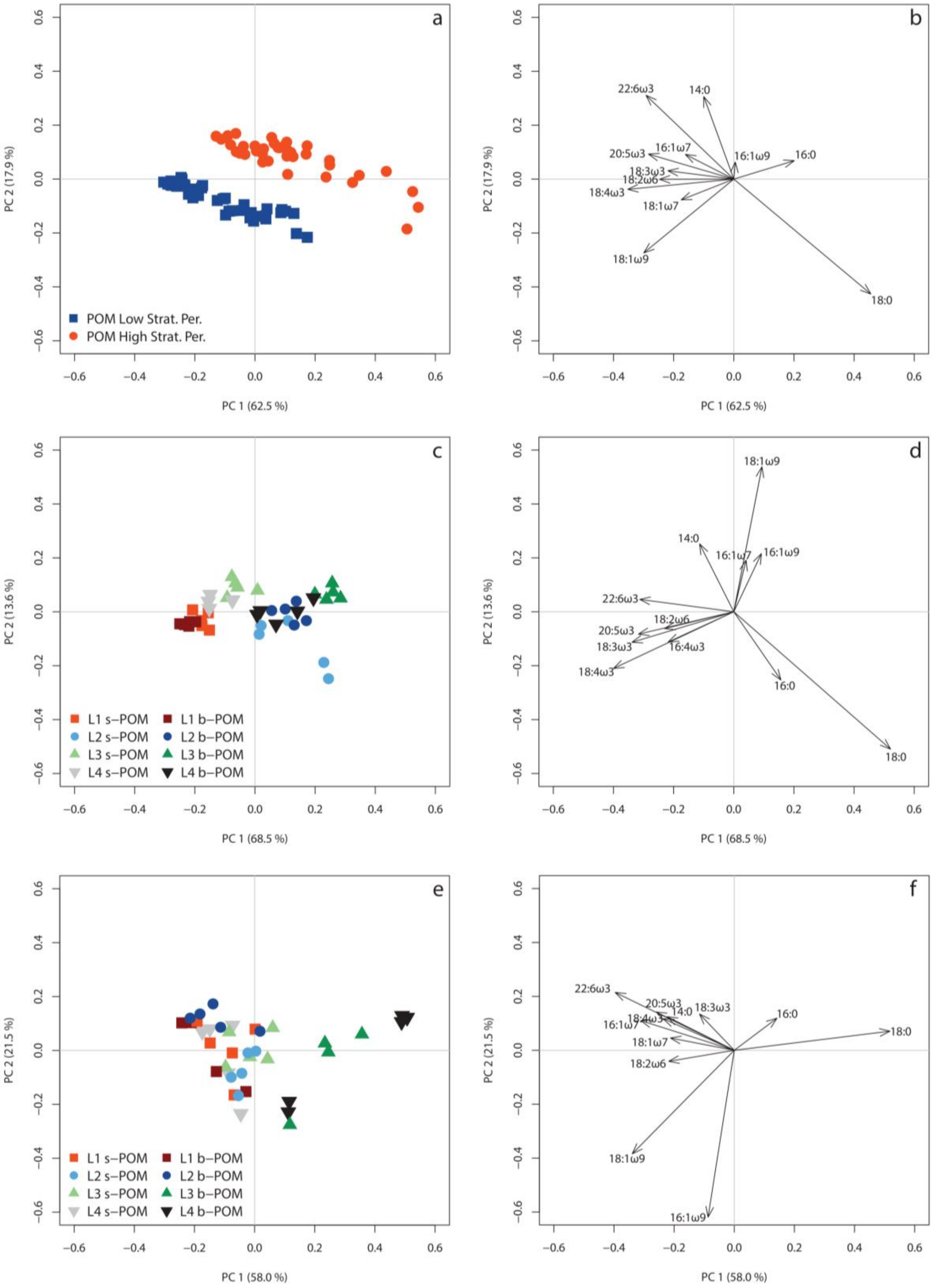

Figure 3: Principal Component Analyses (PCA) based on Hellinger-transformed POM fatty acid percentages from both High and Low Stratification Periods (a, b) as well as from separate Low (c, d) and High (e, f) Stratification Periods. Individual factor maps are represented in left

plots (a, c, e) while variables factor maps are showed and right plots, respectively (b, d, f). Variable factor maps include only the 12 most discriminant fatty acids.

During the Low Stratification Period, all stations showed statistically distinctive POM fatty acid profiles ($p < 0.05$). Spatial variation was particularly pronounced between L1 and the other stations sampled since both s-POM and b-POM samples from L1 displayed the highest relative contributions of PUFAs (especially 18:2ω6, 18:3ω3, 18:4ω3 and 20:5ω3; Figure 3 c, d). Samples collected during the High Stratification Period showed high spatial variation in b-POM fatty acid profiles (Appendix, Table S3). The High Stratification b-POM samples also varied considerably between L1-L2 and L3-L4 stations ($p < 0.01$; Appendix, Table S3). This variation appeared primarily as higher relative contributions of PUFAs (especially 18:2ω6, 18:4ω3, 20:5ω3 and 22:6ω3) at Ll-L2 relative to those measured from L3-L4 (Figure 3e, f).

Sedimentary Organic Matter

Table 3 and Figure S2 show seasonal differences in SOM fatty acid profiles between High and Low Stratification Periods. SOM samples from the Low Stratification Period displayed higher levels of PUFAs (especially for 18:4ω3 and 20:5ω3) compared with samples collected during the High Stratification Period (Σ PUFA = 12.9 % vs 5.7 % for Low and High Stratification Periods, respectively). By contrast, SFA (16:0 and 18:0 in particular) contributions were lower in samples from the Low Stratification Period relative to those collected during the High Stratification Period (Σ SFA = 39 % *vs* 77.4 %). MonoUnsaturated Fatty Acid (MUFA) contributions differed significantly between both seasons (Σ MUFA = 9.3 *vs* 44.8 % for High and Low Stratification Periods, respectively), especially for 16:1ω7 (3.4 *vs* 23.8 %) and 18:1ω9 (1.6 *vs* 9.4 %). However, no spatial variations were observed between L1 and L2 stations during the High Stratification Period ($p > 0.05$).

Table 3: Fatty acid (FA) composition from sand dollar tissue collected in August 2017 and July 2018. Values correspond to mean percentages from 3-9 samples with standard deviation in brackets. SFA, MUFA, PUFA, BrFA and EFA refer to Saturated, MonoUnsaturated, PolyUnsaturated, Branched and Essential fatty acids, respectively. EPA: Eicopensaconoic acid (i.e. 20:5ω3); DHA: Docohexaconoic acid (i.e. 22:6ω3), nd: not detected; tr: traces (fatty acid percentages < 0.2 %). Fatty acid values of less than 0.2 % in all samples are not shown. The entire table is provided in the appendix (see Table S2).

	High Stratification Period (August 2017)				Low Stratification Period (July 2018)			
	Echinarachnius parma			SOM	*Echinarachnius parma*			SOM
	Station 1	Station 2	Station 4	Stations 1 & 2	Station 1	Station 2	Station 3	Station 2
	N = 3	N = 3	N = 4	N = 7	N = 6	N = 5	N = 9	N = 2
14:0	5.2 (1.2)	4.8 (0.4)	4.9 (0.6)	6.7 (1.3)	4.8 (1.2)	5 (0.4)	4.9 (0.7)	6 (0.6)
15:0	0.9 (0.2)	0.9 (0.2)	0.8 (0.1)	2.6 (0.5)	0.8 (0.1)	0.9 (0.3)	0.7 (0.1)	2.2 (0.2)
16:0	9.8 (2.3)	10.8 (1.2)	7.2 (0.8)	43.7 (4.1)	9.6 (1.8)	10.8 (1.4)	8.2 (1.0)	23.5 (1.0)
18:0	5.6 (0.9)	5.2 (0.7)	3.9 (0.3)	17.7 (3.8)	5.3 (1.1)	5.2 (0.8)	4.9 (0.7)	4.7 (0.1)
Σ SFA	23.0 (4.1)	23.4 (2.8)	18.0 (1.2)	77.4 (8.2)	22.1 (3)	23.1 (2.2)	20 (1.4)	39 (0.2)
16:1ω7	7.7 (2.9)	8.1 (0.4)	12.5 (2.5)	3.4 (3.5)	8 (3)	10.9 (3.5)	9.7 (2.4)	23.8 (1.5)
16:1ω9	tr	0.2 (0.0)	0.3 (0.0)	0.5 (0.2)	0.2 (0.1)	0.4 (0.5)	0.2 (0.1)	4.6 (2.2)
18:1ω7	2.5 (0.2)	3.1 (0.6)	3.0 (0.2)	1.2 (1.1)	2.6 (0.3)	2.8 (0.4)	3.2 (0.2)	2.5 (0.1)
18:1ω9	1.9 (0.9)	2.3 (0.3)	1.8 (0.3)	1.6 (1.4)	5.1 (2.3)	4.7 (1.6)	4.2 (1.9)	9.4 (2.2)
20:1ω7	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.4 (0.2)	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.3 (0.0)
20:1ω9	1.2 (0.1)	1.3 (0.1)	1.2 (0.3)	0.3 (0.2)	2.4 (0.9)	1.9 (0.2)	2.3 (0.5)	0.3 (0.0)
20:1ω15	8.8 (2.0)	6.5 (1.5)	5.9 (1.7)	nd	7.4 (1.5)	5.2 (1.2)	6.8 (1.0)	nd
21:1ω9	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	0.5 (0.5)	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	nd
Σ MUFA	29.4 (1.2)	27.9 (1.6)	31.2 (1.1)	9.3 (6.7)	30.4 (1.5)	29.9 (1.3)	30.8 (1.3)	44.8 (1.4)
16:4ω1	1.4 (0.7)	1.3 (0.3)	2.2 (0.5)	nd	1.6 (1)	1.9 (1)	1.7 (0.7)	0.6 (0.0)
18:4ω3	2.1 (0.1)	2.5 (0.5)	2.7 (0.2)	0.4 (0.2)	2.5 (0.5)	2.9 (0.3)	3.2 (0.5)	1.4 (0.4)
20:2 Δ 5, 13	2.2 (0.5)	2.0 (0.1)	2.0 (0.5)	nd	1.8 (0.5)	2 (0.5)	2.2 (0.3)	nd
20:2 Δ 5, 11	5.1 (1.3)	4.1 (0.3)	3.6 (0.8)	nd	4.5 (1.5)	3.5 (0.8)	3.7 (0.5)	nd
20:4ω6	1.8 (0.4)	2.0 (0.2)	2.9 (0.8)	0.4 (0.3)	1.3 (0.4)	1.8 (0.6)	1.6 (0.2)	0.5 (0.0)
20:5ω3	28.5 (4.0)	26.7 (2.2)	28.5 (1.1)	1.3 (1.0)	29.2 (3.4)	26.9 (2.2)	28.7 (2.2)	4.2 (0.5)
22:6ω3	1.7 (0.0)	4.1 (1.8)	2.3 (0.3)	0.4 (0.2)	1.4 (0.3)	1.8 (0.2)	2.1 (0.1)	0.5 (0.1)
Σ PUFA	47.1 (5.4)	47.8 (4.2)	49.8 (2.3)	5.7 (1.7)	47 (3.3)	46 (2.3)	48.3 (2.3)	12.9 (1.0)
Σ BrFA	0.5 (0.1)	0.9 (0.0)	1.0 (0.1)	6.7 (0.7)	0.6 (0.1)	0.9 (0.1)	0.9 (0.2)	3.3 (0.2)
Σ EFA	32.1 (4.3)	32.8 (3.7)	33.8 (2.0)	2.2 (1.3)	32 (3.5)	30.6 (1.9)	32.4 (2.2)	5.2 (0.7)
ΣPUFA/ΣSFA	2.1 (0.6)	2.1 (0.4)	2.8 (0.3)	0.1 (0.0)	2.2 (0.4)	2 (0.3)	2.4 (0.3)	0.3 (0.0)
EPA/DHA	16.9 (2.6)	7.1 (2.4)	12.7 (1.6)	2.9 (1.7)	20.8 (3.2)	15 (1.3)	13.9 (1)	8.3 (1.3)
[FA] (mg/g)	31.7 (23.0)	22.8 (19.7)	52.5 (38.5)	0.2 (0.1)	78.0 (43.0)	63.9 (33.7)	90.3 (23.1)	1.8 (1.1)

Stable isotopes signatures from POM and SOM samples

POM samples showed a general decrease in δ^{13}C and δ^{15}N values from High to Low Stratification Periods ($p < 0.001$, Figure 3). Two-way PERMANOVA detected significant station, depth and station-depth interaction effects on POM's δ^{13}C values ($p < 0.01$) but not δ^{15}N values ($p > 0.05$) during the High Stratification Period. During the Low Stratification Period, station and depth factors exerted influence on POM δ^{13}C values ($p < 0.01$), while only depth factors and station-depth interactions exerted effects on $\delta^{15}N$ values ($p < 0.05$). Supplementary materials list pairwise PERMANOVA results (Table S3).

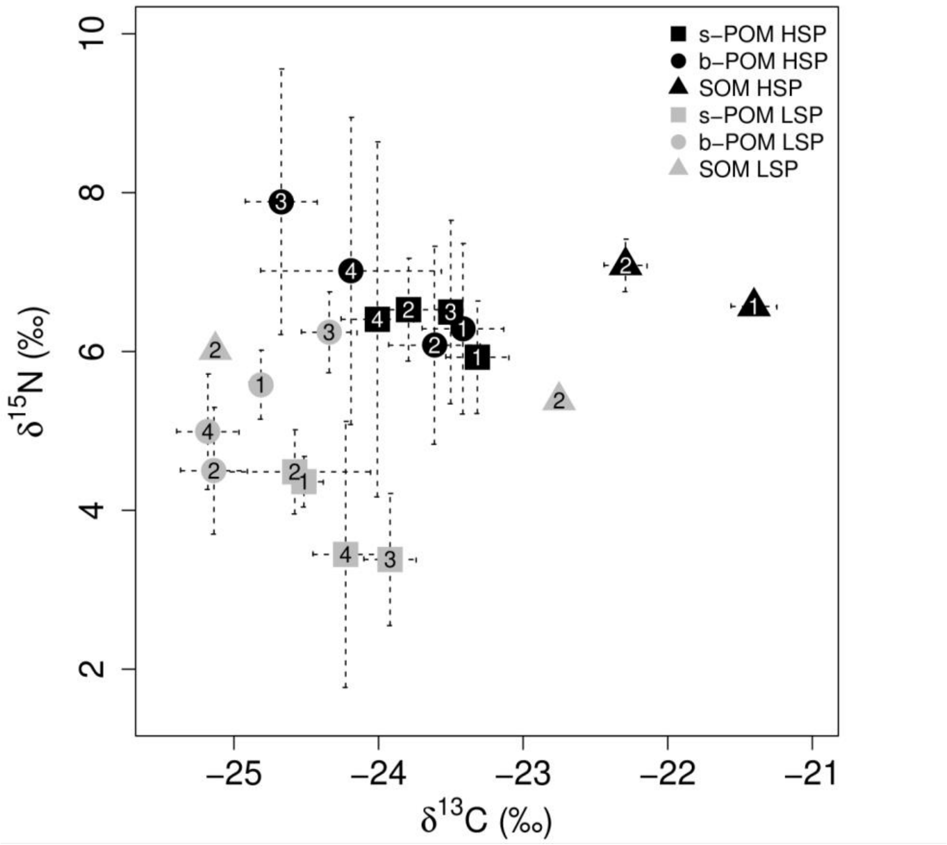

Figure 3: Mean (± SD) stable isotope signatures (δ13C and δ15N) of surface and bottom Particulate Organic Matter (s-POM and b-POM, respectively) and Sedimentary Organic Matter (SOM) samples collected during High Stratification (August 2017, black symbols) and Low Stratification (July 2018, grey symbols) periods. Numbers within symbols refer to sampled stations.

The SOM samples collected during the Low Stratification Period showed more depleted $\delta^{13}C$ and $\delta^{15}N$ values than samples collected during the High Stratification Period (≈ depletion of - 1.6 and - 1.4 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively). During the High Stratification Period, SOM from L2 displayed significantly higher $\delta^{15}N$ and lower $\delta^{13}C$ values than L1 ($p < 0.05$).

Fatty acids profiles and stable isotopes signatures from sand dollars

Overall, fatty acid profiles from *E. parma* stomachs showed relatively low variation between years and stations. All samples contained relatively high proportions of PUFAs (range = 46 – 49.8 %), especially 20:5ω3 (range = 26.7 – 29.2 %). Presence of 16:4ω1, 18:4ω3, 20:4ω6 and

22:6ω3 were also noticed in fatty acid profiles (Table 3). Samples contained lower proportions of SFAs (Σ SFA range = 18 - 23.4 %), which consisted primarily of 14:0, 16:0 and 18:0. Proportions of MUFAs ranged between 27.9 and 31.2 % and were dominated by 16:1ω7 (range = 7.7 – 12.5 %) and 20:1ω15 (range = 5.2 – 8.8 %). Although *E. parma* samples showed significantly different fatty acid profiles between High and Low Stratification Periods ($p < 0.01$), lipid profiles from the two years were highly similar (83.14 % of similarity, Table 3). *E. parma* fatty acid profiles showed significant differences among stations during the High Stratification Period ($p < 0.01$) but not during the Low Stratification Period ($p > 0.05$).

The *E. parma* samples collected during the Low Stratification Period showed slightly enriched carbon isotopic values relative to those collected during the High Stratification Period ($p < 0.01$, Figure 4a, b). *E. parma* samples collected from different stations did not show significant differences in carbon isotopic values ($p > 0.05$). Nitrogen isotopic values from *E. parma* samples differed between L3 and L1-L2 stations ($p < 0.01$) but not between seasons ($p > 0.05$). During the High Stratification Period, *E. parma* and SOM samples had similar respective $\delta^{13}C$ values of -21.4 ± 0.1‰ vs -21.4 ± 0.2‰ for L1 and -22.2 ± 0.3‰ vs -22.3 ± 0.1‰ for L2 (Figure 4a).

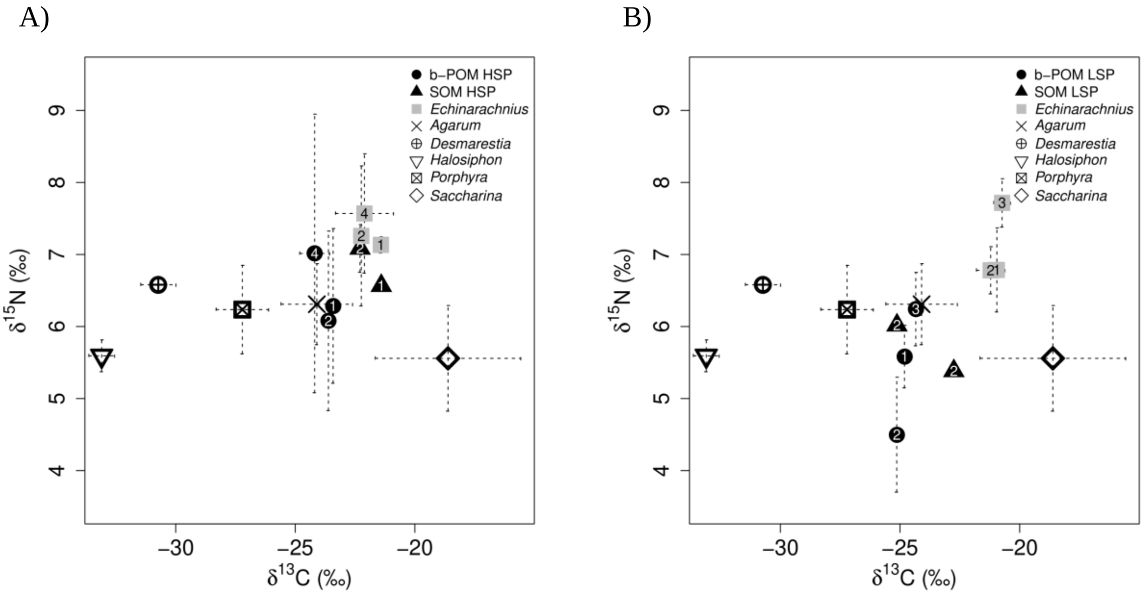

Figure 4: Mean (± SD) stable isotope signatures (δ13C and δ15N) measured from Echinarachnius parma stomachs and the organism's potential food sources during High Stratification (August 2017, A) and Low Stratification (July 2018, B) periods. b-POM: bottom Particulate Organic Matter; SOM: Sedimentary Organic Matter. Numbers within symbols indicate stations.

Discussion

Spatiotemporal variations in POM sources

During both seasons, microalgal fatty acids represented significant proportions of POM fatty acid profiles. Dinoflagellate (22:6ω3, 18:4ω3) and diatom markers (20:5ω3, 16:1ω7) were notably present (Figure 3, Table S1). Macroalgae also made significantly apparent contributions to the organic matter pool as indicated by the presence of 18:2ω6 and 18:3ω3 PUFAs (range Σ (18:2ω6 + 18:3ω3) = 1.4 – 13.5 %, Table S1). Stable isotope signatures were consistent with a contribution from the macroalgae *A. clathratum* and possibly several other mixed species (e.g. *D. aculeata* and *S. latissima*). Higher relative percentages of 18:2ω6 and 18:3ω3 indicated that macroalgal contributions to POM were much higher during the Low Stratification Period relative to the High Stratification Period conditions. On the whole, the Low Stratification Period was characterized by fresh and high quality organic matter as indicated by high levels of EFAs (Essential Fatty Acids) and PUFAs (especially 18:2ω6, 18:4ω3, 20:5ω3). Higher TSS concentrations observed during this season may also indicate higher food availability compared to that available during the High Stratification Period (Table S1).

Our results revealed also major variations along the cross-shore transect. Strong spatial variations were observed in both surface and bottom waters during the Low Stratification Period due to a predominance of macroalgal sources for POM collected from near shore environments while POM from more distal environments (i.e. depth > 20 m) appeared to originate from a mixture of microalgal and macroalgal sources. In contrast, POM sources and quality were homogenous in surface waters during the High Stratification Period. Bottom water samples showed however higher organic matter quality in shallow areas (depth < 30 m) due to higher contributions of microalgal material to POM (fatty acid markers 16:1ω7, 18:4ω3, 20:5ω3, 22:6ω3).

Influence of stratification on POM quality and pelagic-benthic coupling

Differences in pelagic trophic conditions may arise from seasonal drivers of water column stratification and vertical mixing. Seawater surface temperatures at SPM rise in March and increase steadily until mid-September when water column stratification reaches its maximum (Lazure et al. 2018, Poitevin et al. 2018). Nutrient profiles from SPM waters show a typical vertical distribution with depleted nutrient concentrations at the surface (especially for nitrates and silicates) and nutrient-rich bottom waters (C. Jauzein pers. com.) during the stratified period. Extremely high-water column stratification during the High Stratification Period may then act as a barrier to nutrient exchange between surface and sub-surface waters. Limitation in nutrient vertical fluxes during the High Stratification Period and the absence of significant horizontal nutrient input to this oligotrophic environment by rivers (Doré et al. 2020) likely limit primary production compared to the Low Stratification Period. The much lower TSS concentrations recorded during the High Stratification Period ([TSS] = 1.5 ± 1.1 *vs* 4.0 ± 1.0 mg l^{-1} for the High and Low Stratification periods, respectively) support this interpretation.

Spatial variation in POM fatty acid profiles during the High Stratification Period also seems to reflect the influence of stratification on pelagic-benthic coupling and b-POM freshness. Numerous studies have shown that nutrient limitations under increased stratification lead to shifts in the size distributions of phytoplankton communities from a predominance of larger to smaller cells (Kiørboe 1993, Falkowski & Oliver 2007, Finkel et al. 2010). Tighter coupling between smaller phytoplankton cells and heterotrophic bacteria promotes more efficient recycling of organic matter in surface waters (through regenerated primary production) and limits vertical export to sediment (Legendre & Le Fèvre 1995, Bopp et al. 2005, Turner et al. 2015). Warmer surface temperatures during the High Stratification Period may also enhance POM degradation by stimulating heterotrophic microbial activity (Piontek et al. 2009, Wohlers et al. 2009, Turner et al. 2015). Moreover, slower sedimentation rates of smaller cells usually increase the residence time of phytoplankton within the water column extending thus exposure to oxidation and microbial degradation (Turner et al. 2002, Guidi et al. 2009, Marañón 2015). Together, these processes reduce the quantity and freshness of the organic matter reaching the seabed (Budge and Parrish 1998, Parrish et al. 2005, Guidi et al. 2009, Turner et al. 2015). On both deep stations, extremely low PUFA levels were observed in bottom compared to surface waters that could reflect effects of stratification on phytoplankton size structure, microbial degradation and pelagic-benthic coupling strength. The higher relative levels of PUFAs measured in near shore bottom water samples (< 30 m depth) may derive from autotrophic production of organic matter around the pycnocline supported by (small) local nutrient pulses from subsurface waters. Such subsurface autotrophic production has been widely reported in sub-Arctic/Arctic oligotrophic and highly-stratified surface waters. It is usually the result of a compromise between the low nutrient concentrations at the surface and low light availability in deep waters (Martin et al. 2010, Tremblay et al. 2015). Part of the subsurface fluorescence peak observed in this study may also reflect higher photosynthetic pigment concentrations in shade-adapted phytoplankton species growing in subsurface waters (Fennel and Boss 2003, Tremblay et al. 2015). Spatial variation in POM during the Low Stratification Period indicates a more efficient pelagic-benthic coupling under condition of continuous water column stratification. Smaller shifts in PUFA levels between surface and bottom waters during this period support this interpretation (Table S1).

Lower food availability and lower organic matter quality during the High Stratification Period conditions may also reflect the influence of sharp stratification on internal waves. Pronounced water column stratification caused by higher sea surface temperatures can result in more stable internal waves (Nielsen et al. 2004, Woodson 2018) and prevent their breakage (and their action on turbulence and nutrient mixing). This may have especially affected near shore stations (i.e. L1 and L2) during the High Stratification Period. Amplitudes of internal waves are usually dampened by water column stratification (Walter et al. 2014, Woodson 2018). Weaker vertical oscillation of the thermocline during the High Stratification Period may thus limit deep water nutrient inputs to surface waters.

Longer sedimentation rates during the High Stratification Period imply that POM is probably more subjected to horizontal advection during settling. This means that b-POM deposited at a given location may not originate from the same location at the surface. This effect introduces the possibility that seasonal variation in organic matter composition and quantity reflects POM advection rather than differences in stratification. Pronounced differences between surface and bottom currents (i.e. ~ 10 cm s^{-1}) and a low sedimentation rate (e.g. 5 m d^{-1}, i.e. 16 days of sedimentation between the surface and 80 m depth, Turner et al. 2015) would place POM sampled at 80 m depth during the High Stratification Period ~ 130 km from surface waters where it originated. However, primary production and stratification are generally homogeneous around the Newfoundland Shelf (Craig and Colbourne 2002, Cyr and Larouche 2015, Pepin et al. 2017). Therefore, although b-POM may have undergone some advection during the High Stratification Period, this would not influence POM quality and quantity since the impact of stratification on primary production and vertical sedimentation rates are likely homogeneous across the Newfoundland Shelf.

Additional contribution of macroalgae to POM

The high levels of 18:2ω6 and 18:3ω3 (Figure 3, Table S1) reported here suggest that macroalgae represent a major source of POM around SPM, especially during the Low Stratification Period. An additional fatty acid, the 20:4ω6 marker, displays high levels in macroalgae samples but low relative abundance in POM samples (Appendix, Table S4). This may arise from the lower relative chemical stability of certain macroalgal fatty acids. Also, microalgal fatty acids detected in POM derive primarily from living cells whereas macroalgal fatty acids mostly derive from thalli detritus subjected to more intensive degradational processes. The 18:2ω6 and 18:3ω3 may also derive from seagrass or terrestrial organic matter (Kelly and Scheibling 2012, Mathieu-Resuge et al. 2019). The distinctive $\delta^{13}C$ values measured from POM relative to known ranges for seagrass ($\delta^{13}C > -12$ ‰) and terrestrial organic matter ($\delta^{13}C < -28$ ‰) however argue against a contribution from these sources (see Peterson 1999).

Field observation also support the interpretation of a significant autochthonous macroalgal contribution to POM. Scuba diving surveys conducted near the sampling area have found that shallow areas are populated by the two macroalgal species *A. clathratum* and *S. latissima* (P. Poitevin pers. obs.). Kelp forests can constitute major sources of dissolved and particulate organic matter in marine coastal ecosystems via exudation and fragmentation processes (e.g. blade erosion, thalli dislodgment, blade shedding, Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012, Leclerc et al. 2013, Pessarrodona et al. 2018). Fragmentation processes depend on several factors (i.e. grazing, variations of temperature, hydrodynamics) that vary with time and season (Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012, Simonson et al. 2015). Although variation in macroalgal input between Low and High Stratification Periods should depend on such factors, their specific roles are difficult to assess. Larger proportions of macroalgal detritus in the shallowest area likely reflect autochthonous inputs (Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012), whereas lower macroalgae contributions in deeper areas should either reflect different degrees of thalli fragmentation or transport from shallow areas (Krumhansl & Scheibling 2012, Renaud et al. 2015, Filbee-Dexter et al. 2018).

Differentiating macroalgal input from the effects of stratification on the quality and composition of POM is complex. The higher proportions of Σ PUFA found in L2, L3 and L4 POM samples during the Low Stratification Period (e.g. s-POM = 13.7 – 25.8 %) relative to those measured from the High Stratification Period (s-POM = 9.5 – 14.4 %) along with similar concentrations of macroalgal markers (e.g. 18:2ω6, 18:3ω3) suggest that organic matter quality reflects the absence of sharp vertical stratification rather than macroalgal input. By contrast, strong seasonal variation in the macroalgal markers from the L1 POM samples coincided with relatively little variation in microalgal markers (e.g. 16:1ω7, 22:6ω3). This suggests that POM seasonality for most near shore stations reflected macroalgal pulses. Assessing the effects of stratification on the export and sedimentation of macroalgal detritus into deep water areas was not feasible in this study. Other studies have described the salient roles of temperature (Simonson et al. 2015), grazing (Wernberg & Filbee-Dexter 2018) or wave exposure (Krumhansl & Scheibling 2011) on these transfers, but none have yet investigated how stratification may limit such transport and deposition. Detection of fatty acid macroalgae markers in s-POM samples from offshore stations along with their absence from b-POM samples (e.g. 18:2ω6 and 18:3ω3, station L3 and L4, Figure 3, Table S1) suggest that stratification may limit sedimentation of macroalgal detritus. Given the future increases of stratification expected from rising sea surface temperatures, future research should seek to constrain these processes.

Organic matter transfers and spatiotemporal variations in SOM sources

Significant seasonal differences observed in SOM fatty acid profiles reflect different organic matter quality and origins between High and Low Stratification Periods (Table 3). Large levels of SFAs observed during the High Stratification Period (14:0, 16:0 and 18:0, especially) reveal a high degradation state of the organic matter (Table 2). Sources contributing to SOM during the High Stratification Period were limited and consisted of minor inputs from microphytobenthos (Σ of 20:5ω3 and 16:1ω7 < 5%) and macroalgae (Σ of 18:2ω6 and 18:3ω3 < 1%). SOM samples from the Low Stratification Period contained higher concentrations of PUFAs and EFAs (Σ PUFA = 12.9 and Σ EFA = 5.2 for Low Stratification vs Σ PUFA = 5.7 % and Σ EFA = 2.2 % for High Stratification) including diatom markers (16:1ω7, 20:5ω3 and 16:4ω1). These high temporal variations of SOM sources and quality result likely from the microphytobenthos dynamics, with a major bloom during the Low Stratification Period (illustrated by much higher contributions of 16:1ω7, 20:5ω3 and 16:4ω1) turning toward degraded OM during the High Stratification Period (reflected by high levels of Σ SFA). Such a pattern is consistent with the typical dynamics of microphytobenthos which usually includes one single massive bloom per year (e.g. occurring in April in the Gulf of Mexico and in the Bay of Brest, Pinckney & Lee 2008, Chatterjee et al. 2013; in July in the Seto Inland Sea, Yamaguchi et al. 2007). Although POM samples collected during the Low Stratification Period contained higher relative contributions of macroalgal fatty acids, these markers appeared in low concentrations in SOM profiles (Σ 18:2ω6, 18:3ω3, 18:4ω3 and 22:6ω3 < 1.6 %) demonstrating that they represent only a minor source for the SOM pool. Low macroalgal and high microphytobenthic contributions in SOM samples may reflect a strong microbial degradation of macroalgal detritus by benthic heterotrophic bacteria and an effective recycling of nutrients released through this microbial loop by benthic microalgae (e.g. Hardison et al. 2010).

Several authors questioned the trophic ecology of *E. parma*, especially if this species feed either on the sediment or on suspended particles from the water column (e.g. Seilacher 1979, Ellers & Telford 1984, Miller et al. 1992). Some studies have suggested that vertical orientations observed among several sand dollar species (e.g. *Dendraster excentritus*, *Encope michelini*, *Heliophora orbiculus*, *Rotula augusti*, Merrill & Hobson 1970, Lawrence et al. 2004 and references therein) may indicate filter-feeding (Timko 1976, O'Neill 1978) while others (Seilacher 1979, Ellers & Telford 1984, Miller et al. 1992) suggest that deposit-feeding occurs by using podia from both oral and aboral sides to select and transport food particles toward the mouth. Our study supports this latter hypothesis. Since carbon isotopic fractionation between primary and secondary producers is usually relatively low or nonexistent in high-turnover tissue (e.g. digestive glands, Gaillard et al. 2017, De Cesare et al. 2017, Bridier et al. 2019), similar $\delta^{13}C$ values for both SOM and sand dollar samples indicates a diet dominated by SOM. Such hypothesis is also confirmed by fatty acids profiles results: a dominant suspension feeding activity should have implied a high spatial variability of sand dollars' fatty acids profiles reflecting the high spatial variability of b-POM. Our almost identical sand dollars' fatty acids profiles from 10 to 80 m suggest thus a homogenous SOM pool along stations (although we were not able to collect SOM samples in the deepest areas). Previous studies have reported similar findings of homogenous SOM composition between near shore and offshore environments noting that SOM represents long-term accumulation from the water column (Chouvelon et al. 2015, Schaal et al. 2016).

Spatial homogeneity in fatty acid profiles from SOM and sand dollar samples contrasts the above interpretations that stratification diminishes both POM quality and pelagic-benthic coupling. However, the predominance of the 16:1ω7, 16:4ω1 and 20:5ω3 diatom markers indicates that microphytobenthos dominate the SOM pools. This dominance may explain the decoupling of POM and SOM pools. Homogenous benthic production along the bathymetric gradient could reflect the adaptation of microphytobenthos to both low light availabilities and nutrient depletion (by using nutrients released from the sediment, MacIntyre et al. 1996, Leynaert et al. 2009). A major and homogenous contribution of this food source to the diet of

Echinarachnius parma with depth could thus counterbalance the impact of stratification on POM quality and pelagic-benthic coupling strength.

Conclusion

Characterization of organic matter sources and quality revealed multiple negative effects of highly stratified water column on the organic matter sources and quality from a sub-Arctic Archipelago. This study detected weaker pelagic-benthic coupling, lower food availability and more degraded organic matter delivered to benthic compartment during the High Stratification Period. Such observations may be explained by the strong water column stratification that would abate vertical organic matter transfer and limit nutrient replenishment of surface waters by reducing surface/sub-surface nutrient exchanges. By contrast, less pronounced water column stratification would allow more efficient pelagic-benthic coupling and nutrient exchanges around the pycnocline and may facilitate nutrient upwelling through internal waves. Macroalgal material represents a major source of high organic matter quality in shallower areas. Considering complex processes of thalli fragmentation that includes numerous, interrelated environmental and biological factors, the intensity and seasonality of the pulses of macroalgal detritus could however vary significantly in time. In the context of ongoing climate change, our results suggest that intensified water column stratification associated with rising sea surface temperatures may strongly modify pelagic-benthic coupling as well as future quality and composition of POM pools from North-West Atlantic shelf ecosystems. Conversely, shallow areas may be more resilient to changes in water conditions due to local contribution of high-quality organic matter from benthic primary producers.

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Supplementary material *to the article:*

Sources, quality and transfers of organic matter in a highly-stratified sub-Arctic coastal system (Saint-Pierre-et-Miquelon, NW Atlantic)

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Table S1: Fatty acid composition of the surface and bottom Particulate Organic Matter (s-POM and b-POM, respectively) from August 2017 and July 2018 (High and Low Stratification Period, respectively). Values correspond to mean percentages of 2-5 samples with their standard deviation (in brackets). SFA, MUFA, PUFA, BrFA, EFA: Saturated, MonoUnsaturated, PolyUnsaturated, Branched and Essential Fatty Acid. EPA: Eicopensaconoic acid (i.e. 20:5ω3); DHA: Docohexaconoic acid (i.e. 22:6ω3), nd: not detected; tr: traces (i.e. < 0.2 %). Fatty acid lower than 0.2 % in all samples are not shown.

Table S2: Fatty acid composition from sand dollar and Sedimentary Organic Matter (SOM) samples collected in August 2017 and July 2018. Values correspond to mean percentages from 3-9 samples with standard deviation in brackets. SFA, MUFA, PUFA, BrFA and EFA refer to Saturated, MonoUnsaturated, PolyUnsaturated, Branched and Essential fatty acids, respectively. EPA: Eicopensaconoic acid (i.e. 20:5ω3); DHA: Docohexaconoic acid (i.e. 22:6ω3), nd: not detected; tr: traces (i.e. < 0.2 %). Fatty acid lower than 0.2% in all samples are not shown.

Table S3: Results from pairwise PERMANOVAs examining the interactions between Depth and Station factors on POM's (a) fatty acids profiles, (b) carbon ($\delta^{13}C$) and (c) nitrogen ($\delta^{15}N$) isotopic signatures during Low and High Stratification Periods. Samples connected by a same letter are not significantly different from each other ($p \geq 0.05$).

Table S4: Fatty acid composition of 5 macroalgae species (*Agarum clathratum*, *Desmarestia viridis*, *Saccharina latissima*, *Porphyra* spp., *Halosiphon tomentosus*) collected in August 2017. Values correspond to mean percentages of 3 samples with their standard deviation (in brackets). SFA, MUFA, PUFA, EFA: Saturated, MonoUnsaturated, PolyUnsaturated and Essential Fatty acid. EPA: Eicopensaconoic acid (i.e. 20:5ω3); DHA: Docohexaconoic acid (i.e. 22:6ω3), nd: not detected; tr: traces (i.e. < 0.2 %). Fatty acid lower than 0.2 % in all samples are not shown.

Figure S1: Long-term time series (2002-2019) of monthly sea surface chlorophyll-a concentrations over the four sampled stations from Aqua MODIS satellite data.

Figure S2: Relative contributions (%) of the 8 most discriminant fatty acids (according to a SIMPER analysis) between Sedimentary Organic Matter (SOM) from Low and High Stratification Periods (Low Strat. Per. and High Strat. Per., respectively).

Table S1

High Stratification Period (August 2017)					
	Stations 1, 2, 3 & 4	Station 1	Station 2	Station 3	Station 4
	s-POM	b-POM	b-POM	b-POM	b-POM
	N = 20	N = 4	N = 5	N = 4	N = 5
12:0	0.4 (0.3)	0.4 (0.2)	0.3 (0.2)	0.5 (0.3)	0.5 (0.3)
14:0	11.7 (1.8)	11.1 (1.9)	11.7 (1.6)	7.0 (1.2)	4.3 (1.1)
15:0	2.3 (0.7)	2.1 (0.7)	1.5 (0.1)	3.0 (0.8)	2.6 (1)
16:0	34.2 (4.2)	29.2 (0.5)	31 (2.7)	36.5 (5.4)	38.1 (5.5)
17:0	1.1 (0.2)	0.9 (0.3)	0.7 (0)	1.6 (0.1)	1.8 (0.2)
18:0	9.4 (2.3)	7.7 (3.1)	10.3 (6.2)	23.5 (4.9)	28.1 (13.7)
19:0	0.2 (0.1)	tr	tr	0.4 (0.1)	0.4 (0.1)
20:0	0.7 (0.1)	0.6 (0.2)	0.5 (0)	1.1 (0.1)	1.3 (0.2)
21:0	0.2 (0.1)	tr	tr	0.4 (0.1)	0.2 (0.2)
22:0	0.5 (0.1)	0.4 (0.2)	0.5 (0.4)	1.0 (0.3)	1.2 (0.3)
24:0	1 (0.4)	0.7 (0.4)	1.7 (2.4)	1.6 (0.1)	1.7 (0.6)
25:0	0.2 (0.1)	tr	tr	0.4 (0.2)	0.3 (0.2)
Σ SFA	62.1 (6.6)	53.7 (3.9)	58.6 (6.2)	77.1 (10.5)	80.6 (14.6)
14:1ω3	0.3 (0.2)	0.3 (0.1)	tr	0.4 (0.3)	0.2 (0.2)
14:1ω5	0.4 (0.4)	0.4 (0.3)	0.2 (0.1)	0.6 (0.7)	0.4 (0.4)
15:1ω1	0.4 (0.3)	0.3 (0.3)	tr	0.4 (0.6)	0.3 (0.4)
16:1ω5	0.5 (0.1)	0.5 (0)	0.4 (0)	0.5 (0.1)	0.4 (0.2)
16:1ω7	4.5 (1.2)	6.1 (2)	5.8 (0.8)	1.4 (0.8)	0.7 (0.7)
16:1ω9	3.3 (2.8)	3.3 (2.4)	1 (0.2)	3.5 (5.2)	2.6 (3.1)
17:1ω7	tr	tr	tr	tr	0.2 (0.2)
17:1ω9	0.7 (0.5)	0.7 (0.5)	0.4 (0.1)	0.7 (0.7)	0.6 (0.5)
18:1ω5	tr	tr	tr	tr	tr
18:1ω7	2.5 (0.7)	2.8 (0.7)	3 (0.4)	0.8 (0.5)	0.6 (0.6)
18:1ω9	8.8 (2.0)	9.9 (2.4)	6.6 (0.4)	4.6 (3.5)	4.9 (6.6)
20:1ω9	tr	tr	tr	0.3 (0.2)	tr
20:1ω11	0.2 (0.1)	0.2 (0.1)	tr	0.6 (0.6)	tr
22:1ω9	0.2 (0.3)	tr	0.4 (0.6)	0.3 (0.3)	0.5 (0.5)
22:1ω11	0.4 (0.2)	0.4 (0.2)	0.2 (0.1)	0.6 (0.6)	0.9 (1)
Σ MUFA	23.7 (5.4)	25.6 (4)	18.7 (1.3)	14.8 (10.5)	12.8 (12.2)
16:2ω4	nd	nd	nd	nd	nd
16:4ω3	0.2 (0.1)	0.4 (0.1)	0.6 (0.2)	tr	tr
18:2ω6	2.5 (0.6)	3 (0.5)	2.7 (0.4)	0.9 (0.5)	0.8 (0.9)
18:2ω9	0.2 (0.2)	0.2 (0.2)	tr	0.3 (0.3)	tr
18:3ω3	1.7 (0.5)	2 (0.8)	2.4 (0.4)	0.5 (0.1)	0.7 (0.6)
18:3ω6	tr	tr	tr	tr	tr
18:4ω3	1.4 (0.5)	2.1 (1.1)	2.8 (0.9)	0.4 (0.1)	tr
20:2ω6	tr	0.2 (0.1)	tr	tr	tr
20:4ω3	0.3 (0.2)	0.3 (0.2)	0.3 (0.1)	0.3 (0.3)	0.3 (0.2)
20:4ω6	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	0.3 (0.4)	tr
20:5ω3	1.7 (0.7)	3.3 (1.5)	3.6 (1.2)	0.5 (0.1)	0.2 (0.3)
22:5ω3	tr	tr	0.2 (0.1)	tr	tr
22:6ω3	3.2 (1.6)	5.2 (3.3)	6.4 (2)	0.4 (0.3)	tr
Σ PUFA	12.0 (3.9)	17.6 (7.5)	19.7 (5.2)	4.2 (0.8)	3 (1.9)
Σ BrFA	3.3 (0.5)	3.1 (0.2)	2.9 (0.3)	3.9 (0.6)	3.5 (1)
PUFA/SFA	0.2 (0.1)	0.3 (0.2)	0.3 (0.1)	0.1 (0.1)	0 (0)
Σ EFA	5.1 (2.3)	8.8 (4.9)	10.3 (3.3)	1.2 (0.9)	0.4 (0.6)
16:1ω7/16:0	0.1 (0.0)	0.2 (0.1)	0.2 (0)	0 (0.1)	0 (0)
EPA/DHA	0.6 (0.1)	0.7 (0.2)	0.6 (0)	1.3 (0.5)	1.5 (0.7)
[FA] (μg/mg)	6.3 (3.1)	8.9 (3.4)	6.9 (1.7)	4.9 (6.3)	2.0 (1.9)
[TSS] (mg/l)	1.5 (1.3)	1.3 (0.4)	1.0 (0.2)	1.0 (0.6)	2.9 (0.9)

Table S1, continued

Low Stratification Period (July 2018)								
	Station 1		Station 2		Station 3		Station 4	
	s-POM N = 5	b-POM N = 5	s-POM N = 5	b-POM N = 5	s-POM N = 5	b-POM N = 5	s-POM N = 5	b-POM N = 2
12:0	nd	nd	nd	nd	nd	nd	nd	nd
14:0	10 (0.3)	6.9 (0.5)	7 (2.2)	6.4 (1.1)	11.2 (0.4)	6.6 (1.5)	10.8 (1.3)	8.1 (1)
15:0	0.7 (0.1)	0.6 (0)	0.7 (0.2)	1.3 (0.3)	1 (0.1)	2.5 (0.1)	1 (0.1)	1.5 (0.1)
16:0	25.4 (0.5)	26.5 (0.9)	31.5 (6.7)	27.9 (2.1)	23 (2.1)	31.7 (1.5)	25.1 (1.5)	30 (0.3)
17:0	0.4 (0)	0.4 (0)	0.5 (0.1)	0.7 (0.1)	0.4 (0.1)	1.1 (0.1)	0.4 (0)	0.7 (0)
18:0	5.3 (1.5)	3.4 (0.3)	20.9 (7.4)	15.1 (2.6)	6.3 (1.1)	13.9 (1.4)	5.2 (0.9)	14.3 (0.5)
19:0	tr	tr	0.2 (0.1)	0.3 (0.2)	0.3 (0.1)	0.7 (0.1)	0.3 (0.1)	1 (0.1)
20:0	tr	0.1 (0)	0.3 (0)	0.5 (0.1)	0.2 (0)	0.8 (0.2)	tr (0)	0.5 (0.1)
21:0	nd	nd	nd	nd	nd	nd	nd	nd
22:0	tr	tr	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	0.6 (0.2)	0.2 (0)	0.5 (0.1)
24:0	tr	tr	tr	0.3 (0.2)	tr	0.9 (0.4)	0.2 (0.1)	0.4 (0.1)
25:0	nd	nd	nd	nd	nd	nd	nd	nd
Σ SFA	42.4 (2.1)	38.2 (1.7)	61.5 (11.7)	52.9 (4.8)	43 (3.5)	59 (2.7)	43.4 (3.4)	57.1 (0.7)
14:1ω3	tr	tr	tr	tr	tr	0.4 (0.3)	tr	tr
14:1ω5	tr	0.4 (0.1)	tr	tr	tr	tr	tr	0.2 (0.1)
15:1ω1	nd	nd	nd	nd	nd	nd	nd	nd
16:1ω5	0.9 (0.1)	1.4 (0)	0.6 (0.2)	0.4 (0.1)	0.9 (0.1)	0.3 (0.1)	0.9 (0.1)	0.3 (0)
16:1ω7	4.3 (0.3)	3.6 (0.1)	3.1 (1)	5.6 (0.9)	4.1 (0.4)	5.7 (1.5)	4.6 (0.2)	5 (0.3)
16:1ω9	2 (0.4)	1.5 (0.1)	1.9 (0.7)	2.5 (0.9)	2 (0.2)	4.6 (1.2)	2.3 (0.3)	2.1 (0.2)
17:1ω7	nd	nd	nd	nd	nd	nd	nd	nd
17:1ω9	0.6 (0)	0.4 (0)	0.3 (0.1)	0.4 (0.1)	0.4 (0)	tr	0.4 (0)	0.3 (0)
18:1ω5	tr	tr	tr	tr	tr	tr	tr	0.2 (0)
18:1ω7	3.5 (0.3)	3.4 (0.3)	3.2 (1.2)	4.2 (1)	3.4 (0.3)	3.9 (0.4)	4.2 (0.2)	3.8 (0.3)
18:1ω9	10.6 (1.3)	11.5 (0.6)	11.6 (2.6)	16.9 (1.7)	21.5 (3.3)	16.7 (1.5)	13.7 (0.7)	17.6 (1.4)
20:1ω9	tr	tr	tr	0.2 (0.1)	tr	tr	tr	tr
20:1ω11	nd	nd	nd	nd	nd	nd	nd	nd
22:1ω9	tr	tr	tr	tr	tr	tr	tr	tr
22:1ω11	tr	tr	0.4 (0.1)	0.5 (0.1)	0.3 (0)	0.4 (0.1)	0.3 (0)	0.8 (0)
Σ MUFA	22.5 (2.1)	22.7 (0.6)	21.7 (5.7)	31.2 (2.7)	33.1 (2.9)	32.7 (2)	27 (1.1)	30.6 (1.9)
16:2ω4	0.4 (0)	0.3 (0)	0.2 (0.1)	tr	0.3 (0)	tr	0.4 (0)	0.3 (0.1)
16:4ω3	3.5 (0.5)	2.1 (0.2)	1.5 (0.8)	1 (0.2)	1.6 (0.2)	0.3 (0.1)	2.1 (0.3)	0.5 (0.2)
18:2ω6	4.9 (0.4)	7.9 (0.2)	2.5 (0.7)	3.3 (0.4)	3.6 (0.4)	1.8 (0.2)	4 (0.2)	3 (0.4)
18:2ω9	nd	nd	nd	nd	nd	nd	nd	nd
18:3ω3	4.9 (0.2)	5.6 (0.1)	2 (0.7)	1.4 (0.3)	3.5 (0.5)	0.3 (0.1)	3.7 (0.4)	1.1 (0.4)
18:3ω6	0.3 (0.1)	0.3 (0)	0.2 (0.1)	0.2 (0)	0.3 (0.1)	0.3 (0)	0.2 (0.1)	0.4 (0)
18:4ω3	7.1 (0.3)	8.8 (0.5)	3 (1.5)	2.3 (0.4)	3.7 (0.6)	0.7 (0.3)	5.1 (0.8)	1.4 (0.6)
20:2ω6	nd	nd	nd	nd	nd	nd	nd	nd
20:4ω3	0.4 (0)	0.4 (0.1)	0.2 (0.2)	0.2 (0)	tr	tr	0.3 (0)	tr
20:4ω6	tr	tr	tr	tr	tr	tr	tr	tr
20:5ω3	4.6 (0.2)	7 (0.8)	1.7 (1.1)	2.2 (0.7)	2.6 (0.5)	0.9 (0.4)	4.2 (0.9)	1.3 (0.5)
22:5ω3	tr	tr	tr	tr	tr	tr	tr	tr
22:6ω3	4.9 (0.3)	3.9 (0.6)	2 (1.4)	1.6 (0.5)	3.9 (0.9)	0.7 (0.5)	5.6 (1.5)	1 (0.4)
Σ PUFA	31.7 (1.4)	36.7 (2)	13.7 (6.4)	12.8 (2.4)	20.2 (2.6)	5.3 (1)	25.8 (3.9)	9.5 (2.8)
Σ BrFA	3.4 (0.2)	2.5 (0.1)	3.2 (1)	3 (0.3)	3.8 (0.3)	3 (0.4)	3.8 (0.1)	2.8 (0.1)
PUFA/SFA	0.7 (0.1)	1 (0.1)	0.2 (0.1)	0.2 (0.1)	0.5 (0.1)	0.1 (0)	0.6 (0.1)	0.2 (0.1)
Σ EFA	9.7 (0.5)	11 (1.4)	3.8 (2.5)	4 (1.3)	6.6 (1.4)	1.7 (0.6)	9.8 (2.4)	2.4 (0.9)
16:1ω7/16:0	0.2 (0)	0.1 (0)	0.1 (0)	0.2 (0)	0.2 (0)	0.2 (0)	0.2 (0)	0.2 (0)
EPA/DHA	0.9 (0)	1.8 (0.1)	0.9 (0.1)	1.4 (0.2)	0.7 (0.1)	1.9 (1.1)	0.8 (0.1)	1.3 (0)
[FA] (µg/mg)	5.4 (0.9)	10.8 (1.9)	4.1 (1.6)	3.0 (0.4)	3.7 (0.7)	2.3 (0.4)	3.8 (0.8)	1.5 (0.1)
[TSS] (mg/l)	3.8 (0.8)	4.4 (0.6)	3.5 (0.5)	3.5 0.2)	4.0 (0.5)	3.5 (0.2)	4.0 (0.3)	7.4 (1.4)

Table S2

	High Stratification Period (August 2017)				Low Stratification Period (July 2018)			
	Echinarachnius parma			SOM	*Echinarachnius parma*			SOM
	Station 1 N = 3	Station 2 N = 3	Station 4 N = 4	Stations 1 & 2 N = 7	Station 1 N = 6	Station 2 N = 5	Station 3 N = 9	Station 2 N = 2
12:0	nd	nd	nd	0.4 (0.3)	nd	nd	nd	0.8 (0.1)
14:0	5.2 (1.2)	4.8 (0.4)	4.9 (0.6)	6.7 (1.3)	4.8 (1.2)	5 (0.4)	4.9 (0.7)	6 (0.6)
15:0	0.9 (0.2)	0.9 (0.2)	0.8 (0.1)	2.6 (0.5)	0.8 (0.1)	0.9 (0.3)	0.7 (0.1)	2.2 (0.2)
16:0	9.8 (2.3)	10.8 (1.2)	7.2 (0.8)	43.7 (4.1)	9.6 (1.8)	10.8 (1.4)	8.2 (1.0)	23.5 (1.0)
17:0	0.5 (0.1)	0.5 (0.0)	0.4 (0.1)	1.5 (0.2)	0.4 (0.1)	0.4 (0.1)	0.4 (0.1)	0.5 (0.0)
18:0	5.6 (0.9)	5.2 (0.7)	3.9 (0.3)	17.7 (3.8)	5.3 (1.1)	5.2 (0.8)	4.9 (0.7)	4.7 (0.1)
19:0	nd	nd	nd	0.5 (0.4)	nd	nd	nd	0.2 (0.0)
20:0	0.6 (0.1)	0.5 (0.1)	0.4 (0.1)	1.2 (0.2)	0.7 (0.4)	0.4 (0.1)	0.5 (0.1)	0.3 (0.1)
21:0	nd	nd	nd	0.7 (0.2)	nd	nd	nd	tr
22:0	nd	nd	nd	1.0 (0.2)	nd	nd	nd	0.3 (0.0)
24:0	nd	nd	nd	1.0 (0.4)	nd	nd	nd	0.3 (0.1)
25:0	nd	nd	nd	0.4 (0.5)	nd	nd	nd	nd
Σ SFA	23.0 (4.1)	23.4 (2.8)	18.0 (1.2)	77.4 (8.2)	22.1 (3)	23.1 (2.2)	20 (1.4)	39 (0.2)
14:1ω3	nd	nd	nd		nd	nd	nd	0.2 (0.0)
16:1ω5	tr	tr	tr	0.2 (0.1)	tr	tr	0.2 (0.0)	0.7 (0.0)
16:1ω7	7.7 (2.9)	8.1 (0.4)	12.5 (2.5)	3.4 (3.5)	8 (3)	10.9 (3.5)	9.7 (2.4)	23.8 (1.5)
16:1ω9	tr	0.2 (0.0)	0.3 (0.0)	0.5 (0.2)	0.2 (0.1)	0.4 (0.5)	0.2 (0.1)	4.6 (2.2)
17:1ω7	nd	nd	nd	0.2 (0.1)	nd	nd	nd	0.4 (0.0)
17:1ω9	nd	nd	nd	0.5 (0.4)	nd	nd	nd	1.6 (0.1)
18:1ω7	2.5 (0.2)	3.1 (0.6)	3.0 (0.2)	1.2 (1.1)	2.6 (0.3)	2.8 (0.4)	3.2 (0.2)	2.5 (0.1)
18:1ω9	1.9 (0.9)	2.3 (0.3)	1.8 (0.3)	1.6 (1.4)	5.1 (2.3)	4.7 (1.6)	4.2 (1.9)	9.4 (2.2)
18:1ω11	1.1 (0.2)	1.2 (0.1)	1.0 (0.2)	nd	1 (0.4)	1.1 (0.3)	1 (0.1)	nd
19:1ω9	0.7 (0.2)	0.5 (0.1)	0.7 (0.3)	nd	0.6 (0.2)	0.5 (0.1)	0.6 (0.1)	nd
20:1ω7	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.4 (0.2)	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.3 (0.0)
20:1ω9	1.2 (0.1)	1.3 (0.1)	1.2 (0.3)	0.3 (0.2)	2.4 (0.9)	1.9 (0.2)	2.3 (0.5)	0.3 (0.0)
20:1ω11	nd	nd	nd	0.3 (0.2)	1.1 (0.3)	0.8 (0.1)	1 (0.2)	nd
20:1ω15	8.8 (2.0)	6.5 (1.5)	5.9 (1.7)	nd	7.4 (1.5)	5.2 (1.2)	6.8 (1.0)	nd
21:1ω9	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	0.5 (0.5)	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	nd
21:1ω11	0.2 (0.1)	tr	0.3 (0.3)	nd	nd	nd	nd	nd
22:1ω9	nd	nd	nd	0.5 (0.5)	1.7 (0.8)	1.3 (0.4)	1.3 (0.4)	0.4 (0.0)
22:1ω11	nd	nd	nd	0.9 (0.7)	nd	nd	nd	tr
Σ MUFA	29.4 (1.2)	27.9 (1.6)	31.2 (1.1)	9.3 (6.7)	30.4 (1.5)	29.9 (1.3)	30.8 (1.3)	44.8 (1.4)
16:2ω4	0.4 (0.2)	0.4 (0.1)	0.8 (0.2)	nd	0.5 (0.2)	0.7 (0.3)	0.6 (0.2)	1.3 (0.2)
16:2ω6	tr	tr	tr	nd	tr (0.1)	0.2 (0.1)	tr (0.1)	0.4 (0.0)
16:3ω4	0.3 (0.1)	0.5 (0.1)	0.9 (0.2)	nd	0.5 (0.3)	0.8 (0.4)	0.9 (0.3)	1.2 (0.3)
16:4ω1	1.4 (0.7)	1.3 (0.3)	2.2 (0.5)	nd	1.6 (1)	1.9 (1)	1.7 (0.7)	0.6 (0.0)
16:4ω3	nd	nd	nd	nd	nd	nd	nd	0.4 (0.0)
18:2ω3	0.3 (0.0)	0.3 (0.1)	0.4 (0.0)	nd	0.4 (0.1)	0.4 (0.1)	0.5 (0.1)	nd
18:2ω6	0.2 (0.2)	0.6 (0.2)	0.5 (0.2)	0.5 (0.4)	0.6 (0.2)	0.6 (0.1)	0.6 (0.2)	1.2 (0.3)
18:3ω3	0.3 (0.0)	0.4 (0.1)	0.4 (0.2)	0.3 (0.1)	tr	tr	tr	0.4 (0.1)
18:3ω6	tr	tr	tr	tr	tr	0.2 (0.0)	tr	0.6 (0.1)
18:4ω3	2.1 (0.1)	2.5 (0.5)	2.7 (0.2)	0.4 (0.2)	2.5 (0.5)	2.9 (0.3)	3.2 (0.5)	1.4 (0.4)
20:2ω6	0.9 (0.2)	0.9 (0.1)	0.9 (0.2)	tr	0.8 (0.2)	0.7 (0.1)	0.8 (0.1)	nd
20:2ω9	nd	nd	nd	0.6 (0.3)	nd	nd	nd	nd
20:2 Δ 5, 13	2.2 (0.5)	2.0 (0.1)	2.0 (0.5)	nd	1.8 (0.5)	2 (0.5)	2.2 (0.3)	nd
20:2 Δ 5, 11	5.1 (1.3)	4.1 (0.3)	3.6 (0.8)	nd	4.5 (1.5)	3.5 (0.8)	3.7 (0.5)	nd
20:4ω3	nd	nd	nd	1.0 (0.3)	nd	nd	nd	tr
20:4ω6	1.8 (0.4)	2.0 (0.2)	2.9 (0.8)	0.4 (0.3)	1.3 (0.4)	1.8 (0.6)	1.6 (0.2)	0.5 (0.0)
20:5ω3	28.5 (4.0)	26.7 (2.2)	28.5 (1.1)	1.3 (1.0)	29.2 (3.4)	26.9 (2.2)	28.7 (2.2)	4.2 (0.5)
22:2 Δ 7, 15	0.8 (0.3)	0.6 (0.1)	0.7 (0.3)	nd	0.7 (0.2)	0.6 (0.2)	0.7 (0.2)	nd
22:5ω3	0.2 (0.0)	0.4 (0.1)	0.2 (0.0)	tr	tr	tr	tr	tr
22:6ω3	1.7 (0.0)	4.1 (1.8)	2.3 (0.3)	0.4 (0.2)	1.4 (0.3)	1.8 (0.2)	2.1 (0.1)	0.5 (0.1)
Σ PUFA	47.1 (5.4)	47.8 (4.2)	49.8 (2.3)	5.7 (1.7)	47 (3.3)	46 (2.3)	48.3 (2.3)	12.9 (1.0)
Σ BrFA	0.5 (0.1)	0.9 (0.0)	1.0 (0.1)	6.7 (0.7)	0.6 (0.1)	0.9 (0.1)	0.9 (0.2)	3.3 (0.2)
Σ EFA	32.1 (4.3)	32.8 (3.7)	33.8 (2.0)	2.2 (1.3)	32 (3.5)	30.6 (1.9)	32.4 (2.2)	5.2 (0.7)
ΣPUFA/ΣSFA	2.1 (0.6)	2.1 (0.4)	2.8 (0.3)	0.1 (0.0)	2.2 (0.4)	2 (0.3)	2.4 (0.3)	0.3 (0.0)
EPA/DHA	16.9 (2.6)	7.1 (2.4)	12.7 (1.6)	2.9 (1.7)	20.8 (3.2)	15 (1.3)	13.9 (1)	8.3 (1.3)
[FA] (mg/g)	31.7 (23.0)	22.8 (19.7)	52.5 (38.5)	0.2 (0.1)	78.0 (43.0)	63.9 (33.7)	90.3 (23.1)	1.8 (1.1)

Table S3

(a) Fatty acids									
HSP (2017)					LSP (2018)				
Depth	Stations				Depth	Stations			
s-POM	L1^{a}	L2^{a}	L3^{a}	L4^{a}	s-POM	L1	L2	L3	L4
b-POM	L1^{a}	L2^{a}	L3^{b}	L4^{b}	b-POM	L1	L2	L3	L4
Stations	Depth				Stations	Depth			
L1	s-POM^{a}		b-POM^{a}		L1	s-POM		b-POM	
L2	s-POM		b-POM		L2	s-POM^{a}		b-POM^{a}	
L3	s-POM^{a}		b-POM^{a}		L3	s-POM		b-POM	
L4	s-POM		b-POM		L4	s-POM		b-POM	
(b) Stable isotopes : $\delta^{13}C$									
HSP (2017)					LSP (2018)				
Depth	Stations				Depth	Stations			
s-POM	L1^{a}	L2^{b}	L3^{a}	L4^{b}	s-POM	L1^{a}	L2^{a}	L3	L4^{a}
b-POM	L1^{a}	L2^{a,b}	L3^{c}	L4^{b,c}	b-POM	L1	L2^{a}	L3	L4^{a}
Stations	Depth				Stations	Depth			
L1	s-POM^{a}		b-POM^{a}		L1	s-POM		b-POM	
L2	s-POM^{a}		b-POM^{a}		L2	s-POM^{a}		b-POM^{a}	
L3	s-POM		b-POM		L3	s-POM		b-POM	
L4	s-POM^{a}		b-POM^{a}		L4	s-POM		b-POM	
(c) Stable isotopes : $\delta^{15}N$									
HSP (2017)					LSP (2018)				
Depth	Stations				Depth	Stations			
s-POM	Not significant				s-POM	L1^{a}	L2^{a}	L3^{a}	L4^{a}
b-POM					b-POM	L1^{a}	L2^{b}	L3	L4^{a,b}
Stations	Depth				Stations	Depth			
L1	Not significant				L1	s-POM		b-POM	
L2					L2	s-POM^{a}		b-POM^{a}	
L3					L3	s-POM		b-POM	
L4					L4	s-POM^{a}		b-POM^{a}	

Table S4

	Agarum clathratum N = 3 (SD)	*Desmarestia viridis* N = 3 (SD)	*Saccharina latissima* N = 3 (SD)	*Porphyra* spp. N = 3 (SD)	*Halosiphon tomentosus* N = 3 (SD)
12:0	tr	tr	tr	tr	tr
13:0	tr	tr	tr	tr	tr
14:0	2.9 (0.2)	8.5 (1.7)	10.3 (1.7)	0.6 (0.2)	6.7 (0.3)
15:0	1.3 (0.4)	0.4 (0.1)	1.1 (0.2)	0.6 (0.5)	0.3 (0)
16:0	23.4 (4.7)	24.2 (3.9)	31.3 (1.8)	38.2 (6.5)	21.7 (0.9)
17:0	tr	0.2 (0)	0.2 (0)	tr	tr
18:0	1.5 (0.5)	3.6 (0.5)	1.5 (0.1)	1.6 (0.6)	tr
20:0	1 (0.6)	1.4 (0.3)	1 (0.2)	tr	0.3 (0)
22:0	0.4 (0.1)	nd	nd	nd	nd
24:0	tr	nd	nd	nd	nd
Σ SFA	31 (5.8)	38.5 (6.5)	45.7 (2.6)	41.4 (7.8)	29.2 (0.6)
14:1ω3	nd	0.8 (0.1)	tr	0.3 (0.2)	tr
14:1ω5	nd	tr	tr	tr	tr
15:1ω1	0.5 (0.3)	nd	tr	tr	nd
16:1ω5	0.2 (0.1)	2.4 (0.6)	0.4 (0.1)	tr	tr
16:1ω7	13.7 (0.7)	1.4 (0.3)	6.2 (1.5)	0.4 (0.1)	0.8 (0.1)
16:1ω9	2 (3)	0.3 (0.1)	tr	tr	tr
17:1ω9	0.3 (0.2)	tr	0.2 (0.1)	tr	tr
18:1ω5	nd	0.5 (0)	nd	nd	tr
18:1ω7	1 (0.1)	1.8 (0.5)	0.3 (0.1)	1.8 (0.7)	11.7 (1.4)
18:1ω9	4.9 (1.6)	8.4 (1.2)	15.1 (2.7)	3.5 (1.6)	8.4 (0.6)
Σ MUFA	22.6 (2.5)	15.9 (2.8)	22.6 (1.4)	6.4 (2.2)	21.4 (1.9)
16:2ω4	2.1 (0.6)	tr	tr	tr	tr
16:2ω6	0.7 (0.2)	tr	0.7 (0.1)	tr	tr
16:3ω4	2.3 (0.8)	tr	tr	tr	tr
16:4ω1	8.5 (1.4)	tr	tr	tr	nd
16:4ω3	0.3 (0.3)	nd	nd (nd)	nd	tr
18:2ω3	0.8 (0.1)	tr	tr	tr	tr
18:2ω6	1.9 (0.7)	7.5 (0.9)	5.3 (1.1)	4.3 (1.8)	9.6 (0.2)
18:2ω9	nd	tr	tr	0.3 (0.2)	tr
18:3ω3	3.5 (1.3)	8.4 (1.8)	4.2 (1.3)	0.4 (0.3)	8.2 (0.3)
18:3ω6	1.5 (0.5)	0.7 (0.1)	0.5 (0.1)	0.4 (0)	1.3 (0.2)
18:4ω1	0.6 (0.1)	nd	nd	nd	nd
18:4ω3	1.4 (0.4)	7.8 (2.2)	4 (1.1)	0.4 (0.1)	9.7 (0.6)
20:2ω6	nd	tr	tr	2 (0.2)	tr
20:3ω3	nd	tr	tr	0.2 (0.1)	tr
20:3ω6	tr	0.4 (0.1)	0.3 (0.2)	1.5 (0.4)	0.9 (0.1)
20:4ω3	nd	0.6 (0.2)	0.5 (0.1)	0.4 (0.1)	0.6 (0.1)
20:4ω6	6.1 (0.7)	9.7 (2.1)	9.8 (2.8)	7.4 (3.2)	8.3 (0.5)
20:5ω3	4.2 (1.4)	9.6 (2.1)	5.2 (0.3)	34.1 (7.3)	10.3 (0.7)
22:4ω6	0.3 (0.3)	nd	nd	nd	nd
22:5ω3	12.1 (2.6)	tr	tr	tr	tr
22:6ω3	nd	0.2 (0.1)	0.2 (0)	0.2 (0.1)	tr
Σ PUFA	46.4 (3.9)	45.4 (9)	31.6 (1.3)	52.1 (7)	49.4 (2.4)
[FAs] (mg/g)	10.9 (1.7)	17.5 (5.1)	4.4 (1)	7.1 (3.4)	44 (2.9)

Figure S1

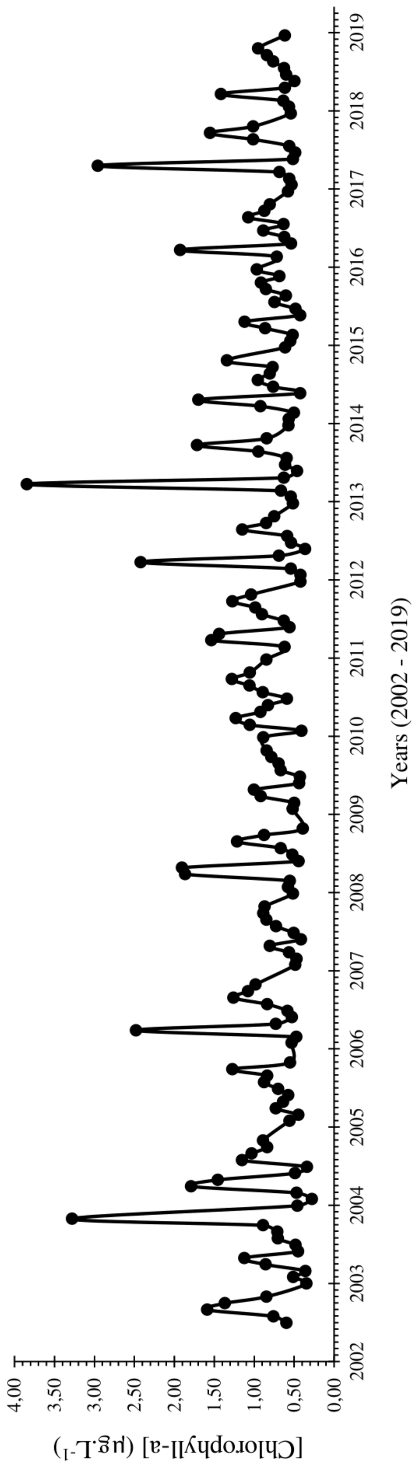
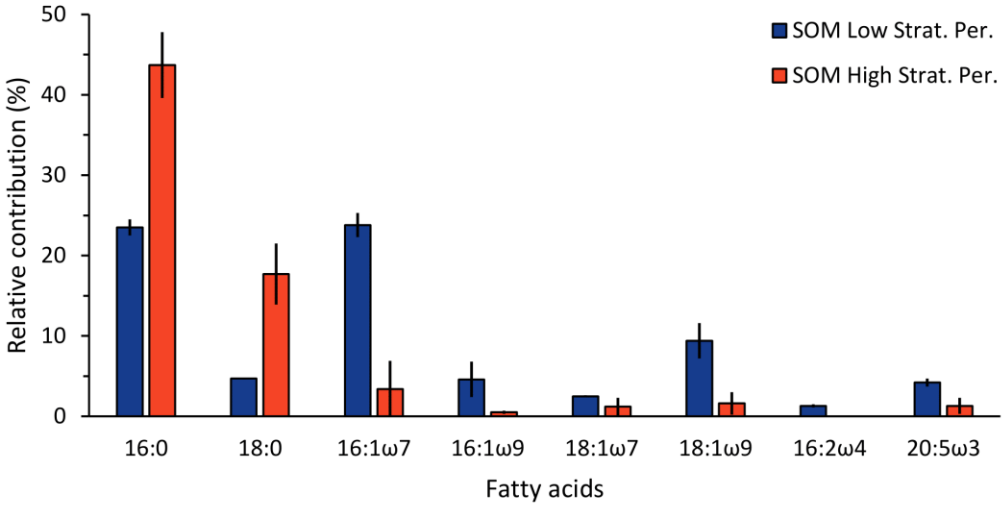

[Chlorophyll-a] (µg.L-1)
4,00
3,50
3,00
2,50
2,00
1,50
1,00
0,50
0,00
Years (2002 - 2019)
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019

Figure S2


Relative contribution (%)
50
40
30
20
10
0
🟦 SOM Low Strat. Per.
🟥 SOM High Strat. Per.
16:0
18:0
16:1ω7
16:1ω9
18:1ω7
18:1ω9
16:2ω4
20:5ω3
Fatty acids

Chapter III

Food source diversity, trophic plasticity, and omnivory enhance the stability of a shallow benthic food web from a high-Arctic fjord exposed to freshwater inputs

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Abstract

Under climate change, many Arctic coastal ecosystems receive increasing amounts of freshwater, with ecological consequences that remain poorly understood. In this study, we investigated how freshwater input may affect the small-scale structure of benthic food webs in a low-production high-Arctic fjord (Young Sound, NE Greenland). We seasonally sampled benthic invertebrates from two stations receiving contrasting freshwater input: an inner station exposed to turbid and nutrient-depleted freshwater flow and an outer station exposed to lower terrestrial influences. Benthic food web structure was described using a stable isotope approach ($\delta^{13}C$ and $\delta^{15}N$), Bayesian models, and community-wide metrics. The results revealed the spatially and temporally homogeneous structure of the benthic food web, characterized by high trophic diversity (i.e., a wide community isotopic niche). Such temporal stability and spatial homogeneity mirror the high degree of trophic plasticity and omnivory of benthic consumers allowing the maintenance of several carbon pathways through the food web despite different food availability. Furthermore, potential large inputs of shelf organic matter together with local benthic primary production (i.e., macroalgae and presumably microphytobenthos) may considerably increase the stability of the benthic food web by providing alternative food sources to locally runoff-impacted pelagic primary production. Future studies should assess beyond which threshold limit a larger increase in freshwater inputs might cancel out these stability factors and lead to marked changes in Arctic benthic ecosystems.

Key words

Arctic benthic ecosystems • Riverine inputs • Climate change • Stable isotopes • Mixing models • Isotopic niche width • Benthic primary producers • Terrestrial Organic Matter • Young Sound • Greenland

Introduction

Arctic ecosystems are experiencing strong modifications of abiotic conditions under climate change, including increasing water temperatures and decreasing sea-ice coverage (AMAP 2017). In addition, freshwater inputs to the coastal domain are currently increasing in many locations along the Arctic coastline (Haine et al. 2015; Sejr et al. 2017). The impacts of such inputs on marine systems can be complex and influenced by numerous factors such as the freshwater origin (e.g., marine- *vs* land-terminating glacier) and local topography (e.g., absence/presence of a sill in fjords; Hopwood et al. 2020). Consequences of increased freshwater on the pelagic compartment include modifications of primary production, water column stratification, turbidity, and nutrient concentrations, but also organic matter quality and quantity (Meire et al. 2017; Paulsen et al. 2017; Bridier et al. 2019), with subsequent impacts on food webs (Middelbo et al. 2018).

Impacts on benthic ecosystems have received little attention, with studies mainly focusing on the disturbance generated by high sedimentation close to marine glaciers (e.g., sediment instabilities, bivalve gill clogging, etc.) that may decrease the species and functional richness of benthic communities (Sejr et al. 2010; Włodarska-Kowalczuk et al. 2019). Food-web studies have revealed significant contributions of terrestrial organic matter to the diet of benthic organisms, but these studies have mainly concerned large hydrological systems (e.g., Mackenzie River) over very large spatial scales (i.e., >100s of km; Bell et al. 2016). By contrast, fjords and coastal subtidal habitats have been less investigated, although they should be the first to be affected by freshwater inputs (i.e., fjords' water masses are more confined and surrounded by land than are shelf water masses). Because benthic organisms are essential for the functioning of marine ecosystems (e.g., through carbon and nutrient cycling, and benthic-pelagic coupling; Griffiths et al. 2017) and are key resources for several marine mammal and seabird species (e.g., Grebmeier et al. 2006), understanding the consequences of environmental changes for benthic food webs should be improved to enable accurate predictions of marine ecosystem responses to climate change.

In this study, we aimed at understanding the effects of local freshwater inputs on the functioning of a high-Arctic fjord by investigating carbon pathways through the benthic food web. For this purpose, we compared stable isotope signatures of benthic organisms and organic matter sources, using $\delta^{13}C$ and $\delta^{15}N$ measurements from two stations located along a gradient of freshwater inputs (controlling other environmental factors, e.g., turbidity, nutrient depletion, and organic matter quality; Meire et al. 2017; Paulsen et al. 2017; Bridier et al. 2019). Ecological studies using stable isotopes have been widely used to trace transfers of organic matter within benthic communities (e.g., Abrantes et al. 2014). Numerous studies have shown the ability of stable isotope mixing models and trophic position models to quantify the relative importance of production originating from various origin and to better understand feeding strategies of benthic invertebrates (e.g., McTigue & Dunton 2017; Michel et al. 2019). In addition, several authors recently suggested that the bivariate $\delta^{13}C$ – $\delta^{15}N$ isotope space (δ-space) filled by a community accurately depicts its isotopic niche (Layman et al. 2007; Jackson et al. 2011). Several metrics describing such isotopic niches (e.g., area, dimensions, and shape of the δ-space) were then developed to assess food-web complexity/stability and to determine the diversity of organic matter sources fueling a community (Layman et al. 2007; Jackson et al. 2011; Reid et al. 2016).

These approaches have shown their ability to describe the functioning of benthic ecosystems exposed to high environmental pressures (e.g., flood events; Abrantes et al. 2014) by tracking changes in organic matter pathways within communities over time and space. However, these methods are still rarely used in polar areas (but see Włodarska-Kowalczuk et al. 2019). Using community-wide trophic niche metrics and stable isotope mixing/trophic position models, we investigated the small-scale variability (i.e., inner *vs* outer fjord communities) of the structure of the benthic food-web in a high-Arctic fjord exposed to freshwater input. The objective of this study is to better understand the effects of freshwater inputs on Arctic benthic food webs and to identify the drivers of community resilience and stability in the context of ongoing climate change.

Materials and Methods

Study sites and sampling stations

This study was conducted in Young Sound, a high-Arctic fjord of NE Greenland (Fig. 1). This fjord ranks among the least-productive coastal ecosystems in the world (pelagic primary production ~10 g C m^2 yr^{-1}; Rysgaard et al. 1999) due to prolonged sea-ice cover (9–10 months per year; Rysgaard et al. 1999) and seasonal stratification generated by strong riverine inputs from land-terminating glaciers (Holding et al. 2019). This low production is partly compensated by high benthic primary production in its shallow coastal areas (i.e., < 30 m) which exceed from 2 to 7 times local phytoplankton production and accounts for 20-40% of the whole outer fjord primary production (Glud et al. 2002; Krause-Jensen et al. 2007; Attard et al. 2016). On the other hand, ice-algae contribute only marginally (i.e., < 1 %) to the overall Young Sound primary production, mainly as a result of high snow cover and low seawater salinity directly under sea-ice (Glud et al. 2002; Limoges et al. 2018).

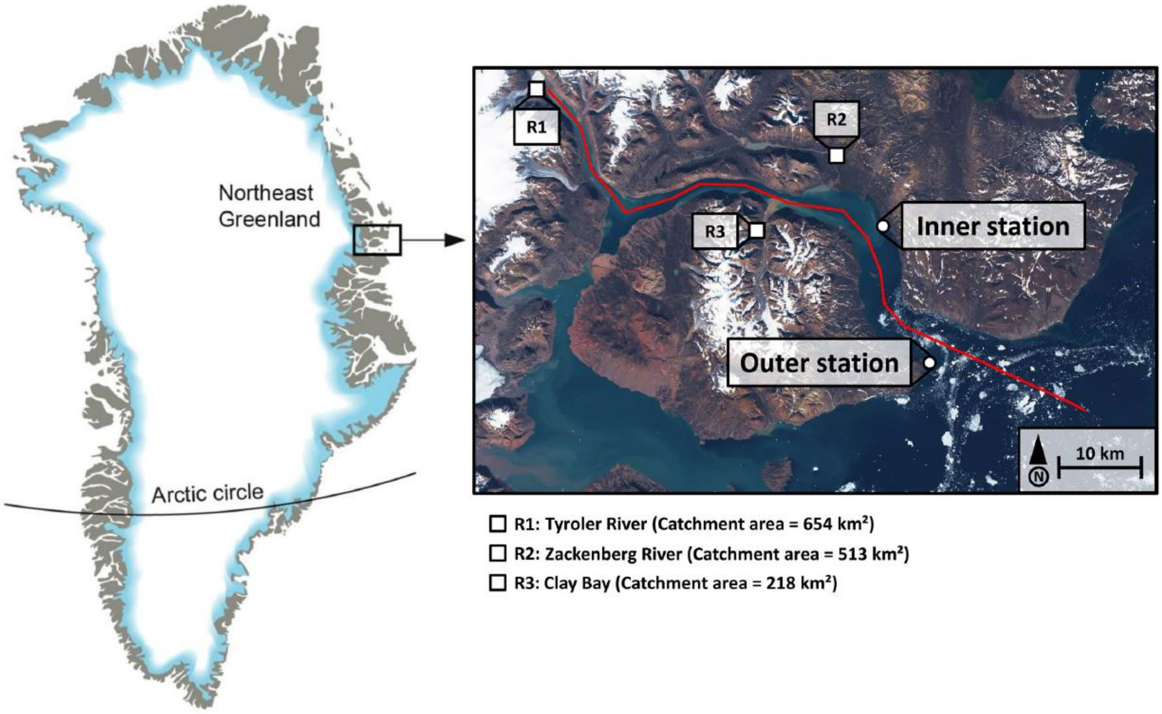

Figure 1: Map representing the two study locations (white circles), the CTD transect (red lines) and the three main rivers (white squares) in the study area (Young Sound fjord, 74°N, NE Greenland). River catchment areas are from Bendtsen et al. (2014).

Two shallow stations (i.e., depth range = 10 – 30 m) were prospected: (1) an inner station (74°24’36’’N – 20°19’48’’W, surveyed in May 2017 and August 2018), close to the Zackenberg River (river discharge = 0.15 – 0.25 km^3 yr$^{–1}$; Citterio et al. 2017), and (2) an outer station (74°12’36’’N – 20°6’36’’W, surveyed in May and August 2018), situated at the fjord mouth. These two localities were selected because of contrasted exposure to freshwater inputs associated to an inner/outer fjord gradient in physical and chemical conditions. Considerable freshwater inputs in Young Sound innermost areas (ranging from 0.9 to 1.4 km^{-3} yr^{-1}; Bendtsen et al. 2014) generate strong spatial variations in surficial water salinity, ranging from 8 in the innermost part of the fjord to 30 in the outermost part (Rysgaard et al. 2003; Bendtsen et al. 2014). Moreover, the inner station is located at the direct vicinity (i.e., ~ 500 – 750 m) of several small deltas and it receives additional inputs in freshwater and sediment while no deltas were reported close to the outer station (Kroon et al. 2017). These contrasted exposure of inner and outer stations to freshwater inputs and inert particles explain the observed differences in sediment grain-size distributions between both sites. Proportion of pelites (particles < 63 µm) in the sediment is three-fold higher at the inner (i.e., 69.2 %) than the outer station (i.e., 21.7 %, see Fig. S1, Supplementary Information), reflecting very contrasting loadings of terrestrial material between these two coastal areas.

This freshwater input gradient leads to contrasting environmental conditions between inner and outer stations. Stronger stratification at the inner station reduces the size of phytoplankton cells (Holding et al. 2019), with potential subsequent impact on marine primary consumers (Middelbo et al. 2018). Higher input of terrestrial material and nutrient depletion at the inner station (Paulsen et al. 2017) is also reported to lessen the quality of the organic matter (Bridier et al. 2019). Finally, a two-fold lower pelagic primary production has been recorded at the inner station compared to the outer station because of the negative impacts of freshwater inputs on inner fjord turbidity and nutrient concentrations (Meire et al. 2017).

Sampling

Benthic consumers were sampled using a triangular dredge (1 mm mesh size, August 2018) or a suction dredge (1 mm mesh size) operated by scuba divers (May 2017 and 2018). All entire individuals were collected for stable isotope analyses in order to meet species diversity requirements for isotopic diversity indices (i.e., n > 20 species; Brind’amour & Dubois 2013). Number of replicates varied from 1 to 9 individuals per benthic species. Three potential food sources were sampled in our study: particulate organic matter (POM), sedimentary organic matter (SOM) and terrestrial organic matter (TOM). Bottom POM samples were collected on each site at 1 meter above the seabed by using a 10 L Niskin bottle (May 2017 and August 2018). Scuba divers collected SOM samples by aspirating the first 1-5 mm of the sediment surface delimited in a 25*25 cm (i.e., 625 cm^2) quadrat with a 450 mL syringe (August 2016). Finally, TOM samples were taken in August 2018 upstream of the Zackenberg River delta (74°28'14.3"N, 20°34'47.4"W, salinity = 0.38) using 10 L bottles. Sampling replication varied from 3 to 6 samples per food source. Water and sedimentary samples were then filtered on precombusted (5 h at 400°C) GF/F filters (pore size = 0.07 µm) until clogging (for further details, see Bridier et al. 2019). In addition, we used the stable isotope signatures of *Fucus* sp. and *Saccharina latissima* measured by De Cesare et al. (2017). All samples were stored at –80°C before laboratory analyses. Finally, surficial waters salinity (i.e., 0 – 30 m) was measured in August 2018 through a set of CTD profiles conducted along the fjord to assess the spatial extent of the freshwater plume (Fig. 1). We also performed two additional CTD profiles at the studied inner and outer stations to record local 0 – 10 m seawater salinity. Additional information on sampling dates and sample replications are available in the Supplementary Information (Table S1 & S2).

Laboratory analyses

Stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) were performed on either one or a pool of complete individuals (guts apart) and muscle tissues from large species (e.g., shrimp, fish; Supplementary Information, Table S1). Animal tissues were freeze-dried for at least 48 h at –50°C and ground to a fine powder in a ball mill (cycles of 10 minutes at 30 Hz). Half of the carbonate-rich tissues were acidified with hydrochloric acid (10% HCl) for carbon isotope analyses to prevent the bias induced by inorganic carbon in $\delta^{13}C$ signatures while the other half remained untreated for nitrogen isotope analyses to avoid acidification bias in $\delta^{15}N$ values (Jacob et al. 2005). Samples were not lipid-extracted, due to the usually low lipid content in Arctic benthic invertebrates (Clarke & Peck 1991) and to avoid potential bias in $\delta^{15}N$ values (Post et al. 2007). No mathematical lipid corrections were done because of the large variability of $\delta^{13}C$ lipid bulk signatures among Arctic species makes questionable the use of generalized mathematical equations based on a constant lipid $\delta^{13}C$ value (Mohan et al. 2016).

All stable isotope analyses were performed at the University of California, Davis (UC Davis Stable Isotope Facility, Department of Plant Sciences, CA, USA). Stable isotope measurements were realized with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa

20-20 isotope ratio mass spectrometer (Sercon, UK). Sample stable isotope ratios were expressed in relation to stable isotope ratios from Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric nitrogen (N_2, $\delta^{15}N$), based on following the equation: $\delta X = [(Rsample / Rstandard) – 1] \times 1000$; where X is the $\delta^{13}C$ or $\delta^{15}N$ value of the analyzed sample and R the corresponding 13C/12C or 15N/14N molar ratio (Peterson & Fry 1987). Standard deviations of stable isotope measurements were estimated at ± 0.2 for $\delta^{13}C$ and ± 0.3 for $\delta^{15}N$, based on replicate measurements of international standards (run every 15th sample) from the International Atomic Energy Agency (IAEA600) and the United States Geological Survey (USGS40, USGS41, USGS62, USGS65).

Data analyses

Community convex hulls (areas compassing all the data) and standard ellipses (95% confidence ellipses encompassing 40% of the data) were plotted in a δ-space to visualize isotopic niches. Potential shifts on the $\delta^{13}C$ or $\delta^{15}N$ axis between community isotopic niches were investigated by computing the overlap between inner and outer standard ellipses (i.e., the percentage shared by two communities in relation to the smallest ellipse). Community trophic niche widths were assessed by calculating the standard ellipse area and mean distance to centroid (i.e., the mean distance of each species to the $\delta^{13}C – \delta^{15}N$ centroid) metrics (Layman et al. 2007; Jackson et al. 2011). Standard ellipses' eccentricities were also calculated to compare the shapes of isotopic niches (e.g., a lower eccentricity would result in a narrower community ellipse range on the $\delta^{13}C$ axis; Reid et al. 2016).

The horizontal structure of benthic food webs was described using Bayesian stable isotope mixing models performed on primary consumer stable isotope signatures to assess the diversity and importance of organic matter sources fueling benthic invertebrates (Parnell et al. 2013). Mixing models were calculated using the simmr package (Parnell et al. 2019) to include the variability of consumer and end-member stable isotope signatures as well as the uncertainty in trophic enrichment factors (TEFs) for diet estimates (Parnell et al. 2013). Although $\delta^{13}C$ TEFs are considered to be similar between primary consumers and carnivores (Post 2002, McCutchan et al. 2003), they are known to be highly variable (e.g., ranging from ~ 0 to 4 ‰) among species from a same guild, depending on animal physiology and/or food source quality (e.g., Caut et al. 2009). In order to integer such variability, we used an intermediate $\delta^{13}C$ TEF with a high level of uncertainty (i.e., 2 ± 2 ‰) which considers that $\delta^{13}C$ fractionation can potentially be very low (e.g., 0 ‰) or very high (e.g., 4 ‰) for some species. Mixing models used Post's TEF for

δ^{15}N signatures (i.e., 3.4 ± 1.0 ‰). Stable isotope signatures of POM and SOM sources as well as those of *Fucus* sp. and *Saccharina latissima* were combined *a posteriori* into two unique sources (i.e., "POM/SOM" and "Benthic sources", respectively) because of their close isotopic compositions (Phillips et al. 2014).

The vertical structure of the benthic food web was studied using a trophic position model (Quezada-Romegialli et al. 2018) to assess the degree of omnivory in food webs by comparing the trophic positions of consumers in relation to their putative food sources. Trophic positions were calculated using two-baseline (i.e. POM/SOM and macroalgae [i.e. *Fucus* sp. and *Saccharina latissima*]) Bayesian models from the tRophicPosition package (Quezada-Romegialli et al. 2019) based on the following equations from Quezada-Romegialli et al. (2018):

$$\delta^{15}\mathrm{N_C} = \Delta\mathrm{N}(\mathrm{TP} + \lambda) + \alpha(\delta^{15}\mathrm{N_{b1}} + \delta^{15}\mathrm{N_{b2}}) - \delta^{15}\mathrm{N_{b2}}$$

and

$$\alpha = \left(\frac{\frac{\delta^{13}\mathrm{C_{b2}} - (\delta^{13}\mathrm{C_c} + \Delta\mathrm{C})}{\mathrm{TP}\ -\ \lambda}}{\delta^{13}\mathrm{C_{b2}} + \delta^{13}\mathrm{C_{b1}}}\right)$$

Where δ^{15}N, $\delta^{15}\mathrm{N_{b1}}$ and $\delta^{15}\mathrm{N_{b2}}$ refer to the δ^{15}N values of consumers, first and second baselines, respectively; $\delta^{13}\mathrm{C_c}$, $\delta^{13}\mathrm{C_{b1}}$ and $\delta^{13}\mathrm{C_{b2}}$ are the δ^{13}C values of consumers, first and second baselines, respectively; ΔN refer to the TEF for nitrogen (i.e., 3.4 ± 1 ‰); ΔC is the TEF for carbon (i.e., 2 ± 2 ‰); TP is the consumer's trophic position and λ is the baseline's trophic position.

Standard ellipse area credibility intervals were calculated on species mean isotope signatures through a Bayesian approach using 200,000 posterior iterations. Standard Ellipses Areas without overlap of their 95% credibility intervals were considered significantly different. Unfortunately, this Bayesian approach could not be applied to estimate mean distance to centroid and ellipse eccentricity credibility intervals because these calculations are based on both intra-group (i.e., dispersion between replicates of a single species) and inter-group (i.e., dispersion among species; Jackson et al. 2011) variability and several species had no replicates. Bayesian mixing and trophic position models were performed only on August samples as replication for May samples was too low. Stable isotope signatures of the main abundant consumers from the inner and outer stations were then pooled to meet replication requirements for the calculation of the residual error term (i.e., n > 4; Parnell et al. 2010). Bayesian mixing and trophic position models were based on 200,000 iterations, 100,000 burn-ins, 500 thinned samples, and 3 chains. Gelman-Rubin convergence statistics were computed to determine if the mixing model had a properly run with a suitable number of iterations (i.e., Gelman-Rubin diagnostics > 1.1 indicates unsatisfactory runs; Gelman et al. 2004). All Gelman-Rubin statistics were below 1.03 and indicated thus satisfactory runs. Each mixing model was built when the range of consumer isotope signatures inside the mixing polygon. Distribution of posterior predictive values were plotted to ensure that the produced model fitted with the original data. All data analyses were performed with R (R Core Team 2019) using scripts provided by N. D. McTigue (from Harris et al. 2018) and L. N. Michel (from Michel et al. 2019).

Results

Spatial variations in summer surface seawater salinity

Seawater salinity in surface waters was highly variable along the fjord transect (Fig. 2). Terrestrial inputs generated a shallow low salinity surface layer (≈ 5 m) ranging from 0 to 15 (Fig. 2) in Young Sound's innermost areas. Salinity then steadily increasing as the plume flowed toward the shelf. Fjord areas in the vicinity of the inner station showed intermediate sea surface salinity (≈ 15 – 20) and halocline depth (≈ 2 – 3 m). On the other hand, highest salinities were measured around the outer station (i.e., 20-25). These salinities were however more variable at small-spatial scale because of the simultaneous exposition of the outer fjord area to both inflowing shelf waters, outflowing fjord waters and southward coastal currents. Salinity profiles conducted at the exact studied station locations also showed strong differences between sites as illustrated by the averaged (0 – 10 m) surface salinity measured at 21.0 and 28.7, in the inner and outer stations, respectively (see Table S3, Supplementary Information).

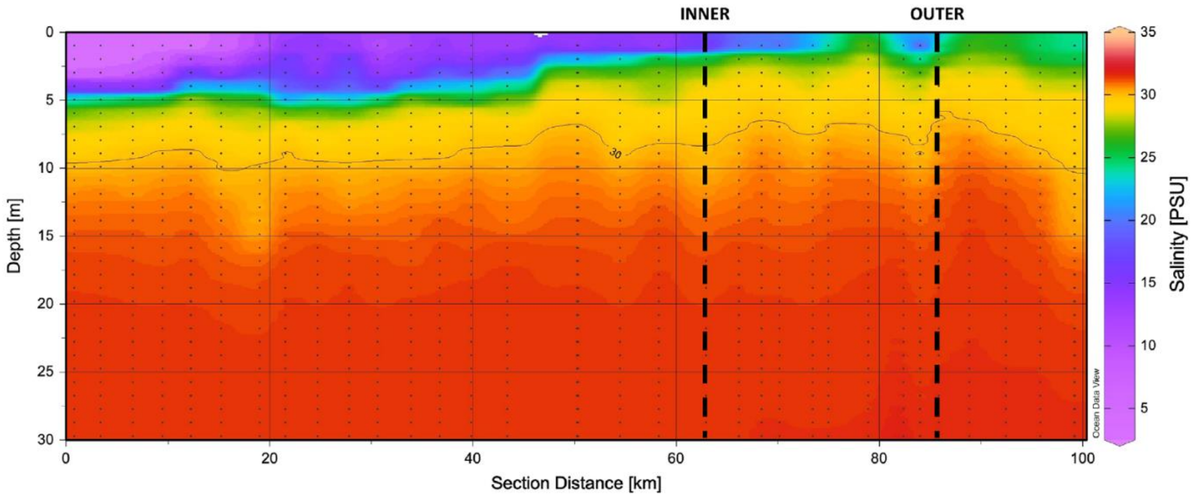

Figure 2: Contour plot representing salinity variation in the upper 30 m of the water column along an inner/outer fjord transect (see Fig. 1). Black dashed lines indicate the position of the inner and outer stations.

Isotopic niches of outer and inner communities

Isotopic niches of the inner and outer communities were highly similar in both seasons as reflected by their high overlap (74.8 and 77.5% during winter and summer, respectively; Fig. 3a, b). Such seasonal stability and spatial homogeneity of Young Sound food webs is confirmed by the absence of significant differences in standard ellipse areas between both stations and seasons ($p > 0.05$, see credibility interval overlaps in Supplementary Information, Fig. S2). Although no statistical analyses could be performed on the Layman metrics (mean distance to centroid and eccentricity) due to the absence of replication for several species (i.e., $n < 5$), the absence of strong variations between seasons and stations suggests no major seasonal or spatial differences of food web structures occurred (Table 1).

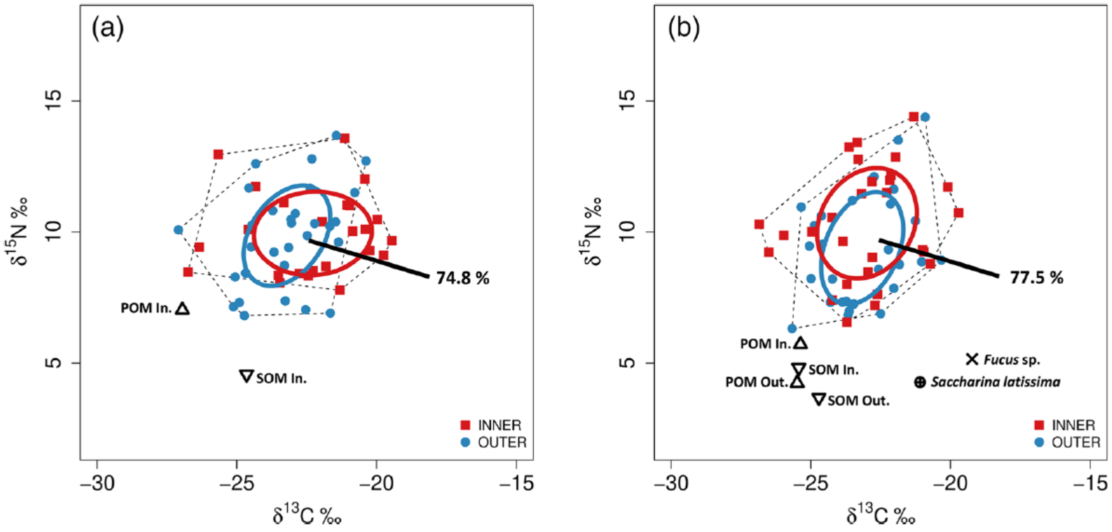

Figure 3: Standard ellipses (solid lines) and convex hulls (dashed lines) of the inner and outer communities during winter (a) and summer (b) seasons, respectively. Isotopic niche overlap is defined as the percentage of δ-space shared between inner and outer communities in relation to the surface of the smallest ellipse. Food sources are represented by black symbols. POM: particulate organic matter, SOM: sedimentary organic matter, Out.: Outer station, In.: Inner station.

Table 1. Standard ellipse area (SEA, ‰2), mean distance to centroid (CD, ‰), mean nearest neighbor distance (MNND, ‰), standard deviation of mean nearest neighbor distance (SDNND, ‰), and SEA eccentricity from the inner and outer communities sampled in winter and summer.

	Winter		Summer	
	Outer	Inner	Outer	Inner
SEA	8.45	10.29	9.07	11.30
CD	2.12	2.34	2.34	2.53
MNND	0.73	0.76	0.65	0.66
SDNND	0.50	0.51	0.40	0.35
Eccentricity	0.77	0.66	0.80	0.64

Benthic food web horizontal structure

Outputs from our mixing models highlighted a low/insignificant contribution of TOM for all primary consumers, except perhaps for the isopod *Arcturus baffini*, Ascidiacea and *Pectinaria hyperborea* which were characterized by large variation in its credibility intervals (Fig. 4). The contribution of other organic matter sources was variable among primary consumers. Several species considered here as suspension (i.e., *Arcturus baffini*, *Astarte moerchi*, *Astarte elliptica*, *Balanus* sp., *Hiatella arctica*) or deposit (i.e., *Margarites coastalis*, *Pectinaria hyperborea*) feeders appeared to feed in significant proportion on benthic sources (from 18.9% for *Balanus* sp. to 47.4% for *Astarte moerchi*, modes of the posterior probability distributions), while for other species its contribution remained low (10.4–14.0%, Fig. 4). Aggregated POM and SOM sources showed large contributions for all species (from 43.3% for *Astarte elliptica* to 85.4% for *Ophiocten sericeum*, modes of the posterior probability distributions).

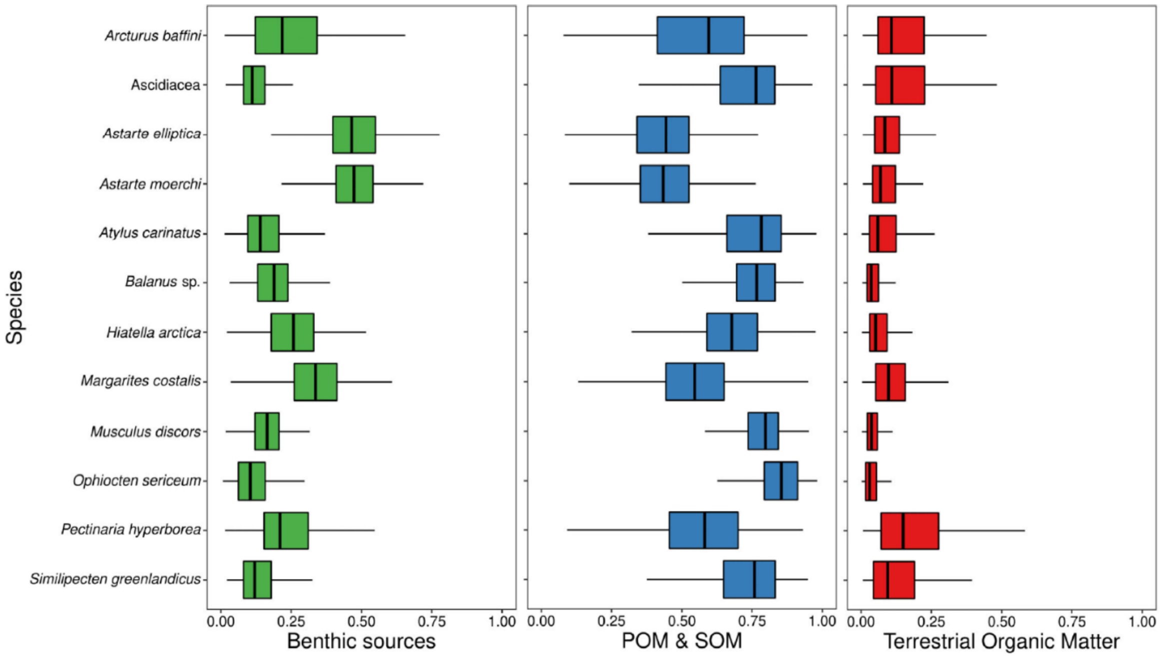

Figure 4: Boxplots representing relative contributions of benthic sources (left); combined particulate organic matter and sedimentary organic matter sources (middle); and terrestrial organic matter (right) to the diet of main primary consumers. The center line, boxes, and error bars represent the modes and 50% and 95% credibility intervals based on posterior probability distributions, respectively. Outliers were omitted for clarity. POM: particulate organic matter; SOM: sedimentary organic matter.

Benthic food web vertical structure

Consumer trophic positions calculated using two-baseline Bayesian models (based on POM and SOM baselines, according to mixing model outputs) were highly variable among species (Fig. 5). The mean trophic position of primary consumers (i.e., suspension and deposit feeders) ranged from 1.7 for *Atylus carinatus* and *Balanus* sp. to 2.6 for *Pectinaria hyperborea*, while for predatory/scavenging consumers (combined together as "carnivores") it ranged from 2.3 for *Metopa glacialis* to 3.8 for *Argis dentata* (Fig. 5). Credibility intervals varied overall over large ranges, exceeding in some cases the extent of one trophic level (e.g., *Colus* sp., *Icelus bicornis*, *Pectinaria hyperborea*, Fig. 5).

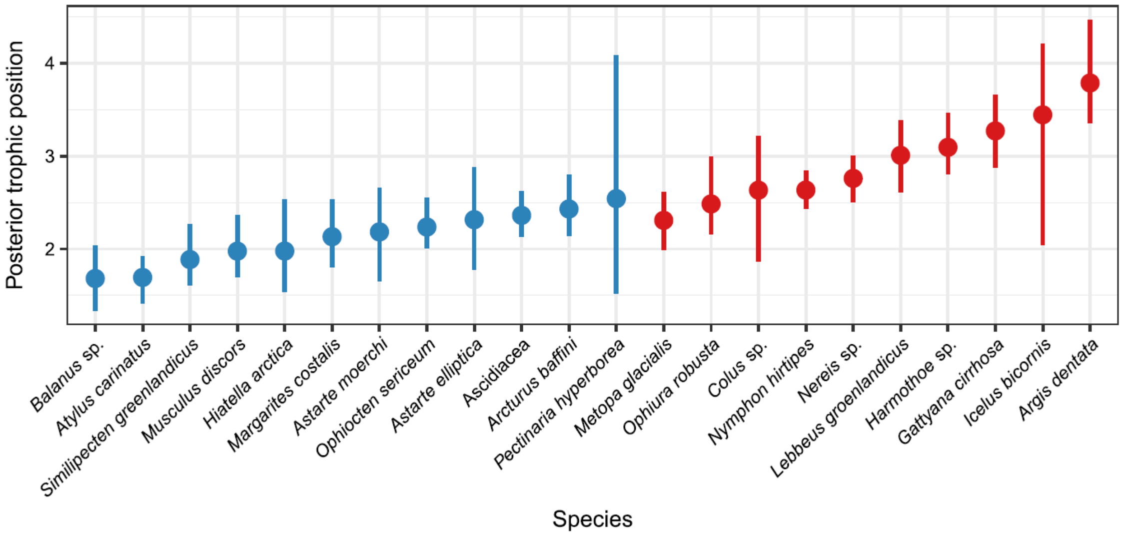

Figure 5. Modal trophic positions of main primary (blue circles) and secondary/tertiary consumers (red circles) with their associated 95% credibility intervals based on posterior probability distributions.

The modal trophic positions of all primary consumers, except for the crustaceans *Atylus carinatus* and *Balanus* sp., were higher than 2, with significant values for *Arcturus baffini*, Ascidiacea, and *Ophiocten sericeum* only (Fig. 5). The modal trophic positions of four taxa initially considered as primary consumers (*Astarte elliptica*, Ascidiacea, *Arcturus baffini*, *Pectinaria hyperborea*) were higher than the lowest value of a secondary consumer (*Metopa glacialis*). In contrast, modal trophic positions of five other species initially considered as secondary consumers (*Colus* sp., *Metopa glacialis*, *Nereis* sp., *Nymphon hirtipes*, *Ophiura robusta*) were lower than 3 (Fig. 5). Finally, all primary consumers' credibility intervals overlapped with those of one or several secondary consumers, except for Atylus carinatus (Fig. 5).

Discussion

Temporal and spatial variability of the benthic food web

Although Young Sound experiences an extreme seasonality (Rysgaard et al. 1999; Rysgaard & Nielsen 2006) and strong spatial gradients associated to freshwater inputs (Fig. 2; Meire et al. 2017; Paulsen et al. 2017; Holding et al. 2019), in the present study we did not observe any spatiotemporal variations in the benthic food-web structures. Such similarity between inner and outer standard ellipse areas and positions on the δ^{13}C axis (reflected by high standard ellipse area overlaps) suggests that both communities are based mostly on the same organic matter sources. Moreover, high mean distance to centroid and eccentricity values in the inner and outer communities indicate that both trophic webs are based on several organic matter sources (Layman et al. 2007). Although these metrics might be highly sensitive to sampling effort, all standard ellipse areas had a sample size sufficient to avoid such potential bias (i.e., n > 20, Brind'Amour & Dubois 2013).

The absence of temporal variability in the benthic food webs despite strong seasonal variation of POM and SOM baselines (Fig. 3a, b) and changes in food source availability (Bridier et al. 2019) may appear surprising. Indeed, several works on Arctic food webs previously highlighted similar temporal stability partly explained by the moderate seasonality of systems that were characterized by multiple pulses of fresh organic matter each year (e.g., Renaud et al. 2011). Considering the extreme seasonality of primary production in Young Sound (i.e., limited to 2 to 4 months per year; Rysgaard et al. 1999; Holding et al. 2019), there is no evidence for regular input of fresh organic matter in this fjord. We rather hypothesize that the temporal stability reflects the low tissue-turnover rates (expected to range from 8 months to more than one year) observed in Arctic benthic invertebrates, which display long lifespan and slow growth (Kaufman et al. 2008; Weems et al. 2012; McMeans et al. 2015). As a consequence, isotope signatures of benthic invertebrates would reflect environmental conditions over the year rather than during one particular season.

Despite strong environmental gradients, which vary at a seasonal scale, we also did not detect any spatial variation in the benthic food webs in Young Sound. Although the sampled stations in this study cover only a part of the fjord's length, significant gradients of salinity (Paulsen et al. 2017; Sejr et al. 2017), organic matter quality (Bridier et al. 2019), and primary production (Meire et al. 2017) have been reported between the same stations. In a similar spatial and salinity gradient of Hornsund (Svalbard), Włodarska-Kowalczuk et al. (2019) highlighted a clear $\delta^{13}C$ shift between benthic food webs of inner and outer fjords, which they attributed to different relative contributions of various organic matter sources. The absence of such a trend in Young Sound may signify that the organic matter pool fueling inner and outer communities is minimally affected by environmental gradients. Considering that the inner and outer communities displayed similar general functioning, we consider that their related consumers should be part of a single benthic food web. We will discuss below the potential origins of this spatial homogeneity that exists despite strong gradients in freshwater inputs.

Importance of the diversity of food sources on benthic food web stability

Based on the horizontal structure of the benthic food web (which extends over 7‰ on the $\delta^{13}C$ axis) and the high standard ellipse area values coupled to low eccentricity metrics, we conclude that primary consumers feed on several organic matter sources (Layman et al. 2007; Reid et al. 2016). We then hypothesize that some of these food sources may support the resilience of benthic food webs in shallow habitats facing high freshwater inputs and low pelagic primary production.

Contrary to several food-web studies conducted in shallow Arctic areas (e.g., Harris et al. 2018), we did not detect significant contributions of TOM in the diet of primary consumers in the Young Sound fjord. Although stable isotope signatures of terrestrial material may be modified by bacteria, $\delta^{15}N$ signatures of TOM (–2.2 ‰) appear too depleted to reach the $\delta^{15}N$ signatures of marine POM and SOM, even after bacterial degradation (Lehmann et al. 2002). Several hypotheses can be proposed to explain these constrasting results. Firstly, it is possible that our sampling missed species feeding massively on TOM. However, while the highest reliance on terrestrial material is usually shown by sub-surface deposit feeders (e.g., Orbinidae, Maldanidae; Harris et al. 2018; McGovern et al. 2020), these species exhibited relatively enriched $\delta^{13}C$ signatures in the present study (Supplementary Information, Table S1) leading us to reject this hypothesis. Secondly, both the outer and inner sampling stations could be located too far out of the zone of influence of the Zackenberg River delta to receive significant contributions of TOM. However, this would not have been the case for the inner station, located ~5 km from the delta and where a significant influence of terrestrial material input was detected (Bridier et al. 2019). Therefore, we hypothesize that such opposite results might reflect differences in the quality and quantity of TOM inputs across Arctic regions. Indeed, soils from Scandinavia, Siberia or Canada/Alaska contain much more organic carbon than soils from Greenland (i.e., 100-260 *vs* < 30 $kg.m^{-2}$, respectively; Parmentier et al. 2017). Moreover, Siberian and Alaskan rivers usually flow through permafrost areas covered with abundant vegetation (Walker et al. 2005) while most of the Young Sound river inputs are from glacial meltwater flowing on rocky sediment basin bare from any vegetation (Bendtsen et al. 2014; Paulsen et al. 2017). These geographical features are likely to reduce the quantity and quality of TOM inputs in Young Sound and may thus explain the poor assimilation of this food source in the benthic food web. Contrary to previous shallow food-web studies (e.g., Harris et al. 2018), this negligible contribution of TOM to the benthic food web implies that the negative impact of freshwater inputs on the Young Sound POM quality and availability cannot be balanced by local additional contribution from terrestrial materials.

In contrast, benthic primary consumers fed substantially on the POM/SOM pool. Although carbon stable isotope signatures usually provide a powerful tool to discriminate organic matter sources in marine ecosystems, POM and SOM sources measured in this study were weakly discriminated which precluded the evaluation of their respective contribution to the benthic food web. Such stable isotope signatures overlap probably reflects strong resuspension of sedimentary materials toward the overlying bottom waters (i.e., one meter above the seabed). The relatively low degradation of settled particles in polar ecosystems usually leads to the accumulation of a persistent sediment food bank of labile detritus (Smith et al. 2006; Mincks et al. 2008). The re-suspension of these labile detritus (through bottom currents or bioturbation) has a considerable importance for arctic benthic food webs facing periods of low food availability by providing an alternative food source for suspension feeders (Smith et al. 2006; Włodarska-Kowalczuk et al. 2019). We hypothesize that such resuspension events in Young Sound might thus partly increase the temporal stability and spatial homogeneity of the benthic food web in the face of strong spatiotemporal variations in primary production and organic matter quality (Meire et al. 2017; Bridier et al. 2019).

Finally, benthic sources (i.e., *Fucus* sp. and *Saccharina latissima*) appear to constitute an additional major source of organic matter for biomass dominating primary consumers (e.g., *Astarte elliptica*, *Hiatella arctica*, *Margarites coastalis*). Such contribution is in line with in situ measurements of seabed primary production that revealed substantial production of benthic micro- and macroalgae (2–7 times higher compared with phytoplankton production above 30 m; Glud et al. 2002; Krause-Jensen et al. 2007; Attard et al. 2016). Macroalgae account for the main part of the benthic primary production (Glud et al. 2002; Rysgaard & Glud 2007), mainly through the production of three species (i.e., *Desmarestia aculeata*, Fucus sp. and *Saccharina latissima*) together representing more than 90% of the overall macroalgal production (Glud et al. 2002; Krause-Jensen et al. 2007). However, it appears that *Desmarestia aculeata* is unlikely to be a major source of organic matter for the benthic food web because of its poor palatability for benthic invertebrates (e.g., Wessels et al. 2006). In contrast, numerous studies showed that both *Fucus* sp. and *Saccharina latissima* productions are able to provide a considerable part of food web carbon requirements of arctic shallow benthic ecosystems (Renaud et al. 2015; Gaillard et al. 2017). These two macroalgae might thus offer essential alternative food sources to the Young Sound benthic food web in a context of low pelagic primary production.

Benthic microalgae represent also a non-negligible part of the benthic primary production in Young Sound (i.e., 16% of the overall outer fjord primary production; Glud et al. 2002). These benthic microalgae are often far neglected in arctic food webs studies, notably because of the great difficulties to obtain accurate isotopic signature in arctic for these primary producers (McTigue & Dunton 2017). Both benthic micro- and macroalgae isotope signatures are known to be ^{13}C-enriched compared to those from pelagic organic matter sources (France 1995). In the case of Young Sound, we cannot exclude that a part of the enriched ^{13}C signal in several benthic invertebrates (e.g., *Astarte elliptica*, *Margarites coastalis*, *Hiatella arctica*) could also reflect the assimilation of such benthic microalgae as a food source. While enriched-δ^{13}C ice algae would also theoretically constitute an additional potential food source, their extremely low production in Young Sound (i.e., 0.0% of the overall outer fjord primary production; Glud et al. 2002) seems obviously too small to drive such δ^{13}C enrichment in several biomass-dominant consumers (e.g., *Astarte moerchi*, *Hiatella arctica*; Sejr et al. 2000).

Overall, the horizontal structure of the food web suggests a significant contribution of carbon of benthic origin to the diet of primary consumers (i.e., species from Fig. 4 fed in average at 25.2% on benthic sources), in agreement with what has been reported from other Arctic locations (e.g., Dunton & Schell 1987, Renaud et al. 2015). This finding is also consistent with two annual carbon budgets showing that Young Sound is a net heterotrophic fjord (Rysgaard & Nielsen 2006; Glud & Rysgaard 2007). In this ecosystem, local pelagic primary production provides a minor part of food-web carbon requirements, which are balanced by additional supplies of local benthic primary production and allochthonous inputs from the shelf (both providing ~3 times more organic carbon than local primary production; Glud & Rysgaard 2007). Although this study is not able to distinguish relative contributions from local (i.e., fjord) and shelf primary production to the POM pools, these results suggest that a major part of POM/SOM contributions in primary consumers would actually be related to an assimilation of shelf primary production. Such dominant contributions of both benthic primary production and allochthonous organic matter to the benthic food web would actually signify that both food sources are less impacted by freshwater inputs than are the phytoplankton.

For instance, benthic primary production is not as directly impacted by inputs of turbid and nutrient-depleted freshwaters as pelagic primary production. Benthic primary producers are usually more adapted to nutrient depletion because of the direct access of benthic microalgae to the nutrients released from sediments (MacIntyre et al. 1996) and the relatively low nutrient requirements of perennial macroalgae (Pedersen & Borum 1996). Such adaptations are reflected by the balance of pelagic and benthic primary production by nutrient regimes of shallow coastal ecosystems. Oligotrophic systems generally promote benthic primary production over pelagic primary production, while eutrophic settings favor the dominance of phytoplankton at the expense of benthic micro- and macroalgae (Duarte 1995; Glud et al. 2009). Therefore, we believe that nutrient depletion could affect benthic primary producers to a lesser degree than pelagic producers, which would in turn display homogeneous production along our spatial gradient.

Whereas it may be argued that freshwater inputs impact pelagic and benthic primary production through increased turbidity and sedimentation, several studies have shown that pelagic and benthic primary producers are both well adapted to low-light conditions in Young Sound (Glud et al. 2002; Krause-Jensen et al. 2007; Holding et al. 2019). Similarly, although strong sedimentation may inhibit the settlement of macroalgae (Filbee-Dexter et al. 2019), benthic micro- and macroalgae tolerate moderate sedimentation rates (Wulff et al. 1997; Ronowicz et al. 2020). For these reasons, we believe that nutrient concentration rather than turbidity is the main factor controlling primary production in the Young Sound fjord.

Moreover, although turbid and nutrient-depleted freshwater inputs strongly impact primary production toward the fjord head, production on the adjacent shelf remains relatively unaffected due to higher light and nutrient availability (Meire et al. 2017; Holding et al. 2019). Large inflows of shelf waters into the fjord generated by the seasonal estuarine circulation (Bendtsen et al. 2014) permit the supply of high-quality allochthonous organic matter to the benthic food web (Rysgaard & Nielsen 2006; Glud & Rysgaard 2007). Higher resilience of benthic primary producers and lower exposure of offshore phytoplankton to freshwater inputs may thus explain why these two components make such large contributions to the benthic food web. Therefore, although local pelagic production shows strong spatial variation (Meire et al. 2017), its contribution to the diet of primary consumers is not sufficient to mirror the gradient in the benthic food-web structure.

Potential role of omnivory and trophic redundancy on benthic food-web stability

The absence of spatial variation in the benthic food web may also result from large trophic adaptations of the community to local carbon availability. According to the benthic food-web structure, the fact that numerous consumers seem to feed on several food sources or several trophic levels could be interpreted as a means to cope with variable resource availability in the ecosystem. We hypothesize that such flexible foraging behavior of benthic invertebrates may enhance the food web's stability in a context of strong seasonal and spatial variations of food availability and quality.

Several species confirmed our trophic assignments and showed modal trophic positions consistent with their putative trophic levels (e.g., *Hiatella arctica* or *Musculus discors* primary consumer, *Argis dentata* predator). In contrast, the trophic positions of some taxa usually considered suspension or deposit feeders (Ascidiacea, *Arcturus baffini*, *Ophiocten sericeum*) were significantly above those of the strict primary consumers. Also, numerous species considered carnivores were actually below the trophic levels of strict secondary consumers (e.g., *Metopa glacialis*, *Nereis* sp., *Nymphon hirtipes*, *Ophiura robusta*). Such observed trophic positions could reflect a wide trophic plasticity of primary consumers but also high levels of omnivory in secondary/tertiary consumers. Indeed, when confronted with conditions of low food availability, primary consumers may broaden their forage base by feeding on various δ^{15}N-enriched animal/(macro)algal detritus (Mincks et al. 2008). In addition, secondary consumers may also expand their diet to several trophic levels in summer by feeding on both nutritive prey and abundant primary producers (McMeans et al. 2015). These two feeding strategies (i.e., trophic plasticity and omnivory) may thus considerably increase the stability of benthic communities by sustaining large carbon fluxes through the food web throughout the year despite strong freshwater input gradients and extreme seasonality.

High levels of omnivory highlighted by the trophic position models may also be a result of the TEFs used in this study. For instance, the low modal trophic positions of *Atylus carinatus* and *Balanus* sp. primary consumers (significantly below 2) may indicate that Post's fractionation factors are actually too high for aquatic consumers (McCutchan et al. 2003). However, neither Post's nor McCutchan's fractionation factors seemed appropriate for our trophic position estimates (see McCutchan's equivalent to Fig. 5 in Supplementary Information, Fig. S3). The high overlap (not dependent on the applied TEFs) between primary and secondary consumers shows in any case that either trophic plasticity or omnivory is a key feature of the benthic food web. A lower fractionation factor would only imply that more primary consumers would exhibit high trophic plasticity by feeding on δ^{15}N-enriched detritus, while fewer secondary consumers would be omnivorous.

Perspectives

Our study reveals that contributions of alternative food sources (i.e., benthic production and allochthonous inputs of organic matter) and trophic adaptations of benthic consumers (i.e., omnivory, trophic plasticity) are key to the stability of benthic food webs exposed to freshwater inputs. However, future research might assess whether these factors will be able to maintain such stability as these freshwater inputs continue to increase.

For instance, deep communities (i.e., below the euphotic zone) probably have less access to benthic micro- and macroalgae as they rely on the export of benthic production from shallow coastal habitats (Krumhansl & Scheibling 2012). Considering the negative impact of freshwater inputs on phytoplankton productivity (Meire et al. 2017), further studies might thus investigate whether deeper habitats will be more sensitive to forthcoming increases in terrestrial inputs than shallower communities, as their food webs might be less able to adjust their energy requirements to benthic primary production.

In addition, it might be interesting to examine how increasing freshwater inputs would alter supplies of benthic primary production and allochthonous organic matter in benthic food webs. Benthic primary producers will not necessary be adapted to increased sedimentation under a climate change scenario. Although benthic primary producers can cope with moderate sedimentation (Wulff et al. 1997, Ronowicz et al. 2020), abrupt and extreme sedimentation events may exceed their tolerance threshold, leading to a considerable decline in their productivity (Sahade et al. 2015). In contrast, increasing freshwater inputs may at the same time enhance the fjord’s estuarine circulation (i.e., surface outflows of turbid freshwater plumes and subsurface inflows of shelf water masses), increasing in turn inputs of allochthonous organic matter to the fjord (Rysgaard et al. 2003; Glud and Rysgaard 2007). The balance between these two scenarios deserves further interest in forthcoming studies, in order to better assess the sensitivity of the benthic food web, as well as the whole system’s functioning, to such changes.

Acknowledgements

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Supplementary material *to the article:*

Food source diversity, trophic plasticity, and omnivory enhance the stability of a shallow benthic food web from a high-Arctic fjord exposed to freshwater inputs

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Table S1. Stable isotope ratio averages ($\delta^{13}C$ & $\delta^{15}N$) and standard deviations (SD $\delta^{13}C$ & SD $\delta^{15}N$) of benthic invertebrates collected in inner and outer stations and sampled during winter and summer seasons. For each species, we specified the tissue used for the analyses (Tissue), the absence/presence of sample acidification (Acid.), the feeding trait used in trophic group analyses as well as the species replication (n).

Table S2. Stable isotope ratio averages ($\delta^{13}C$ & $\delta^{15}N$) and standard deviations (SD $\delta^{13}C$ & SD $\delta^{15}N$) of food sources, with the number of species replicates as well as the corresponding sampling dates and references. SOM: Sedimentary Organic Matter, POM: Particulate Organic Matter, TOM: terrestrial Organic Matter.

Table S3. Salinity profile (0 – 10 m) at the inner and outer stations.

Fig. S1. Sediment grain-size distribution composition at the inner and outer stations.

Fig. S2. Boxplots of the standard ellipse area (‰²) of the inner and outer communities from winter and summer seasons. Dark gray, intermediate gray, and light gray boxes represent respectively the 50%, 75%, and 95% credibility intervals estimated from the distribution of posterior values generated by the Bayesian model. Standard ellipse areas without overlap in their 95% credibility intervals are considered significantly different. Black dots represent mean Bayesian SEA estimates.

Fig. S3. Modal trophic positions of main primary (blue circles) and secondary/tertiary consumers (red circles) with their associated 95% credibility intervals based on posterior probability distributions. Trophic position estimates were built on McCutchan's (2003) fractionation factors (i.e. 0.4 ± 0.2 ‰ for $\delta^{13}C$ and 2.3 ± 0.3 ‰ for $\delta^{15}N$).

Table S1

				OUTER - SUMMER (08/08/2018)						n	OUTER - WINTER (12/05/2018)						n	INNER - SUMMER (11/08/2018)						n	INNER - WINTER (19/05/2017)						n
ID	Tissu	Acid.	Feeding trait	δ13C	SD δ13C	δ15N	SD δ15N	C/N	SD C/N		δ13C	SD δ13C	δ15N	SD δ15N	C/N	SD C/N		δ13C	SD δ13C	δ15N	SD δ15N	C/N	SD C/N		δ13C	SD δ13C	δ15N	SD δ15N	C/N	SD C/N	
NEMERTEA																															
Nemertea	Whole body	No	Carnivore								-22.3	0.3	12.8	1.3	3.9	0.0	2								-20.4		12.0		3.4		1
POLYCHAETA																															
Ampharete sp.	Whole body	No	Deposit feeder															-24.2	0.0	7.4	0.6	4.0	0.0	2	-23.5	0.2	8.1	0.4	4.2	0.0	2
Axionice maculata	Whole body	No	Deposit feeder	-23.9	0.2	7.3	0.9	4.6	0.4	2																					
Capitella capitata	Whole body	No	Deposit feeder								-25.1		8.3		5.2		1														
Cirratulidae	Whole body	No	Deposit feeder								-23.0	0.7	10.3	2.4	3.7	0.7	2														
Cossura longocirrata	Whole body	No	Deposit feeder								-21.7		6.9		3.5		1														
Eunicidae	Whole body	No	Deposit feeder								-22.5		7.0		4.0		1														
Flabelligeridae	Whole body	No	Deposit feeder																						-19.8		9.1		3.6		1
Gattyana cirrhosa	Whole body	No	Carnivore	-22.7	0.9	12.1	0.5	3.8	0.3	3								-22.0	0.7	12.9	0.8	3.4	0.1	4							
Harmothoe sp.	Whole body	No	Carnivore	-22.8	0.3	12.0	0.5	3.4	0.1	3	-23.1	0.2	10.5	0.2	3.5	0.1	4	-22.2	0.4	12.0	0.6	3.5	0.1	5	-22.0	1.1	10.4	0.1	3.4	0.0	2
Hesionidae	Whole body	No	Deposit feeder								-22.2		10.3		3.6		1														
Maldane sarsi	Whole body	No	Deposit feeder																						-21.1		11.0		4.0		1
Nephtys sp.	Whole body	No	Carnivore																						-21.1		13.6		3.9		1
Nereis sp.	Whole body	No	Deposit feeder	-24.6	0.7	10.6	0.3	3.6	0.1	6	-23.7		10.8		3.6		1	-22.3	0.6	11.5	0.5	3.5	0.1	4							
Owenia sp.	Whole body	No	Deposit feeder																						-22.4		8.3		5.7		1
Pectinaria hyperborea	Whole body	No	Deposit feeder	-23.5	0.5	11.2	0.0	4.1	0.1	2								-22.8	2.2	9.0	3.3	3.9	0.5	2	-20.9		10.0		3.6		1
Phyllodoce groenlandica	Whole body	No	Carnivore								-22.4	0.5	11.7	0.9	4.0	0.2	3	-22.8		11.9		3.8		1							

Table S1, continued

Oweniidae	Whole body	No	Deposit feeder								-23.3	0.4	8.7	1.0	4.6	0.1	2														
Scoloplos sp.	Whole body	No	Deposit feeder								-23.1		9.4		4.2		1														
Sigalionidae	Whole body	No	Carnivore								-24.6		11.7		4.0		1														
Terebellides sp.	Whole body	No	Deposit feeder								-22.9		10.7		4.1		1								-21.8		8.7		3.7		1
SIPUNCULA																															
Golfingia sp.	Whole body	No	Deposit feeder															-19.7		10.7		3.3		1	-19.5		9.7		3.4		1
MOLLUSCA																															
Astarte elliptica	Adductor muscle	No	Suspension feeder	-22.6	0.3	8.6	0.3	3.0	0.1	2								-21.0	0.6	9.3	0.7	3.4	0.3	6							
Astarte moerchi	Adductor muscle	No	Suspension feeder	-21.0	0.6	8.9	0.3	3.1	0.2	4								-20.7	0.3	8.8	0.6	3.2	0.3	3	-20.2	0.3	9.3	0.3	3.5	0.2	4
Caudofoveata	Whole body	No	Deposit feeder	-20.3	1.7	8.9	0.6	5.6	1.2	2																					
Ciliatocardium ciliatum	Adductor muscle	No	Suspension feeder	-23.7		6.8		3.5		1								-23.7	0.4	6.6	0.4	3.3	0.0	3							
Colus sp.	Foot muscle	No	Carnivore	-21.3	0.7	10.4	1.0	3.6	0.2	5	-21.4	0.3	9.6	0.1	3.5	0.1	3								-21.0	0.2	11.0	0.1	3.5	0.1	3
Cylichna sp.	Whole body	No	Carnivore	-22.0	0.4	11.6	0.2	3.5	0.0	2																					
Hiatella arctica	Adductor muscle	No	Suspension feeder	-23.5	0.5	7.3	0.1	3.3	0.0	4	-25.1		7.2		4.0		1	-21.0	1.3	9.2	1.1	3.3	0.1	5	-22.3	0.9	8.5	0.7	3.4	0.1	4
Margarites costalis	Foot muscle	No	Deposit feeder	-21.8	0.4	8.8	0.2	3.5	0.1	5	-23.7		9.2		3.5		1														
Margarites helicinus	Foot muscle	No	Deposit feeder								-22.5		9.9		3.7		1														
Musculus discors	Adductor muscle	No	Suspension feeder	-22.0	0.1	7.9	0.2	3.3	0.0	5	-23.3	0.7	7.4	0.4	3.4	0.1	3	-22.9	1.5	8.5	1.2	3.7	0.7	9	-21.3	0.3	7.8	0.5	3.6	0.4	3
Mya truncata	Adductor muscle	No	Suspension feeder								-24.7		6.8		3.9		1														
Nuculana pernula	Foot muscle	No	Deposit feeder	-23.7		7.4		3.6		1																					
Nudibranchia	Foot muscle	No	Carnivore																						-24.3		11.7		3.8		1
Opisthobranchia	Whole body	No	Carnivore	-21.9	0.1	13.5	0.6	3.6	0.1	2	-21.4		13.7		3.8		1														

Table S1, continued

Retusa sp.	Whole body	No	Carnivore								-21.7		10.2		4.2		1								-20.0		10.5		4.0		1
Serripes groenlandicus	Adductor muscle	No	Suspension feeder	-23.6	0.9	7.0	0.3	3.5	0.1	2																					
Similipecten greenlandicus	Adductor muscle	No	Suspension feeder	-24.2	0.2	8.2	0.8	3.6	0.1	6								-25.0		10.0		3.5		1	-22.8		8.4		3.1		1
CRUSTACEA																															
Aeginina longicornis	Whole body	Yes	Deposit feeder	-25.0	0.6	9.5	0.5	4.8	0.1	2																					
Ampelisca sp.	Whole body	No	Suspension feeder								-24.9		7.3		8.4		1														
Arcturus baffini	Whole body	Yes	Suspension feeder															-26.0	0.4	9.9	0.4	4.7	0.3	5							
Argis dentata	Whole body	No	Carnivore															-21.3	1.1	14.4	0.4	3.3	0.1	4							
Atylus carinatus	Whole body	Yes	Deposit feeder	-24.3	0.2	7.3	0.4	5.7	0.7	4								-22.7		7.2		6.6		1							
Balanus sp.	Whole soft tissue	No	Suspension feeder	-22.5	1.1	6.9	0.3	3.9	0.2	5								-22.6	0.3	7.6	0.6	3.8	0.3	4							
Crangonidae	Dorsal muscle	No	Carnivore																						-20.4		10.1		3.5		1
Ischyroceridae	Whole body	No	Deposit feeder																						-23.5	0.0	8.4	0.1	4.5	0.1	2
Lebbeus groenlandicus	Dorsal muscle	No	Carnivore	-22.1	0.4	11.1	0.4	3.3	0.1	5								-23.3	0.2	12.8	0.1	3.5	0.1	3							
Lysianassidae sp. 1	Whole body	No	Carnivore								-20.8	1.0	11.5	2.4	7.1	2.3	2														
Lysianassidae sp. 2	Whole body	No	Carnivore								-24.3	0.5	12.6	0.2	5.6	1.1	2														
Metopa glacialis	Whole body	No	Carnivore	-24.6	1.1	9.5	0.6	4.9	0.7	5	-24.5	0.7	9.4	0.3	4.6	0.2	6														
Monoculodes sp.	Whole body	No	Carnivore								-21.5	1.1	10.4	1.5	4.3	0.6	3														
Ostracoda	Whole body	No	Suspension feeder																						-23.3	1.0	11.1	0.3	4.2	0.4	4
Pandalidae	Dorsal muscle	No	Carnivore								-24.5	0.5	10.3	1.7	5.7	0.3	2														
Sclerocrangon boreas	Dorsal muscle	No	Carnivore	-20.9	1.8	14.4	0.7	3.4	0.3	2																					
Socarnes sp.	Whole body	No	Carnivore								-20.4	1.3	12.7	1.0	5.3	0.2	3	-20.1		11.7		5.2		1							

Table S1, continued

ECHINODERMATA																															
Holothuroidea	Whole body	Yes	Deposit feeder															-23.7	0.5	8.0	0.6	4.0	0.4	2							
Ophiocten sericeum	Whole body	Yes	Carnivore	-22.2	3.3	9.3	0.6	7.3	0.8	7								-26.5	0.4	9.2	0.7	8.0	1.0	4	-26.3	1.1	9.4	0.5	7.5	0.5	5
Ophiopleura borealis	Whole body	Yes	Carnivore															-23.3	0.6	13.4	0.3	4.6	0.4	3	-25.7	0.2	13.0	0.5	8.2	2.3	2
Ophiura robusta	Whole body	Yes	Carnivore								-27.1	2.0	10.1	0.5	7.3	0.8	5	-26.8	4.3	10.3	0.9	7.8	0.8	2	-26.7		8.5		6.0		1
Strongylocentrotus sp.	Gonade	No	Deposit feeder	-25.7		6.3		4.5		1																					
PYCNOGONIDA																															
Boreonymphon abyssorum	Whole body	No	Carnivore															-22.1		12.2		4.0		1							
Nymphon hirtipes	Whole body	No	Carnivore	-25.3	0.0	10.9	0.0	5.4	0.4	2								-24.2	1.2	10.5	0.5	4.6	1.0	10							
Nymphon longimanum	Whole body	No	Carnivore															-23.2	0.3	11.5	0.2	4.2	0.1	3							
TUNICATA																															
Ascidiacea	Ectoderm	No	Suspension feeder															-23.8	0.6	9.6	0.4	4.8	1.6	8	-24.6		10.1		3.7		1
Pedondulate Ascidiacea	Ectoderm	No	Suspension feeder								-24.7		8.4		3.6		1														
HYDROZOA																															
Hydrozoa	Whole body	Yes	Suspension feeder	-25.0	0.2	8.2	0.5	4.5	0.3	3																					
NEMATODA																															
Nematoda	Whole body	No	Carnivore	-24.9	0.6	10.2	0.1	5.5	0.7	2																					
PISCES																															
Icelus bicornis	Dorsal muscle	No	Carnivore															-23.6	1.1	13.2	1.4	3.3	0.0	4							

Table S2

Food sources	δ13C	SD δ13C	δ15N	SD δ15N	n	Sampling Date	Publication
SOM Inner Summer	-24.7	0.1	3.7	0.5	3	09/08/2016	Bridier et al. (2019)
SOM Outer Summer	-25.4	0.2	4.8	0.2	4	08/08/2016	Bridier et al. (2019)
POM Inner Summer	-25.5	0.1	4.2	0.5	3	11/08/2018	This study
POM Outer Summer	-25.4	0.3	5.7	1.1	6	08/08/2018	This study
SOM Inner Winter	-24.7	0.3	4.6	0.4	4	19/05/2017	Bridier et al. (2019)
POM Inner Winter	-27.0	0.8	7.0	0.2	5	12/05/2018	Bridier et al. (2019)
TOM Summer	-26.9	0.5	-2.2	0.5	6	13/08/2018	This study
Fucus sp.	-19.2	2.2	5.2	1.6	3	08/2014	De Cesare et al. (2017)
Saccharina latissima	-21.1	0.0	4.3	1.9	3	08/2014	De Cesare et al. (2017)

Table S3

Depth	Inner station	Outer station
1	21.44	23.56
2	20.34	24.58
3	19.00	26.84
4	20.37	28.09
5	21.95	29.74
6	21.30	30.76
7	20.38	30.80
8	21.25	30.85
9	22.81	30.89
10	21.29	30.91
Average	21.01	28.70

Figure S1

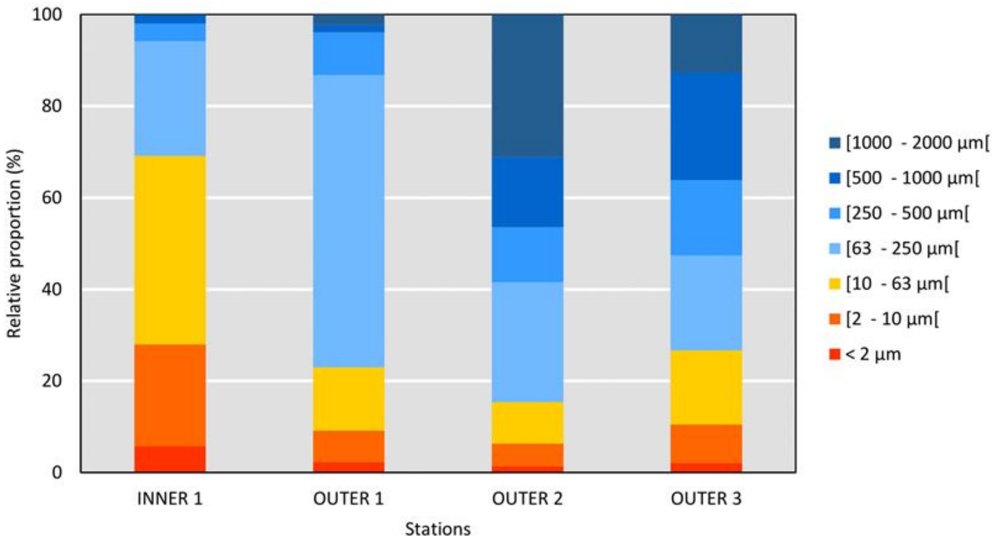

100
80
60
40
20
0
Relative proportion (%)
INNER 1
OUTER 1
OUTER 2
OUTER 3
Stations
[1000 - 2000 µm[
[500 - 1000 µm[
[250 - 500 µm[
[63 - 250 µm[
[10 - 63 µm[
[2 - 10 µm[
< 2 µm

Figure S2

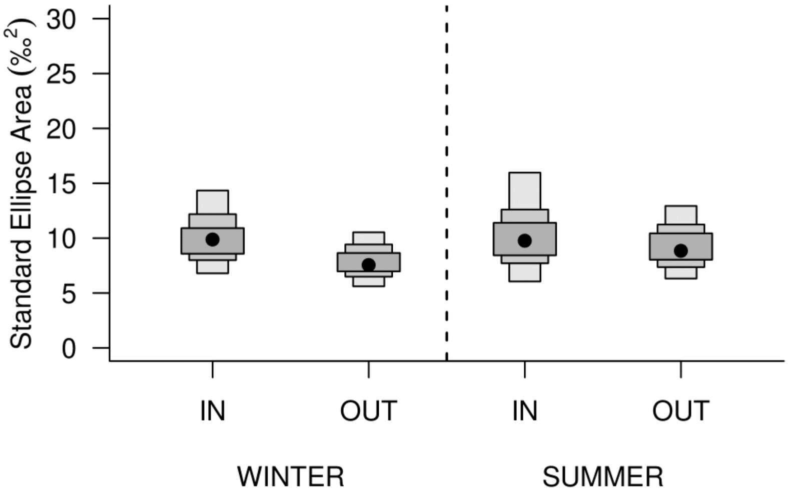
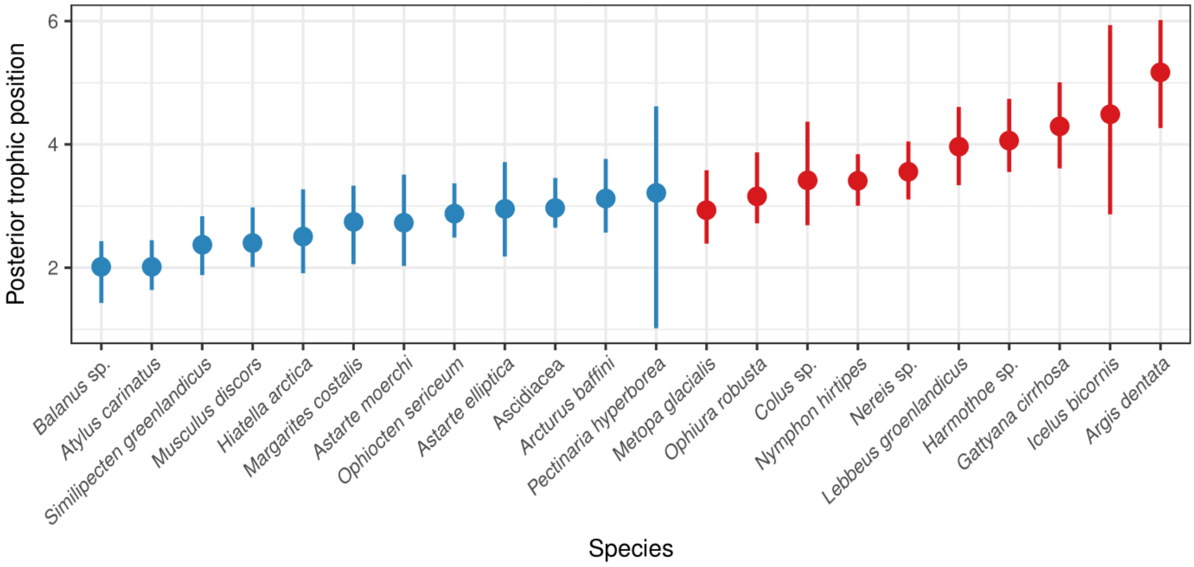


Figure S3



Chapter IV

Thermal stratification does not change the food web structure and functioning of a shallow benthic ecosystem from a sub-Arctic archipelago

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Abstract

Sub-Arctic/Arctic marine ecosystems are experiencing one of the most drastic increases in seawater surface temperatures in the world. In recent decades, such global warming has strengthened the water column stratification, reducing in turn the phytoplankton production and the quality of the pelagic organic matter. However, impacts of such changes on benthic food webs as well as organic matter transfers toward higher trophic levels (e.g. fishes) are still poorly understood. Within this context, this study investigates the spatial and temporal variability in the food web structure of a fine soft-bottom sub-Arctic benthic community submitted to contrasted conditions in thermal stratification. Benthic fauna and several fish species were sampled along a cross-shore transect (2 stratified *vs* 2 unstratified stations) east of the Miquelon island (Saint-Pierre and Miquelon archipelago, Newfoundland Shelf) over two seasons corresponding to low and high stratification periods. Food web structure and organic matter transfers were investigated through analyses of carbon and nitrogen stables isotopes signatures including community-wide metrics and mixing models. Results revealed low spatial and temporal variability in food web structure and organic matter transfers. Most benthic primary consumers displayed in both stratified and unstratified stations a high trophic plasticity by feeding on both phytoplankton and benthic carbon sources while most fishes strongly relied on benthic preys. In the future context of thermal stratification increase with global warming, we hypothesize that benthic primary production may be less sensitive to nutrient depletion than phytoplankton. A high contribution of benthic primary producers to organic matter transfers in shallow food webs might therefore considerably increase the resilience of benthic food web under a changing climate.

Key words

Seasonal stratification • Climate change • Benthic ecosystems • Food web structure • Stable isotopes • Sub-Arctic ecosystems • Saint-Pierre et Miquelon • Newfoundland Shelf

Introduction

Arctic and sub-Arctic shelves usually host large benthic biomass on the seafloor (Grebmeier et al. 1988, Dunton et al. 2005, Piepenburg et al. 2005) resulting from tight sympagic-pelagic-benthic coupling at high-latitudes (Ambrose and Renaud 1995, Fortier et al. 2002, Cochrane et al. 2009, Grebmeier et al. 2012). Such abundant benthic invertebrates play a key role in marine food webs by sustaining large carbon stocks for benthic fishes (e.g. *Hippoglossoides platessoides*, *Pleuronectes platessa*, Sherwood and Rose 2005, Silberberger et al. 2018) and for marine mammals (e.g. walrus, Born et al. 2003) which can ultimately provide seafood for human populations (Grebmeier et al. 2006, Darnis et al. 2012). However, pelagic-benthic coupling intensity is linked to wide variety of factors including phytoplankton productivity, grazing pressure, activity of pelagic microbial communities as well as sedimentation of phytoplankton cells (Renaud et al. 2008, Kędra et al. 2015, Turner et al. 2015). Therefore, any future environmental changes, such as the expected surface seawater warming, that would impact the strength of pelagic-benthic coupling and/or the intensity of primary production, should ultimately impact benthic stocks.

Over the last decades, arctic and sub-arctic latitudes have been experiencing considerable warming, somewhat 2-3 times higher than the global average (AMAP 2017). It is widely accepted that associated ongoing increase of seawater temperatures and ice melting (from sea-ice and ice sheet) will considerably enhance stratification during the XXI century (Capontondi et al. 2012, Nummelin et al. 2016). Several studies evidenced that such forthcoming changes will considerably impact pelagic-benthic coupling in future Arctic seas (e.g. Wassmann and Reigstad 2011, Ardyna and Arrigo 2020, Wassmann et al. 2020). Indeed, decrease in vertical nutrient fluxes related to increased stratification may actually directly limit primary production by limiting nutrient concentration in surface waters (Tremblay and Gagnon 2009, Tremblay et al. 2015). Moreover, surface water nutrient depletions are expected to shift phytoplankton communities size structure toward smaller cells (e.g. Li et al. 2009), which in turn affect phytoplankton sedimentation rates and can diminish the organic matter quantity/quality reaching the seabed (Bopp et al. 2005, Turner et al. 2015). Considering the crucial role of food quantity and quality on benthic biomass and food web structure (e.g. Campanyà-Llovet et al. 2017), stratification should impact both pelagic primary production and organic matter quality and, as a result, influence benthic ecosystems dynamics. Yet, little is known on the role of water column stratification on organic matter transfer to coastal benthic food webs up to predators, including commercial fish species.

In this context, this study investigated the benthic food web structure and organic matter transfers toward several fish species under contrasted stratification conditions in a sub-Arctic coastal ecosystem (Saint-Pierre and Miquelon (SPM) archipelago – Newfoundland). We identified the Newfoundland shelf as an exceptional study area for such investigation since seawater temperatures experienced one of the greatest warming in recent decades in the world (+ 1°C between 1982 and 2006, Belkin 2009) increasing considerably stratification (Cyr et al. 2020). Moreover, the Scotian/Newfoundland shelf represents a major region for fisheries providing an important economic resource for Canada's maritime populations by employing about 80 000 people (Baum and Fuller 2016). In 2018, landings of benthic invertebrates (e.g. *Homarus americanus, Placopecten magellanicus*) from the Canadian Atlantic coast reached 364,000 tons and have been valued at $2.8 billion, while benthic fish landings (e.g. *Hippoglossus hippoglossus, Melanogrammus aeglefinus, Reinhardtius hippoglossoides*) reached 87,000 tons for a value of $200 million (DFO 2018). However, overfishing may lead to a collapse of fish stocks as observed for cod (*Gadus morhua*) in the last decades and cause restructuring of fish food webs (e.g. Hutchings and Myers 1994, Pauly et al. 2001). To better preserve the economical and ecological values of fisheries in a context of high fishing pressure, it is therefore crucial to predict how fish stocks will evolve in response to expected changes in primary production and pelagic-benthic coupling due to stratification's intensification.

To this aim, we sampled benthic assemblages during either low or high stratification periods along a cross-shore transect. Shallow stations of this transect (i.e. 10 and 30 m) represented unstratified stratifications as they are always located above the thermocline (≈ 15 – 25 m, Bridier et al. 2021) while deeper stations (i.e. 60 and 80 m) are considered as stratified stations as they remained below the thermocline during the stratified season. We hypothesize that during the stratified season benthic invertebrates from unstratified stations could have a direct access to feeding sources from the surface/subsurface primary production whereas species from stratified stations should relate only on the vertical export of organic matter from surface waters. We have also hypothesized that fish relying on benthic stocks might be vulnerable to changes in pelagic primary production and pelagic-benthic coupling as lower carbon exports toward the seabed may result in lower benthic biomass.

The main goals of this study conducted on a subarctic coastal benthic ecosystem were to: (1) describe the spatial and temporal variability of the structure of associated food webs, (2) assess the impact of stratification on organic matter transfers and (3) evaluate the potential vulnerability/resilience of local fisheries facing future expected intensified stratification.

Materials and Methods

Study site

The study was conducted in SPM (46°50’N, 56°20’W), a sub-Arctic Archipelago localized on the Newfoundland Shelf (Figure 1). This site is characterized by large seasonal variations in surface temperatures (i.e. ranging from 0-2°C in March-April up to 18°C in August-September) but annually stable temperatures in deeper waters (< 80m depth, Lazure et al. 2018, Poitevin et al. 2018). These decoupled seasonal variations in seawater temperatures lead to the formation of a sharp thermocline in late-summer occurring at depth between 20 and 40 m (Lazure et al. 2018). This induces a significant reduction in POM quantity/quality and pelagic-benthic coupling strength (Bridier et al. 2021). The dynamics of pelagic primary production is usually characterized by a single bloom occurring in March-April (Harrison et al. 2013, Pepin et al. 2017) although there can be a secondary phytoplankton bloom in late autumn (Pepin et al. 2017, Bridier et al. 2021).

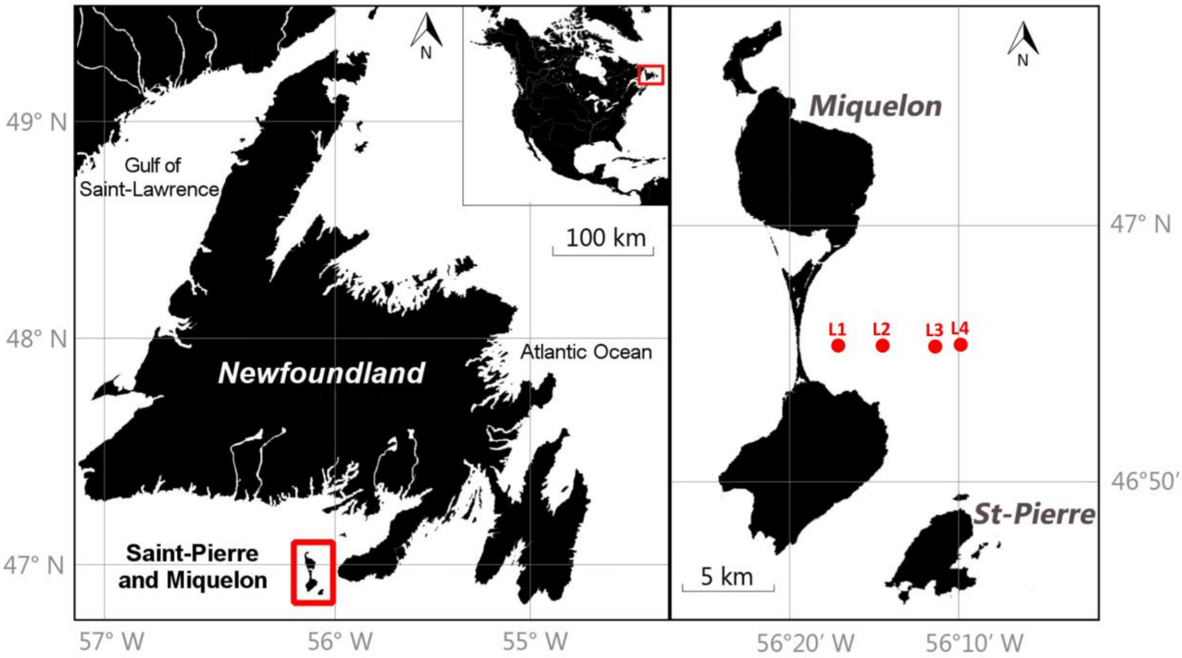

Figure 1: Localization of the Saint-Pierre and Miquelon Archipelago in relation to Newfoundland (left) and geographical positions of the four sampled stations (right, modified from Poitevin et al. 2018).

The four sampling stations are distributed along a small cross-shore gradient (L1, L2, L3 & L4 depths = 10, 30, 60 and 80 m, respectively, Figure 1). Sediment grain-size distribution was similar along the gradient and dominated by fine sand particles (85 % of the particle size fraction ranges between 100 and 200 µm, Robin 2007). Sampling stations are exposed to contrasted thermal conditions, with the shallow area (10-30 m) experiencing strong thermal seasonal variations (ranging from 1°C in March/April to 18°C in August/September) while seawater temperature in deeper area (60- 80 m) remains stable and cold (below 2°C) throughout the year (Poitevin et al. 2018, Lazure et al. 2018). Benthic assemblages respond to such contrasting thermal conditions with boreal species (e.g. *Arctica islandica*) colonizing the shallow zone whereas polar species (e.g. *Astarte montagui*) are restricted to the deeper ones (J. Grall and F. Olivier, pers. com.).

Sampling

Sampling was conducted over two successive years (August 2017 and July 2018) in order to detect potential inter-annual variability in the benthic food web structure. Benthic organisms were collected using a Rallier du Baty dredge (1 mm square mesh size). All collected species were identified directly onboard at the lowest taxonomic level possible then let in seawater at 4°C during 4 – 6 h to eliminate gut contents. All species were dissected or not according to their size and packed separately in aluminum foils and then stored at -20°C before analyses (see Table S1 for more details on tissue selection).

Main organic matter sources were collected to identify carbon pathways in the benthic food web. Particulate Organic Matter (POM) was sampled at every sampling station by filtering 10 liters of seawater collected at one meter above the seabed and filtered on GF/F microfiber filters (pore = 0.7 µm). Upper sediment surface (≈ first 0 – 3 mm) was collected for SOM samples on shallow stations (L1 & L2 in August 2017 and only L2 in July 2018) using a 450 mL syringe operated by scuba divers. Sediment samples (i.e. mixture of microphytobenthos, various detritus and inorganic particles) were mixed in one liter of filtered seawater and let settled during one hour before filtering the supernatant SOM on GF/F filters. Finally, several dominant and palatable macroalgae species were sampled in 2017 by scuba divers, namely *Agarum clathratum*, *Desmarestia viridis*, *Halosiphon tomentosus*, *Porphyra* spp., *Saccharina latissima*. Microphytobenthos was not sampled in this study but we investigated its role in the benthic food web by using an average of 26 microphytobenthos stable isotope values found in the literature ($\delta^{13}C$ = -16.9, $\delta^{15}N$ = 6.4, see McTigue and Dunton 2017).

Laboratory analyses

All animal tissue and macroalgae were freeze-dried at – 50°C during at least 48 hours. Dried tissues were then ground using a ball mill (30 Hz, cycles of 10 minutes) into fine powder. Carbonate-rich tissues were split in two parts: one half were acidified in order to avoid bias related to carbonates on $\delta^{13}C$ analyses (Søreide et al. 2006) while the other half were not acidified to avoid the impact on $\delta^{15}N$ analyses (Jacob et al. 2005). No lipid extraction was realized considering the usually low lipid concentration in benthic invertebrates (Clarke and Peck 1991) and potentials bias of lipid extractions on $\delta^{15}N$ values (Bodin et al. 2007, Post et al. 2007). Following Mohan et al. (2016), no mathematical corrections were applied due to the inaccuracy of lipid-normalization equations using constant lipid $\delta^{13}C$ value despite the large variability of $\delta^{13}C$ lipid bulk signatures in Arctic marine species.

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

Where δX is $\delta^{13}C$ or $\delta^{15}N$ and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio.

Data analyses

Statistical tests and standard ellipses

Two-way PERMANOVAs were performed for all species and each trophic group (i.e. suspension-feeders, deposit-feeders and carnivores) in order to test the effect of station (S), year (Y) and the interaction of these two factors (S * Y) on stable isotopes signatures ($\delta^{13}C$, $\delta^{15}N$). This permutational analysis was preferred to the more common ANOVAs because of its robustness to normality and homoscedasticity issues (Anderson and Walsh 2013). In addition, pairwise PERMANOVAs were realized when one factor showed a significant effect to identify which pairs of factors were significantly different from each other. The same procedure was applied for each trophic group in order to investigate whether trends observed at the community scale were transferable to trophic guilds. Benthic organisms were separated into three trophic guilds based on each taxa trophic ecology (Fauchald and Jumars 1979; Macdonald et al. 2010; Degen and Faulwetter 2019) using the classification made by Włodarska-Kowalczuk et al. (2019): suspension-feeders, deposit-feeders (i.e. surface/subsurface deposit-feeders and grazers) and carnivores (i.e. predators and scavengers). Stable isotope signatures from pairs of factors without significant differences between them were pooled together in subsequent statistical analyses. Stable isotope signature and standard ellipses from each significant pairs of factor levels were plotted in a δ-space in order to visualize the dimension of their trophic niche (i.e. food web length and basal food source diversity). Standard ellipse overlaps (defined as the percentage of δ-space shared between two ellipses in relation to the smallest ellipse) were then assessed to identify shift in food source contributions fueling benthic food webs.

Reliance on benthic sources

In order to distinguish the relative contribution of phytoplankton and benthic primary production to primary/secondary consumers (i.e. benthic invertebrates and fishes), we estimated the reliance of each taxon on benthic carbon sources. Percentages of reliance on benthic carbon sources were calculated based on the equation below (see Figure 2a) adapted from Vander Zanden and Vadeboncoeur (2002), Sherwood and Rose (2005) and Le Loc'h et al. (2008) for a primary producer baseline.

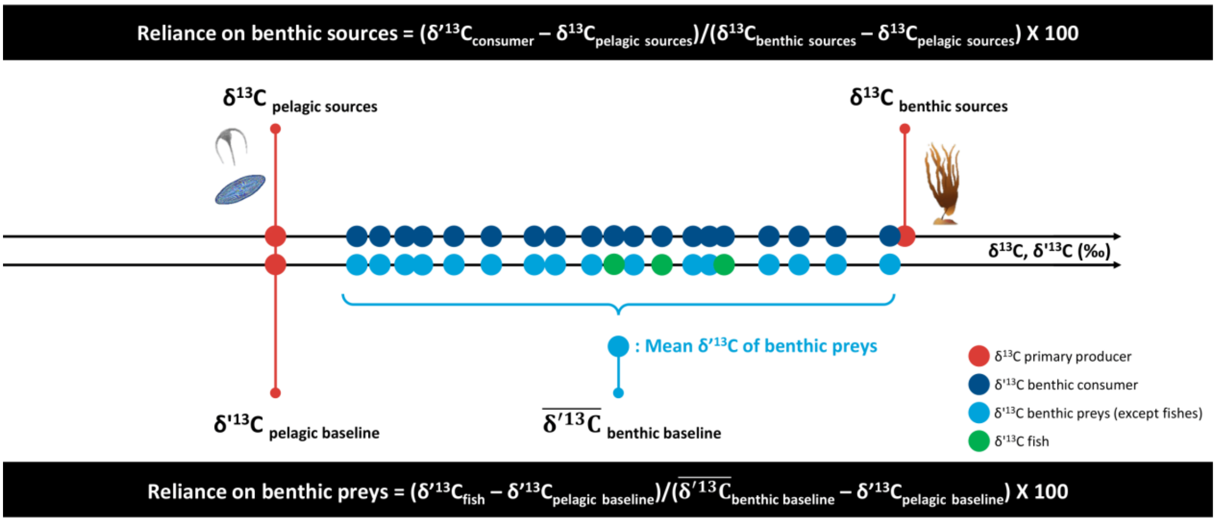

Figure 2: Conceptual diagram representing the selection of benthic baseline δ'^{13}C values for the calculation of equation I and II of benthic reliance on benthic preys.

Pelagic sources carbon isotopic signatures (δ^{13}C pelagic sources) was chosen as the average value of POM δ^{13}C from both unstratified and stratified stations. Benthic sources carbon isotopic signatures (δ^{13}C benthic sources) were calculated from the average between *Saccharina latissima* and microphytobenthos δ^{13}C signatures. Depleted macroalgae sources were not included in this mixing model because we could not clearly distinguish their δ^{13}C signatures from those of the POM pool. All δ^{13}C stable isotope signatures were corrected (δ'^{13}C) individually for each taxon to standardize all consumers on the same trophic levels (i.e. primary producer baseline, i.e. TL = 1), assuming a fractionation factor of 1 ‰ per trophic levels (Post 2002):

$$\delta'^{13}\mathrm{C}_{\mathrm{consumer}} = \delta^{13}\mathrm{C}_{\mathrm{consumer}} - (\mathrm{TL}_{\mathrm{consumer}} - 1) \times 1\text{‰}$$

where $\mathrm{TL}_{\mathrm{consumer}}$ is the trophic level of one consumer related to primary producer baselines:

$$\mathrm{TL}_{\mathrm{consumer}} = 1 + \frac{\delta^{15}\mathrm{N}_{\mathrm{consumer}} - (\delta^{15}\mathrm{N}_{\mathrm{benthic\ sources}} \times 0.5 - \delta^{15}\mathrm{N}_{\mathrm{pelagic\ sources}} \times 0.5)}{\Delta^{15}\mathrm{N}}$$

and Δ^{15}N correspond to the trophic enrichment in δ^{15}N observed between two trophic levels, based on a fractionation factor of 3.4 ‰ per trophic level (Post 2002, DeNiro and Epstein 1981).

Reliance on benthic preys

The reliance of fish on benthic preys was calculated to assess the connectivity of fish species to pelagic and benthic food webs. The equation of fish reliance on benthic prey (see Figure 2b) is derived from the previous equation but uses benthic preys (i.e. all benthic consumers except fishes) as benthic baselines. Then, the pelagic baseline corresponds to a virtual δ’^{13}C signature of pelagic primary consumer (i.e. δ’^{13}C = δ^{13}C – 1) that exclusively feeds on POM (i.e. δ’^{13}C pelagic baseline = δ^{13}C POM). The benthic baseline was defined following the equation used by Vander Zanden and Vadeboncoeur (2002) and Scherwood and Rose (2005) by averaging all benthic consumer δ’^{13}C signatures (i.e. $\overline{\delta'^{13}\mathrm{C}}$). When a fish δ’^{13}C signature is outside the range of pelagic and benthic baselines (i.e. either δ’^{13}C fish < δ’^{13}C pelagic baseline or δ’^{13}C fish > $\overline{\delta'^{13}\mathrm{C}}$ benthic baseline), we set its reliance either to 0 % or 100 %. All fishes displaying percentages of reliance on benthic preys lower than 25 % or higher than 75 % were considered as exclusively connected to pelagic and benthic food webs, respectively (Sherwood and Rose 2005). Fishes displaying intermediate reliance were considered as part of both pelagic and benthic food webs (Sherwood and Rose 2005).

Results

We did not observe any differences between 2017 and 2018 in terms of structure of the whole benthic food web ($p < 0.05$, two-way PERMANOVAs, Table 1). Weak spatial variations were detected in $\delta^{15}N$ signatures ($p < 0.05$, two-ways PERMANOVAs) while none occurred for $\delta^{13}C$ signatures. According to Pairwise PERMANOVAs, differences in $\delta^{15}N$ signatures were only significant between L1 and L3-L4 stations ($p < 0.05$). Based on these results, we chose to pool stable isotope signatures into two groups representing “unstratified stations” (L1 & L2) and “stratified stations” (L3 & L4) from both seasons. Despite this new data arrangement, standard ellipses of both communities still display high overlapping (i.e. 73.2 %), confirming the relatively low spatial variability along the transect (Figure 2a). The position of the standard ellipse of the stratified stations community was slightly higher on the $\delta^{15}N$ axis than that of the shallow benthic community (Figure 2a, $p < 0.05$, two-way PERMANOVAs). Statistical analyses performed separately on each trophic group gave similar results than those performed on the entire benthic community. No between-year variations were observed and spatial variations were only significant for $\delta^{15}N$ signatures, except for deposit-feeders for which significant spatial variations for both $\delta^{13}C$ and $\delta^{15}N$ signatures were observed ($p < 0.05$, two-way PERMANOVAs, Table 1). Moreover, all trophic groups from stratified stations showed higher position on the $\delta^{15}N$ axis than those from unstratified ones. Deposit-feeder standard ellipses showed the lowest overlap between unstratified and stratified stations (i.e. 46.6 %).

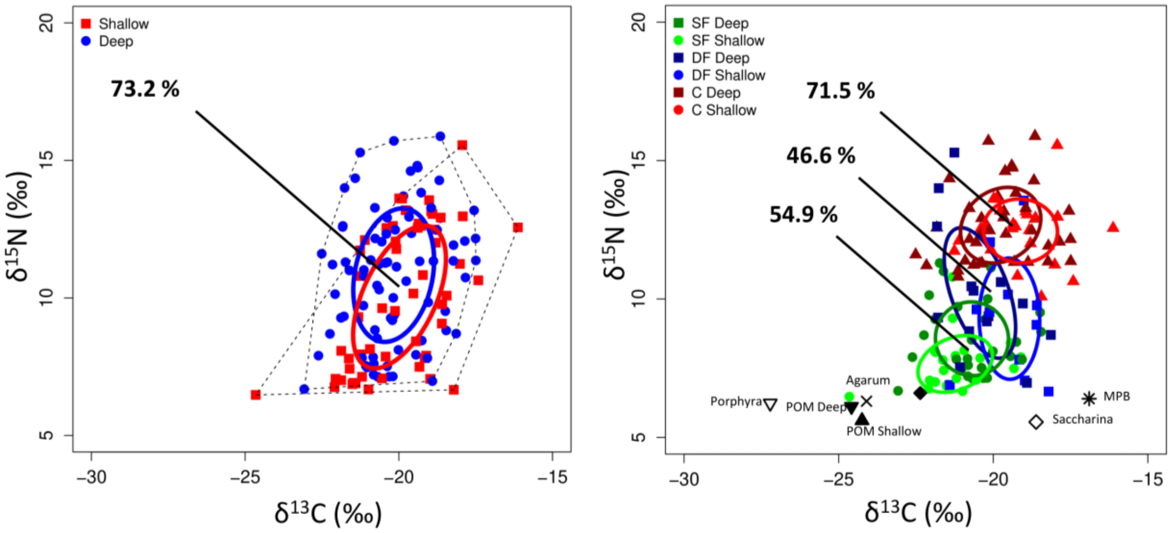

Figure 2: Standard ellipses (solid lines) and convex hulls (dashed lines) of unstratified and stratified benthic assemblages based on either A) all species or B) each trophic group (suspension-feeders SF, deposit-feeders DF, carnivores C).

Table 1: Results from PERMANOVA analyses performed on $\delta^{13}C$ and $\delta^{15}N$ signatures from all species as well as each trophic group (Suspension-feeders, deposit-feeders and carnivores). Two sources of variations were tested: Station (S, fixed with 4 levels) and Year (Y, fixed with two levels). Significant p-value (p) are represented in ***bold****.*

Feeding group	Isotope ratio	Effect	F-statistic (df)	*p*
All fauna	$\delta^{13}C$	S	1.09 (3)	0.36
		Y	1.19 (1)	0.27
		S * Y	0.59 (3)	0.62
	$\delta^{15}N$	S	2.73 (3)	**< 0.05**
		Y	1.81 (1)	0.18
		S * Y	0.19 (3)	0.90
Suspension-feeders	$\delta^{13}C$	S	2.30 (3)	0.09
		Y	1.43 (1)	0.24
		S * Y	0.18 (3)	0.91
	$\delta^{15}N$	S	4.70 (3)	**0.01**
		Y	0.49 (1)	0.48
		S * Y	0.33 (3)	0.81
Deposit-feeders	$\delta^{13}C$	S	3.60 (3)	**0.03**
		Y	0.00 (1)	0.99
		S * Y	0.88 (3)	0.47
	$\delta^{15}N$	S	3.08 (3)	**0.04**
		Y	0.03 (1)	0.86
		S * Y	1.00 (3)	0.40
Carnivores	$\delta^{13}C$	S	0.98 (3)	0.41
		Y	0.16 (1)	0.69
		S * Y	0.67 (3)	0.57
	$\delta^{15}N$	S	2.94 (3)	**0.03**
		Y	0.78 (1)	0.38
		S * Y	0.15 (3)	0.93

Stable isotope signatures of benthic organisms from both unstratified and stratified stations showed an overall large range over $\delta^{13}C$ and $\delta^{15}N$ axis (Figure 2b, Table 2). Based on a common $\delta^{15}N$ enrichment factor of 3.4 ‰, food web length spanned nearly over three trophic levels at both stations ($\Delta\ \delta^{15}N$ range = 9.1 and 9.2 ‰ in unstratified and stratified stations). Large range of stable isotope signatures over the $\delta^{13}C$ axis were also reflected by substantial variations in the reliance on benthic sources among benthic consumers (Figure 3). The reliance on benthic sources ranged from 0 % (Caprellidae) to 96.4 % (*Buccinum undatum*) at the shallow stations (Figure 3a) and from 4.7 % (Pycnogonida) to 82.5 % (Turritellidae) at the deep stations (Figure 3b). The ranges in reliance on benthic sources were homogeneous among trophic groups and varied principally from 20 to 80% (mean reliance = 51.0 and 43.9 % for unstratified and stratified stations, respectively).

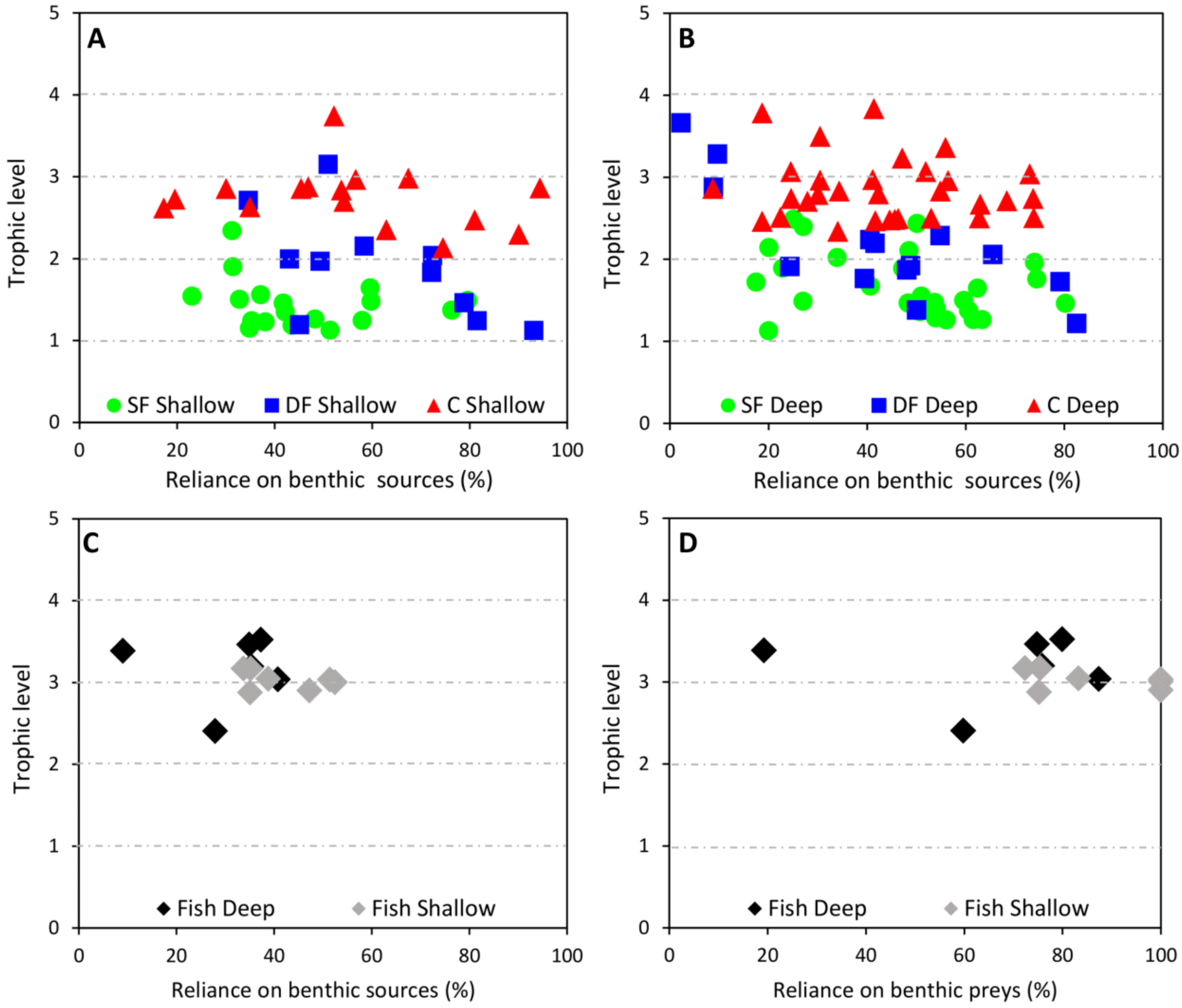

Figure 3: Plots representing the reliance on benthic sources/preys of each taxon with it related trophic level. Upper plots showed the reliance on benthic sources of all benthic species (except fish) from shallow (A) and deep stations (B) according to their feeding groups (suspensive feeders, deposit feeders and carnivores). Lower plots showed the reliance of fish on benthic sources (C) and benthic preys (D).

Percentages of fish reliance on benthic sources showed a moderate reliance of fish on the benthic primary production. Almost all estimates were below 50 %, ranging from 9.0 % for

Eumicrotremus spinosus to 52.5 % for *Hippoglossoides platessoides* (mean reliance = 36.8, Table 2). In contrast, percentages of fish reliance on benthic preys were substantially higher ranging from 59.8 for *Cyclopterus lumpus* to 100 % for *Hippoglossoides platessoides* (mean reliance = 77.2), except for *Eumicrotremus spinosus* (19.3 %).

Table 2: Percentages of fish reliance on benthic sources and preys with associated a priori and δ13C-derived assignations.

Species	Reliance on benthic sources (%)	Reliance on benthic preys (%)	A priori trophic assignation	δ^{13}C-derived trophic assignation
Eumicrotremus spinosus	9.0	19.3	pelagic	pelagic
Cyclopterus lumpus	27.9	59.8	mixed	mixed
Pholis gunnellus	33.7	72.4	mixed	mixed
Artediellus uncinatus	34.9	74.8	benthic	mixed
Cottidae (Shallow)	35.0	75.2	benthic	benthic
Myoxocephalus scorpius	35.2	75.5	mixed	benthic
Hippoglossoides platessoides (Deep)	35.3	75.8	benthic	benthic
Gymnocanthus tricuspis	37.2	79.9	mixed	benthic
Gadus morhua	38.8	83.2	mixed	benthic
Cottidae (Deep)	40.7	87.4	benthic	benthic
Zoarces americanus	47.2	100	benthic	benthic
Lumpeninae	51.4	100	benthic	benthic
Hippoglossoides platessoides (Shallow)	52.5	100	benthic	benthic
Total mean	36.8	77.2		

Discussion

Structure of the benthic food web of Saint-Pierre and Miquelon

Year-to-year variations in the benthic food web structure

Despite strong seasonal variations in trophic conditions (Bridier et al. 2021), the benthic food web structure did not differ between low and high stratification periods. While some might suggest that these results signify that the seasonal stratification has no effects on the structure of benthic food webs, we believe that they are rather related to animal tissue isotopic turnover rates. Previous temporal studies showed that benthic invertebrates can show highly variable integration times (ranging from a month, e.g. Norström et al. 2009, Rodil et al. 2020, to year, e.g. Fry et al. 2006, Wing et al. 2012), depending on tissue type, animal growth rate or ambient temperatures (Vander Zanden et al. 2015). Therefore, the slow growth rates of long-lived benthic invertebrates in cold polar/sub-polar waters are probably associated to low turnover rates (i.e. long integration times) exceeding several months or a year (Wing et al. 2012, McMeans et al. 2015). Therefore, we hypothesize that the time-lag between low and high stratification conditions (i.e. ≈ 2 months) is too short for benthic invertebrates to reach their isotopic equilibrium. In addition, it might be questioned how far food availability and quality might influence the rates of isotopic incorporation in animal tissues (Martínez del Rio et al. 2009). High food quality and availability during the phytoplankton bloom (March/April, Pepin et al. 2017) may lead to a higher food assimilation and isotopic incorporations in invertebrate tissues than during periods outside phytoplankton blooms. Isotopic signatures of benthic invertebrates from both low and high stratification periods could then in fact reflect trophic conditions during the previous phytoplankton bloom.

Benthic food web vertical structure

The vertical structure of the benthic food web showed only minor spatial variations in δ^{15}N signatures along the cross-shore transect. The benthic food wed length (from primary producer to uppermost predators) was estimated in both stratified and unstratified areas to ≈ 3.7 – 3.8 trophic levels, a common value within those known in marine food webs (Vander Zanden and Fetzer 2007). However, the majority of suspension-feeder signatures surprisingly remained below their putative trophic levels (i.e. TL primary consumer range = 1.07 – 2.34 and 1.13 – 2.49, mean = 1.42 and 1.69, in unstratified and stratified stations, respectively). Several factors may explain such unexpected observations. Firstly, the δ^{15}N fractionation factor applied here

($\Delta\delta^{15}N$ = 3.4 ‰, Post 2002) might actually be somehow high compared to the effective fractionation in aquatic invertebrates as reported by McCutchan et (2003) and Vanderklift and Ponsard (2003). The McCutchan factor ($\Delta\delta^{15}N$ = 2.3 ‰, McCutchan et al. 2003) seems effectively closer to the observed $\delta^{15}N$ fractionation between primary producers and primary consumers. However, this factor seems paradoxically unsuitable for upper trophic levels since the mean $\delta^{15}N$ fractionation between primary and secondary consumers ranges in our study between 3.5 and 4.5 ‰ (i.e. ≈ 1.5 to 2 times higher than McCutchan factor). Such trend is rather contradictory with what is generally observed in marine food webs since isotope discrimination usually decreases when dealing with upper trophic levels (Hussey et al. 2014). Therefore, the fractionation factor is probably not able to explain the low trophic level observed in suspension-feeders.

On the other hand, low trophic positions in suspension-feeders have been already reported from other locations and interpreted as a possible indicator of food selection. Some suspension-feeders may indeed select a specific type/size of particles, depending on their anatomy as well as on the quality and/or availability of suspended organic matter, thus showing distinct (depleted) $\delta^{15}N$ signature from the POM bulk (Fry et al. 1988, Iken et al. 2005, Le Loc'h et al. 2008).

Finally, an alternative hypothesis is that $\delta^{15}N$ signatures of the organic matter sources sampled during this study are higher than those of the organic matter sources assimilated by benthic invertebrates during previous period (months to year). Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of trophic baselines (e.g. phytoplankton, macroalgae) are rarely stable over the whole season/year (e.g. Nordström et al. 2009, Dethier et al. 2013). As a result, the isotopic signatures of benthic consumers are not always in equilibrium and can sometimes reflect the isotopic signature of trophic baselines from the previous season (Woodland et al. 2012, McMeans et al. 2015). A time lagged sampling of trophic baselines and primary consumers' tissues, as recommended by McMeans et al. (2015), might have shown a more consistent fractionation between primary producers and primary consumers. The slight variations in POM $\delta^{15}N$ signatures observed between 2017 and 2018 ($\delta^{15}N$ = 6.6 and 4.4 ‰, respectively) could validate this hypothesis. These outcomes may imply that the benthic food web of Saint-Pierre and Miquelon is actually one trophic level higher than our estimate.

Benthic food web horizontal structure

The horizontal dimension of the benthic food web is similar in both stations and shows a large extent on the $\delta^{13}C$ axis (ranging over 8.5 ‰), reflecting the contribution of several food sources with contrasted $\delta^{13}C$ signatures (Layman et al. 2007). According to the percentages of reliance on benthic sources, numerous benthic consumers actually feed on a mixed diet of both pelagic (i.e. POM) and benthic (i.e. macroalgae and/or microphytobenthos) sources (i.e. 85 % of benthic consumers relied between 20 and 80 % on benthic sources). In contrast, some species seem to feed exclusively on pelagic- (such as Caprellidae, Cumaceae) or on benthic-origin sources (e.g. *Lacuna vincta*, *Siphonoecetes* sp., *Tellina* sp.).

The absence of spatial variation in the benthic food web horizontal structure suggest that species assemblages from both unstratified and stratified stations are based on the same organic matter sources. This result might be surprising with regard to previous cross-shelf studies showing that benthic primary production and stratification conditions can induce strong spatial variation in primary consumer $\delta^{13}C$ and $\delta^{15}N$ signatures between shallow and deep stations (stratified *vs* unstratified). For instance, the relative increase of benthic primary production over phytoplankton production in shallow areas is usually linked to an increase in primary consumer $\delta^{13}C$ signatures (e.g. Miller et al. 2008, Nérot et al. 2012, Carlier et al. 2015). In our study, the absence of such spatial shift might thus imply that contribution of benthic sources (i.e. macroalgae and microphytobenthos) is homogeneous along the cross-shore transect (see the part “Contribution of the benthic primary production and its role in coastal ecosystems”). Moreover, previous studies have shown that contrasted stratification conditions along cross-shelf gradients can lead to differences in trophic functioning between weakly- and highly-stratified areas (e.g. González et al. 2013, Chouvelon et al. 2015, Day et al. 2019). For example, Chouvelon et al. (2015) observed a decrease in $\delta^{13}C$ signatures of primary consumers along a cross-shelf transect that they attribute to a shift from a microalgae-based (low stratified stations) to a microbial-based (high stratified stations) trophic functioning.

Although strong variations in the trophic environment, i.e. organic matter availability, sources and quality, were observed between unstratified and stratified stations (Bridier et al. 2021), they did not induce subsequent variations in primary consumer $\delta^{13}C$ signatures or benthic food web structure. We propose two hypotheses to explain this lack of spatial variation in the food web structure that we will discuss in the next section: (1) impact of stratification on benthic food webs may vary according to the synchronization/desynchronization between phytoplankton blooms and stratification onsets and (2) contribution of alternatives organic matter sources to the pelagic tropic environment could also limit the consequences of stratification on benthic food webs.

Mismatch between phytoplankton bloom and stratification onsets

The impact of trophic constraints may strongly depend on the timing of stratification onset and especially on its duration. Firstly, although the Newfoundland Shelf ranks among the most highly stratified marine systems at subarctic latitudes (e.g. Harrison et al. 2013), the period of such extreme occurrence is quite limited in time. Moderate stratification conditions are usually observed on the Newfoundland Shelf in May/June and October/November while strong stratification conditions are observed in the summer only from July to September (Craig and Colbourne 2002, Harrison et al. 2013, Cyr et al. 2020). Outside this timeframe, all the SPM stations have access to the same water masse and are likely to feed on the same POM pool. Therefore, the duration of the trophic forcing related to high stratification conditions may be not long enough in time to have a detectable impact on the benthic food web structure. In addition, and perhaps even more importantly, the short duration of strong stratification conditions in SPM might not correspond to a period of high pelagic primary productivity. Indeed, the main part of the annual pelagic primary production on the Newfoundland Shelf is actually attributable to a single bloom occurring in March-April (i.e. three months before the high stratification period, Harrison et al. 2013, Pepin et al. 2017, Maillet et al. 2019). Consequently, we believe that benthic organisms in SPM might be relatively unaffected by harsh trophic conditions during the period of high stratification as they probably assimilate the main part of their annual carbon requirements before the stratification onset. Such hypothesis suggests therefore that the coupling between stratification and the appearance of phytoplankton blooms could be a key factor controlling the impact of stratification on benthic food webs especially if organic matter transfers mainly imply the use of pelagic sources. Under climate changes, the sub-Arctic zones characterized by a similar mismatch between phytoplankton blooms and high stratification period could therefore be relatively unaffected in case of intensification of thermal stratification. On the other hand, a large part of the annual primary production in high-arctic areas is triggered by a match between sea ice retreat and high stratification conditions (e.g. Wassmann and Reigstad 2011, Holding et al. 2019). In such case, forthcoming strengthening in stratification should thus have a deeper impact on the annual primary production budget.

Contribution of the benthic primary production and its role in coastal ecosystems

The present work emphasizes a strong contribution of benthic sources (i.e. macroalgae and microphytobenthos) to the diet of benthic consumers from unstratified and stratified stations that could explain the lack of spatial variation in the food web structure. Percentages of reliance on benthic sources reveal that benthic primary production provide at least half of the community carbon requirements, but with strong disparities between benthic consumers since some species feed only on pelagic sources while others feed exclusively on benthic sources. These percentages of reliance on benthic sources must be considered in this study as low estimates since our mixing model does not include macroalgae with less enriched isotopic signatures (e.g. *Agarum chlathratum* was not include as we cannot discriminate this source from the POM pool). Such a high contribution of macroalgae along the cross-shore transect might be surprising as a previous study showed that macroalgal contribution to the POM pool was only restricted to the shallowest stations (Bridier et al. 2021). However, macroalgae erosion and detritus export to the POM can be potentially very variable in space and time, depending on numerous local abiotic and biotic factors (Krumhansl and Scheibling 2011, Krumhansl and Scheibling 2012, Wernberg and Filbee-Dexter 2018). In addition, POM composition is usually highly variable over time (i.e. from few hours to few days) in shallow areas since particles present in the water column during sampling are strongly related to coastal hydrological processes (i.e. tidal cycles, short upwelling/downwelling events, e.g. Moynihan et al. 2016, David et al. 2019, Dyer et al. 2019). This might be particularly the case in SPM where diurnal internal waves (see Lazure et al. 2018) can change rapidly the nearshore POM composition by bringing deep waters toward the surface or surface waters toward the bottom (Woodson 2018). Our sampling strategy based on a single POM sampling per station would not detect variations in POM composition and sporadic pulses of macroalgae detritus.

The high contributions of macroalgae and microphytobenthos along the cross-shore transect implies that most benthic consumers could be quite independent from the pelagic primary production and potentially less sensitive to changes in POM quality/quantity occurring under high stratification conditions. While several authors predict that increases in stratification should reduce both primary production and organic matter quality in the pelagic compartment (e.g. Wassmann and Reigstad 2011, Turner et al. 2015, Bridier et al. 2021), it remains questionable for the benthic compartment. For example, microphytobenthos is well adapted to pelagic nutrient depletions as benthic diatoms can use nutrients released directly from the seabed and at the same time benefit from lower seawater turbidity due to lower phytoplankton biomasses (MacIntyre et al. 1996, Glud et al. 2009, Griffiths et al. 2017). In addition, perennial macroalgae are also less sensitive to pelagic nutrient depletion because they usually require less nutrients than phytoplankton species for optimal growth (Pedersen and Borum 1996). As a result, the relative importance of benthic and pelagic primary production in coastal ecosystems is often set by local nutrient regimes, with oligotrophic conditions favoring the former and eutrophic conditions favoring the latter (Duarte 1995, Cloern 2001, Riemann et al. 2016). Such a paradigm suggests that future increases in stratification might have contrasted impacts on Arctic ecosystems, depending on their stratification regimes (i.e. either haline or temperature-based stratification, but see in Ardyna and Arrigo 2020). In shallow nearshore areas exposed to enhanced temperature-based stratification (e.g. SPM), such a contribution of the benthic primary production could be crucial for the resilience of benthic ecosystems facing higher nutrient depletion. Benthic primary producers may actually provide an alternative organic matter source to the pool of pelagic organic matter and their relative contribution in benthic food webs might be even expected to increase as pelagic primary production decreases. However, such contribution of benthic primary producers is more uncertain in Arctic ecosystems facing increasing haline-based stratification since the high turbidities associated with freshwater inputs (e.g. Murray et al. 2015) could impact both pelagic and benthic primary production.

Implications for fisheries

According to estimates of fish dependency on benthic sources in this study, benthic primary producers constitute a significant source of organic matter for fishes (mean benthic reliance = 37%, range = 9 – 53 %) that probably reflect a tight coupling in shallow areas since studies conducted in deeper areas (i.e. > 100 m) generally showed a dominant reliance on phytoplankton (e.g. Le Loc'h et al. 2008, Cresson et al. 2020). Previous works highlighted a major contribution of benthic primary producers to fish food webs in shallow zones such as the Eastern English Channel (≈ 50%, Kopp et al. 2015, Cresson et al. 2020), the west Norwegian (33 – 68%, Fredriksen 2003) and Northwest American coasts (32 – 89 %, von Biela et al. 2016) or the Wadden Sea (Christianen et al. 2017). The differences of benthic reliance between SPM and the other sites could be related to depth since the previous cited studies were conducted on shallower zones than in the present work.

Estimates of fish reliance on benthic preys indicate that almost all fishes exclusively feed on benthic prey (benthic reliance > 75 %), apart from the lumpfish *Cyclopterus lumpus* and the

Atlantic spiny lumpsucker *Eumicrotremus spinosus*. The mixed reliance on benthic and pelagic preys of *Cyclopterus lumpus* (benthic reliance = 59 %) is in accordance with previous data showing that the lumpfish feed both on benthic harpacticoids and pelagic calanoids (Daborn and Gregory 1982, Ingólfsson and Kristjánsson 2002). By contrast, Roshchin (2006) and Berge and Nahrgang (2013) observed that *Eumicrotremus spinosus* mainly predates on *Themisto* spp. amphipods, that could explain its exclusive feeding in SPM on pelagic preys (benthic reliance < 25 %).

It could be argued that the present study underestimates the contribution of phytoplankton and pelagic prey to the overall fish food web since our sampling did not include strict pelagic fish species. However, previous studies have shown that distinguishing pelagic from benthic fishes is less relevant in shallow habitats where both pelagic and benthic preys occur in the same habitat (Kopp et al. 2015, Giraldo et al. 2017). Therefore, it is possible that the benthic primary production may also partly benefit to pelagic fish species if they partly feed on benthic prey.

The future of sub-Arctic fisheries will evidently depend first and foremost on the regulation of fishing industries and the implementation of new management policies controlling fishing pressure (e.g. Jørgensen et al. 2017). However, it might be interesting to investigate the extent to which the evolution of sub-Arctic fisheries may also partly depend on the evolution of benthic and pelagic sources under a warmer and more stratified ocean. Future increases in stratification will likely reduce the phytoplankton production and decrease the quality of the pelagic organic matter (Wassmann and Reigstad 2011, Tremblay et al. 2015, Bridier et al. 2021). In such context, the benthic primary production might be potentially less impacted by increased stratification due to their lower sensitivity to nutrient depletion. We believe that the contrasted sensitivity of pelagic and benthic primary producers to nutrient depletion might potentially have subsequent implications on fisheries. Fish species connected to the pelagic food chain are likely to be vulnerable to such changes as the decrease in phytoplankton production and pelagic organic matter quality will probably impact the carbon transfers trough the pelagic food web. In contrast, fish species connected to the benthic food webs might be potentially less vulnerable to these changes, depending on the trophic plasticity of benthic invertebrates and their ability to increase their reliance to the benthic primary production. Such differential vulnerability of fish species would obviously depend on the local shelf bathymetry. Shallow shelves where a significant part of the benthic primary production might fuel benthic food webs with organic carbon might probably increase the resilience of fish species connected to the benthic food web compared to their counterpart connected to the pelagic food chain. However, such differences would be probably not observed in deeper areas where benthic invertebrates depend almost exclusively of the pelagic primary production.

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Supplementary material *to the article:*

Thermal stratification does not change the food web structure and functioning of a shallow benthic ecosystem from a sub-Arctic archipelago

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Table S1: Stable isotope ratio average ($\delta^{13}C$ & $\delta^{15}N$) and associated standard deviation (SD) of benthic invertebrates collected in shallow and deep stations. Tissue selection for stable isotope analyses, laboratory method (with or without acidification) and species feeding trait were specified by “Tissu”, “Acid.” and “Feeding traits” columns, respectively.

Table S1

Species	Tissu	Acid.	Feeding traits	Shallow					Deep				
				δ^{13}C	SD	δ^{15}N	SD	N	δ^{13}C	SD	δ^{15}N	SD	N
POLYCHAETA													
Aphroditidae	Parapodia	No	Carnivore	-17,9		15,6		1					
Euclymene sp.	Whole body	No	Deposit feeder						-21,8		12,6		1
Glyceriidae	Whole body	No	Carnivore	-20,4		12,5		1	-20,1	0,1	12,5	2,4	3
Hesionidae	Whole body	No	Carnivore	-18,0	0,8	11,2	0,6	7					
Maldanidae	Whole body	No	Deposit feeder	-18,6		9,8		1					
Nepthydae	Whole body	No	Carnivore	-17,9		13,0		1	-17,5	0,3	13,2	0,1	2
Nereidae	Whole body	No	Deposit feeder						-20,9	0,5	11,4	0,4	7
Orbiniidae	Whole body	No	Deposit feeder	-19,0	0,3	13,6	1,0	3					
Pectinaria granulata	Whole body	No	Deposit feeder						-21,3	0,7	15,3	2,4	8
Phyllodoce sp.	Whole body	No	Carnivore						-22,2		11,2		1
Opheliidae	Whole body	No	Carnivore	-19,4		12,5		1					
Polychaete tubulaire	Whole body	No	Deposit feeder	-20,1	0,4	12,1	0,1	3	-21,8	0,7	14,0	0,9	7
PolychŠte tube sp. 1	Whole body	No	Deposit feeder						-20,2	0,7	9,4	0,4	4
Polynoidae	Whole body	No	Carnivore	-19,2		10,8		1	-20,6	0,7	12,3	0,8	14
Sigalionidae	Whole body	No	Carnivore	-21,3		11,7		1	-20,6	0,8	12,0	1,1	8
Terebellidae	Whole body	No	Deposit feeder						-21,8	0,6	9,3	0,4	9
SIPUNCULA													
Golfingiidae	Whole body	No	Deposit feeder						-20,2		9,2		1
MOLLUSCA													
Anomiidae	Adductor muscle	No	Suspension feeder	-20,4	0,2	7,9	0,3	5	-20,0	1,3	8,1	0,8	2
Aporrhais occidentalis	Foot muscle	No	Deposit feeder						-19,0	0,2	9,8	0,3	
Arctica islandica	Adductor muscle	No	Suspension feeder	-22,3	0,2	7,2	0,2	8	-20,7	0,2	7,1	0,1	7
Astarte elliptica	Adductor muscle	No	Suspension feeder						-20,3	0,3	9,3	1,1	2
Astarte montagui	Adductor muscle	No	Suspension feeder						-20,2	0,8	10,0	0,8	3
Buccinum undatum	Foot muscle	No	Carnivore	-16,1	0,6	12,6	0,1	2	-18,6	0,7	12,9	1,3	16
Chlamys islandica	Adductor muscle	No	Suspension feeder						-20,7	0,2	8,5	0,4	4

Table S1, continued

Clinocardium sp.	Adductor muscle	No	Suspension feeder						-19,4		7,9		1
Crenella decussata	Adductor muscle	No	Suspension feeder	-21,6	0,7	7,8	0,2	10	-21,0	0,2	7,5	0,1	2
Cylichna sp.	Whole body	No	Carnivore						-19,6		12,4		1
Cyrtodaria siliqua	Adductor muscle	No	Suspension feeder						-18,5	0,2	8,8	0,2	5
Ensis leei	Siphon muscle	No	Suspension feeder	-20,5	0,3	7,1	0,4	7					
Euspira heros	Adductor muscle	No	Carnivore	-18,4		10,1		1					
Hiatella arctica	Adductor muscle	No	Suspension feeder						-20,8	0,4	7,2	0,4	4
Lacuna vincta	Whole body	No	Deposit feeders	-18,2	0,8	6,7	0,6	6					
Liocyma fluctuosa	Adductor muscle	No	Suspension feeder						-20,8	0,3	7,6	0,2	13
Macoma calcarea	Adductor muscle	No	Deposit feeders	-19,1	0,2	7,9	0,3	4					
Margarites umbilicatus	Foot muscle	No	Deposit feeders	-20,5	0,0	9,6	0,3	2	-20,6	0,2	10,2	0,5	6
Margarites costalis	Foot muscle	No	Deposit feeders						-19,8	0,2	10,6	0,3	7
Mytilidae	Adductor muscle	No	Suspension feeder	-22,1		6,8		1					
Naticidae	Foot muscle	No	Carnivore						-18,7		15,9		1
Neptunea despecta	Foot muscle	No	Carnivore						-17,5		12,2		1
Neptunea lyrata	Foot muscle	No	Carnivore						-19,3		11,3		1
Helichlamys ??	Adductor muscle	No							-20,6	0,1	11,2	0,3	5
Ocenebra	Whole body	No	Carnivore						-21,8		12,6		1
Ocenebrinae	Whole body	No	Carnivore						-18,9	0,6	11,3	0,2	3
Pandora gouldiana	Adductor muscle	No	Suspension feeder	-20,9	0,4	8,1	0,5	3					
Parvicardium pinnulatum	Adductor muscle	No	Suspension feeder						-21,2		7,8		1
Placopecten magellanicus	Adductor muscle	No	Suspension feeder	-19,4	0,0	8,4	0,1	3					
Serripes groenlandicus	Adductor muscle	No	Suspension feeder						-20,4	0,6	7,5	0,2	5
Risoidae sp. 1	Adductor muscle	No	Deposit feeders	-19,5		10,2		1					
Sepiola sp.	Adductor muscle	No	Carnivore						-18,7		14,3		1
Solamen glandula	Adductor muscle	No	Suspension feeder	-21,5	0,1	6,9	0,2	2					
Spisula solidissima	Adductor muscle	No	Suspension feeder	-21,2		7,1		1					
Tellina sp.	Adductor muscle	No	Deposit feeders	-19,2	1,1	7,8	0,5	3					
Tonicella marmorea	Whole shoft tissue	No	Deposit feeders	-20,4	1,7	9,6	0,4	5					
Trichotropis bicarinata	Adductor muscle	No	Suspension feeder						-19,1	0,0	7,8	0,1	2

Table S1, continued

Trophon sp.	Adductor muscle	No	Carnivore						-17,9	0,2	12,1	0,5	3
Turritellidae	Adductor muscle	No	Suspension feeder						-18,1	1,9	8,7	0,6	2
CRUSTACEA													
Ampelisca sp.	Whole body	No	Suspension feeder	-19,3		7,5		1	-20,3	0,9	7,1	0,8	7
Amphipode	Whole body	No	Suspension feeder	-21,2	0,4	7,9	0,3	3					
Amphipode 2	Whole body	No	Suspension feeder	-21,5	0,4	6,9	0,9	2	-22,6	1,3	7,9	0,3	7
Balanus sp.	Whole soft tissue	No	Suspension feeder						-18,5		9,5		1
Cancer irroratus	Claw tissue	No	Carnivore	-18,8	0,6	12,5	0,4	9	-18,8	0,8	12,5	1,5	3
Caprelles rouges	Whole body	No	Suspension feeder	-24,7	0,3	6,5	0,8	8					
Caprellidae	Whole body	No	Suspension feeder	-21,9	1,1	7,0	1,9	15	-20,8	0,4	7,8	0,9	2
Chionoecetes opilio	Claw tissue	No	Carnivore						-19,6	0,8	14,6	1,5	20
Crangon sp.	Dorsal muscle	No	Carnivore						-19,4	1,1	14,7	0,5	2
Crangonidae	Dorsal muscle	No	Carnivore	-18,6	0,6	12,9	0,7	6					
Lebbeus sp.	Dorsal muscle	No	Carnivore	-21,1		12,1		1					
Cumaceae sp. 1	Whole body	Yes	Suspension feeder	-21,0	0,9	6,7	0,5	6					
Cumaceae sp. 2	Whole body	Yes	Suspension feeder						-23,1	2,0	6,7	0,5	6
Hyas araneus	Claw tissue	No	Carnivore						-18,2	2,0	11,3	1,6	7
Hyas coarctatus	Claw tissue	No	Carnivore						-18,2	1,7	11,9	1,4	6
Lysianassidae	Whole body	No	Carnivore	-17,4	0,6	10,6	0,1	2	-17,5	1,0	11,4	0,3	3
Mysida	Whole body	No	Carnivore						-21,1		10,8		1
Oedicerotidae	Whole body	No	Carnivore						-20,4	1,0	11,3	0,7	10
Paguridae	Claw tissue	No	Carnivore	-19,6	1,6	12,1	0,2	7	-19,7	0,1	12,9	0,1	3
Palaemonidae	Dorsal muscle	No	Carnivore						-20,4		11,3		1
Pandalus sp.	Dorsal muscle	No	Carnivore						-20,4		12,9		1
Pontoporeiidae	Whole body	No	Deposit feeders	-21,9	1,8	8,1	0,3	3					
Siphonoecetes	Whole body	No	Suspension feeder	-19,0		7,1		1	-18,9	0,3	7,0	1,2	3
Spirontocaris sp.	Dorsal muscle	No	Carnivore						-20,8	0,7	13,3	1,7	12
Isopoda	Whole body	Yes	Suspension feeder	-21,3	0,5	9,3		3	-21,2	0,9	9,7	0,6	3
ECHINODERMATA													

Table S1, continued

Cucumaria frondosa	Whole body	No	Suspension feeder						-19,3	0,7	8,4	0,5	2
Edwaardariidae	Dorsal muscle	No	Carnivore	-20,1		11,8		1					
Gorgonocephalidae	Arms	Yes	Deposit feeders						-21,6	0,2	11,0	0,4	6
Holothurie	Whole body	No	Deposit feeders						-20,8	0,6	8,8	0,1	2
Oursin	Stomach	No	Deposit feeders						-19,0	0,3	13,3	0,5	7
Echinarachnius parma	Stomach	Yes	Deposit feeders	-21,4	0,6	6,9	0,5		-21,1	0,9	7,5	0,5	
PYCNOGONIDA													
Pycnogonida	Whole body	No	Carnivore						-22,5		11,6		1
TUNICATA													
Ascidiacea	Ectoderm	No	Suspension feeder	-21,3		10,8		1	-21,9		9,3		1
Ascidiacea 2	Ectoderm	No	Suspension feeder						-22,5	0,1	8,4	0,1	5
Ascidiacea 3	Ectoderm	No	Suspension feeder						-20,1	0,7	11,1	0,6	5
Boltenia ovifera	Ectoderm	No	Suspension feeder						-21,9	0,3	10,1	0,1	5
CNIDARIA													
Scleractinia	Whole body	No	Suspension feeder						-17,8	0,3	10,7	0,0	4
PORIFERA													
Porifera	Whole body	No	Suspension feeder						-21,7	0,5	11,3	1,7	7
PISCES													
Artediellus uncinatus	Dorsal muscle	No	Carnivore						-19,6		14,6		1
Cottidae	Dorsal muscle	No	Carnivore	-20,2		12,6		1	-19,7	0,5	13,2	0,5	2
Cyclopterus lumpus	Dorsal muscle	No	Carnivore						-21,1		11,0		1
Eumicrotremus spinosus	Dorsal muscle	No	Carnivore						-21,4	0,2	14,4	0,1	2
Gadus morhua	Dorsal muscle	No	Carnivore	-19,8	0,4	13,2	0,5	5					
Gymnocanthus tricuspis	Dorsal muscle	No	Carnivore						-19,4	0,2	14,8	0,3	3
Hippoglossoides platessoides	Dorsal muscle	No	Carnivore	-18,9	0,6	13,1	0,9	6	-19,9		13,7		1
Lumpeninae	Dorsal muscle	No	Carnivore	-18,9	0,2	13,2	0,6	4					
Myoxocephalus scorpius	Dorsal muscle	No	Carnivore	-19,9	0,5	13,6	0,9	4					

Table S1, continued

Pholis gunnellus	Dorsal muscle	No	Carnivore	-20,0	0,2	13,6	0,1	5
Pseudopleuronectes americanus	Dorsal muscle	No	Carnivore	-19,3	0,1	12,6	0,0	3
Zoarces americanus	Dorsal muscle	No	Carnivore	-19,4	0,4	12,7	0,2	10

Chapter V

Diversity and spatial variability of shallow benthic macrofaunal assemblages in a high-Arctic fjord (Young Sound, North-East Greenland)

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Abstract

Although knowledge of Arctic benthic biodiversity has increased considerably in recent decades, some regional areas remain poorly studied, such as the coastal ecosystems of North-East Greenland. The aim of the present study was to complete an earlier benthic species inventory from Young Sound, a high Arctic fjord (74°N), through a survey of shallow benthic assemblages along an inner/outer fjord transect corresponding to a gradient of decreasing influence of freshwater input. New benthic assemblages were highly diversified (i.e. 124 species were identified for a total sampling surface of 0.8725 m^2) and total species richness, including a previous inventory, was estimated to 192 species over the most marine part of the fjord. Strong variations in the species richness and structure of benthic assemblages were observed between inner and outer parts of the fjord, confirming the general patterns observed in other Arctic fjords. The outer fjord section was dominated in abundance by diverse mollusk assemblages (e.g. *Hiatella arctica*, *Musculus discors* and *Mya truncata*) while numerous polychaetes were found in the middle fjord section (e.g. *Abyssoninoe* sp., *Laphania boecki* and *Nereimyra aphroditoides*). By contrast, the innermost benthic assemblage was dominated by crustaceans (Ostracods, *Metopa glacialis*) and polychaetes (*Maldane sarsi*, *Owenia borealis*, *Leitoscoloplos mammosus*). This inner fjord section showed some similarities with both impacted- and sheltered-freshwater input areas, suggesting that this zone is transitional between inner and outer fjord conditions. Future samplings toward the innermost (namely Tyrolerfjord) or deepest areas (up to 350 m) could further complete the current inventory of Young Sound benthic biodiversity.

Key words

Benthic ecosystems • Macrofauna • Community structure • Spatial variability • Freshwater inputs • Arctic fjord • Young Sound • North-East Greenland

Introduction

Arctic benthic biodiversity remains poorly studied to date although species found at seabed constitute 90 % of the total estimated species richness of Arctic invertebrates (Sirenko 2001, Gradinger et al. 2010). While Arctic benthic ecosystems were previously considered as areas of low specific diversity (e.g. Knox and Lowry 1977), there is now increasing evidences that such assumption is probably biased by low sampling efforts at high latitudes (Piepenburg et al. 2005, Piepenburg et al. 2011). Recent inventories estimate the diversity of Arctic benthic species over 4600 species, a much higher number than previously assessed, while several thousands of species probably remain to be discovered (Bluhm et al. 2011, Josefson et al. 2013). Despite a considerable reduction of knowledge gap in biodiversity in the last decades, some geographical areas are still understudied (e.g. East Greenland, Piepenburg et al. 2011).

As a result of climate change, Arctic benthic ecosystems are expected to undergo major modifications in seawater salinity and temperature, acidification or sedimentation over the XXIth century (AMAP 2017). It is likely that these modifications will alter the benthic biodiversity, especially in coastal areas which are expected to be the most exposed to these forthcoming environmental changes (Węsławski et al. 2011). The expansion of boreal species toward high latitudes is also expected to impact benthic biodiversity by bringing new species to Arctic areas (Węsławski et al. 2011, Renaud et al. 2015). Recent expansions of several engineer species of boreal affinities toward the high Arctic (e.g. blue mussel *Mytilus edulis* or *Laminaria hyperborea* kelp) may have also deep influences on biodiversity structure of shallow benthic ecosystems by increasing habitat diversity and supporting the arrival of new species (Berge et al. 2005, Krause-Jensen and Duarte 2014, Filbee-Dexter et al. 2019). Numerous questions remain however unresolved regarding how endemic benthic species will cope with these new abiotic conditions (increases in temperature or sedimentation, decrease in seawater salinity) and associated changes on biotic interactions (e.g. arrivals of new predators or competitors, Renaud et al. 2015). Assessing the vulnerability of Arctic benthic communities experiencing these environmental change and arrivals of new boreal species remains thus challenging without initial references states in benthic biodiversity throughout Arctic ecoregions.

In this context, any increase of our knowledge on the benthic biodiversity of poorly characterized Arctic ecoregions is crucial, particularly in shallow coastal ecosystems for which rare data are available although they are expected to be the most impacted by climate change

(Węsławski et al. 2011). For example, the sole studies conducted in the North-Eastern coasts of Greenland focused on epifauna and/or megafauna shelf communities (e.g. Piepenburg and Schmid 1996, Brandt and Schnack 1999, Starmans et al. 1999, Fredriksen et al. 2020). To our knowledge, for such real *Terra Incognita* of the Arctic ecoregions (Piepenburg et al. 2011), only Sejr et al. (2000) provided quantitative datasets on shallow macrozoobenthos assemblages in a high-Arctic fjord (Young Sound, NE Greenland). Although numerous older studies from the mid XX^{th} century have been conducted on shallow habitat (e.g. Ockelmann 1958), they usually focused on single taxa distribution rather than give insights on macrobenthic community structure and diversity.

The aim of the present study is to complete the benthic biodiversity inventory conducted by Sejr et al. (2000) in North East Greenland (Young Sound, 74°N) by studying additional stations. While Sejr et al. (2000) studied the vertical zonation of macrofaunal communities (from 20 to 85 m), we decided to prospects new benthic assemblages by sampling macrofaunal communities along an inner/outer fjord gradient (reflecting differential exposition of freshwater inputs). The species assemblage descriptions provided by this present study and Sejr et al. (2000) will provide a baseline for future studies investigating the temporal variability of shallow coastal communities and their response to climate change.

Materials and Methods

Study sites

Young Sound is a high Arctic fjord located in North-East Greenland (Figure 1) of about 90 km long and 2-7 km wide (Rysgaard et al. 2003). A sill is located at its outer section (≈ 45 m depth) limiting seawater exchanges between the inner parts of the fjord and the shelf (Bendtsen et al. 2007) where average and maximum depths reaching 100 and 360 m, respectively (Rysgaard et al. 2003). This fjord is characterized by extreme seasonal variations, thick sea ice (> 100 cm) and snow layers (20 – 100 m) covering the fjord for 9 to 10 months per year (Glud et al. 2007) and strongly limiting the annual primary production estimated at ca. 10 g m-2 yr^{-1} (Rysgaard et al. 1999). During summer, glacier and snow melt generate strong river flows ranging annually from 0.9 to 1.4 km^{3} (annual total runoff, Bendtsen et al. 2014). Such freshwater inputs induce strong spatial salinity and temperature gradients in summer surface waters, with temperature decreasing from 9 to 2°C and salinity increasing from 8 to 30, from the inner to the outer part of the fjord, respectively (Bendtsen et al. 2007). By contrast, deeper waters (> 10 m) remain generally stable throughout the year (i.e. > 2° C) along the entire fjord length (Bendtsen et a. 2007, Middelbo et al. 2019).

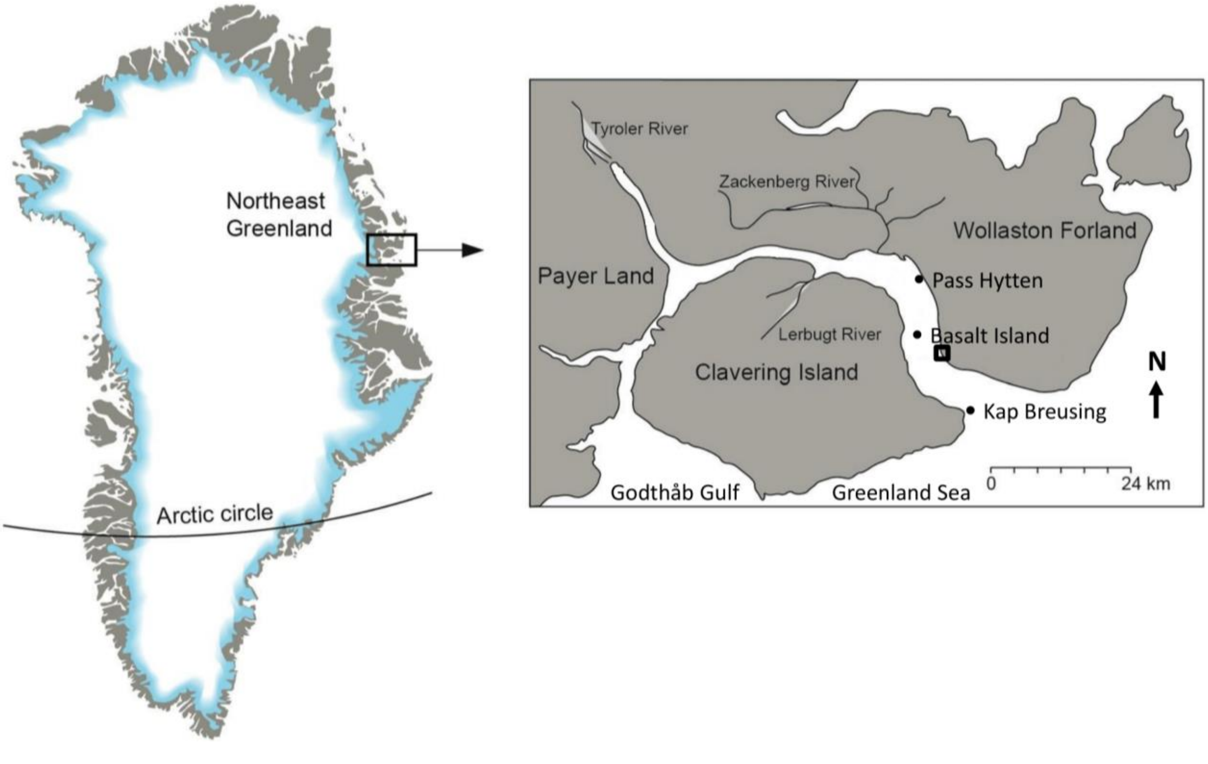

Figure 1: Map indicating location of sampling stations in Young Sound, North-East Greenland (modified from Ribeiro et al. 2017). Black square represents the Daneborg research station.

Sampling and laboratory analyses

Sampling was conducted in August 2016 at three stations distributed along an inner/outer fjord gradient: Pass Hytten (depth = 18 m, 74.41° N, 20.33° W), Basalt Island (depth = 21.5 m, 74.33° N, 20.36° W) and Kap Breusing (depth = 20 m, 74.21° N, 20.11° W, Figure 1). Macrofauna samples were collected at each station by scuba divers using a suction dredge (square mesh size = 1 mm) over a surface of 900 cm² (except one replicate from Kap Breusing which was collected on 625 cm²). Macrofauna samples were directly fixed in 10% formalin after sampling. Sediment samples were also collected at both Pass Hytten and Kap Breusing using small sediment cores for grain-size analysis.

Dredged samples were sent to the LEMAR laboratory (UMR 6539 CNRS, Brest, France) for species identification. Animals were sorted and then transferred to 70% ethanol before identification to the lowest taxonomic level. Sediment samples were analyzed at the private company "*Eurofins – Analyses pour l'environnement*" (Saverne, France) using laser methods: all samples were sieved through a 2 mm square mesh then analyzed by a Malvern Mastersizer 2000 laser particle size analyzer to provide various size fractions ranging from 2 to 2000 µm.

The knowledge on macroalgal species assemblages in Young Sound is still limited to date. Therefore, although primary benthic producers are outside the scope of the present study, we provide here a first non-exhaustive list of specimen species collected by the suction dredge in Kap Breusing.

Statistical analyses

Spatial differences in community structure were visualized using Principal Component Analysis (PCA) realized on Hellinger-transformed fauna abundances. This transformation was selected to reduce the weight of rare species in the analysis (Legendre and Gallagher 2001). The first eighteen species explaining the most the spatial pattern in the ordination were represented in a second plot in order to visualize which species contributed to each station benthic structure. Spatial differences in community structure was tested through one-way permutational multivariate analysis of variance (PERMANOVA) performed on Bray-Curtis-transformed fauna abundances. Homoscedasticity was checked through a permutational analysis of multivariate dispersions (PERMDISP) test to ensure that data dispersion do not influence PERMANOVA result (Anderson et al. 2008, Anderson and Walsh 2013).

Species rarefaction curves were calculated for each replicate in order to compare trends in species richness among stations. Species richness was compared among replicates based on rarefaction curves by standardizing all data to a same abundance (corresponding to the number of individuals in the replicate with the lowest abundance) to remove any bias of abundance on taxa richness (Gotelli and Colwell 2001). An additional rarefaction curve was plotted to assess roughly the specific richness for the entire Young Sound system. Jacknife1 Chao2 estimates were calculated and plotted as accumulation curves to estimate the total species richness in case species rarefaction curves did not reach their asymptotes (Colwell et al. 2004, Chao and Chiu 2016).

Results

Benthic community structure

Significant spatial differences in community structure were observed between sampling stations (one-way PERMANOVA, $p < 0.001$). The homoscedasticity of faunal abundances was validated by a PERMDISP test ($p > 0.05$). Pairwise analyses revealed that such differences were observed between all stations ($p < 0.001$). PCA analysis showed that over half of the spatial variability was explained by the first two principal components (PC1 and PC2 explained 32.97 and 27.68 % of community variations, respectively); low variability was observed among replicates of each station (Figure 1).

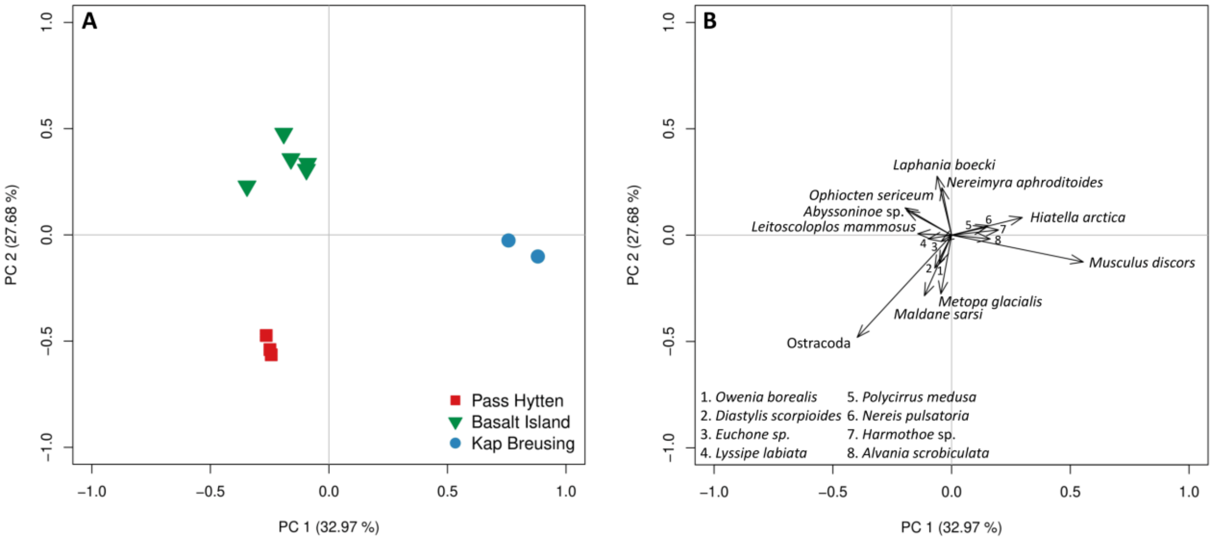

Figure 1: Principal component analysis based on Hellinger-transformed fauna abundances. Left plot (A) represents the position of each replicate while right plot (B) represents the position of the first eighteen species explaining most of spatial variations.

Kap Breusing benthic assemblages were strongly dominated by mollusks, with 67.8 – 69.0 % of the total abundance (Figure 2a), mainly due to both *Hiatella arctica* and *Musculus discors* filter-feeding bivalves (> 50%, Figure 1b). Community structure in Basalt Island was slightly more homogeneous among taxa (Figure 2a), with polychaetes being the most dominant group (relative abundance = 44.9 – 45.9 %). *Abyssoninoe* sp. *Laphania boecki* and *Nereimyra aphroditoides* dominated the polychaetes' assemblage (Figure 1b, 2a). Finally, crustaceans constituted the dominant taxonomic group in Pass Hytten (relative abundance = 52.9 – 78.0 %,

Figure 1a), largely represented by high densities of Ostracoda and amphipod *Metopa glacialis* (Figure 1b).

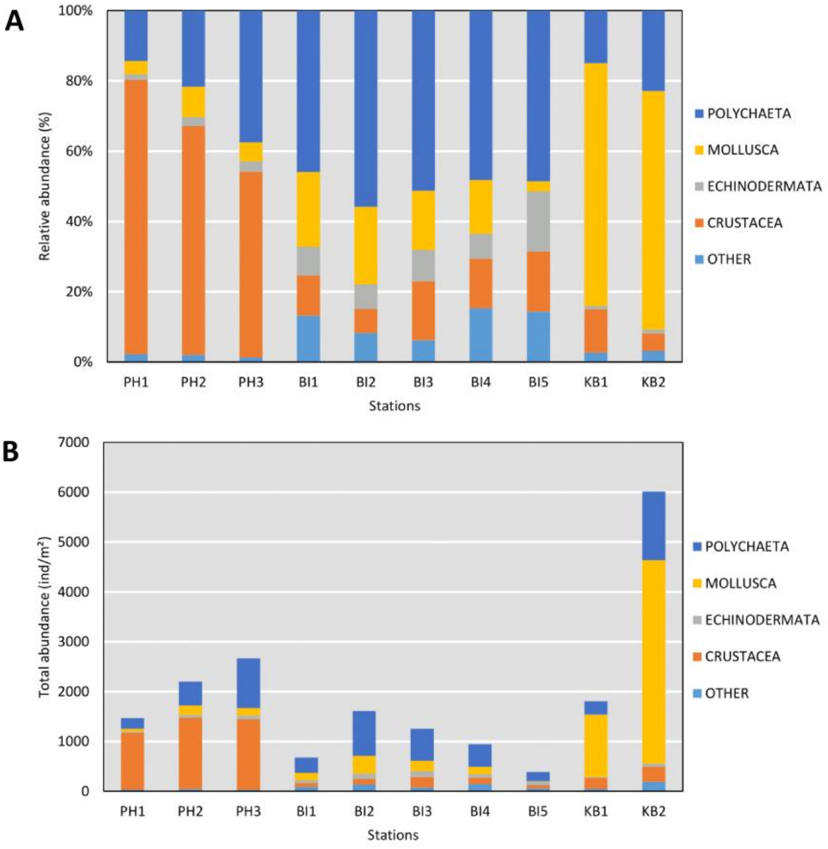

Figure 2: Relative abundance (%, A) and total abundance (individuals/m², B) of major taxonomic groups from Pass Hytten (from PH 1 to PH 3), Basalt Island (from BI 1 to BI 5) and Kap Breusing (KB 1 & KB 2) stations.

Total abundances showed large variation among stations and replicates (Figure 2b). The highest abundances were observed in the second replicate from Kap Breusing (reaching 6011 individuals/m^2, Figure 2b). In contrast, the first replicate from Kap Breusing showed however substantially lower total abundance (1808 individuals/m^2) which were similar to the abundances observed in Pass Hytten (1467 to 2667 individuals/m^2, Figure 2b). Finally, the lowest total abundance was observed in Basalt Island (389 to 1611 individuals/m^2, Figure 2b).

Abiotic and biotic description of benthic habitats

Pass Hytten

Sediment from Pass Hytten is dominated by fine silt particles (55% of the total size fraction for particles < 63 µm) mixed with fine sand (25%) and gravels (20%, Figure S1). Significant bioturbation activity occurs probably due to high abundances of epifauna (e.g. *Ophiocten sericeum*, see Figure 3a) and burrowing shrimps (e.g. *Sclerocrangon boreas*, L. Chauvaud pers. obs.).

Pass Hytten's species assemblage is characterized by a low species evenness. Only ten taxa, accounting for 83.5% of total abundance (Table 1), dominated by hyperbenthic crustaceans such as ostracods, the amphipod *Metopa glacialis* and the cumacean *Diastylis scorpioides* (representing 59 % of total abundance). Strict benthic species (epifauna and endofauna) were mostly represented by tube-dwelling (*Euchone* sp. [see high abundances in Figure3a], *Lyssipe labiate*, *Maldane sarsi* and *Owenia borealis*) and errant polychaetes (*Abyssoninoe* sp. and *Leitoscoloplos mammosus*). In much lower proportion (< 15 % total abundance) the bivalves *Astarte moerchi*, *Hiatella arctica*, *Mya truncata* and *Musculus discors*) were also present.

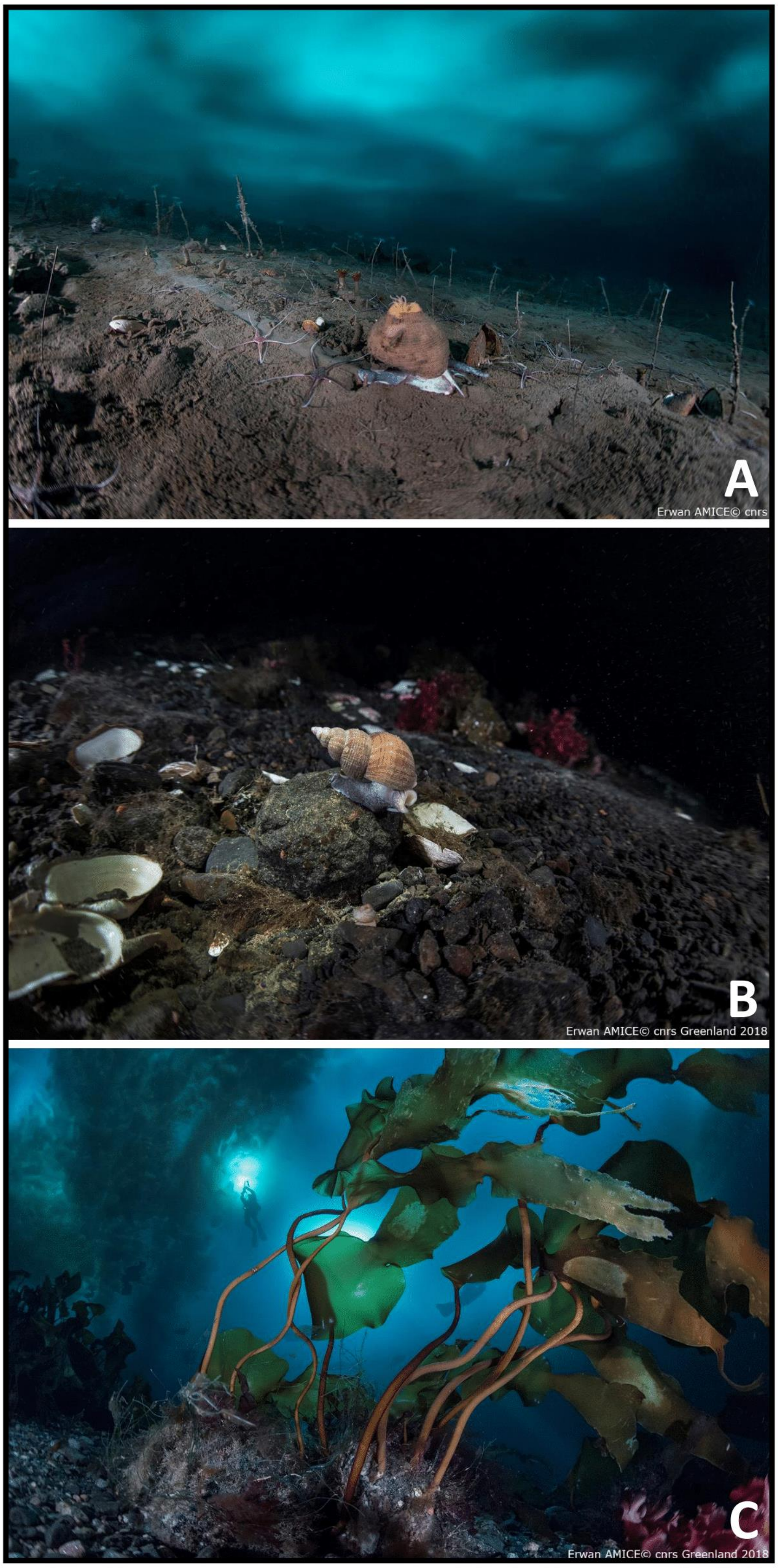

Figure 3: Submarine landscape of Pass Hytten (A), Basalt Island (B) and Kap Breusing stations (C). Photo credits: Erwan Amice

Table 1: List of the ten most common taxa for each station, with their related relative abundance (%), cumulative relative abundance (Cum. %) and density (Dens., individuals/m²).

Species	Phylum	Abund.	%	Cum. %
Pass Hytten				
Ostracoda Latreille, 1802	Arthropoda	996.3	47.2	47.2
Metopa glacialis (Krøyer, 1842)	Arthropoda	185.2	8.8	56.0
Maldane sarsi Malmgren, 1865	Polychaeta	166.7	7.9	63.9
Owenia borealis Koh, Bhaud & Jirkov, 2003	Polychaeta	114.8	5.4	69.3
Leitoscoloplos mammosus Mackie, 1987	Polychaeta	63.0	3.0	72.3
Diastylis scorpioides (Lepechin, 1780)	Arthropoda	63.0	3.0	75.3
Abyssoninoe sp. Orensanz, 1990	Polychaeta	48.1	2.3	77.5
Euchone sp. Malmgren, 1866	Polychaeta	44.4	2.1	79.6
Lysippe labiata Malmgren, 1866	Polychaeta	44.4	2.1	81.8
Musculus discors (Linnaeus, 1767)	Mollusca	37.0	1.8	83.5
Basalt Island				
Laphania boecki Malmgren, 1866	Polychaeta	64.4	6.6	6.6
Ostracoda Latreille, 1802	Arthropoda	57.8	5.9	12.5
Abyssoninoe sp. Orensanz, 1990	Polychaeta	55.6	5.7	18.2
Nereimyra aphroditoides (O. Fabricius, 1780)	Polychaeta	55.6	5.7	23.9
Nematoda	Nematoda	55.6	5.7	29.6
Ophiocten sericeum (Forbes, 1852)	Echinodermata	51.1	5.2	34.9
Astarte moerchi Hopner Petersen, 2001	Mollusca	46.7	4.8	39.6
Clymenura sp. Verrill, 1900	Polychaeta	42.2	4.3	44.0
Pholoe sp. Johnston, 1839	Polychaeta	40.0	4.1	48.1
Nemertea	Nemertea	31.1	3.2	51.3
Kap Breusing				
Musculus discors (Linnaeus, 1767)	Mollusca	1881.6	43.7	43.7
Hiatella arctica (Linnaeus, 1767)	Mollusca	802.6	18.7	62.4
Harmothoe sp. Kinberg, 1856	Polychaeta	223.7	5.2	67.6
Nereis zonata Malmgren, 1867	Polychaeta	177.6	4.1	71.7
Polycirrus medusa Grube, 1850	Polychaeta	118.4	2.8	74.5
Alvania scrobiculata (Møller, 1842)	Polychaeta	78.9	1.8	76.3
Mya truncata Linnaeus, 1758	Mollusca	65.8	1.5	77.8
Nereimyra aphroditoides (O. Fabricius, 1780)	Polychaeta	46.1	1.1	78.9
Apherusa sarsi Shoemaker, 1930	Polychaeta	46.1	1.1	80.0
Syllis sp. Lamarck, 1818	Polychaeta	39.5	0.9	80.9

Basalt Island

Basalt Island's sediment is composed of a mixture of sand and small gravels (2-5 millimetres) associated with detrital organic matter (mainly macroalgae and shell debris) accumulated on the seabed (Figure 3b). Due to the dominance of stones, we were not able to sample the sediment at this station. The steep slope of the seafloor (steepness grade ≈ 80 – 100 %, see Figure 3b) probably makes the soil unstable due to the downward export of mineral materials toward deep fjord basins.

The species assemblage at Basalt Island shows greater species evenness than at the other two sites since the ten most dominant species account for only 51.3% of total abundance (Table 1). Polychaetes dominate the species assemblage with *Abyssoninoe* sp., *Clymenura* sp., *Laphania boecki*, *Nereimyra aphroditoides* and *Pholoe* sp. representing 26.4 % of the total abundance. Less abundant, several bivalves such as *A. moerchi*, *H. arctica* or *M. truncata* were also found on the site, as well as the brittle-star *Ophiocten sericeum* (Table 1, Table S1). Among hyperbenthic species, ostracods show high abundance (5.9 %, Table 1).

Kap Breusing

The grain-size distribution of Kap Breusing was variable between replicates, but overall this sandy sediment includes particles larger than 63 µm and smaller than 2000 µm (ranging from 53 to 80 %, Figure S1). Heterogeneous medium/coarse sand (38 to 55 % of the grain-size particle were between 250 and 2000 µm) was found for two of the three samples, the other was largely composed of fine sand (61 % of the grain-size particle was between 63 and 250 µm).

The species assemblage was associated here with a rock wall close to the location where sediment samples were collected and included Sertulariidae hydrozoans and *Musculus discors* bivalves (L. Chauvaud, pers. obs., see background of Figure 3c). Both species generate a complex three-dimensional structure hosting a highly diversified assemblage including the gastropod *Alvania scrobiculata* and the bivalves *A. moerchi*, *H. arctica*, *M. discords* and *M. truncata* that represent more than 68% of the total abundance (Table 1). Four polychaete vagile species were also found as *Harmothoe* sp., *Nereimyra aphroditoides*, *Nereis* sp. and *Syllis* sp. (11.3 % of total abundance) as well as the sedentary terebellid *Polycirrus medusa* (2.8 %; Table 1).

Biodiversity estimates of benthic habitats

From a sampled surface of 0.8725 m^2 collected through 10 suction dredge replicates, we collected a total of 1663 individuals belonging to 123 species (Table S1). Polychaetes represented the most diversified phylum (49 species), followed by crustaceans (34 species) and mollusks (24 species). Nemerteans, sipunculans, pycnogonids, tunicates, nematodes, brachiopods and platylhelminths were also collected but they display a much lower species richness.

In addition, 16 macroalgae species were identified at Kap Breusing (Table S2). Florideophyceae represented the most diversified phylum with 9 species: *Coccotylus truncatus*, *Euthora cristata*, *Neodilsea integra*, *Phycodrys rubens*, *Polysiphonia* sp. 1, *Polysiphonia* sp. 2, *Ptilota serrata*, *Scagelothamnion pusillum*, *Turnerella pennyi*. Phaeophyceae showed a slightly lower diversity with 6 species (*Chaetopteris plumosa*, *Desmarestia aculeata*, *Desmarestia viridis*, *Halosiphon tomentosus*, *Laminaria solidungula*, *Saccorhiza dermatodea*) while only one of Ulvophyceae (*Chaetomorpha melagonium*) was observed. We recognize that this inventory is incomplete since our sampling was conducted at only one station (Kap Breusing) and one depth (i.e. 20 m).

Species accumulation curves failed to reach their asymptotes for all stations (Figure 4). Initial slope of species accumulation curves showed strong variations among stations but were rather consistent between intra-site replicates. Based on the lowest number of individuals (i.e. 35 in the 5th Basalt Island replicate), estimated species richness in Pass Hytten and Kap Breusing (i.e. range S = 9 – 13 and 12 – 13 for Pass Hytten and Kap Breusing respectively) was lower than in Basalt Island (range S = 19 – 22). Based on the total number of species per replicates, species richness was usually lower in Pass Hytten and Kap Breusing (S = 17 – 31) than Basalt Island (S = 19 – 45), except for one replicate at Kap Breusing (S = 58 for KB 2). A rarefaction curve based on the entire set of fauna samples from the three sampled stations also does not reach reaches its asymptote despite the substantially higher number of individuals (i.e. > 1500).

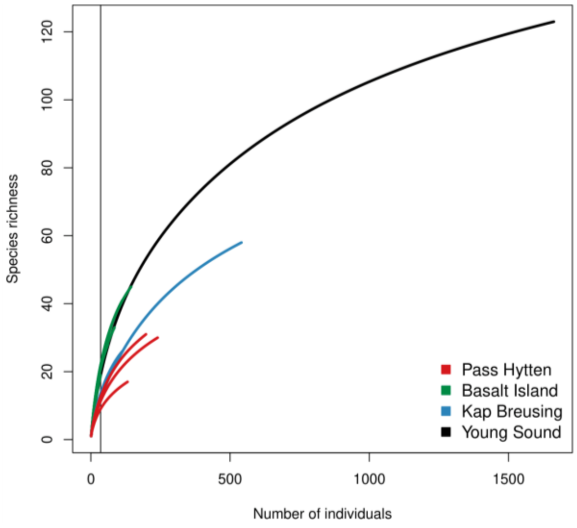

Figure 4: Accumulation curves for each replicate from Pass Hytten, Basalt Island and Kap Breusing stations and the entire Young Sound site (combining 10 replicate samples). Vertical line represents the number of individuals chosen for inter-replicate comparisons.

Results based species rarefaction curves and Chao2 and Jackkniffe1 estimates slightly differ from species accumulation curves (Figure 5). Biodiversity estimators were lowest at Pass Hytten (Chao2 = 60 and Jackknife1 = 62). For Basalt Island and Kap Breusing, biodiversity estimators were rather similar for both Jacknife1 (99 and 90 for Basalt Island and Kap Breusing, respectively) and Chao2 estimates (90 and 96 for Basalt Island and Kap Breusing, respectively). When considering the whole dataset based, Chao2 and Jackknife1 estimates predicted a total species richness of 164 and 169 species, respectively. Overall, it seemed that Kap Breusing harbored a higher number of rare and unique species than the two other stations when considering the slope of the curves for two replicates (see Figure 5)

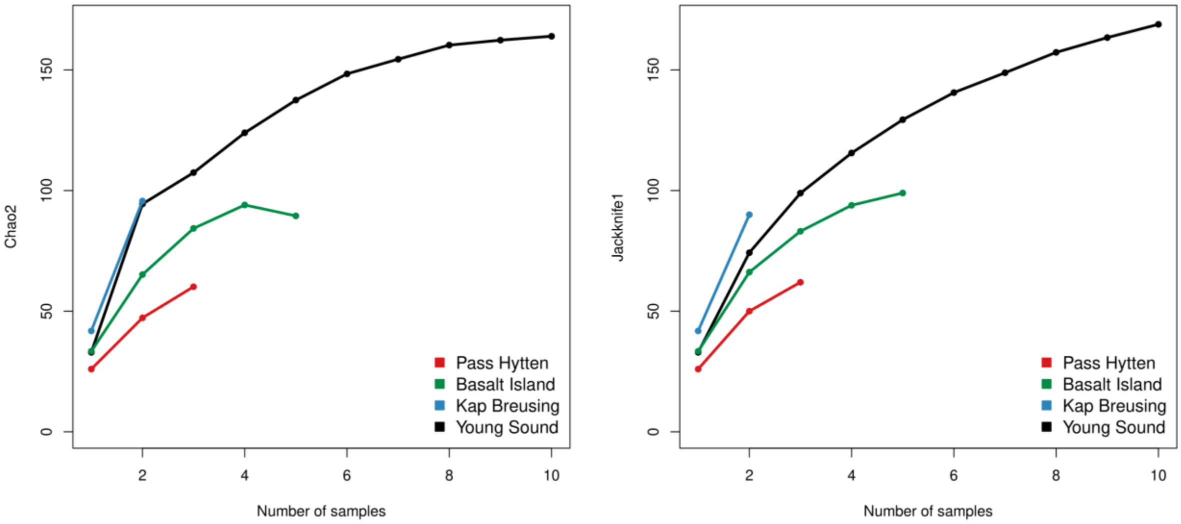

Figure 5: Chao2 (left plot) and Jackknife1 (right plot) accumulation curves calculated for Pass Hytten, Basalt Island, Kap Breusing and the three stations combined. .

Discussion

Spatial variations in species assemblages

The present study complements the seminal work of Sejr et al. (2000) conducted twenty years ago in Young Sound that described space limited gradual changes in species assemblages along a depth gradient (from 20 to 85 m) in the vicinity of Daneborg station (see Figure 1). Our study reveals strong spatial variations among shallow (above 20 m depth) stations distributed along an inner/outer fjord gradient. Therefore, the shallow benthic community of Young Sound appears not to be homogeneous but rather composed of a succession of species assemblages know to respond to environmental gradients between the inner and outer fjord. Such results are in accordance with previous studies conducted in others Arctic fjord investigating spatial gradient in macrofaunal communities (e.g. Gulliksen et al. 1985, Wlodarska-Kowalczuk and Pearson 2004, Sejr et al. 2010).

The community structure in Kap Breusing is dominated by large suspension-feeding bivalves (*Hiatella arctica, Musculus discors* and *Mya truncata*) and motile polychaetes (e.g. *Harmothoe* sp., *Nereimyra aphroditoides* and *Nereis zonata*). This high dominance of suspension feeding bivalves is rather consistent with the common species associations observed on stable sandy seafloors protected from sediment disturbances generated either by freshwater inputs or burrowing species (Włodarska-Kowalczuk 2007). However, the predominance of motile polychaetes reported here is rather in contrast with the observations from other Arctic fjords showing down-fjord increases (i.e. inner-outer fjord) in the proportion of tube-dwelling polychaetes over motile species (e.g. Gulliksen et al. 1985, Renaud et al. 2007b, Włodarska-Kowalczuk et al. 2012). Such a trend in our study may reflect the importance of biological interactions (e.g. ecological facilitation) on the structure of the outer fjord polychaete communities (Kędra et al. 2013). Tremendous abundance of *M. discors* in Kap Breusing probably exert a strong control on the specific composition of polychaete assemblages by modifying the habitat complexity. *M. discors*’ populations may transform the physical habitat into a nest of byssus threads forming a complex three-dimensional structure which can be then colonized by diverse species (e.g. hydroids, bryozans, bivalves, polychaetes, Merril and Turner 1963, Tandberg et al. 2010). The high abundance and diversity of motile polychaetes in our assemblage probably reflect such structuring effect of *M. discors* on the habitat as several taxa such as Nereididae, Polynoidae or Syllidae are often found in complex three-dimensional habitats (e.g. maerl beds, kelp holdfast, artificial structures…, Grall et al. 2006, Yakovis et al. 2007, Pabis and Sicinski 2010).

In contrast to Kap Breusing, the benthic community structure in Basalt Island is largely dominated by polychaetes and to a lesser extent by mollusk species. These differences in community structure probably reflect the contrasted habitats between these two stations (i.e. rocky wall at Kap Breusing vs bare sediment at Basalt Island). Hard substrates such as in Kap Breusing probably exclude the settlement of endofauna and favor the colonization of epifauna. In contrast, the bare sediment on Basalt Island probably favors the installation of endofauna over epifauna since the latter cannot take shelter in a 3D structure such as the hydrozoans – *M. discors* assemblage. The species distribution in the Basalt Island assemblage within the different phyla (mollusks, polychaetes, echinoderms and crustaceans) is relatively similar to the inventory conducted in Daneborg by Sejr et al. (2000) which suggests that both stations are characterized by similar habitat and species associations.

Tube-dwelling polychaetes (e.g. *Maldane sarsi*, *Owenia borealis*, *Euchone* sp.) and hyperbenthic crustaceans dominate benthic assemblages at Pass Hytten. Surprisingly, several species described in the literature as typical species from either outer or inner fjord assemblages are found together in Pass Hytten. For instance, the sub-surface deposit feeder *Maldane sarsi* is the most dominant polychaete in Pass Hytten although this species is typical of outer fjord assemblages (Gulliksen et al. 1985, Renaud et al. 2007b) and excluded from inner fjord areas (Włodarska-Kowalczuk et al. 2012). By contrast, surface deposit-feeding thyasirids and nuculanids are found in low abundance in Pass Hytten although they usually dominate benthic assemblages in inner fjord areas (Włodarska-Kowalczuk and Pearson 2004). The presence of *Euchone* sp. or *Leitoscoloplos mammosus* polychaetes in Pass Hytten are in line with previous observations conducted in shallow and deep areas exposed to high sedimentation rates (Sejr et al. 2010, Kędra et al. 2013, McGovern et al. 2020). Therefore, the coexistence of several typical species from both outer and inner fjord assemblages in Pass Hytten suggests that this location constitutes a transitional zone between typical outer and inner fjord areas. We hypothesize future sampling upward the fjord may allow to identify new species associations typical of glacial/freshwater input areas.

Diversity of species assemblages

Young Sound benthic biodiversity

The present study provides a complementary census of 124 benthic species, including numerically dominant polychaetes (49 species), crustaceans (34 species) and mollusks (24 species) that complete previous work of Sejr et al. (2000) which listed 100 species. With only 32 common species between both studies, the total number of benthic species found in Young Sound now reaches a total of 192 species. The low number of taxa shared between the two inventories reflects the complementarity of both sampling strategies. The bathymetric sampling conducted by Sejr et al. (2000) targeted species assemblages from increasing depths while our sampling along an inner/outer fjord gradient allowed to identify species assemblages from different shallow habitats (i.e. silt, sand/gravel, rocky wall). Both studies then give a first insight of the variability of benthic assemblages in Young Sound in response to strong environmental gradients, i.e. depth and substrate type.

However, we believe that the low number of common species between the two strategies may also result from the different sampling techniques used between both studies as deep buried species could have been missed or not well collected by the suction dredge. Furthermore, identification biases cannot be excluded as it is possible that the same species might have been described under two different names. As an example, this could be the case of *Scoloplos armiger* (identified solely by Sejr et al. 2000) and *Leitoscolopos mammosus* (identified solely in the present study) which have been reported to be subject to taxonomic confusion (Mackie 1987, Renaud et al. 2007b). Further efforts should thus include harmonization of the two species list with the experts that were involved in the identifications. Finally, it might also be argued that the low number of species shared between our inventory and the Sejr et al. (2000) study could reflect long-term variability in the benthic community structure. However, previous studies conducted in other arctic silled-fjord highlight a high stability in the benthic food web structure over several decades (Renaud et al. 2007b) in contrast with open fjords (Beuchel et al. 2006, Kędra et al. 2010a, Kortsch et al. 2012). Therefore, we assume that the present inventory is temporally comparable with the Sejr et al. (2000) study.

The slope of species accumulation curves suggests that the benthic biodiversity inventory in this fjord is far from being complete as many rare species probably remain to be recorded at each study site. Based on Chao2 and jackknife1 estimates, we predict a maximum species richness at shallow sites to exceed 164-169 species while species richness is very likely much more than 200 species when considering the data of Sejr et al. (2000). Overall we were only able to sample a very limited part of the shallow Young Sound fjord. Studies exploring both shallow and deep depths as well as outer and inner fjord areas usually highlight much higher species diversity than in the present study. For instance, Kędra et al. (2010b) recorded over 300 taxa after an extensive multi-year sampling covering the entire soft-bottom habitats from Hornsund (SW Svalbard, from 30 m to 250 m), and Voronkov et al. (2013) identified 403 benthic taxa in shallow hard-bottom communities from Kongsfjorden (NW Svalbard). Therefore, when comparing our data to these studies, it might be hypothesized that the current Young Sound benthic species inventory is still far from being exhaustive. Further sampling will be needed in Young Sound to complete our knowledge of its benthic habitat types, biodiversity, and their structure, dynamics and functioning. Additional sampling should prioritize the deep silty basins (up to 350 m) as well as the innermost section of the fjord (namely Tyrolerfjord) exposed to strong freshwater and sedimentation inputs, and yet to be explored. According to the literature, these environments should be dominated by opportunistic species (e.g. such as the cirratulid polychaete *Chaetozone* sp.) and mollusks surface-deposit feeder such as small thyasirid and nuculanid bivalves (e.g. Włodarska-Kowalczuk and Pearson 2004, Sejr et al. 2010, Włodarska-Kowalczuk et al. 2012). Forthcoming sampling strategies should include deeper investigations of several substrate type and focus in particular on epifaunal communities colonizing hard bottom substrates (such as in Voronkov et al. 2013). Finally, the utilization of several sampling gears (e.g. dredges, grabs, epibenthic sledges, suction dredges, bottom trawls) would undoubtedly allow to sample a wider number of species that are un-sampled in studies using only one sampling gear (e.g. endofauna is poorly sampled by bottom trawls while hyperbenthos is under-sampled by grabs).

Spatial trends in benthic biodiversity

In agreement with previous studies conducted in other Arctic fjords (e.g. Gulliksen et al. 1985, Schmid and Piepenburg 1993, Sejr et al. 2010), we have emphasized clear biodiversity gradients between inner and outer parts of Young Sound. The mechanisms behind these biodiversity gradients have already been summarized by numerous studies and are mainly related to gradients in environmental conditions (Sejr et al. 2010, Meyer et al. 2015). The environmental filtering associated to the strong sedimentation rates in inner fjord areas generally limit settlement in the habitat to a limited number of species adapted to such harsh conditions (usually mobile and deposit-feeding species, Włodarska-Kowalczuk et al. 2012, McGovern et al. 2020).

In contrast, more stable environmental conditions in the outer fjords usually allow a greater number of species to coexist. Some studies have also shown that bottom water deoxygenation in boreal fjord/enclosed-bays might directly drive the structure of benthic food webs by inducing strong decrease in species abundances and diversity and favoring selection of opportunistic species (Rosenberg et al. 2002, Holte et al. 2005, Griffiths et al. 2017). It has however to be noticed that since bottom waters remain well oxygenated throughout the whole year in Young Sound, even at the deepest depth (Oxygen saturation > 80 % at 350 m, Dmitrenko et al. 2015, Sejr et al. 2016), this process probably does not affect the benthic biodiversity in Young Sound.

In our study, the specific habitat structure in Kap Breusing (i.e. a 3D structure produced by *Musculus discors* and Sertulariidae hydrozoans) might also locally modify the biodiversity spatial gradient previously observed since species assemblages associated to engineer species usually exhibit higher local biodiversity (e.g. Rigolet et al. 2014). This specific habitat may also partly explain the low number of species shared between inner and outer benthic assemblages since species living in the 3D structure are not necessarily adapted to bare ground sediments and vice versa.

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Supplementary material ***to the article:***

Diversity and spatial variability of shallow benthic macrofaunal assemblages in a high-Arctic fjord (Young Sound, North-East Greenland)

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Table S1: Young Sound species list

Table S2: Short (and non-exhaustive) species list of Young Sound (Kap Breusing) macroalgae.

Figure S1: Sediment composition in Pass Hytten (PH 1) and Kap Breusing stations (KB 1, KB 2, KB 3).

Table S1

	Pass Hytten			Basalt Island					Kap Breusing	
	PH1	PH2	PH3	BI1	BI2	BI3	BI4	BI5	KB1	KB2
NEMERTEA										
Cerebratulus sp. Renier, 1804				1	1					
Micrura sp. Ehrenberg, 1828										3
Nemertea				3	5	1		5		2
POLYCHAETA										
Abyssoninoe sp. Orensanz, 1990	1	7	5	1	4	9	7	4		
Ampharete sp. Malmgren, 1866								1		1
Axionice sp. Malmgren, 1866										3
Capitella capitata (Fabricius, 1780)			1		1	2				
Chaetozone sp. 1 Malmgren, 1867				1						1
Chaetozone sp. 2 Malmgren, 1867										1
Chone sp. Krøyer, 1856						1	1	1	1	2
Cirratulus sp. Lamarck, 1818										1
Cirratulidae Ryckholt, 1852							1	1		
Clymenura sp. Verrill, 1900		4		3	9	2	4	1		
Cossura sp. Webster & Benedict, 1887								1		
Dipolydora sp. Verrill, 1881		1							1	
Eteone longa (Fabricius, 1780)	1			1			2			2
Euchone sp. Malmgren, 1866		11	1	2	1					2
Flabelligera affinis M. Sars, 1829						1				1
Gattyana amondseni (Malmgren, 1867)			1	1		2				4
Harmothoe sp. Kinberg, 1856						4			5	29
Laphania boecki Malmgren, 1866				9	9	7	4			2
Leaena ebranchiata (M. Sars, 1865)									2	
Leitoscoloplos mammosus Mackie, 1987	7	3	7	2	3	2	5	1		1
Lysippe labiata Malmgren, 1866		2	10	1			2	1		
Magelona sp. F. Müller, 1858										3
Maldane sarsi Malmgren, 1865	6	11	28							
Mediomastus sp. Hartman, 1944					2					
Nereis zonata Malmgren, 1867					1		1		2	25
Nereimyra aphroditoides (O. Fabricius, 1780)					13	8	3	1		7
Nicolea sp. Malmgren, 1866										2
Ophelina sp. Örsted, 1843	1		1				1			1
Owenia borealis Koh, Bhaud & Jirkov, 2003			31							
Parasabella sp. Bush, 1905										1
Parougia sp. Wolf, 1986				2	2					
Pholoe sp. Johnston, 1839	1	2		1	12	1	3	1		4
Polycirrus medusa Grube, 1850				1		2			5	13
Polycirrus sp. 1 Grube, 1850						1				
Polynoinae sp. 1 Kinberg, 1856					2					
Polynoinae sp. 2 Kinberg, 1856					4	2	4	3		
Polynoinae sp. 3 Kinberg, 1856	1	1	2						1	2
Protodorvillea sp. Pettibone, 1961					3	3				
Sabellidae Latreille, 1825		1								
Samythella sp. Verrill, 1873					1	2				
Scalibregma inflatum Rathke, 1843					2	1				4
Scoletoma sp. Blainville, 1828				1	2					
Sigalionidae sp. 1 Kinberg, 1856					1					
Sphaerodorum sp. Örsted, 1843			1			1				
Syllis sp. Lamarck, 1818										6
Terebellidae H. Adams & A. Adams, 1854			2							
Terebellides sp. Sars, 1835	1				5	2	2	1		6

Table S1, continued

	Pass Hytten			Basalt Island					Kap Breusing	
	PH1	PH2	PH3	BI1	BI2	BI3	BI4	BI5	KB1	KB2
Trichobranchus glacialis Malmgren, 1866				1	4	5	1			
Rhodine sp. Malmgren, 1866				1						
SIPUNCULA										
Golfingiidae sp. 1 Stephen & Edmonds, 1972				1						
Golfingiidae sp. 2 Stephen & Edmonds, 1972										1
Sipuncula		1								
MOLLUSCA										
Alvania scrobiculata (Møller, 1842)									6	6
Astarte moerchi Hopner Petersen, 2001		4	1	4	11	3	2	1		
Bullidae Gray, 1827					1					
Caudofoveata sp. 1										1
Ciliatocardium ciliatum (Fabricius, 1780)		1		3		2	1			
Cylichna sp. Lovén, 1846			1							
Hiatella arctica (Linnaeus, 1767)		3		5	3	3			13	109
Macoma calcarea (Gmelin, 1791)		1		1	1	5				1
Margarites groenlandicus (Gmelin, 1791)					2	1			2	
Margarites helicinus (Phipps, 1774)					3	1			3	
Moelleria costulata (Møller, 1842)					1		2		1	1
Musculus discors (Linnaeus, 1767)	3	1	6			1	5		51	235
Musculus niger (J.E. Gray, 1824)		1	2		2					
Mya truncata Linnaeus, 1758	2	3	1		1	2	1		2	8
Nuculana pernula (O. F. Müller, 1779)			1							
Oenopota sp. Mörch, 1852										1
Opisthobranchia					1		1			
Philinidae Gray, 1850 (1815)										1
Portlandia arctica (Gray, 1824)		1	1							
Similipecten greenlandicus (G. B. Sowerby II, 1842)		2					1			1
Rissoidae Gray, 1847					1					
Thyasira sp. Lamarck, 1818					2	1				2
Trochidae Rafinesque, 1815					3					
Velutina velutina (O. F. Müller, 1776)										1
CRUSTACEA										
Akanthophoreus gracilis (Krøyer, 1842)					1					
Amphipoda sp. 1							1			
Anonyx lilljeborgi Boeck, 1871							1			
Anonyx sp. Krøyer, 1838		1		1		1				
Apherusa sarsi Shoemaker, 1930									3	4
Arrhis sp. Stebbing, 1906		2	1							
Calliopiidae G.O. Sars, 1893							1			
Caridea (mauvais état) Dana, 1852									1	
Cumella (Cumella) carinata (Hansen, 1887)						1	4			
Diastylis scorpioides (Lepechin, 1780)	6	5	6		2					1
Ericthonius rubricornis (Stimpson, 1853)			2							
Haploops sp. Liljeborg, 1856		1								
Ischyrocerus sp. Krøyer, 1838			4							
Ischyroceridae sp. 1 Stebbing, 1899										3
Lebbeus groenlandicus (Fabricius, 1775)									2	2
Lebbeus polaris (Sabine, 1824)									1	
Leucon (Leucon) nasica (Krøyer, 1841)					1					

Table S1, continued

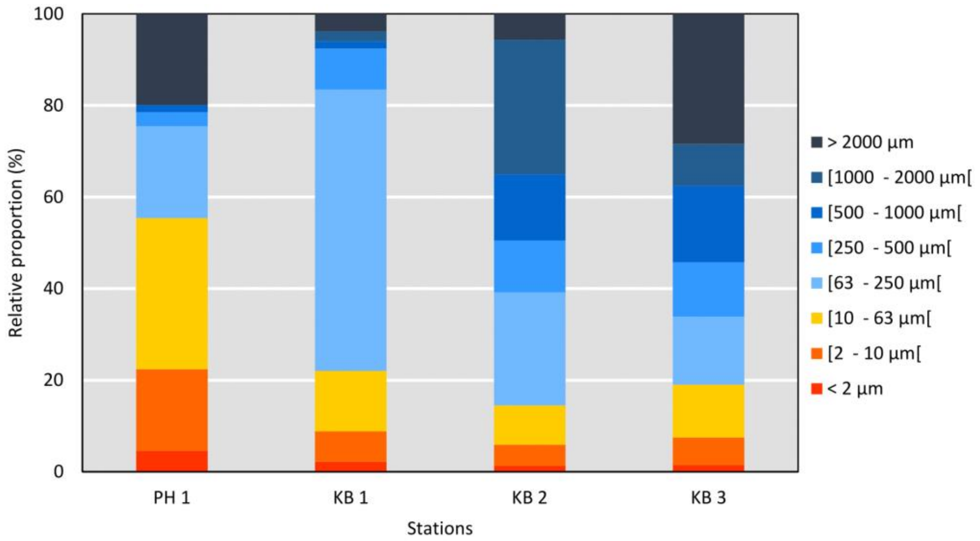
	Pass Hytten			Basalt Island					Kap Breusing	
	PH1	PH2	PH3	BI1	BI2	BI3	BI4	BI5	KB1	KB2
Lysianassa sp. H. Milne Edwards, 1830								1	1	
Melitidae Bousfield, 1973			2							
Metopa glacialis (Krøyer, 1842)	16	34							1	1
Monoculodes borealis Boeck, 1871	2		2	3	2	2		1		
Mysida Boas, 1883		1								
Neopleustes sp. Stebbing, 1906										1
Oedicerotidae Lilljeborg, 1865							1			
Ostracoda Latreille, 1802	78	82	109	3	4	12	3	4		4
Pardalisca cuspidata Krøyer, 1842						1			2	
Phoxocephalidae G.O. Sars, 1891			1							
Pleurogonium spinosissimum (G. O. Sars, 1866)							1			
Pleusymtes sp. J.L. Barnard, 1969										1
Pontoporeia femorata Krøyer, 1842	1	3								
Rachotropis inflata (G.O. Sars, 1883)						1			2	1
Socarnes vahlii (Krøyer, 1838)									1	4
Stenothoidae sp. 1 Boeck, 1871										5
Tryphosella rotundata (Stephensen, 1925)						1				
ECHINODERMATA										
Amphiura sp. Forbes, 1843		1	3							2
Ophiacantha bidentata (Bruzelius, 1805)					1	1				
Ophiocten sericeum (Forbes, 1852)	2	4	4	2	7	5	4	5		
Ophiura robusta (Ayres, 1852)				3	2	4	2	1		1
Stephanasterias albula (Stimpson, 1853)									1	3
PYCNOGONIDA										
Eurycyde hispida (Krøyer, 1844)					1		2			
TUNICATA										
Styelidae Sluiter, 1895									2	1
NEMATODA										
Nematoda	3	3	3	3	5	6	11			5
BRACHIOPODA										
Brachiopoda sp. Duméril, 1805									1	3
PLATYHELMINTHES										
Platyhelminthes Minot, 1876										2
CNIDARIA										
Sertulariidae Lamouroux, 1812									NC*	NC*

*Not Counted

Table S2

Phylum	Species
Ulvophyceae	*Chaetomorpha melagonium* (F. Weber & D. Mohr) Kützing 1845
Florideophyceae	*Coccotylus truncatus* (Pallas) M. J. Wynne & J. N. Heine 1992
Florideophyceae	*Euthora cristata* (C. Agardh) J. Agardh 1847
Florideophyceae	*Phycodrys rubens* (Linnaeus) Batters 1902
Florideophyceae	*Neodilsea integra* (Kjellman) A. D. Zinova 1961
Florideophyceae	*Polysiphonia* sp. 1 Greville, 1823
Florideophyceae	*Polysiphonia* sp. 2 Greville, 1823
Florideophyceae	*Ptilota serrata* Kützing 1847
Florideophyceae	*Scagelothamnion pusillum* (Ruprecht) Athanasiadis 1996
Florideophyceae	*Turnerella pennyi* (Harvey) F. Schmitz 1893
Phaeophyceae	*Chaetopteris plumosa* (Lyngbye) Kützing 1843
Phaeophyceae	*Desmarestia aculeata* (Linnaeus) J. V. Lamouroux 1813
Phaeophyceae	*Desmarestia viridis* (O. F. Müller) J. V. Lamouroux 1813
Phaeophyceae	*Halosiphon tomentosus* (Lyngbye) Jaasund 1957
Phaeophyceae	*Laminaria solidungula* J. Agardh 1868
Phaeophyceae	*Saccorhiza dermatodea* (Bachelot Pylaie) J. Agardh 1868

Figure S1



Conclusion

The main goal of the present work was to describe and compare the functioning of Arctic and sub-Arctic shallow benthic ecosystems from highly stratified coastal systems and to understand how they could evolve under increased stratification due to climate change. The two selected study sites selected were: (1) the archipelago of Saint-Pierre-et-Miquelon, a sub-Arctic area characterized by strong seasonal variations of surface temperatures (0-18°C) contrasting with those annually steady at the bottom (0-2°C at 80 m depth, Lazure et al. 2018, Poitevin et al. 2018) and (2) the Young Sound High-Arctic Fjord which is exposed to strong seasonal freshening of surface waters due to the inputs of turbid and nutrient-depleted freshwaters (Meire et al. 2016, Paulsen et al. 2017). According to climate model projections, both ecosystems are expected to experience one of the largest increases in stratification in the world, mainly caused by a strong increase of surface temperatures in the North-West Atlantic and a major freshening of the seawater surface in High-Arctic seas (Belkin et al. 2009, Capotondi et al. 2012).

Throughout this manuscript, I gather elements to answer the two following questions: what is the impact of increased stratification on the sources and quality of organic matter that fuel primary consumers? and (2) how such potential changes in the trophic environments may impact the structure of shallow benthic food webs?

Impact of stratification on sources, quality and transfers of the organic matter

The results from the first two chapters, although based on two contrasted sites, showed similar impacts of stratification on the trophic environment as evidenced by the substantial decrease of POM quality (Chapter I & II) and decline of POM quantity (Chapter II). Periods and/or stations related to higher stratification were usually characterized by lower relative contributions of microalgal (e.g. 16:1ω7, 16:4ω1, 18:4ω3) and essential fatty acids (20:5ω3, 22:6ω3) to the POM pool. Such results should reflect the control of stratification on vertical nutrient exchanges between surface/subsurface waters, which in turn limits nutrient availability in surface waters and primary production (Tremblay and Gagnon 2009, Randelhoff et al. 2020). For example, Mayzaud et al. (2013) showed that decreasing nutrient availability and primary production during periods of high stratification increase the fraction of detrital material (e.g. senescent detrital particles, richer in SFAs) relative to living cells in the water column (richer in PUFAs). Moreover, nutrient limitations in surface waters can induce a shift in phytoplankton cell metabolism towards less growth (and hence less production of polar lipids rich in PUFAs) and more reserve (and hence more production of neutral lipids, rich in SFAs and MUFAs), resulting in a global decrease in the quality of the particulate organic matter (Parrish et al. 2005, Leu et al. 2006). Such outcomes (i.e. decrease of primary production and phytoplankton physiological states) may thus explain the decrease of the organic matter quality under condition of elevated stratification.

Contrary to the pelagic compartment, the composition and quality of SOM from both Saint-Pierre-et-Miquelon and Young Sound did not vary along spatial gradients of stratification. Such decoupling between pelagic and benthic compartment is surprising since the upper sediment surface (i.e. the first 0-3 mm) of shallow coastal habitats is usually highly responsive to the spatiotemporal variations in pelagic primary production (e.g. Vizzini and Mazzola 2006). We hypothesized that spatially homogenous SOM profiles in our studies might thus reflect a strong and homogeneous production of benthic microalgae. Such hypothesis is in accordance with the dominance of several diatom fatty acid markers (16:1ω7, 16:4ω1, 20:5ω3) found in all SOM lipid profiles from Young Sound. Although SOM was not sampled at all stations from Saint-Pierre-et-Miquelon, the high dominance of diatom makers observed in all lipid profiles of *Echinarachnius parma* also suggest a spatially stable production of benthic microalgae along the bathymetric gradient. These observations suggest that microphytobenthos is fairly independent from nutrient depletion processes that may occur within the water column. Such hypothesis would be in line with what we know about the ecological characteristics of microphytobenthos, that has a preferential access to the nutrients released from the sediment surface (MacIntyre et al. 1996).

As for benthic microalgae, macroalgae are probably less sensitive to pelagic nutrient depletion than phytoplankton because of their lower nutrient requirements (Pedersen and Borum 1996). The high relative contribution of macroalgae fatty acids markers (e.g. 18:2ω6, 18:3ω3) in POM samples from Saint-Pierre-et-Miquelon during the high stratification period suggests that macroalgae can provide high quality detritus to the pelagic compartment which may offset the negative impact of enhanced stratification on POM quality. However, according to several studies, pulses of macroalgae detritus usually relate on numerous environmental factors such as seawater temperatures (Simonson et al. 2015), grazing (Krumhansl and Scheibling 2011, Wernberg and Filbee-Dexter 2018), hydrodynamics (Krumhansl and Scheibling 2011) or kelp reproduction (de Bettignies et al. 2013). This alternative contribution of macroalgae to decreases in POM quality/quantity under conditions of enhanced stratification may thus largely depend on local environmental conditions and may potentially be highly variable among systems. Future studies should therefore aim at better understanding how kelp erosion processes may vary depending on local environmental conditions in order to further assess the macroalgal contribution to the POM.

Impact of stratification on the structure of benthic food webs

Despite the large spatial variations observed in the trophic environment (see Chapter I), the Young Sound benthic food web exhibit low spatial variations between its inner and outer sections that can be explained by several factors. First, to overcome low food availability conditions, many benthic consumers feed on several basal food sources (diet extended horizontally) or on several trophic levels (diet extended vertically) depending on the availability of primary/secondary producers in the ecosystem (Norkko et al. 2007, Mincks et al. 2008, McMeans et al. 2015). Through such trophic adjustments, benthic consumers may adapt to the influence of stratification on the pelagic primary production by broadening their foraging base according to the food sources available in the ecosystem, thus optimizing energy flows in the food web. Secondly, several benthic consumers with high trophic plasticity may be able to redirect their diet toward multiple alternative sources potentially less impacted by stratification than phytoplankton. We hypothesized in Chapters II & III that benthic primary producers may be significantly less impacted by stratification (and by the associated nutrient depletions) than the pelagic compartment because of their ability to cope with nutrient depletions (MacIntyre et al. 1996, Pedersen and Borum 1996, Glud et al. 2009). Therefore, a substantial contribution of such food sources in the benthic food web should increase the resilience of benthic invertebrates that are submitted to a decrease of primary production under increased stratification conditions. Data from stable isotope mixing models reveal that carbon requirements for several mollusk species can be fulfilled by high contribution of benthic primary producers, up to 50% by microphytobenthos for *Astarte moerchi*, *Hiatella arctica* and *Margarites costalis,* confirming what was already observed in shallow coastal food webs from Chukchi and Beaufort Seas (McTigue and Dunton 2017, Harris et al. 2018). Although we were not able to clearly discriminate the isotope signatures of macroalgae from pools of POM and SOM, Dunton and Schell (1987), Fredriksen (2003) and Renaud et al. (2015) previously highlighted the crucial role of this carbon source for Arctic/sub-Arctic benthic food webs, and such results suggest that macroalgae probably are also major food sources for several primary consumers in Young Sound.

In order to better assess the export of macroalgae to deeper habitats and to determine their role in food web stability, we compared in Chapter IV the benthic food web structure of Saint-Pierre-et-Miquelon along a small bathymetric gradient (10 km long, depth from 10 to 80 m). This cross-shore transect included contrasting kelp coverage level (high above 30 m and low below) as well as contrasted stratification conditions with shallow (i.e. > 30 m) or deeper stations (i.e. 30 – 80 m) either unstratified throughout the year or stratified during summer respectively (Craig and Colbourne 2002, Harrison et al. 2013, Cyr et al. 2020). Despite spatial differences in habitats and environmental conditions, no variations were observed in the benthic food web structure along the transect. Because of similar isotopic signatures, we were not able to distinguish the contribution of *Agarum clathratum* from that of POM and SOM pools. However, we have shown that *A. clathratum* can punctually contribute to POM pool through pulses of detritus (see Chapter II). Consequently, we cannot exclude along the whole bathymetric gradient that macroalgae potentially contribute to benthic food web and could explain its spatial stability despite the strong variations of environmental conditions. Such absence of spatial variability may also signify that the stratification has no impact on the benthic food web structure of Saint-Pierre and Miquelon. The decoupling between spring bloom and stratification seasonal increase resulting from sea surface warming, could be one other possible explanation of this food web spatial steadiness. According to AquaModis data (Chapter II, Supplementary material), most of the annual primary production in Saint-Pierre-et-Miquelon is due to a spring (April) phytoplankton bloom (Chapter II) that is not synchronized to the dynamics of thermal stratification. In the Newfoundland region, stratification starts around the end of May and reach it maximum in late-August/early-September (Harrison et al. 2013, Pepin et al. 2017). It is therefore possible that qualitative changes in the trophic environment during periods of high stratification have only a limited impact on food web structure as benthic consumers potentially assimilate most of the food for their energy requirements during the spring bloom. However, this decoupling does not constitute an alternative hypothesis to the absence of spatial variation in Young Sound because primary production starts almost simultaneously with the seasonal increase of haline stratification (Rysgaard et al. 1999, Holding et al. 2019).

Impacts of enhanced stratification on sub-Arctic/Arctic coastal ecosystems: Role of specific environmental features

Through the description of the functioning of two contrasting sub-Arctic/Arctic coastal ecosystems, the present work identifies several key environmental features that are likely to affect their sensitivity to forthcoming increases in stratification. Such features imply that coastal and offshore ecosystems would not necessarily undergo the same evolution under increasing stratification. Some of the main environmental features deserving further investigations as (1) the role of alternative food sources and (2) the importance of Subsurface Chlorophyll Maximum at shallow depths. In addition, specific local factors might affect at a local scale (10s of km) the response of costal benthic food webs to increased stratification.

The role of alternative food sources

Throughout this manuscript, our research highlights that shallow subtidal Arctic and sub-Arctic ecosystems usually relate on more diverse sources of organic matter than deeper ones. In such coastal ecosystems, light availability at the seabed stimulates high benthic primary production (i.e microphytobenthos and macroalgae) which generally far exceed the pelagic primary production (i.e. < 40 m, Glud et al. 2002, Krause-Jensen et al. 2007, Attard et al. 2016). In Chapter II we hypothesized that seasonal macroalgae pulses can even buffer the effect of stratification on the quality of the pelagic trophic environment by providing an additional source of high organic matter quality to the pool of POM. Furthermore, these alternative organic matter sources can substantially fuel shallow coastal benthic food webs while local phytoplankton production provides sometimes only a minor part of the community carbon requirement (Rysgaard and Nielsen 2006, Glud and Rysgaard 2007, Chapter III & IV). Under a scenario of increased stratification, surface coastal waters could experience significant nutrient depletion if the decrease in vertical nutrient fluxes is not compensated by additional horizontal inputs. According to the paradigms developed in eutrophication studies, perennial macroalgae (e.g. kelp), usually adapted to low nutrient availability (Pedersen and Borum 1996), often dominate the primary production in oligotrophic systems. By contrast, increases in nutrient levels lead to a dominance of fast-growing macroalgae and ultimately phytoplankton (Duarte et al. 1995, Grall and Chauvaud 2002, Krause-Jensen et al. 2012, Riemann et al. 2016). Although microphytobenthos is rather independent of nutrient concentrations in the water column (using those released from sediments, e.g. MacIntyre et al. 1996), benthic microalgae are usually also favored in oligotrophic systems due to the higher light availability on the seabed related to lower phytoplankton biomass in the water column (Glud et al. 2009). Considering these characteristics of benthic micro- and macroalgae, further nutrient depletion in surface coastal water under conditions of enhanced stratification might not necessarily impact the benthic primary production at the same level as it would impact phytoplankton production. Therefore, the contribution of microphytobenthos and macroalgae derived carbon to coastal food webs appears to be potentially a significant resilience factor for benthic communities that would have to face increased stratification.

In addition, coastal shallow food webs may locally benefit from inputs of terrestrial organic matter supplied by rivers and soil erosion. Although such contributions were not observed in Young Sound (nor in Saint-Pierre and Miquelon as this site is not exposed to river inputs), several studies highlighted a major contribution of terrestrial organic matter in shallow benthic food webs exposed to strong river flows (Dunton et al. 2012, Bell et al. 2016, Harris et al. 2018). These contrasted contributions of terrestrial organic matter across Arctic locations probably reflect the importance of organic matter bioavailability for the assimilation of terrestrial materials by the benthic food webs. For example, rivers flowing through vegetated catchment such as in northern Alaska (e.g. Harris et al. 2018) or northern Norway (e.g. McGovern et al. 2020) can probably provide a significant amount of terrestrial organic matter that is relatively bioavailable. However, this is probably not the case for rivers in High-Arctic fjords such as in Young Sound, where the limited catchment vegetation and the predominance of glacial meltwater (Paulsen et al. 2017) provide probably a poorly bioavailable organic matter.

Subsurface Chlorophyll Maximum

Subsurface/deep chlorophyll maxima (SCM [or DCM]) constitute a dominant feature of sub-Arctic/Arctic oligotrophic and highly-stratified waters (Martin et al. 2010, Tremblay et al. 2015). Results from Chapter II and Holding et al. (2019) confirm this common feature of sub-Arctic/Arctic oligotrophic waters since both Young Sound and Saint-Pierre-et-Miquelon exhibit SCM at 25 m in late summer (August/September). Such subsurface accumulation of phytoplankton reflects a compromise between low nutrient concentration at the surface and low luminosity at depth, favoring the growth of shade-adapted phytoplankton species at intermediate depth (mean depth = 45 m – range = 12–75 m, Martin et al. 2010, 2012, Tremblay et al. 2015). These species also usually host high quantities of photosynthetic pigment, including chlorophyll-a, in order to maximize the light harvesting at subsurface depth (Fennel and Boss 2003, Tremblay et al. 2015).

Under a scenario of increased stratification and surface-water nutrient depletion, the relative importance of SCM to the overall pelagic primary production would likely increase (Martin et al. 2010). While deep benthic community may suffer from lower carbon export in condition of enhanced stratification (Bopp et al. 2005, Turner et al. 2015), coastal communities that have access to the subsurface phytoplankton production are likely to be less impacted. However, the usually limited thickness of SCM (e.g. median thickness = 18 m in the Canadian Arctic, Martin et al. 2010) may imply that only a restricted portion of the seabed may directly access to this subsurface production. Some studies showed that internal waves can move the pycnocline vertically and thus transport the associated phytoplankton production upward/downward relative to the mean SCM depth (Woodson 2018). Under these high-frequency vertical oscillations, benthic communities located above or below the SCM depth may punctually benefit of the subsurface phytoplankton production (Woodson 2018) and would therefore be potentially less sensitive to increased stratification than localities without such physical features.

Small-scale variability

In addition to general features of coastal ecosystems (i.e. higher access to alternative organic matter sources and subsurface primary production), specific local factors also affect the response of benthic food web to increased stratification as benthic coastal ecosystems show substantial variations in abiotic conditions at small-spatial scale (i.e. 10s of km). Coastal ecosystems can be sometimes exposed locally to strong seawater turbidity, amplifying the impacts of freshwater inputs on primary production (e.g. Murray et al. 2015, Holding et al. 2019), while others shallow sites can be prevented or only moderately exposed to these freshwater turbid flows. Moreover, benthic food webs can be differently impacted by enhanced stratification/freshwater inputs, depending on nutrient concentrations in freshwater flows: while depleted-nutrient rivers might dilute surface waters and thus amplify the consequences of stratification on primary production (e.g. Holding et al. 2019), nutrient-rich rivers may induce an opposite effect by compensating the lower vertical nutrient fluxes with higher horizontal nutrient inputs. Such importance of additional nutrient inputs can be illustrated by the example of land- and marine-terminating glaciers. Ice-melt from land-terminating glaciers usually induce nutrient-depleted and turbid freshwater plumes in coastal ecosystems which reduces the primary production whereas subsurface melt from marine-terminating glaciers generally generates nutrient-rich freshwater plumes (upwelled from deep waters at glacier fronts) which stimulate primary productivity (Meire et al. 2017). Finally, the absence or presence of a sill is also likely to influence the sensitivity of coastal benthic food web to increased stratification through the renewal of fjord’s bottom waters and/or estuarine exchanges (Bendtsen et al. 2007, Cottier et al. 2010, Boone et al. 2018).

Rivers inputs may also have contrasted influences on coastal ecosystems at a small-spatial scale depending on local trade-off between the reduction of vertical nutrient inputs (controlled by stratification and thus river inputs) and potential local increases in horizontal nutrient supplies (potentially increasing with river flows). Results from Young Sound illustrate such a trade-off as the fjord gradient in POM quality do not exactly follow the stratification/freshwater input gradient (i.e. the middle station, Basalt Island, displayed the lowest organic matter quality). Lower organic matter quality in the inner and middle stations (Pass Hytten and Basalt Island) most likely reflect the impact of freshwater inputs on water column stratification and turbidity (Figure 1). In contrast, higher organic matter quality in the outer station (Kap Breusing) probably result from a lower exposition to freshwater inputs implying higher light and greater vertical mixing. However, while both inner and middle stations are submitted to high stratification and low vertical nutrient fluxes, the impact in the inner station might be partly dampened by the moderate nutrient inputs from the Zackenberg river (Figure 1). Therefore, although the middle station is more distant from the Zackenberg river than the inner station, the combined effects of high stratification/turbidity and no additional nutrient inputs may result in worst trophic conditions in the middle station.

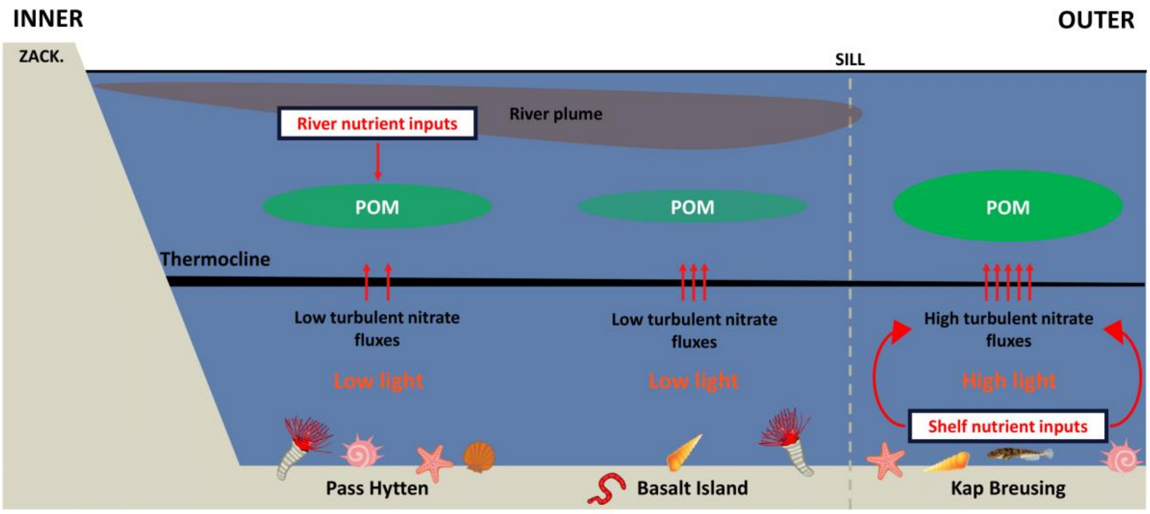


Figure 1: Conceptual model representing the combined effect of stratification as well as river and shelf inputs on primary production in Young Sound. Brightness and areas of POM ellipses are proportional to the POM production and quality. Intensity of vertical nutrient fluxes are represented by red vertical arrows. POM: Particulate Organic Matter, ZACK.: Zackenberg river.

This example underlines the need to consider the local variability of environmental conditions in coastal ecosystems to better understand and assess the effects of increased stratification on their functioning. While consequences of enhanced stratification on the functioning of offshore marine ecosystems can be applied at the regional scale (e.g. inflow/outflow shelves, American/Eurasian basin, Brown et al. 2020), such approach is much more complex in coastal areas because of the wide variety of factors acting at small-spatial scale. Therefore, additional studies are required in order to propose realistic evolution scenarios relative to several fjord types (land-/marine-terminating glaciers, with/without sills, fjord/lagoons/open sea).

Functioning of sub-Arctic and Arctic benthic food webs under enhanced stratification: conceptual models

Basic conceptual model

We propose here a conceptual model synthetizing the main achievements regarding the potential evolution of shallow and deeper benthic ecosystems (i.e. in the euphotic zone/above the thermocline *vs* below the euphotic zone/thermocline respectively) under increased stratification. Note that this model only considers general features of coastal ecosystems (i.e.

access to alternatives organic matter sources and subsurface primary production) and does not take into account their potential small-scale variability (e.g. vertical/horizontal nutrient supplies, low/high sea water turbidity…). The POM compartment includes here various suspended material, including phytoplankton, macroalgae detritus and terrestrial organic matter, while the SOM includes various settled materials, including phytoplankton/macroalgae detritus and microphytobenthos.

In Figure 2 we show that shallow benthic food webs presently benefit from both fresh POM and benthic primary production in the form of microphytobenthos and macroalgae (A). Future increase in stratification associated to a decrease in vertical nutrient fluxes lead to POM diminishing in both quality and quantity. In parallel, the relative production of benthic micro- and macroalgae to the overall primary production would be expected to increase because of their lower sensitivity to nutrient depletion (Chapter I & II). Consequently, benthic food webs in coastal areas may partly dampen the decrease in pelagic POM quality/quantity by increasing their reliance on alternative organic matter sources (Chapter III & IV, B). In contrast, deeper benthic food webs currently rely only on lower-quality settled POM (which undergo some degradation during the sedimentation, e.g. Budge and Parrish 1998, Parrish et al. 2005) and resuspended SOM (C). Decrease in POM production and quality as well as weakened pelagic-benthic coupling under increased stratification conditions should therefore reduce the quality and quantity of organic materials reaching the seabed (Chapter II). Contrary to coastal ecosystems, deep benthic food webs would not compensate these reductions of carbon fluxes by feeding on alternative organic matter sources. Such outcome may ultimately conduct to a decrease in benthic biomass in these deeper ecosystems (D).

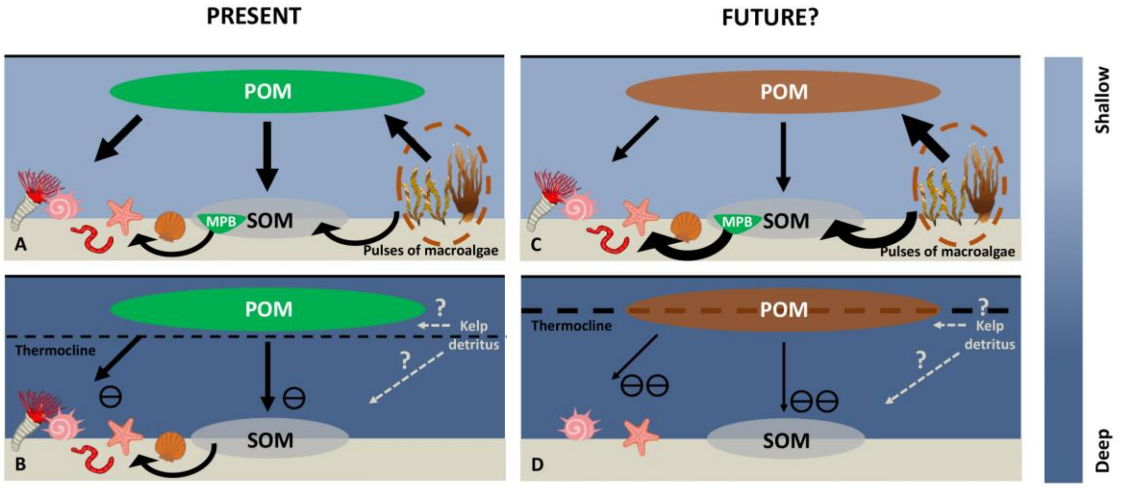


Figure 2: Conceptual model showing the present functioning of shallow (A) and deep (B) benthic communities as well as their potential future functioning under a scenario of increased stratification (C & D, for shallow and deep habitats, respectively). Direction of organic matter fluxes are indicated by black arrows and their intensity is proportional to arrow widths. The negative impact of stratification and sedimentation on POM quality are represented by brown color and ⊖ symbols. POM: Particulate Organic Matter, SOM: Sedimentary Organic Matter, MPB: microphytobenthos.

Consequently, the deepening and northern expansion of kelp forest with reduced sea-ice cover (e.g. Krausen-Jensen et al. 2012) may constitute an unexpected source of resilience for coastal benthic food-webs that might face weak pelagic-benthic coupling in the future. In addition, export of kelp detritus from the euphotic zone toward deeper habitats (Sokołowski et al. 2014, Renaud et al. 2015, Cari et al. 2020) might also increase the stability of deeper benthic food web. Such export was not quantified in our study but should deserve further investigations. However, such points must be dampened because kelp production is controlled in part by light availability which is likely to decrease in case of higher turbidity due to higher freshwater inputs and permafrost erosion (Filbee-Dexter et al. 2019).

Advanced conceptual model

Our conceptual model is somehow incomplete as sub-Arctic/Arctic marine ecosystems can be highly variable at both regional and local scales. For instance, impacts of enhanced stratification vary considerably in offshore areas depending on regional trophic status (oligotrophic vs eutrophic) and on exposure to nutrient inputs (vertical vs horizontal) (Ardyna et al. 2011, Brown et al. 2020). Moreover, consequences of increased stratification in coastal areas may also substantially differ according to local environmental conditions such as exposure to freshwater inputs and by cascade to changes in water turbidity and nutrient inputs to surficial waters (Murray et al. 2015, Paulsen et al. 2017). In that context, we must be prudent and not generalize the results of this study in both Young Sound and Saint-Pierre-et-Miquelon to a pan-Arctic scale. We below detail an advanced conceptual model to better describe the combined effects of local factors and stratification on primary production and specify various types of ecosystems concerned for each scenario (Figure 3).

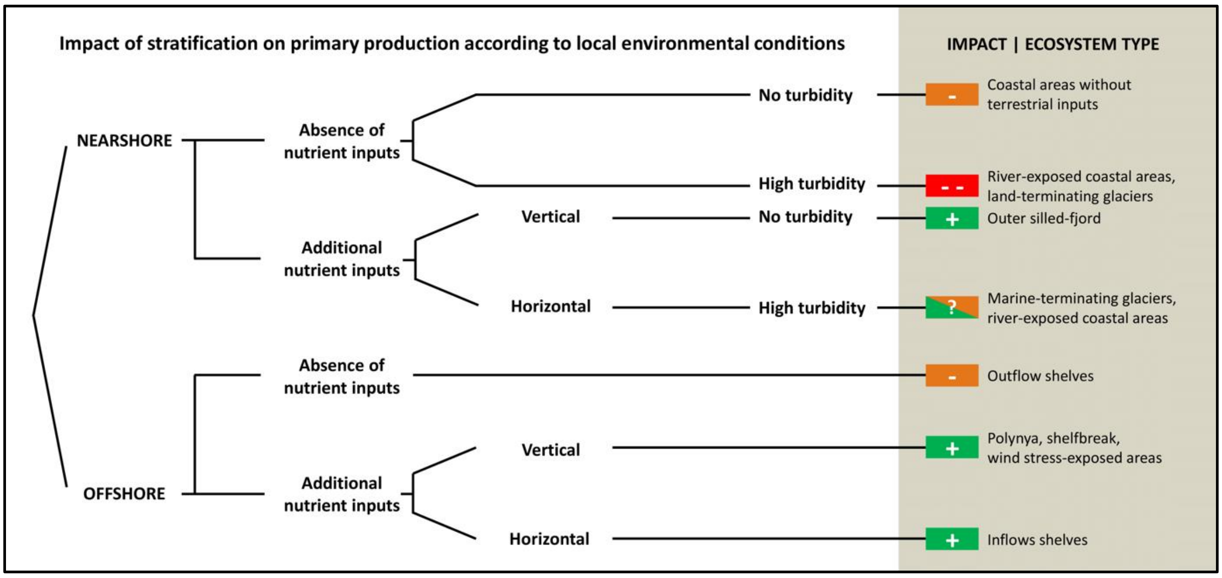


Figure 3: Conceptual model representing the potential contrasted effects of stratification on primary production according to local environmental conditions. Positive, negative and highly negative effects are depicted by green (+), orange (-) and red (- -) colors (symbols), respectively. The beige box on the right specify the types of ecosystems potentially concerned for each scenario. Question mark represents uncertain evolutions in primary production.

While offshore highly-stratified systems without additional nutrient inputs (e.g. outflow shelves) are likely to experience a decrease in primary production, this would probably not be the case within offshore areas receiving large additional nutrient inputs from subarctic seas (e.g. inflow shelves, Hunt et al. 2016, Lewis et al. 2020) or from vertical inputs (upwelling at the shelf break, wind-driven vertical mixing; Ardyna et al. 2014, Williams and Carmack 2015). When considering coastal ecosystems, areas deprived from additional nutrient inputs are likely to experience a decrease in primary production, even amplified by turbidity increase in river-exposed areas (e.g. fjord with land-terminating glaciers, Chapter I, Holding et al. 2019). In contrast, coastal localities away from high turbidity zones may experience higher primary production (e.g. outer silled-fjord with low turbidity, Meire et al. 2016) due to vertical nutrient fluxes. Finally, the evolution of primary production in coastal areas receiving large horizontal nutrient inputs from rivers and/or marine terminating glaciers is much more difficult to predict as positive influence of nutrient supply is counterbalanced by higher seawater turbidity.

Perspectives

This work reveals that increases in stratification with ongoing warming and freshening of sub-Arctic and Arctic surface waters may impact quality of the trophic environment in coastal marine systems. However, such changes could not necessarily impact the structure of benthic food webs because of various trophic adaptations (e.g. trophic plasticity, omnivory) of benthic species to overcome the changing local trophic conditions. Moreover, the benthic primary production in shallow coastal habitats might also provide alternative food sources to stratification-impacted pelagic organic matter for primary consumers.

In the present work, we were not able to clearly assess the relative contributions of benthic primary producers to shallow benthic food webs because of the overlap of stable isotopic signatures in pelagic and benthic sources. Moreover, the seasonality of benthic food webs was difficult to assess, limiting thus our ability to detect the sensitivity of benthic consumers to changes in the trophic environment. Finally, because local specificities may strongly influence the sensitivity of benthic food webs to increased stratification, it is also questionable in which extent our results from two shallow coastal ecosystems may be generalizable to arctic systems in general. Below are detailed several points that we believe should deserve further research when trying to understand the impact of increased stratification on the functioning of sub-Arctic and Arctic marine ecosystems.

Better assessment of benthic primary producers contribution to shallow benthic food webs

Throughout the different chapters of this manuscript, we observed that stable isotopes fail to clearly discriminate different food sources, as attested by similar stable isotope signatures between POM, SOM and macroalgae (*Laminaria* sp. and *Agarum clathratum*, in Chapter III & IV, respectively). For these reasons, we were not able to quantify separately the relative contribution of macroalgae, POM and SOM in the benthic food webs and thus to assess accurately the role of the different benthic primary producers. Such limitations of stable isotopes to discriminate benthic food web' transfers of organic matter sources have already been underlined by several authors (e.g. Richoux and Froneman 2007, Jaschinski et al. 2011, Gaillard et al. 2017, Silberberger et al. 2018).

One main improvement to solve this challenge would to stimulate research coupling the use of tools of trophic ecology with those of other disciplines as biogeochemistry. For example, oxygen microsensors (Glud et al. 2002, Krause-Jensen et al. 2007) or aquatic eddy covariance (Attard et al. 2014, 2016) methods are efficient to assess the relative contributions of benthic vs pelagic primary production in coastal food webs. The integration of such data into ecosystem-scale carbon budgets (e.g. Rysgaard and Nielsen 2006, Glud and Rysgaard 2007) appears as a promising tool helping to quantify the potential weights of such sources for the ecosystem carbon balance. Although these approaches do not directly demonstrate the assimilation of organic matter of benthic origin by consumers (contrary to stable isotopes), they provide conceptual evidences that these organic matter sources may be essential to meet the carbon requirements of the benthic food webs.

Because of the limited number of studies conducted in shallow environments, the contribution of microphytobenthos in Arctic and sub-Arctic food webs has been rarely considered (but see McTigue and Dunton 2017, Harris et al. 2018). Studies conducted in shallow habitats often consider the potential contribution of this source in food webs (e.g. Kędra et al. 2012, Renaud et al. 2015, Stasko et al. 2018), but they do not quantify it because a paucity of credible isotopic values for this food source at high latitudes. Although mixing models, used in McTigue and Dunton (2017), Harris et al. (2018) and Chapters III & IV have partially estimated the contribution of microphytobenthos, the use of a globally averaged isotope value makes these estimates inaccurate. Indeed, Oxtoby et al. (2016) suggested that such averaged values may be too enriched relative to the true values for microphytobenthos at high latitudes, leading to a potential underestimate of the contribution of this source in above studies. Considering the high productivity of microphytobenthos at high latitudes (e.g. Glud et al. 2009, Attard et al. 2016), it seems crucial that future research attempts to acquire the accurate stable isotope signature of this source, if possible in several Arctic localities, in order to better assess the role of microphytobenthos in High Arctic food webs.

Novel methods developed in trophic ecology might also help to better discriminate the contribution of micro- and macroalgae within benthic food webs. For example, Oakes et al. (2010, 2016) and Legrand et al. (2018) revealed the great potential of δ^{13}C labelling to trace transfers of microphytobenthos and macroalgae into benthic food webs. Isotopic δ^{13}C labelling should thus be of great interest when the natural stable isotope signature of benthic (i.e. microphytobenthos and/or macroalgae) overlap with the signature of pelagic primary producers. Compound-Specific Stable Isotopes (CSIA) also allow better discrimination between benthic and pelagic-settled diatoms on the seabed by comparing $\delta^{13}C$ signatures of diatom marker fatty acids (e.g. 16:1ω7, 20:5ω3) of POM and SOM (e.g. De Cesare et al. 2017). Finally, multi-marker approaches (e.g. stable isotopes, fatty acids, sterols) are pertinent to assess diets of several primary consumers (as in Chapter I but extended to more species) in order to better identify the organic matter sources entering the food web (Kelly and Scheibling 2012, Gaillard et al. 2017, Mathieu-Resuge et al. 2019).

Detection of seasonal shifts in the functioning of Arctic and sub-Arctic benthic food webs

No seasonal variations were observed in the structure of benthic food webs from Saint-Pierre-et-Miquelon and Young Sound. However, considering the strong seasonality of these study sites, it seems unlikely that both food webs function similarly during winter and summer. We hypothesize that such weak temporal variability rather reflects low tissue turnover rates of Arctic benthic invertebrates that are generally characterized by slow growth and long lifespans (Wing et al. 2012, McMeans et al. 2015). Although many authors focused on intermediate turnover rates tissues (adductor muscle, foot, siphon) and did not detect any temporal variability in benthic food webs (e.g. Renaud et al. 2011, Kędra et al. 2012), few have focused on faster turnover rates tissues (organs, hemolymph, McMeans et al. 2015). Moreover, we do not know the trophic activities of benthic invertebrates during wintertime and that restrict a lot our understanding of sensibility of benthic invertebrates under climate change inducing intensification of stratification and modifications of the pelagic-benthic coupling.

Chapter I showed that the digestive gland constitute a good tissue candidate for tracking seasonal variations in species' diet. Indeed, digestive gland fatty acid profiles and stable isotope signatures of the bivalves *Astarte moerchi* and *Mya truncata* revealed that these species were able to switch from a diatom-based diet in summer to a pause in the feeding activities during winter. Such "dormancy" suggests that filter-feeding bivalves may be sensitive to future alterations in organic matter quality as they relate exclusively of the summer primary production. Analyses of bivalves' lipid reserves partly confirm this hypothesis: while *Astarte moerchi* was able to maintain a high level of lipid reserves during winter, this was not the case for *Mya truncata* which exhibited low levels of saturated and monounsaturated fatty acids in its digestive glands (generally related to lipid reserves). We hypothesize that these intra-taxa differences reflect contrasted abilities to reduce bivalves' metabolism during winter: *A. moerchi* would be able to preserve its lipid reserves by reducing its metabolism during winter while *M. truncata* would not. Unfortunately, because neutral and polar lipid fractions were not separated in the present study, we were unable to test this hypothesis.

However, such seasonal switch in feeding activities may not concern all benthic species. It would be thus interesting to analyze the composition of high turnover rate tissues from other species to investigate which species maintain their feeding activities during winter, by consuming for instance various detritus (McMeans et al. 2015). In addition, the ability of certain species to reduce their metabolism rate during winter should also deserve further interest as it may affect the ability of benthic invertebrates to maintain a high level of lipid reserves throughout the winter season. Based on these objectives, we chose during this PhD to investigate the feeding activities as well as physiological status and metabolisms of several biomass-dominant species from the Young Sound fjord. Four bivalve species were selected for that (i.e. *A. moerchi*, *M. truncata*, *Hiatella arctica* and *Musculus discors*) and sampled in both May and August 2018. We focused the analyses on the fatty acid composition of polar lipids from the gills and neutral lipids from the digestive glands, which were found to be suitable indicators of bivalves' metabolism and lipid reserve, respectively (e.g. Pernet et al. 2007). In addition, we measured the total lipid, protein and carbohydrate contents in the whole body in order to estimates the overall energy content of each bivalve species (see Clements et al. 2018). These analyses realized on 80 specimens (5 analyses per species, i.e. a total of 400 analyses) were carried out under the supervision of Dr. Réjean Tremblay, during 3 months stay (January – March 2020) at the "Université du Québec à Rimouski" (UQAR, Rimouski, Québec/Canada) funded by an "Isblue" mobility PhD grant (2500 euros). Unfortunately, the results of this work are still not available because of the closure of the university's GC-MS analysis platform due to the COVID-19 outbreak. Results should be available and published in 2021.

Studying the functioning of contrasted coastal ecosystems

This PhD thesis was based on the comparison of two specific shallow and highly-stratified coastal systems, the sub-Arctic Archipelago of Saint-Pierre-et-Miquelon and the High-Arctic Young Sound fjord. Although results from these studies allow to better understand the impact of stratification on the functioning of shallow benthic ecosystems, they might be also partly influenced by their environment. The characterization of several contrasted coastal ecosystems would allow better assessment of the way those local characteristics are likely to influence the functioning of these ecosystems. We identified below several habitat features that may influence the sensitivity/resilience of shallow coastal ecosystems and therefore deserves further investigations.

Studying the importance of food source diversity

We previously hypothesized that a high diversity of food sources may be crucial for the stability of benthic food webs in providing alternative sources of organic matter to pelagic primary production for benthic primary consumers under strong environmental variations. This hypothesis deserves further investigations by comparing the functioning of several benthic food webs characterized by different access to benthic primary production. Further studies should also try to understand to what extent the benthic primary production may fuel the benthic food webs below the euphotic zone. In addition, although we did not identify any contribution of terrestrial organic matter in the benthic food webs of Saint-Pierre-et-Miquelon and Young Sound, several studies across the Arctic have shown that this food source may fuel a considerable part of shallow benthic food web (Dunton et al. 2006, Harris et al. 2018, McGovern et al. 2020). These different results probably reflect the contrasted bioavailability of terrestrial organic matter across the Arctic. At the above study sites, it may be interesting to investigate at which extent increased supplies of terrestrial organic matter (which can potentially be assimilated by benthic food webs) could offset the negative impacts of freshwater inputs on pelagic primary production.

Studying the importance of fjord topography

Fjord topography (both above and below the sea-level) may also influence the sensitivity of benthic communities to increased stratification. For instance, inclination of the catchment area (e.g. slight or steep slope) probably alters the speed of river flows which could in turn changes the quantity and size of particles transported toward marine habitats. These modifications may also induce subsequent changes in sedimentation and turbidity gradients along the fjords and thus modify the exposure of benthic communities to high sedimentation and water turbidity. Moreover, fjord bathymetry could control the diversity of organic matter sources available in deep habitat. Steep slopes should allow a more efficient transport of the macroalgae thalli from the euphotic zone to deeper habitats which may then accumulate around particular topography features (deep basin, sill) and locally fuel deep benthic food webs (Krumhansl and Scheibling 2012, Filbee-Dexter et al. 2018).

Studying the importance of freshwater input origin

Next studies should further investigate to what extent the negative impact of stratification and freshwater inputs on POM quality and pelagic-benthic coupling strength may be dampened by local nutrient regimes (i.e. oligotrophic or eutrophic waters). For instance, Meire et al. (2017) evidenced opposite effects of glacier inputs on fjord primary production, depending on whether freshwater was supplied by a land- or marine-terminating glacier (in Young Sound and Godthåbsfjord, respectively). Although both fjords are highly stratified, sub-surface meltwater plumes generated by marine-terminating glaciers induce a considerable vertical mixing of water masses close to the glaciers which bring bottom nutrients toward the surface. These nutrients are then transported toward the fjord mouth and potentially offset or even surpass the nutrient loss generated by stratification. Consequently, contrary to land-terminating glaciers, freshwater inputs from marine-terminating glaciers usually stimulate the pelagic primary production (Meire et al. 2017). However, it may be questioned whether the increased primary production in fjords with marine-terminating glaciers benefit equally to benthic and pelagic food webs since the high stratification could still limit the flow of organic matter to benthic communities (which would then be mainly channeled in pelagic food webs). Therefore, it would be interesting to study the spatial variability of benthic biomass and food web structures in these fjords to see whether organisms are able to benefit from this higher primary production.

Investigate potential multiples effects of increased stratification on benthic ecosystems

The present PhD did not consider two other potential effects of increased stratification on benthic ecosystems that deserve further interest.

Firstly, in addition to stratification intensification due to depth density gradient, climate change likely influences the timing of seasonal increases in sea surface temperature (Burrows et al. 2011). Onset of phytoplankton blooms at northern latitudes (> 40°N) is triggered by the seasonal light increase associated to higher irradiance in spring/summer, lower vertical mixing of phytoplankton cells (above the critical mixing depth) and/or sea-ice retreat (Kahru et al. 2011, Winder and Sommer 2012, Boyce et al. 2017). Although seasonal increases in irradiance do not relate exclusively on vertical increases in stratification, it might be questioned if earlier season increase in seawater stratification may lead to earlier phytoplankton blooms. This potential effect of climate change has been poorly investigated although some authors suggested that such changes may lead to earlier phytoplankton blooms (e.g. Winder and Sommer 2012, Henson et al. 2013, Henson et al. 2018). Changes in phytoplankton phenology with climate change have been particularly well studied in the Arctic. Many studies showed that earlier sea ice retreats correlated with earlier phytoplankton blooms (e.g. Kahru et al. 2011, Ji et al. 2013). Such phenology changes were hypothesized to lead potential mismatch between phytoplankton blooms and reproductive cycle of some key arctic species (e.g. Calanus glacialis, Søreide et al. 2010, Leu et al. 2011). Therefore, future researches should focus on effect of earlier seasonal sea surface warming and potential earlier phytoplankton blooms on the reproductive cycle of zooplankton or benthic species. Such changes in high latitudes would not necessary impact the timing of phytoplankton blooms driven either by sea-ice break up or seasonal increase in light (Kahru et al. 2011). However, we believe that such earlier increase in sea surface temperature in lower latitudes and ice-free areas may impact some marine species which have currently synchronized their reproductive cycle to spring phytoplankton blooms.

Secondly, the present work did not address the effects of stratification on vertical gas fluxes as oxygen exchanges which are reduced. In bottom waters, when oxygen consumption through respiration or chemical processes is not compensated by advection, mixing or diffusion of the oxygen throughout the water column, stratification can lead to hypoxia (Rabalais et al. 2009). This phenomenon is often observed in semi-closed marine basins exposed to both high anthropogenic inputs of organic matter and limited renewal of their bottom waters (e.g. fjords, Baltic sea, e.g. Rosenberg et al. 2002, Holte et al. 2005, Carstensen et al. 2014, Griffiths et al. 2017). Such events can induce high mortalities in benthic communities and potentially result in a seabed totally devoid of macrofauna (so called “dead zones”, Rosenberg et al. 2002, Vaquer-Sunyer and Duarte 2008, Cloern et al. 2016). Although climate change and associated increases in stratification will probably exacerbate hypoxia events in these urbanized coastal areas (e.g. Baltic sea, Norwegian fjords), it might be interesting to also assess the vulnerability of arctic-silled fjord prevented from anthropogenic organic matter inputs. Future increases of freshwater inputs and coastal erosions could potentially induce such similar hypoxia events due to the deposition of high quantity of terrestrial organic matter from melting permafrost catchments (Bianchi et al. 2020). Young Sound might be a good study site candidate for such investigation as this deep fjord has a sill at is entrance (maximum and sill depths = 365 and 45 m, Rysgaard et al. 2003) and is prevented from anthropogenic influence. Boone et al. (2018) already observed that renewal of Young Sound bottom waters was diminishing due to freshening of Greenland coastal waters since 2004-2005 years. Therefore, this high-arctic fjord may deserve further long-term monitoring studies (such as those conducted by the Marine Basis Program) on benthic assemblages to investigate if future increases in terrestrial organic matter inputs may lead to a restructuration of benthic communities living in deep basins without bottom water renewal.

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DOCTORAT / SCIENCES
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UBO
Université de Bretagne Occidentale

Titre : Fonctionnement des écosystèmes benthiques peu profonds Arctiques et sub-Arctiques en système côtier hautement stratifié

Mots clés : Macrofaune benthique • Stratification • Réseaux trophiques • Écosystèmes côtiers peu profonds • Haut-Arctique • Sub-Arctique

Résumé : Face au changement climatique, les systèmes côtiers Arctiques et sub-Arctiques subissent l'une des plus fortes augmentions de stratification à l'échelle de la planète en raison d'un réchauffement et/ou une dessalure des eaux de surface. Cependant les conséquences ultérieures de ces changements environnementaux sur le fonctionnement des écosystèmes benthiques côtiers restent encore peu comprises à ce jour. Cette thèse vise ainsi à mieux comprendre comment les futures augmentations de stratification dans ces écosystèmes pourraient influencer leur fonctionnement en terme de qualité des sources de matière organique, d'intensité du couplage pélagique-benthique ainsi que de structure des réseaux trophiques benthiques. Deux systèmes côtiers subissant de fortes variations saisonnières de température et de salinité des eaux de surface ont été étudiés : un fjord haut-arctique (Young Sound, NE Groenland) caractérisé par une forte stratification haline et un archipel sub-Arctique (Saint-Pierre-et-Miquelon, plateau continental de Terre-Neuve) exposé à une forte stratification thermique. La première partie de la thèse montre qu'une forte stratification réduit la qualité des sources de matière organique pélagique et l'intensité des transferts de matière organique des eaux de surface vers le compartiment benthique. En revanche, aucun impact n'a été observé sur la qualité des sources de matières organiques benthiques. La deuxième partie de la thèse montre que la stratification n'affecte pas les réseaux trophiques benthiques en raison de la forte plasticité trophique des consommateurs primaires et des niveaux élevés d'omnivorie au sein de la communauté. En outre, la production primaire benthique en zone côtière pourrait potentiellement fournir une source de matière organique alternative à la production primaire pélagique vers les consommateurs primaires en condition de forte stratification. A travers ces résultats, nous proposons plusieurs schémas conceptuels décrivant les possibles évolutions de ces écosystèmes dans le contexte du changement climatique et nous montrons l'importance de considérer la singularité propre à chaque écosystème côtier ainsi que leur variation spatiale à petite échelle.

Title: Functioning of Arctic and sub-Arctic shallow benthic ecosystems in highly-stratified coastal systems

Keywords: Benthic macrofauna • Stratification • Food webs • Shallow coastal ecosystems • High-Arctic • Sub-Arctic

Abstract: Under climate change, Arctic and sub-Arctic coastal systems experience one of the largest increases in stratification at the global scale due to warming and/or freshening of their surface waters. However, the subsequent impacts of these environmental changes on the functioning of coastal benthic ecosystems is still poorly understood. This thesis aims to study how future increases in stratification in these ecosystems could affect the organic matter quality, pelagic-benthic coupling intensity and benthic food web structures. Two coastal systems subject to strong seasonal variations in sea surface temperature and salinity were studied: a high-arctic fjord (Young Sound, NE Greenland) characterized by strong haline stratification and a sub-Arctic archipelago (Saint-Pierre-et-Miquelon, Newfoundland continental shelf) exposed to strong thermal stratification. In the first part of this PhD we show that strong stratification reduces the quality of pelagic organic matter sources and intensity of organic matter transfers from surface waters toward the benthic compartment. On the other hand, no impact was observed on the quality of benthic organic matter sources. In the second part we show that stratification does not alter benthic food web structures thanks to the high trophic plasticity of primary consumers and high levels of omnivory in the community. In addition, benthic primary production in coastal environment could potentially provide an alternative source of organic matter to pelagic primary production for primary consumers during high stratification conditions. Through these results, we propose several conceptual models describing the potential evolutions of these ecosystems under climate change and we show the importance of considering the singularity of coastal ecosystems as well as their small-scale spatial variations.