UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Ecological transitions in Arctic marine ecosystems

Macroalgal settlement, pelagic density, and fish community shifts associated with glacier retreat and Atlantification

Víctor González Triginer

A dissertation for the degree of Philosophiae Doctor - June 2025

Cover photo by Víctor González Triginer

Ecological transitions in Arctic marine ecosystems

Macroalgal settlement, pelagic density, and fish community shifts associated with glacier retreat and Atlantification

Víctor González Triginer

A dissertation for the degree of Philosophiae Doctor
June 2025

Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

The University Centre in Svalbard
Department of Arctic Biology

Table of Contents

Acknowledgements

Everyone talks about how challenging it is to do a PhD and how it is not a walk in the park. In this case, a more relevant metaphor might be a hike through a frozen polar desert with slippery ice underfoot and hungry polar bears lurking in every corner. To be honest, it was a bit like that, and there were many challenges and obstacles from the very beginning. The very first day we tested the experimental setup in the fjord, our autonomous vehicle and main research tool very nearly got crashed into and sunk by a tourist ship. On the first day at our sampling site, we got caught in a storm that pushed our equipment and us to the very limit. A few days later, a female polar bear and her cubs decided that our USV looked delicious and swam towards it to get a taste. There are many more stories like that, and it became clear from the start that this was not going to be easy, but good, worthwhile things rarely are. In hindsight, this has been a singular, unexpected and wonderful journey, and one that I feel deeply thankful to have gone through.

An old proverb says that “it takes a village to raise a child”, and it certainly feels fitting for a PhD too. It would not have been possible to achieve this without the help and support of family, friends and colleagues. First, I would like to thank my advisors, to Arunima for always being there when it really counted, to Børge for setting a high bar and trusting me to reach it, to Max for sharing his valuable advice and knowledge even from far away, and to Jørgen for helping make things happen. Thanks to Milan, we started this together and through sheer determination, stubbornness and probably some degree of divine intervention we managed to succeed. To Claudia, a great mentor and friend. A huge thank you to the UNIS Arctic Biology PhD gang, who made the polar night less dark, to Emelie, Robynne, Bec, Snorre, Cheshtaa, Sam and Sil. Thanks to Raphaëlle for being a great office mate and always offering good advice, and to Ane Cecilie for nice and long coffee breaks. To Ask, Mishka, Jonatan, Nil, Clement, Gordon, Diogo, and all my friends back in Spain. A special merci to Clara for putting up with me during these crazy last months. And to Hope, my dear USV, who didn’t always live up to her name but in the end made me proud.

Thanks to Charlie, Mikko, Bård, Marcos, Sebastian, Arve, Piera and Stig for their help during long days in the field, to Kathy Dunlop for helping with the BRUV and to Emily Venables for her support with the Blueye ROVs. Thanks to Steve and all the great colleagues in the AB department. To Ben, Samira and all the students who have helped along the way. Thank you to the crew members of Helmer Hanssen, G.O. Sars and Polarsyssel, and to the scientists at the Institute of Marine Research for collecting the oceanographic and fish data for Paper III. A big thanks to Kai, and all the great FACE-IT colleagues, it has been a pleasure to be a part of a big international team!

Finally, to my family, who have supported me unconditionally for all these years. I could not wish for anything more.

Advisors

Professor Børge Damsgård

Department of Arctic Biology

The University Centre in Svalbard

P.O. Box 156 N-9171

Longyearbyen, Svalbard, Norway

Associate Professor Arunima Sen

Department of Arctic Biology

The University Centre in Svalbard

P.O. Box 156 N-9171

Longyearbyen, Svalbard, Norway

Dr. Maxime Geoffroy

Centre for Fisheries Ecosystems Research

Fisheries and Marine Institute of Memorial University of Newfoundland

St. John’s, Newfoundland, Canada

Professor Jørgen Berge

Department of Arctic and Marine Biology

Faculty of Biosciences, Fisheries and Economics

The Arctic University of Norway

Tromsø, Norway

List of papers and author contributions

Paper I: Gonzalez Triginer, V., Beck, M., Sen, A., Bischof, K., Damsgård, B. (2024). Acoustic mapping reveals macroalgal settlement following a retreating glacier front in the High Arctic. Frontiers in Marine Science, 11: 1438332. https://doi.org/10.3389/fmars.2024.1438332

Paper II: Gonzalez Triginer, V., Sen, A., Geoffroy, M., Damsgård, B. (2025). Loss of pelagic fish and zooplankton density associated with subglacial upwelling in high Arctic estuaries may be mitigated by benthic habitat expansion following tidewater glacier retreat. Arctic Science. https://doi.org/10.1139/as-2024-0040

Paper III: Gonzalez Triginer V., Geoffroy, M., Eriksen, E., Damsgård, B., Sen, A. (2025). Borealization of pelagic fish communities in the high Arctic during the polar night. Estuarine, Coastal and Shelf Science. In review.

Contributions/roles	Paper I	Paper II	Paper III
Concept and idea	VGT, MB, BD, KB	VGT, BD, MG, AS	VGT, BD, MG, AS
Study design and methods	VGT, MB, BD	VGT, BD, MG, AS	VGT, BD, MG, AS, EE
Data gathering and interpretation	VGT, MB, BD, AS	VGT, BD, MG, AS	VGT, BD, MG, AS, EE
Manuscript preparation	VGT, MB, BD, KB, AS	VGT, BD, MG, AS	VGT, BD, MG, AS, EE

VGT = Victor Gonzalez Triginer

MG = Maxime Geoffroy

AS = Arunima Sen

MB = Milan Beck

KB = Kai Bischof

BD = Børge Damsgård

BD = Børge Damsgård

EE = Elena Eriksen

Other authored publications cited in this thesis:

Van der Kamp, A., **Gonzalez Triginer, V**., Sen, A. (2025). Billefjorden's benthic biodiversity: the impact of glacier retreat on faunal communities in a high Arctic fjord. Polar Biology 48, 71. https://doi.org/10.1007/s00300-025-03390-w

Abbreviations

AUV – Autonomous underwater vehicle

BRUV – Baited remote underwater video system

CTD – Conductivity, temperature and depth sensor

GNSS – Global navigation satellite system

NTU – Nephelometric turbidity units

POM – Particulate organic matter

PSU – Practical salinity units

RCP – Representative concentration pathways

ROV – Remotely operated vehicle

R/V – Research vessel

SSP – Shared socioeconomic pathways

Sv – Volume backscattering strength

USV – Uncrewed surface vehicle

VCS – Vehicle control station

Summary

The Arctic is warming at an unprecedented rate, driving severe changes in marine ecosystems. Glacier retreat, increased sedimentation rates, and reduced sea ice cover are reshaping Arctic fjords, where terrestrial, freshwater, and marine influences interact. Glacier fronts influence fjord biogeochemistry and marine ecosystems across multiple trophic levels, and localized effects of glacier retreat on coastal ecosystems remain poorly understood due to logistical challenges of studying these areas. Simultaneously, the northward influx of temperate species, a process known as borealization, is altering Arctic marine communities. This thesis documents the localized and regional processes associated with glacier retreat and borealization in the Arctic, while also developing and testing sustainable technologies for studying these remote environments.

Papers I and II explored the effects of tidewater glacier retreat, particularly the transition from marine- to land-terminating glaciers, on the underwater coastscape and marine ecosystems of a high Arctic fjord in Svalbard. Sampling stations were established along a gradient of glacier retreat: at a recently land-terminating glacier front, in a river bay with terrestrial input from inland glaciers, and at a site with minimal glacial influence. Using hydroacoustics and autonomous vehicles, Paper I investigated macroalgal coverage and oceanographic conditions along the fjord coastline. This study revealed high variability in macroalgal presence, with abundant coverage in areas with little land runoff and virtually no macroalgae in the river bays or at the marine-terminating glacier front. Notably, kelp was observed near the land-terminating glacier front, highlighting the potential for rapid macroalgal colonization on newly available substrates following glacier retreat.

Paper II extended this research to include pelagic organisms, investigating the density and vertical distribution of fish and zooplankton along the same gradient of glacier retreat. Pelagic density was lowest near the land-terminating glacier front and highest at the site with minimal glacial input, which also featured a rich benthic habitat dominated by kelp beds. These findings suggest that the loss of pelagic productivity associated with the disappearance of subglacial upwelling may be mitigated by benthic habitat expansion. However, macroalgal growth will depend on factors such as fjord topography, sedimentation rates, and substrate availability, which are likely to be affected by higher melting rates and increased turbidity in Arctic waters.

These localized shifts in Arctic fjords are linked to large-scale regional transitions, such as the influx of boreal species into higher latitudes. Paper III upscaled the scope of this thesis by examining spatial differences in fish community composition and pelagic density across Svalbard during the polar night, and assessing the effectiveness of this extreme period as a barrier for borealization. Acoustic-trawl surveys and oceanographic measurements revealed distinct spatial patterns, with western fjords exhibiting lower pelagic density but higher species diversity compared to eastern sites, which were dominated by schooling mesopelagic fish. Interestingly, borealization was equally pronounced in the eastern, more Arctic-influenced sites as in the western, Atlantic-influenced fjords, suggesting that the extreme light regime of the polar night does not act as a strong seasonal barrier to borealization. This study discusses the interplay between wide-scale borealization processes and habitat shifts in Arctic fjords, and explores the potential role of benthic habitat expansion in facilitating the expansion of boreal species into Arctic waters.

This thesis advances our understanding of the localized effects of glacier retreat on Arctic fjord ecosystems and the broader patterns of borealization in the region. By integrating hydroacoustics with autonomous vehicles, this research provides efficient and sustainable protocols for studying coastal areas and glacier fronts, offering valuable tools for monitoring and managing Arctic marine ecosystems in a rapidly changing world.

1 Introduction

1.1 A changing cryosphere

The cryosphere refers to the frozen parts of the Earth system, including snow, glaciers and sea ice, and plays a key role in Earth's climate, acting as an indicator of climate change. Shifts in the cryosphere are a well-studied consequence of climate change, and there is extensive literature on retreating glaciers and decreasing sea ice cover (e.g. Box et al., 2019; IPCC, 2022; Notz & Stroeve, 2016; Zemp et al., 2019). Snow and ice exhibit a high albedo effect, which helps regulate the planet's temperature by reflecting a significant portion of solar radiation back into space. As the cryosphere shrinks due to increased temperatures, this reflective capacity is reduced, leading to further warming through a positive feedback loop. This feedback mechanism is a key driver of the accelerated warming observed in polar regions, with studies showing that the Arctic is warming nearly four times faster than the rest of the planet (Rantanen et al., 2022). Moreover, extreme weather events in the Arctic, including marine heatwaves, storms, and high temperature variability, are occurring at an unprecedented rate and are projected to intensify due to Arctic sea ice decline (He et al., 2024; Overland, 2022).

Svalbard's climate is closely tied to the system of ocean currents that encircle this Arctic archipelago. The North Atlantic Current extends into the West Spitsbergen Current, carrying warm and saline Atlantic water into the region and giving Svalbard a milder climate than other areas at similarly high latitudes (Ingvaldsen et al., 2021; Nilsen et al., 2008). Atlantic water from the West Spitsbergen Current floods into the western fjords of Svalbard, greatly influencing the physical and biological systems within Svalbard fjords and shaping local ecosystems. The other main ocean current in Svalbard is the East Spitsbergen Current, which brings cold, fresher Arctic water from the north and contributes to more Arctic conditions in eastern Svalbard. The interplay between these currents has significant implications for the sea ice extent in the region, as the warm Atlantic water leads to reduced sea ice cover and earlier melt in western Svalbard, while the opposite occurs in the east (Nilsen et al., 2016).

In recent years, the Arctic has experienced a significant increase in the transport of warm Atlantic water, a phenomenon known as Atlantification (Ingvaldsen et al., 2021; Polyakov et al., 2023). This influx of warmer, more saline waters into the Barents Sea and Arctic Ocean is altering the thermal structure and physical oceanography of the region, leading to a decrease in sea ice extent and thickness in the Barents Sea (Onarheim et al., 2018). Sea ice is a critical component of Arctic ecosystems, providing habitat for a wide range of species and playing a vital role in regulating local and global climate (Overland et al., 2014; Stroeve & Notz, 2018). Consequently, the dramatic decline in Arctic sea ice extent across all seasons has important implications for local ecosystems, affecting species distribution and disrupting trophic web dynamics (Leu et al., 2011; Søreide et al., 2006).

Additionally, glaciers globally are retreating at a rapid rate in response to rising temperatures and changing precipitation patterns (Zemp et al., 2015). Arctic glaciers are integral to the cryosphere and have shown consistent mass loss over recent decades (Gardner et al., 2013), driven primarily by increased surface melting and calving rates linked to rising global air and sea temperatures (Jacob et al., 2012). While the contributions of melting glaciers to global sea level rise are well documented, little is known about the effects of retreating glaciers on marine ecosystems at a local scale (Gardner et al., 2013; Kaser et al., 2006; Zemp et al., 2019). Glaciers play a key role in shaping the biological, chemical, and physical characteristics of Arctic fjords, and the heightened freshwater influx from melting glaciers alters the biogeochemistry of marine fjord systems and affects food web dynamics (Meire et al., 2023; van der Kamp et al., 2025; Wassmann et al., 2011). Subglacial meltwater, typically colder and less saline than seawater, is discharged at the base of marine-terminating glaciers and rises through the water column (Straneo & Cenedese, 2015). This process upwells nutrient-rich deep waters to the surface, fuelling phytoplankton blooms and creating highly productive zones near tidewater glacier fronts (Hopwood et al., 2020). These areas support diverse communities of zooplankton, fish, seabirds, and marine mammals that rely on the abundant food resources generated by glacial upwelling (Hop et al., 2023; Lydersen et al., 2014; Meire et al., 2017). As glaciers retreat and transition from marine- to land-terminating, this upwelling process disappears, with consequences for local fjord productivity and energy transfer across trophic levels (Meire et al., 2023).

Beyond driving nutrient upwelling, glaciers are also important sources of silica, iron and phosphorus, which are supplied to Arctic coastal waters through glacial rivers and calving events (Bhatia et al., 2013; Hawkings et al., 2016). Simultaneously, meltwater discharge carries large amounts of suspended particles and sediments, increasing turbidity near glacial outlets and reducing light penetration (Hopwood et al., 2020; Meire et al., 2017). These turbid, low-light conditions limit photosynthesis, and hence primary production is low at glacier fronts, and productivity increases with distance from the glacier plume as light availability rises.

1.2 Macroalgae as key elements of coastal systems

Macroalgae are multicellular photosynthetic organisms that thrive in coastal marine environments and form the backbone of many coastal ecosystems (Dayton, 1985). They range from small structures to dense, towering forests and are classified into brown, red and green algae based on their pigmentation. Kelp are large brown algae in the order Laminariales, but this term is often used to include large non-laminarian brown algae such as Fucoids, as done in this thesis (Fraser, 2012; Thomsen et al., 2024). Kelp create complex three-dimensional habitats that are essential for coastal ecosystems in the Arctic and North Atlantic (Fredriksen, 2003). These organisms rely on hard substrate for attachment, and they are commonly found on rocky shores in sublittoral regions throughout the Arctic (Steneck et al., 2002).

Kelp forests are among the most productive ecosystems on Earth and play a crucial role in carbon sequestration and nutrient cycling (Duggins et al., 1989). Macroalgae, as part of "blue carbon" ecosystems, capture CO_2 through photosynthesis and store it as organic carbon (Duarte et al., 2005; Krause-Jensen & Duarte, 2016), and their carbon sequestration rates are comparable to those of terrestrial forests (Macreadie et al., 2019; Mcleod et al., 2011). Additionally, macroalgae stabilize sediments, enhance carbon burial in the seabed, and protect shorelines by absorbing wave energy, buffering coastal areas from erosion and extreme weather events (Duarte et al., 2013; Løvås & Tørum, 2001; Mork, 1996). Research has shown that macroalgal detritus is an important source of carbon for near-shore Arctic food webs as well as deep-sea ecosystems (Krause-Jensen & Duarte, 2016; Krumhansl & Scheibling, 2012; Renaud et al., 2015). Macroalgae also serve as critical habitats, providing nursery and feeding areas, shelter, and food for a wide range of organisms, including invertebrates, fish, and marine mammals (Teagle et al., 2017).

In the Arctic, macroalgae face unique challenges due to extreme environmental conditions, including pronounced seasonality in light regimes, ice scouring, and low temperatures (Filbee-Dexter et al., 2019; Krause-Jensen et al., 2012). Their growth depends on light, but the extreme seasonality in high latitudes results in several months of darkness and extensive ice cover, which limits light availability for photosynthesis (Düsedau et al., 2024; Niedzwiedz & Bischof, 2023). To adapt to these conditions, Arctic macroalgae accumulate nutrients during winter, when availability is higher, and use these reserves to support photosynthesis and growth during the summer (Pueschel & Korb, 2001). However, cold water temperatures constrain their metabolic rates and sea ice and icebergs can physically damage macroalgal structures (Krause-Jensen et al., 2012). In summer, increased glacial meltwater and river runoff influence light penetration and nutrient dynamics, further affecting macroalgal growth (Niedzwiedz & Bischof, 2023). As glaciers retreat onto land and melting and precipitation rates increase due to warming, terrestrial influx to the sea and sedimentation rates in Arctic fjords are expected to increase (Hopwood et al., 2020). High sediment loads can reduce light penetration in the water column, limiting the levels of photosynthetically available radiation, and as macroalgae rely on sufficient light to sustain their photosynthetic processes, increased turbidity can significantly impact their growth (Hanelt et al., 2001; Ronowicz et al., 2020). These alterations in the underwater light climate have been shown to limit both the horizontal and vertical distribution of macroalgal communities in the Arctic (Düsedau et al., 2024).

Data on the current distribution and extent of kelp in the Arctic is scarce, and while they are known to range along most Arctic coasts, their distribution is limited by the availability of hard substrate. Riverine and glacial runoff lead to shallow coastal areas often being dominated by sediment, and rocky substrate only accounts for about 35% of the Arctic coastline (Lantuit et al., 2012). Kelp are found as far north as >80° N in Svalbard, but most records of Arctic kelp come from northern Norway, western Greenland, northwestern USA and eastern Canada (Bartsch et al., 2016; Filbee-Dexter et al., 2019). Arctic kelp thrive on stable rocky shores with seasonal sea ice cover, and their vertical distribution is constrained by ice scouring at the upper limit and light penetration at the lower limit.

Climate change is driving significant changes in macroalgal distribution. Rising temperatures, decreasing sea ice cover and increasing turbidity are key factors influencing kelp populations (Filbee-Dexter et al., 2019; Krause-Jensen et al., 2020). Warmer temperatures are expected to enhance growth rates and recruitment of warm-adapted temperate kelps, potentially allowing them to outcompete and displace cold-adapted Arctic species (Assis et al., 2022; Krause-Jensen & Duarte, 2014; Wernberg et al., 2013). Models project a major expansion of macroalgae in the Arctic under climate change, but the scale of this expansion will depend on climate scenarios (Figure 1), as well as local environmental conditions including substrate type, sedimentation rates and light availability. Nonetheless, predicting shifts in kelp distribution under climate change remains challenging. Although models predict a significant northward expansion of kelp, these projections may be overestimated, as increased glacial and river runoff driven by warming temperatures could elevate turbidity and reduce light penetration, limiting kelp growth (Filbee-Dexter et al., 2019; Niedzwiedz & Bischof, 2023). Studies in Svalbard have documented increased macroalgal biomass over the last 30 years, attributed to reduced sea ice scouring and newly available substrate for settlement (Bartsch et al., 2016; Fredriksen et al., 2015), but high-resolution data in shallow coastal areas and near retreating glacier fronts remain limited, highlighting a key research gap.

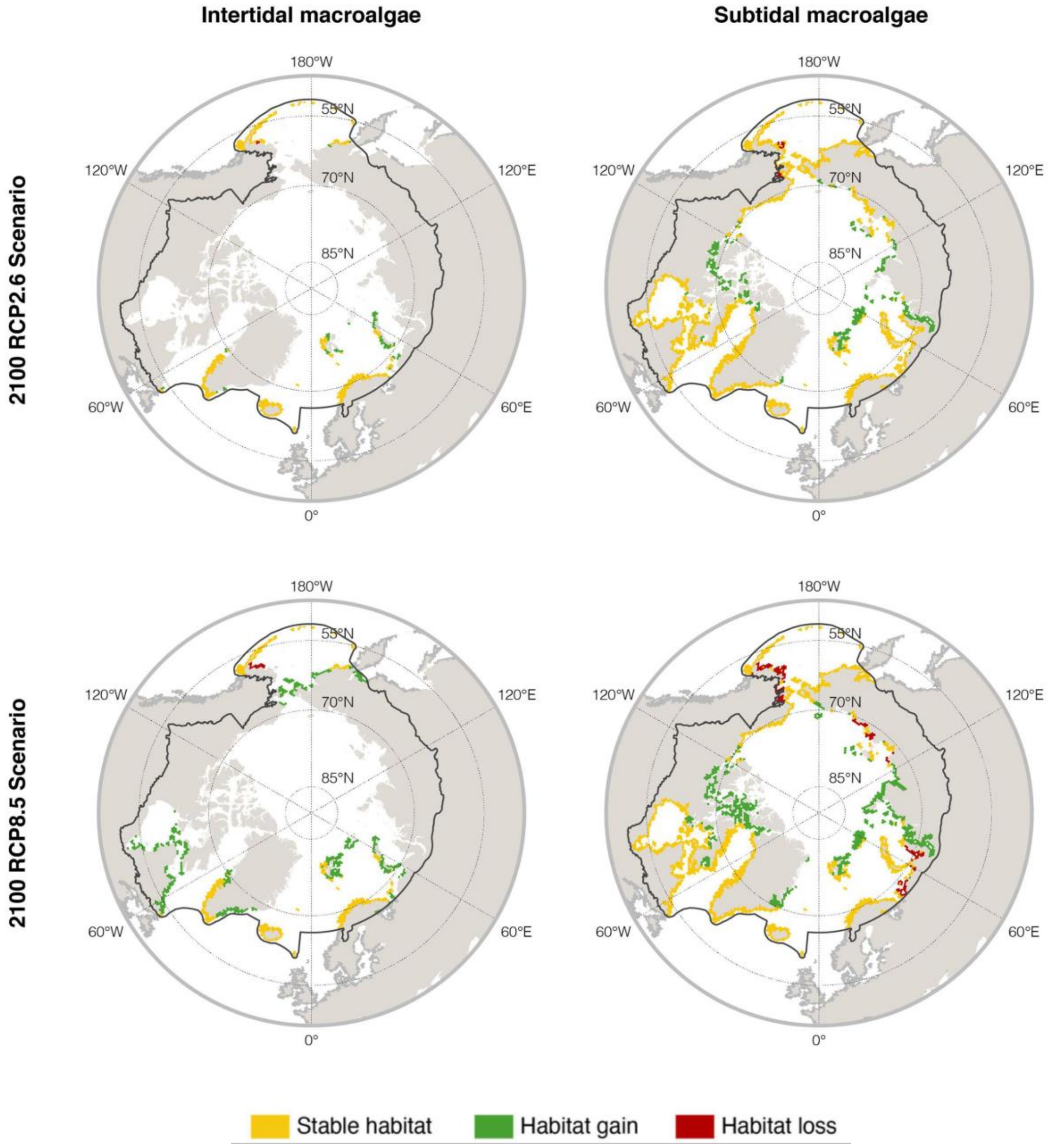


Figure 1. Predicted changes in habitat suitability for subtidal and intertidal pan-Arctic macroalgae based on species distribution models, from the present to 2090-2100 (expansion in green, losses in red and stable habitats in yellow). Projections are shown under two scenarios of greenhouse gas emissions (Representative Concentration Pathways (RCP) 2.6 and 8.5). Adapted from Assis et al. 2022.

As ecosystem engineers, macroalgae support key functions in the marine environment, and their northward expansion due to climate change has significant ecological implications. Increased macroalgal biomass enhances habitat and nursery areas for fish and invertebrates, boosting biomass and biodiversity (Bertocci et al., 2015; Teagle et al., 2017). This expansion into higher latitudes may also provide foraging grounds for boreal fish species and refuge from predators (Gotceitas et al., 1995; James & Whitfield, 2023), and areas near kelp forests have reported higher fish catches (Krause-Jensen & Duarte, 2014). Macroalgal expansion in the Arctic may contribute to increased carbon sequestration, with implications for both local and global carbon levels. Thus, vegetated coastal habitats have significant potential for climate change mitigation, highlighting the importance of understanding their poleward expansion and the potential associated effects on Arctic marine ecosystems (Duarte et al., 2013; Filbee-Dexter et al., 2019).

1.3 Distribution shifts of marine fish fauna

Arctic marine species face multiple physiological challenges as rising temperatures exceed their thermal tolerance. Increased metabolic rates elevate energy demands, which, combined with a changing prey field and potential scarcity of preferred prey, can negatively impact growth and survival (Laurel et al., 2017). Many Arctic organisms rely on energy reserves to survive prolonged periods of low productivity, and these reserves can be depleted more rapidly under enhanced metabolic rates. Additionally, elevated temperatures can accelerate growth rates, leading to earlier maturation at smaller sizes, potentially reducing reproductive output (Crozier & Hutchings, 2014).

While thermal tolerance is a key driver of latitudinal range shifts (Sunday et al., 2012), other factors, such as climate velocity, i.e. the rate of climate shifts, play a critical role. Studies suggest that the responses of marine organisms to climate change closely track local climate velocities, with distribution shifts more pronounced in areas experiencing faster environmental changes, such as the Arctic (Burrows et al., 2011; Dulvy et al., 2008; Pinsky et al., 2013). Habitat loss further compounds these challenges. Declining sea ice reduces essential spawning and nursery habitats, threatening egg survival and foraging success of key Arctic species such as polar cod (*Boreogadus saida*) (Geoffroy et al., 2023; Huserbråten et al., 2019).

Additionally, Arctic species are exposed to heightened biotic stressors, such as increased predation and competition. For example, polar cod are increasingly exposed to such pressures from boreal species like Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), which are expanding into Arctic habitats (Bengtsson et al., 2024; Dupont et al., 2024; Geoffroy et al., 2023). Arctic species, highly specialized for extreme polar environments, may be outcompeted by generalist boreal newcomers as rapid environmental changes lead to niche overlap (Hollowed et al., 2013). Shifts in the distribution and abundance of zooplankton, a key prey item for many Arctic fish, further complicate these dynamics. Changes in bloom timing and phenology may result in mismatches between prey availability and critical feeding periods for larval and juvenile fish (Dalpadado et al., 2014; Edwards & Richardson, 2004).

Polar cod and other forage fish are critical to Arctic marine ecosystems, serving as a link between zooplankton and higher trophic levels, including other fish, birds and marine mammals (Geoffroy et al., 2023). Declines in polar cod populations could disrupt these trophic connections, creating bottlenecks in energy transfer and impacting broader ecosystem productivity and stability (Kortsch et al., 2015). Although forage fish such as herring (*Clupea harengus*) and capelin (*Mallotus villosus*) are expanding their ranges northward, it remains uncertain whether they can fill this ecological niche. For example, diet studies on ringed seals (*Pusa hispida*) along Svalbard's west coast revealed that polar cod remains their primary prey, despite major shifts in fish communities and an increase in Atlantic fish species in this area over recent decades (Bengtsson et al., 2020). This suggests that some Arctic predators are highly specialized and may have limited capacity to adapt to alternative prey species.

Climate change is driving substantial shifts in the distribution of marine species, particularly in Arctic and sub-Arctic waters where warming is occurring at an accelerated rate. Poleward shifts have been widely observed across various taxa, including benthic invertebrates, phytoplankton, zooplankton and fish (Doney et al., 2012; Poloczanska et al., 2013). In the North Atlantic and Arctic regions, notable changes in the distribution of marine fish species have been documented and are predicted to continue under future climate scenarios (Figure 2) (Gordó-Vilaseca et al., 2024; Hollowed et al., 2013; Perry et al., 2005; Rose, 2005). For example, species such as Atlantic cod, mackerel (*Scomber scombrus*) and haddock are increasingly found in the Barents Sea and high Arctic fjords (Drinkwater, 2005; Fossheim et al., 2015), and high biomass of herring has been reported in Svalbard waters in recent years (Eriksen et al., 2025). Recent studies highlight an abrupt poleward shift of approximately 800 km in the spawning sites of herring in Norwegian waters, driven primarily by fisheries but likely facilitated by warming temperatures (Slotte et al., 2025).

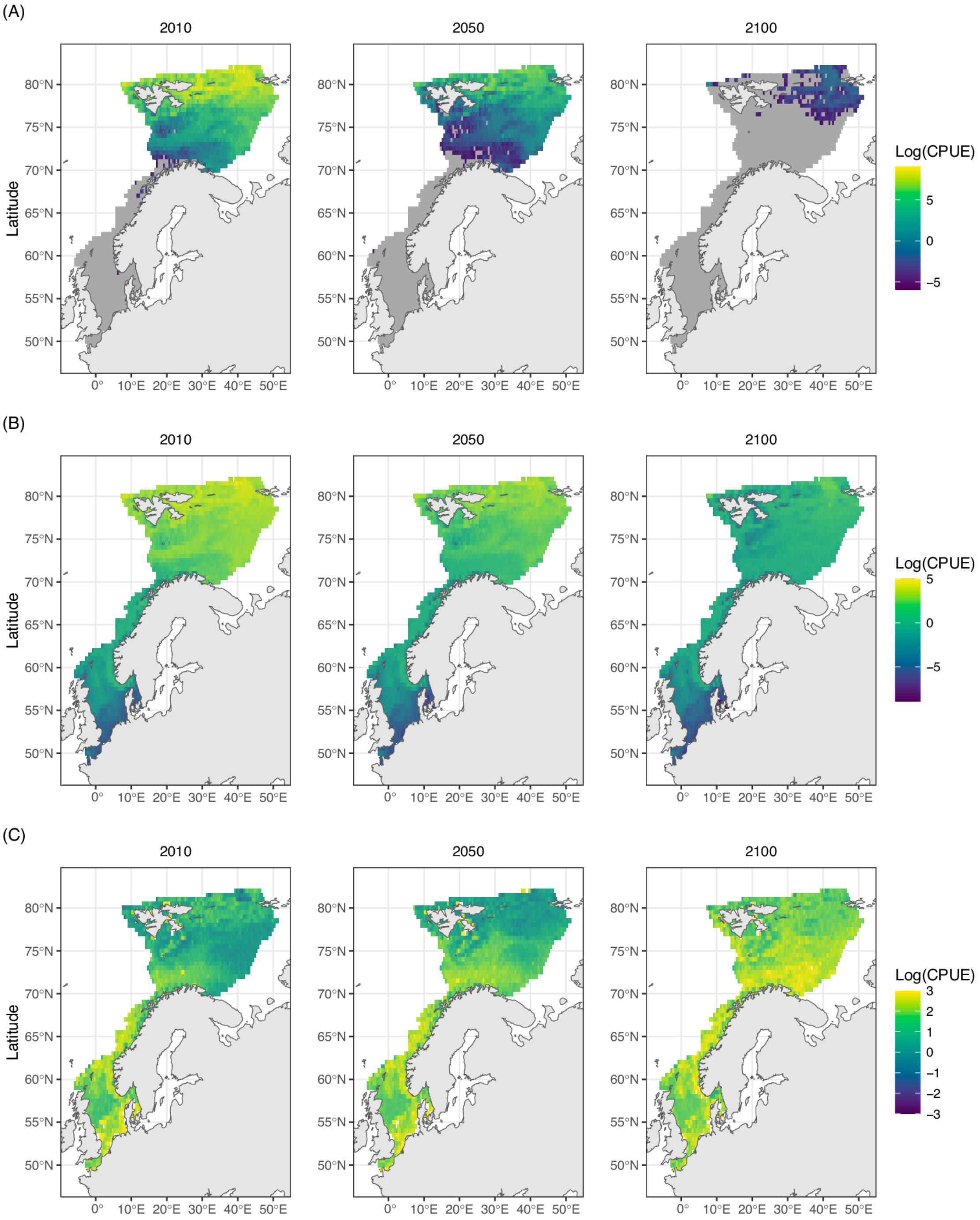


Figure 2. Projections of mean future fish biomass under SSP5-8.5 (Shared Socio-economic Pathway) for (A) Arctic (n=3 species), (B) Arctic-boreal (n=8) and (C) boreal (n=40) species. LogCPUE corresponds to log of catch per unit of effort. Figure adapted from Gordó-Vilaseca et al. 2024.

Climate change has weakened several barriers that historically prevented boreal species from expanding northward, such as cold temperatures and sea ice cover (IPCC, 2022; Stroeve & Notz, 2018). However, one key barrier that remains unaffected by warming is the extreme light regime in the Arctic, which may limit the northward expansion of boreal species. The prolonged daylight of the midnight sun during summer increases predation pressure on mesopelagic fish, while the extended darkness of Arctic winters depletes energy reserves (Langbehn et al., 2022; Ljungström et al., 2021). Many boreal fish are visual predators that rely on light for foraging, making the polar night a significant challenge for their survival. In contrast, Arctic fish are adapted to use minimal light cues for foraging and vertical migrations (Benoit et al., 2010), suggesting that boreal species lacking these adaptations would struggle under such conditions. Surprisingly, studies have shown that some Atlantic species, such as cod and haddock, are capable of foraging during the polar night (Bengtsson et al., 2024; Larsen et al., 2023), and the effectiveness of the Arctic light regime as a barrier to borealization remains uncertain.

The northward movement of temperate marine species into Arctic regions is not only altering the distribution of these newcomers but also displacing endemic Arctic species. These endemic species face a range of ecological challenges, including habitat loss, increased competition, and predation pressures (Hollowed et al., 2013; Kortsch et al., 2015). Arctic marine fish, adapted to cold environments and specific ecological niches, are forced to either adapt to the changing conditions or migrate further north to maintain their ecological and physiological niches (Geoffroy et al., 2023). In addition to latitudinal shifts, Arctic species are adjusting their vertical distribution and depth ranges. As geographical constraints limit further northward movement, species may migrate to deeper, cooler waters to maintain access to suitable thermal conditions for growth and reproduction (Dulvy et al., 2008; Perry et al., 2005). However, the potential of vertical movements to mitigate climate change effects will depend on the availability of suitable habitats and the physiological and ecological constraints of deeper waters (Hollowed et al., 2013). Ultimately, species with more flexible depth tolerance may be better equipped to cope with environmental changes and remain more resilient to risks of population decline.

Box 1: Key marine fish species in Svalbard waters

Polar cod (*Boreogadus saida*)

Morphology and life history: The most abundant forage fish in the Arctic, forming dense aggregations. Small in size (adult length ≤ 25 cm) and short lived (<7 years) (Benoit et al. 2010). Physiological optimum between 3 °C and 10 °C (Geoffroy et al. 2023).

Diet: Varies by size, region and season. Primarily feeds on calanoid copepods, hyperiid amphipods and benthic crustaceans (Geoffroy et al. 2023).

Distribution: Circumpolar distribution, often associated with ice. Spawning occurs mainly in southeast Svalbard (Husebråten et al., 2019). High potential for northward expansion into the Arctic Ocean (Hollowed et al., 2013).

Climate Change stressors: Vulnerable to rising water temperatures, sea ice decline, changing prey field and increased competition and predation pressures.

Atlantic cod (*Gadus morhua*)

Morphology and life history: Key commercial species in the North Atlantic. Typically grows to 100-150 cm of length but can exceed 180 cm and 50 kg in weight, with a lifespan of over 20 years (Rose, 1993). Thrives in a wide temperature range (0-20 °C) (Drinkwater, 2005).

Diet: Opportunistic feeders. Juveniles consume small crustaceans, while adults prey on fish (e.g. capelin, herring), molluscs and large crustaceans.

Distribution: Widely distributed across the North Atlantic, from the Bay of Biscay to the Barents Sea and Svalbard. Demersal fish that undertake seasonal migrations for spawning and feeding.

Climate Change stressors: Northward distribution shifts due to warming temperatures, increased competition and changing prey field (Rose, 2005).

Box 1: Key marine fish species in Svalbard waters (continued)

Atlantic herring (*Clupea harengus*)

Morphology and life history: Small schooling pelagic fish, reaching lengths of 20-40 cm and living up to 15 years (Blaxter & Hunter, 1982). Tolerates temperatures between 1 °C and 20 °C (Whitehead et al. 1988).

Diet: Primarily feeds on zooplankton, including calanoid copepods, krill and fish larvae.

Distribution: Widely distributed across the North Atlantic, from the North and Norwegian Seas to the Barents Sea. Undergoes extensive migrations between spawning and feeding grounds.

Climate Change stressors: Warming may affect spawning success, migration timing and distribution. Changes in plankton communities could reduce food availability, impacting growth and survival rates (Allan et al., 2022).

Capelin (*Mallotus villosus*)

Morphology and life history: Small, slender pelagic fish that play a crucial role as forage species. Typically grows to 12-20 cm and lives up to 6 years (Carscadden & Vilhjálmsson, 2002).

Diet: Feeds primarily on zooplankton, krill and amphipods (Gjøsæter 1998).

Distribution: Abundant in the Barents Sea and around Iceland and Greenland. Undertakes extensive feeding migrations.

Climate Change stressors: Sensitive to warming waters, which affect distribution, spawning success and migration timing. Changes in prey abundance and distribution impact their growth and survival (Dalpadado et al., 2014).

1.4 Hydroacoustics and autonomous vehicles

As the Arctic faces mounting environmental pressures, it is critical to develop and utilise sustainable research methodologies that minimize ecological impact, and this has been an important factor in this thesis.

Hydroacoustic technology, which uses sound waves to detect and quantify marine life, provides detailed information on the distribution, abundance, and movement of fish and other marine organisms. By emitting sound pulses into the water and analysing the echoes reflected by marine organisms, this method can determine the distance, size, and density of targets. Hydroacoustics has been extensively used in fisheries and fish stock assessments, enabling the monitoring of fish populations and tracking changes in their distributions over large areas (Simmonds & MacLennan, 2005). Additionally, acoustic technology plays a crucial role in mapping seafloor topography and studying benthic habitats, providing insights into underwater ecosystems without the need for invasive sampling.

Autonomous vehicles, such as uncrewed surface vehicles (USVs) and autonomous underwater vehicles (AUVs), are revolutionizing marine research by providing innovative ways to monitor the environment with minimal human intervention (Handegard et al., 2024; Patterson et al., 2025). These vehicles are particularly valuable for accessing difficult-to-reach areas, such as glacier fronts and shallow coastal regions, where traditional research methods are often constrained by ice cover, extreme weather, and the risks associated with glacier calving.

Traditional sampling methods, such as trawling and dredging, often have significant environmental impacts. These methods physically disturb the seafloor, damage benthic habitats, and result in bycatch, which can disrupt ecosystems. Hydroacoustics offers a non-invasive alternative by using sound waves to collect data and reducing habitat disturbance. Autonomous vehicles further enhance sustainability by reducing the carbon footprint of research, as, unlike large research vessels, which consume significant amounts of fuel, they are often powered by electric systems. Additionally, their smaller size and quieter operation minimize noise pollution, which can disrupt marine life and affect the quality of data collection (Berge et al., 2020; Ludvigsen et al., 2018).

2 Aims

This thesis addresses critical research gaps by investigating the localized changes in benthic and pelagic communities associated with glacier retreat in Arctic fjords, with a focus on macroalgal expansion and the density of fish and zooplankton near glacier fronts. Furthermore, it explores spatial variability in fish community composition across Svalbard during the understudied polar night and examines the limitations of the Arctic winter as a seasonal barrier to borealization. By leveraging innovative, low-impact technologies like autonomous vehicles and hydroacoustics, this work advances the current understanding of Arctic marine ecosystems and their responses to rapid environmental change.

Research question 1: How does glacier retreat influence the distribution and settlement of macroalgae in Arctic fjords?

> **Hypothesis 1.1**: Macroalgal presence will decrease with increasing proximity to glacier fronts and river bays due to high sedimentation rates and reduced light availability.
>
> **Hypothesis 1.2**: There may be an optimal proximity to the glacier fronts that allows for macroalgal growth, where there is increased nutrient concentration and new substrate available, but where turbidity and mechanical disturbances are not high enough to prevent macroalgal settlement.

Research question 2: How does pelagic density and vertical distribution vary along a gradient of glacier retreat in Arctic fjords?

> **Hypothesis 2.1**: Areas with high land and glacial runoff, such as river bays and land-terminating glacier fronts, will exhibit low productivity and low density of fish and zooplankton due to high sedimentation rates and reduced light availability for primary producers.

Research question 3: What are the patterns of composition, distribution, and borealization of pelagic fish communities across Svalbard during the polar night, and how are they associated with the extreme light regime and regional oceanographic conditions?

> **Hypothesis 3.1**: Borealization will be more pronounced in western Svalbard, where Atlantic water masses dominate, compared to eastern Svalbard, which is more influenced by Arctic water masses.

Together, these three studies provide novel insights into the effects of cryosphere changes on Arctic coastal marine ecosystems. **Papers I and II** investigate the localized impacts of glacier retreat on benthic (macroalgae) and pelagic (fish and zooplankton) distribution, highlighting how environmental shifts influence ecosystem structure. **Paper III** builds on these studies by scaling up to examine how regional oceanographic conditions and the extreme light regime of the polar night shape fish community composition and borealization across Svalbard. By integrating these localized and regional perspectives, this thesis advances our understanding of the interplay between cryosphere changes, species distributions, and ecosystem dynamics in a rapidly changing Arctic. Additionally, this work provides a detailed methodological protocol for the efficient and sustainable investigation of glacier fronts and shallow coastal areas in Arctic fjords using cutting-edge research technology.

3 Methods

3.1 Study area

The high Arctic archipelago of Svalbard, located between 74° and 81° N, is shaped by the influence of two major ocean currents: the warm, saline West Spitsbergen Current and the colder, fresher Arctic water masses dominating the eastern side (Nilsen et al., 2016; Svendsen et al., 2002). The interaction between Atlantic and Arctic water masses creates distinct environmental gradients that shape regional ecosystems. Svalbard's fjords are particularly sensitive to climate change, with rapid glacier retreat, reduced sea ice cover, and increasing Atlantic water inflow driving significant physical and ecological shifts (Ingvaldsen et al., 2021).

Billefjorden is a 32 km long and 5-8 km wide fjord connected to the larger Isfjorden system in western Spitsbergen (Figure 3). The fjord features an outer sill (70 m depth) and an inner sill (50 m depth), which limit the inflow of warm Atlantic water from offshoots of the West Spitsbergen Current and allow for a deep layer of winter-cooled water in the inner basin (Nilsen et al., 2008). The coastscape of Billefjorden is diverse, with one tidewater glacier (Nordenskiöldbreen) and several land-terminating glaciers that drain into the fjord via rivers (notably in Petuniabukta). The Nordenskiöldbreen glacier, located at the inner part of the fjord, is divided into two sides by a rocky peninsula. The glacier has been retreating rapidly, with the northern side transitioning from marine- to land-terminating in 2017 (Kavan et al., 2023), while the southern side remains predominantly marine-terminating as of 2025. Petuniabukta is located northwest of Nordenskiöldbreen and receives significant freshwater and sediment runoff from surrounding land-terminating glaciers and rivers.

Billefjorden offers a unique natural laboratory, with sites in close proximity representing different stages of glacier retreat: a marine-terminating glacier, a recently land-terminating glacier, a river bay influenced by inland glaciers, and areas with minimal glacial influence. This diversity makes it an ideal study site for **Papers I and II**. Additionally, its proximity to Longyearbyen allows for relatively accessible and frequent sampling, which is particularly valuable in the challenging conditions of high Arctic environments.

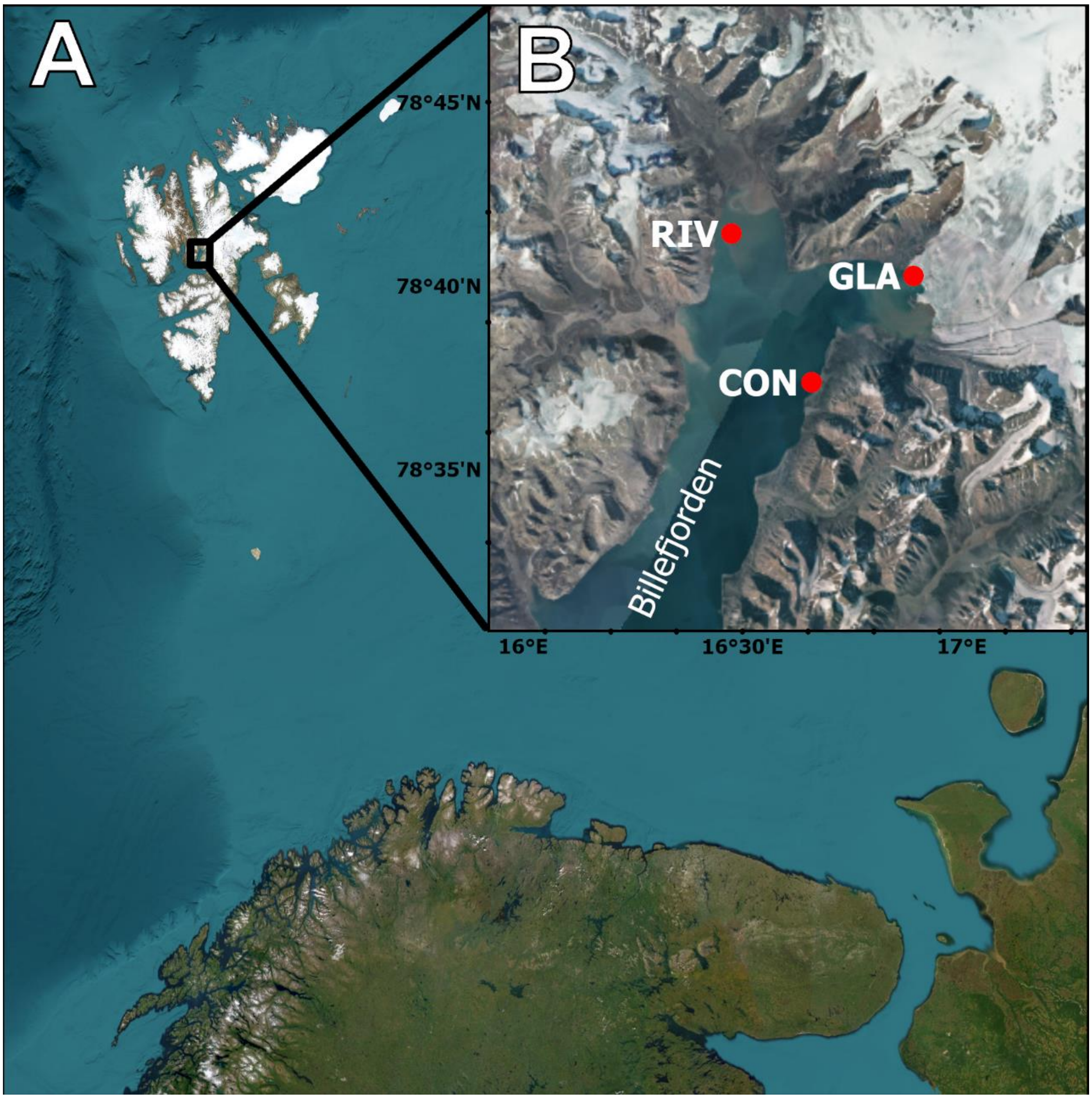


Figure 3. Svalbard is located north of continental Norway (A). The study locations for **Papers I and II** are located in Billefjorden (B) and include a recently land-terminating glacier front (GLA), a river bay with influence from inland glaciers (RIV) and a site with minimal glacial input (CON). Map source: Earthstar Geographics and Norwegian Polar Institute. Figure from Paper II.

For **Paper III**, multiple sites around Svalbard were sampled during the "Polar cod connectivity cruise" on board R/V *G.O. Sars*. This scientific cruise included sampling in Isfjorden, Billefjorden, Nordfjorden, Kongsfjorden, Storfjorden and several sites southeast of Svalbard (Figure 4). This selection of sampling stations allowed for a comparison between the western and eastern regions, enabling an investigation of how Atlantic and Arctic water masses influence fish community composition during the polar night.

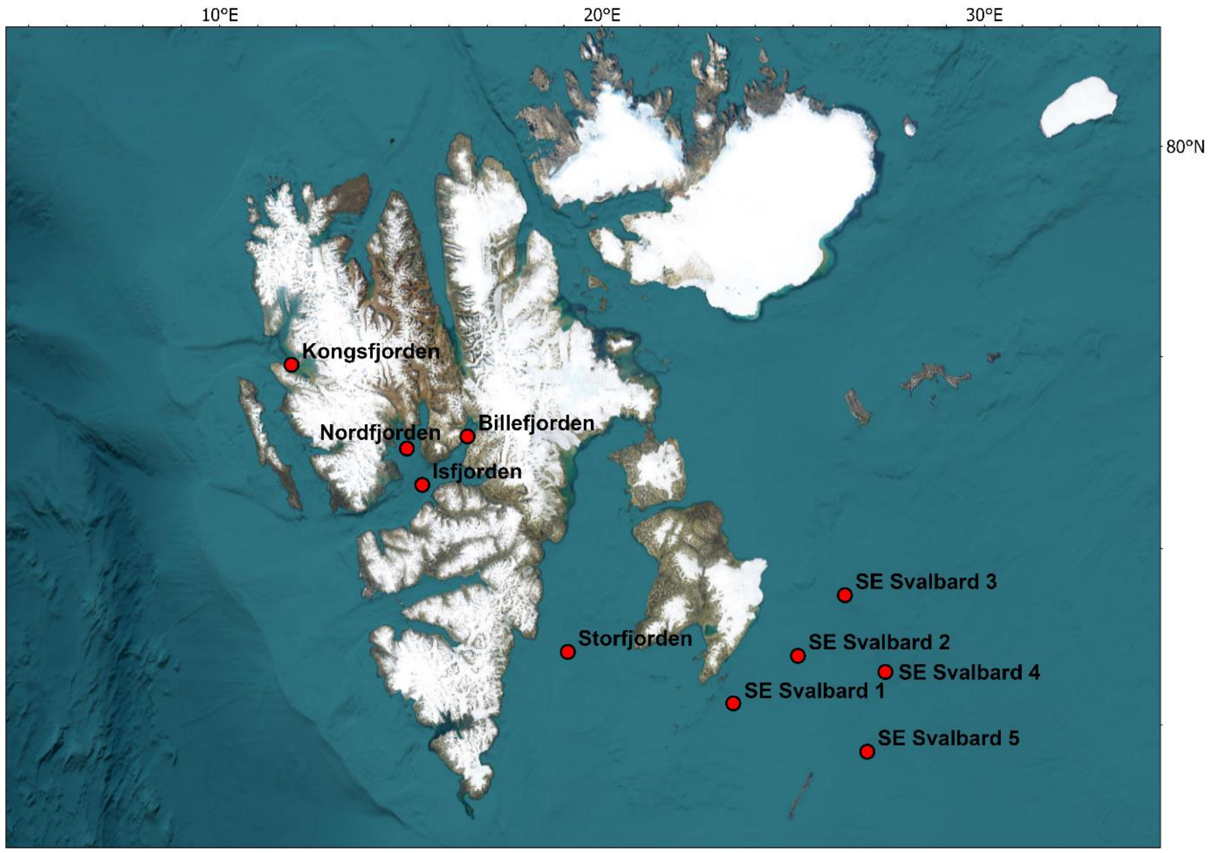


Figure 4. Map of the sampling stations in **Paper III**. The study sites were classified as western stations (Kongsfjorden, Nordfjorden, Billefjorden and Isjorden) and eastern stations (Storfjorden and Southeast Svalbard sites 1-5). Map source: Earthstar Geographics. Figure from Paper III.

3.2 Fieldwork and data collection

The primary tool used for data collection in **Papers I and II** was an uncrewed surface vehicle (USV). The model "Otter", manufactured by Maritime Robotics AS (Trondheim, Norway), is an electric catamaran measuring 200 x 108 x 106 cm and equipped with two electric thrusters. The USV was outfitted with a forward-facing camera, a winch, a frontal attachment with a CTD mount, and a scientific sonar system (Figure 5). It was remotely controlled via broadband communication radio (Direct link 5150 – 5875 MHz with a 2 km line-of-sight range) from a nearby vessel, and its onboard Global Navigation Satellite System (GNSS) was used for georeferencing the collected data.

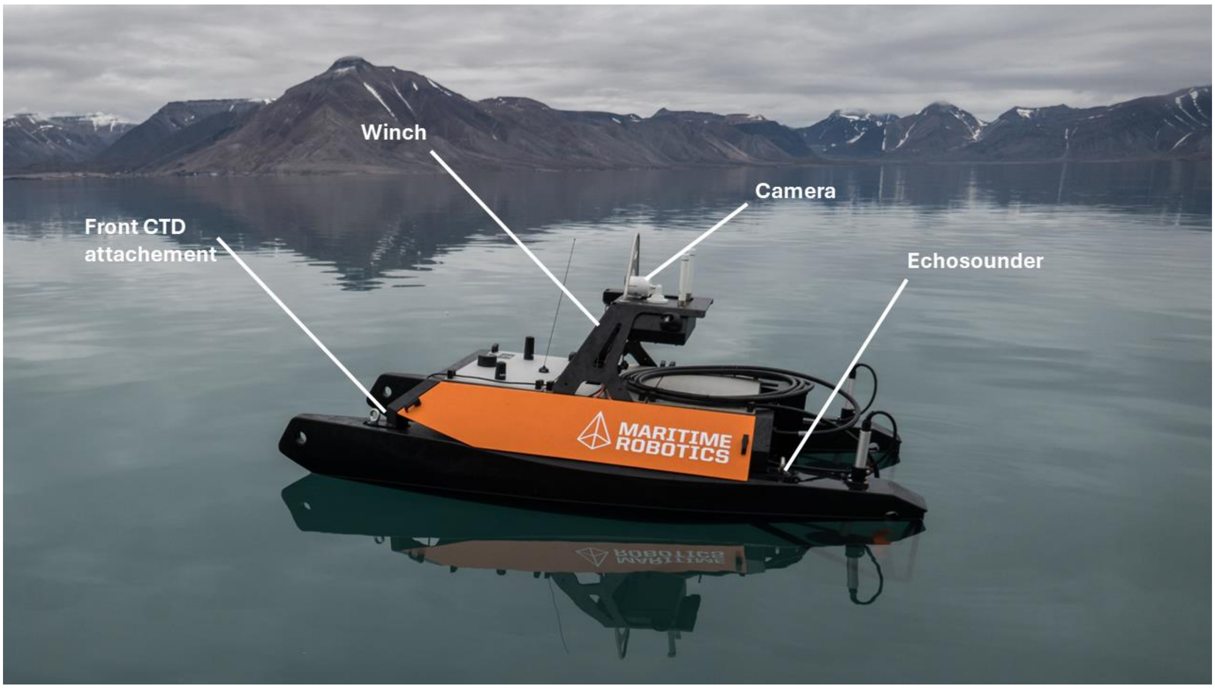


Figure 5. Otter USV in Billefjorden during fieldwork.

The USV was operated through the vehicle control station (VCS), which was installed on a laptop and used onboard UNIS' boats (Figure 6). The VCS allows for both pre-programmed paths and manual driving, with all settings for the USV and sonar system adjustable remotely. A live feed from the camera enabled safe navigation, avoiding obstacles such as ice floes and rocks. The USV was deployed by hand in 2021 and 2022 from Polarcirkel boats, and in 2023 it was deployed using an A-frame winch onboard the vessel *Hanna Resvoll*.

Sensor logging

S	Name	Last RX	Size	Rate
!	DT-X	11:40:54	14.85 MB	68.91 kB/s
	GNSS	11:40:54	5.93 MB	3.69 kB/s

Vehicles: Selected vehicle Otter-33
Available vehicles 1
Channel/USV: Otter-Radio

Bat 2 86 %
Bat 3 87 %

Waypoint info:
Current waypoint
Number 13
Position 78° 40.0221' N 016° 55.5061' E
Leg speed 3.0 kn
Leg length 0.13 NM (237 m)
Distance to waypoint 103 m
ETA to waypoint 1 m, 7 s
Plan name 2023 GLA
Distance left 1.55 NM (2875 m)
ETA 31 m, 7 s

Energy 87 %
Power 375.4 W
Pos. 78° 39.9901' N 016° 55.2541' E
Depth (DUK) 39.7 m

Mode WAYPOINT
SOG 3.0 kn
COG 059.1 °
Yaw --- °
Vel. 3.0 kn
Course --- °
Heading --- °

Figure 6. Snapshot of the vehicle control station (VCS) during sampling with the USV. The image shows the transect path followed by the USV and the live view from the camera.

The main scientific instrument used with the USV was a downward-facing scientific split-beam echosounder (BioSonics DT-X Extreme, BioSonics, Seattle, USA). The echosounder, mounted at the back of the USV, operated at a frequency of 200 kHz with a beam angle of 6.9°x 6.9°, a ping rate of 5 Hz, and a pulse duration of 0.4 ms. While recording the acoustic data, the USV was driven at an approximate speed of 3 knots. The echosounder was calibrated prior to the field season using the standard sphere method (Demer et al., 2015). A frequency of 200 kHz was selected as it strikes a balance between providing sufficient detail for detecting pelagic fish and zooplankton while still being able to reach the seafloor in our coastal, relatively shallow study areas. This allowed us to use the same frequency to study both pelagic organisms and benthic habitats, making it suitable for the dual focus of these studies. The ping rate of 5 Hz was chosen as it is a commonly used setting for detailed studies of underwater features, allowing sufficient temporal resolution to capture fine-scale variations in the water column and along the seafloor.

Additional instruments included a Valeport SWiFT Turbidity CTDplus (Valeport Ltd., Totnes, UK) for collecting temperature, salinity, and turbidity data. The CTD was mounted at the front of the USV for continuous surface measurements and deployed with the winch to collect water column data. A Paralenz Vaquita drop-camera (Paralenz, Rødovre, Denmark) was attached to the winch to capture seafloor images at 1.5 m above the bottom, which were cross-referenced with acoustic data to validate macroalgal coverage detection. Baited remote underwater cameras (BRUV) were used for further validation and benthic habitat characterization was included in **Paper II**. Additionally, Blueye remotely operated vehicles (ROVs; Blueye Robotics, Trondheim, Norway) were used to complement acoustic data with visual observations of the seafloor, although the footage was not included in the papers due to its qualitative nature.

3.2.1 Fieldwork for Papers I and II

For **Paper I**, data collection took place in July and August 2021 and August 2022. This included acoustic data, CTD surface measurements, underwater images from the USV setup, BRUV deployments, and CTD water column sampling in Billefjorden. For **Paper II**, data were collected in August 2022 and August 2023, focusing on acoustic data from the USV and CTD water column sampling. A large survey of Billefjorden's coastline took place in the summer of 2021 to collect seafloor mapping data. The USV was run along the coastline at 3 knots, collecting acoustic, CTD, and drop-camera data, with a focus on depths suitable for macroalgal growth (1-20 m, mean of 7 m). Over four days, 50 km of coastline were surveyed, including shallow areas (< 5 m depth) and at both the tidewater and land-terminating glacier fronts. Data from the first day (approximately 10 km of the southeastern section) were excluded due to poor weather and wavy conditions affecting the quality of the acoustic data. CTD water column measurements were conducted at the three study stations.

For **Paper II**, the USV was run in transects perpendicular to the shore at each of the three study sites, covering depths of 24-42 m and a mean depth of 30 m. Transects were located 200-800 m away from the shore to sample pelagic communities in shallow coastal areas. Sampling for fish using baited traps was attempted but was unsuccessful due to challenging weather conditions. Instead, BRUV recordings of 1 hour at each station were used to document benthic and demersal habitats.

3.2.2 Fieldwork for Paper III

For **Paper III**, data was collected in November 2022 during the "Polar Cod Connectivity Cruise" onboard R/V *G.O. Sars*. A hull-mounted Simrad EK80 scientific echosounder (Kongsberg, Norway) was used to collect the acoustic data at 18, 38, 70, 120, and 200 kHz. Acoustic data were recorded continuously throughout the cruise. A Sea-Bird SBE 9 CTD collected environmental data and sound speed measurements to calibrate the acoustics. A Harstad pelagic trawl was deployed to sample fish density and community composition at each study site.

3.3 Hydroacoustic system

Split-beam echosounders are a type of single-beam sonar designed to provide precise and detailed measurements of marine life and underwater structures. Unlike multibeam echosounders, which use multiple transducers to cover a wide swath, split-beam echosounders use a specialized transducer divided into several segments. This design allows the device to emit and receive sound waves from different angles, making it particularly effective for detecting and measuring fish abundance, size distribution, and swimming behaviour (Simmonds & MacLennan, 2005).

While multibeam echosounders are commonly used for detailed benthic and bathymetric mapping due to their ability to cover large areas (Brown et al., 2011), split-beam echosounders have also been successfully employed to map seafloor features and macroalgal distribution in the Arctic (Kruss et al., 2017; Wiktor et al., 2022). Their ability to provide precise target detection makes them suitable for mapping even a patchy distribution of macroalgae. The USV acoustic system was designed to serve as a versatile platform for sampling both pelagic and benthic ecosystems, with a focus on detail and accuracy rather than large-scale coverage. For this reason, a scientific split-beam echosounder was the chosen tool for **Papers I and II.**

3.3.1 Acoustic processing and analyses

Submerged vegetation scatters acoustic signals differently than unvegetated seafloor, and analysing the strength of acoustic echoes allows researchers to identify boundaries between different layers or structures, such as the seafloor and macroalgae (Simmonds & MacLennan, 2005). Accurate detection requires setting appropriate thresholds, and for this study, thresholds of -40 dB for the seafloor and -70 dB for macroalgae detection were selected based on existing literature and validation during field testing (Radomski & Holbrook, 2015; Simmonds & MacLennan, 2005).

For **Paper I**, acoustic data were processed using BioSonics' software Visual Aquatic/Acquisition. For **Papers II and III**, data processing was conducted in Echoview (Echoview Ltd, Tasmania, Australia). Postprocessing and statistical analyses were performed using the R statistical software for **Papers I and II**, and Python was used for **Paper III** (R Core Team, 2021; Raybaut, 2009). In all papers, the spatial data and maps were processed using ArcGIS (ESRI, 2011).

Box 2: Acoustic parameters used in **Papers I, II and III**

Volume backscattering strength (Sv)

Units: dB (logarithmic) or m^2/m^3 (linear)

Description: A measure of the intensity of sound scattered by a volume of water, providing information on the density of acoustic scatterers (e.g. fish, zooplankton). Acoustic backscattering strength is directly related to biological density (Iida et al., 1996, Simmonds & MacLennan, 2005).

Centre of mass

Units: m

Description: Refers to the average position of acoustic scatterers within a defined volume (e.g. water column), calculated by weighting the position of each scatterer by its backscattering strength (Sv). This metric provides a spatial representation of where the majority of acoustic energy is reflected (Urmy et al., 2012). When applied to the water column, it helps identify the vertical distribution of fish schools and zooplankton aggregations.

Inertia

Units: m^2

Description: A measure of the dispersion of acoustic scatterers, calculated as the sum of squared distances from the centre of mass. Inertia indicates how concentrated or spread out the scatterers are within the studied volume (Urmy et al., 2012). High inertia reflects a wide distribution of scatterers, while low inertia suggests a more concentrated grouping.

4 Main findings

4.1 Paper I

Acoustic mapping reveals macroalgal settlement following a retreating glacier front in the high Arctic

Marine forests are projected to expand in the Arctic due to climate warming, with increasing water temperatures and sea ice loss facilitating this process (Assis et al., 2022; Krause-Jensen et al., 2020). While macroalgal biomass in the littoral areas of Svalbard has been increasing (Bartsch et al., 2016; Weslawski et al., 2010), little is known about macroalgal expansion following glacier retreat in Arctic fjords. This paper mapped macroalgal presence along a gradient of glacier retreat in Billefjorden, Svalbard, and investigated the roles of turbidity, temperature, and salinity in macroalgal establishment (Figure 7). Additionally, this study developed and tested a protocol using hydroacoustics and remote vehicles for surveying shallow coastal environments and glacier fronts.

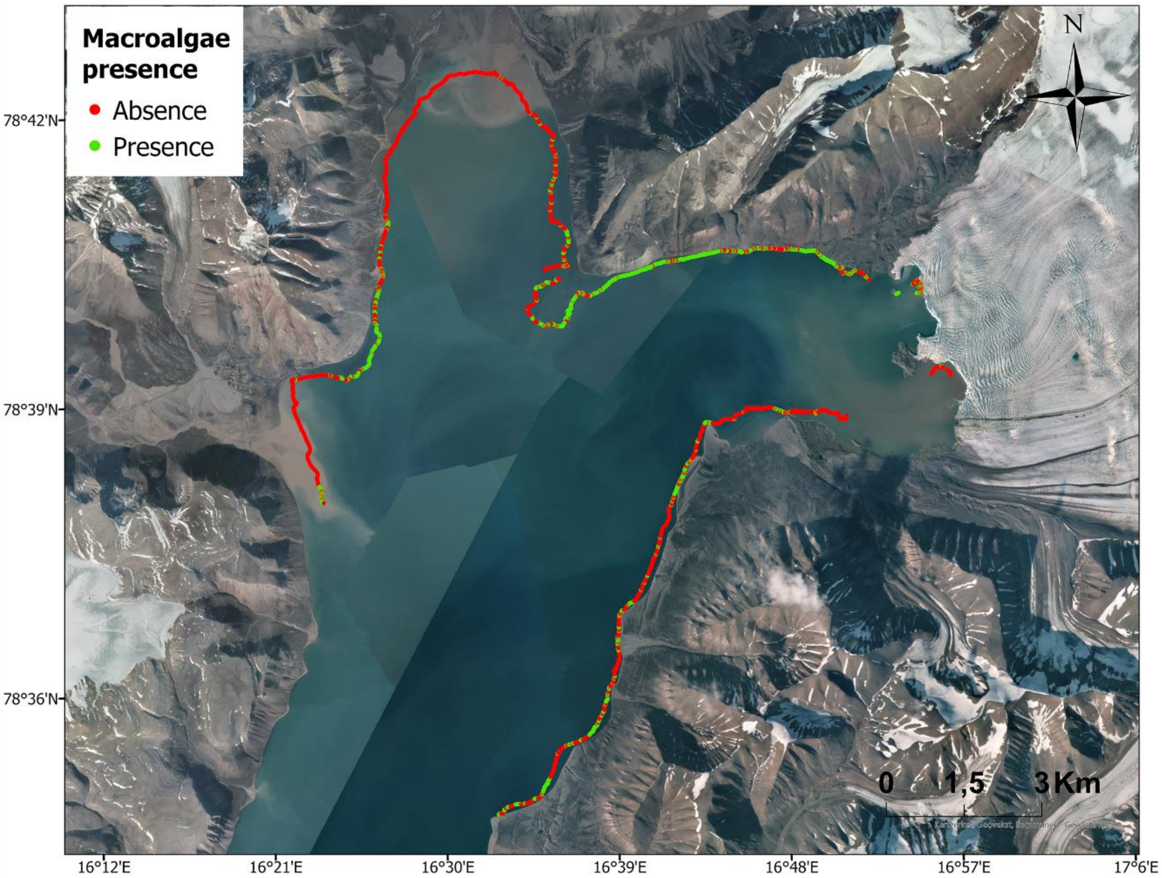


Figure 7. Macroalgal presence/absence (threshold at 50% coverage) along the inner coastline of Billefjorden. Adapted from Figure 4 in Paper I.

Key findings:

- Macroalgal presence was highly heterogeneous along the coastline, with abundant coverage in the northern part of Adolfbukta and virtually no macroalgae in the river bays or near the marine-terminating glacier front.
- Macroalgae were observed at the glacier front which had recently transitioned from marine- to land-terminating, demonstrating the potential for rapid macroalgal settlement on newly available substrate following glacier retreat.
- Temperature, salinity, and turbidity were significantly and negatively correlated with macroalgal presence, but these factors explained only a small portion of the variation. Substrate type and nutrient availability are likely stronger predictors of macroalgal distribution.
- The acoustic algorithm achieved a 93% success rate in identifying macroalgal presence, demonstrating the potential of this approach for efficient and sustainable surveying of coastal ecosystems.

4.2 Paper II

Loss of pelagic fish and zooplankton density associated with subglacial upwelling in high Arctic estuaries may be mitigated by benthic habitat expansion following tidewater glacier retreat

Tidewater glacier fronts are hotspots of pelagic productivity due to subglacial upwelling, which circulates nutrient-rich bottom waters and supports dense fish and zooplankton communities (Hop et al., 2023). As glaciers retreat and transition from marine- to land-terminating, this upwelling ceases, leading to declines in pelagic productivity (Hopwood et al., 2020; Meire et al., 2017). This study investigated pelagic density and vertical distribution along a gradient of glacier retreat in Billefjorden, Svalbard, and explored how cryosphere-related environmental conditions influence fish and zooplankton density (Figure 8). Additionally, a sustainable protocol for using hydroacoustics and autonomous vehicles was developed for studying the pelagic environment in these challenging areas.

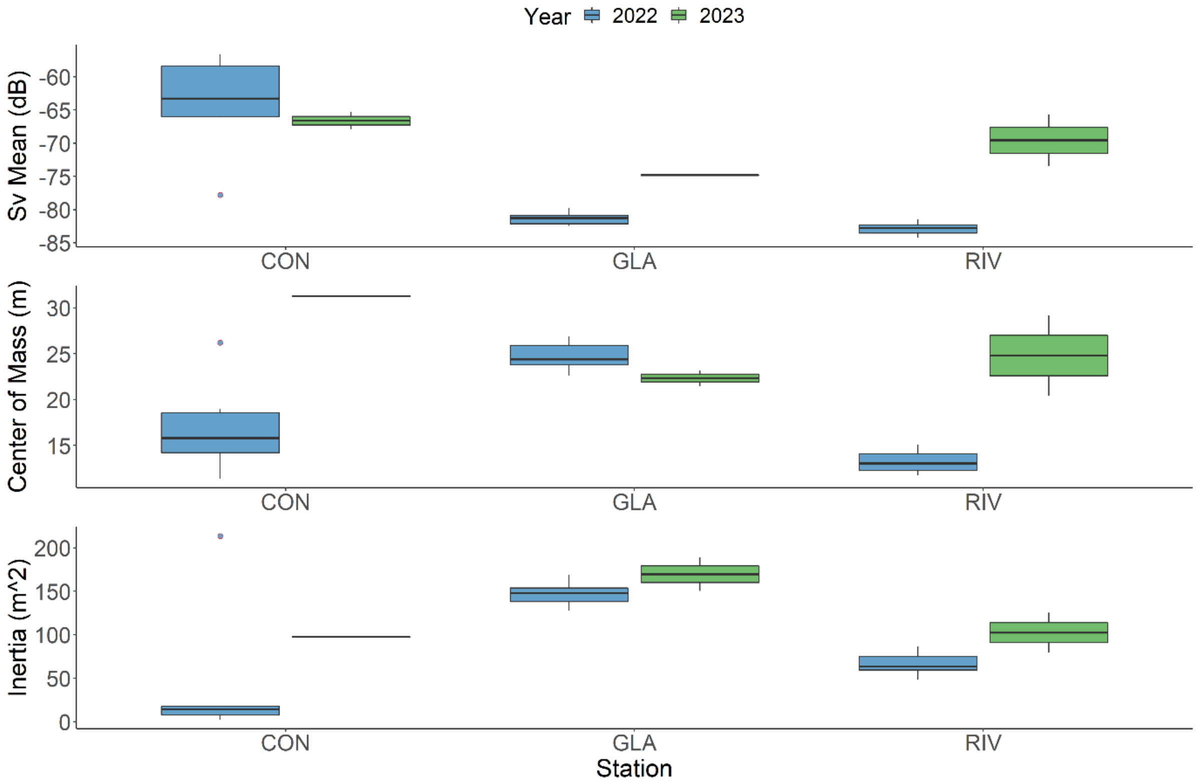


Figure 8. Differences in backscattering strength (Sv), centre of mass and inertia among the three study sites (recently land-terminating glacier front – GLA, river bay with influx from inland glaciers – RIV, and reference location – CON) in 2022 and 2023. Figure 4 from Paper II.

Key findings:

- Pelagic density was lowest at the recently transitioned land-terminating glacier front (GLA) and highest at the site with minimal glacial input (CON).
- The CON site, characterized by dense kelp beds, exhibited large pelagic aggregations and a dynamic environment. The rich demersal habitat likely contributed to the high pelagic density.
- Oceanographic factors explained little of the variation, suggesting that other factors, such as habitat complexity and benthic-pelagic coupling, play a more significant role in shaping the local pelagic systems.
- Hydroacoustics and autonomous vehicles proved to be powerful tools for studying pelagic communities in retreating glacier fronts and shallow coastal areas.

4.3 Paper III

Borealization of pelagic fish communities in the high Arctic during the polar night

The northward expansion of temperate species into the Arctic has significant implications for marine ecosystems, introducing competition and predation pressures for Arctic species while creating new opportunities for fisheries. In Svalbard, Atlantic species such as cod, haddock, and herring have become increasingly prevalent, while potentially displacing key Arctic species like polar cod (Fossheim et al., 2015; Misund et al., 2016). The polar night is a typically understudied period, and it is uncertain how the extreme light regime acts as a seasonal barrier to borealization. This study investigated fish community composition, pelagic density and vertical distribution across the western, more Atlantic-influenced region and the eastern, more Arctic-influenced region in Svalbard during the polar night, and compared the representation of boreal species in fish communities between these regions (Figure 9).

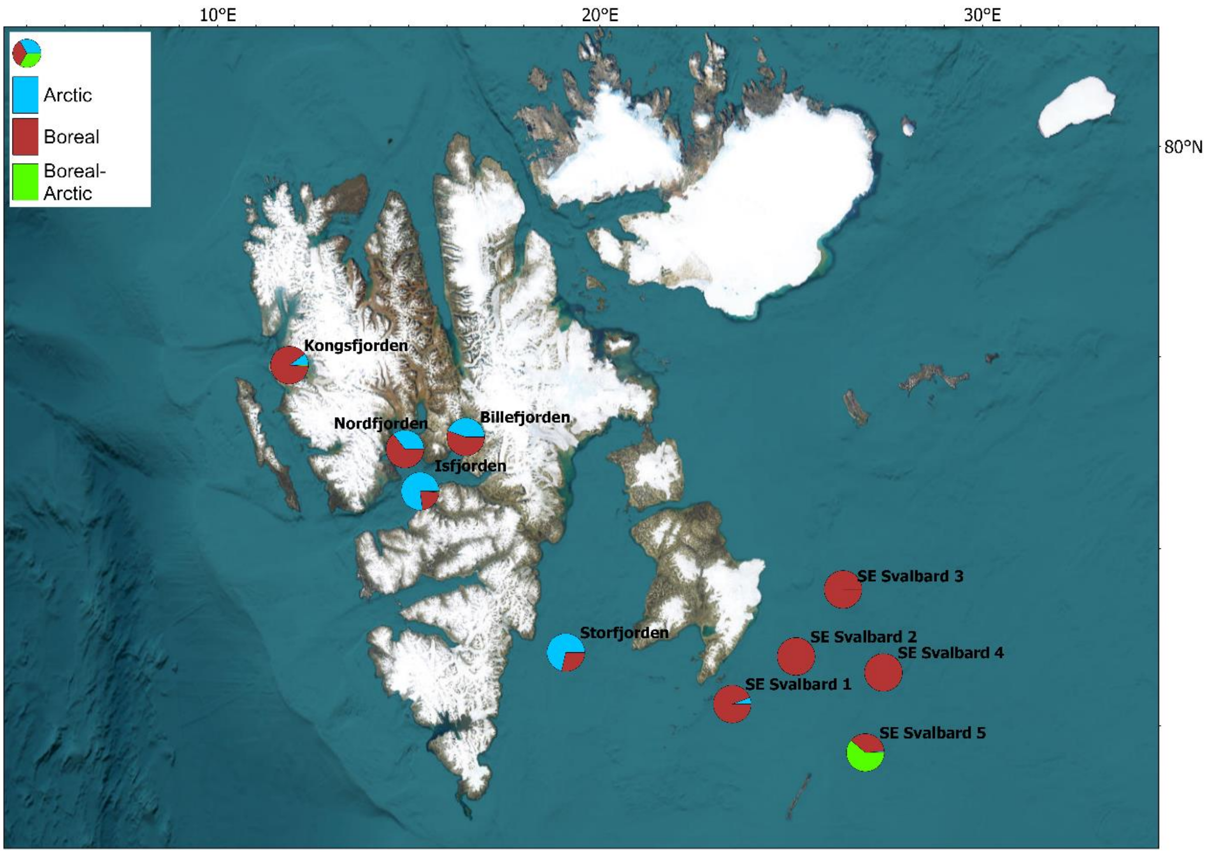


Figure 9. Spatial distribution of fish community composition across sampling stations. Pie charts represent the proportions of Arctic (blue), boreal (red) and boreal-Arctic (green) fish species caught at each station based on fish density values. Figure 5 from Paper III.

Key findings:

- Distinct spatial patterns were observed, with western fjords exhibiting lower pelagic densities but higher species diversity compared to eastern sites, which were dominated by schooling species such as herring and capelin.
- Western fjords showed a deeper centre of mass, indicating a demersal-dominated system, while eastern sites exhibited a shallower, pelagic-dominated system.
- Despite some differences in community composition and vertical distribution, the representation of boreal species in fish communities was not significantly different between western and eastern sites. Boreal species, including Atlantic cod, haddock, and herring, were found at nearly all stations, demonstrating their ability to persist under the extreme light and temperature conditions of the polar night.
- These findings suggest that boreal species are present year-round, as the polar night does not act as a strong seasonal barrier to borealization, potentially leading to enhanced predation and competition pressures on Arctic species.

5 Discussion

Arctic marine ecosystems are undergoing significant changes driven by climate warming, with cascading effects across physical and biological dimensions. Diminishing sea ice cover, retreating glaciers, and altered oceanographic conditions are reshaping both the marine and terrestrial environments, with implications for biodiversity, ecosystem functioning and human activities. This thesis presents three interconnected studies that explore the ecological impacts of glacier retreat and borealization in Arctic fjords, focusing on macroalgal expansion, pelagic density and the role of the polar night as a seasonal barrier to borealization. Together, these studies provide insights into the intricate interactions and interplay between physical and biological processes in a rapidly changing Arctic, while simultaneously showcasing the strength of sustainable, sophisticated and science-driven research technologies.

5.1 Macroalgal expansion and ecosystem engineering in Arctic fjords

Paper I sets the stage in characterising the coastline of an Arctic fjord and highlights the potential for macroalgal expansion following glacier retreat. Billefjorden, with its diverse coastal features including marine- and land-terminating glaciers and river bays, served as a natural laboratory to study how varying degrees of glacial and terrestrial input influence macroalgal settlement.

Macroalgae are ecosystem engineers, contributing to carbon sequestration, nutrient cycling and habitat provision for fish and invertebrates (Filbee-Dexter et al., 2019; Smale et al., 2013; Teagle et al., 2017), and understanding their shifts in distribution is critical for ecosystem management. Their expansion in the Arctic has been widely reported (Assis et al., 2022; Bartsch et al., 2016; Krause-Jensen & Duarte, 2014), as well as in newly ice-free areas in Antarctica (Deregibus et al., 2023; Quartino et al., 2013), and these findings are consistent with the results of **Paper I** which revealed rapid macroalgal colonisation at the recently land-terminating glacier front. However, macroalgal settlement is highly dependent on environmental conditions, particularly substrate type and sedimentation rates (Düsedau et al., 2024; Niedzwiedz & Bischof, 2023), which vary greatly both regionally and seasonally in the Arctic.

Paper I found that macroalgal presence was limited in areas with high sedimentation, such as the river bay and the marine-terminating glacier front, where soft-bottom substrate and reduced light penetration hinder settlement and growth. In contrast, the recently land-terminating glacier front supported macroalgal growth, likely due to the availability of rocky substrate and comparatively reduced sediment influx. Turbidity measurements from **Paper I** and other studies (Szeligowska et al., 2021), as well as satellite imagery, show a large sediment plume at the marine-terminating glacier front, while the northern front is partially sheltered from the sediment influx due to fjord circulation patterns and a small peninsula that separates both sides of the glacier.

Environmental measurements such as temperature, salinity and turbidity explained little variation in macroalgal presence. This may be because these parameters vary greatly on a seasonal scale, while macroalgae are sessile organisms that persist over longer timescales. As a result, factors like substrate type and deposition rates are likely more critical in determining macroalgal settlement and growth. ROV surveys confirmed the presence of macroalgae at the recently land-terminating glacier front, and, while kelp was observed with substantial sediment accumulation on its laminas, turbidity was substantially lower than at the marine-terminating side. This suggests that macroalgae can thrive even under heightened sedimentation rates, provided other conditions, such as substrate availability and light penetration, are favourable.

Therefore, **Paper I** highlights how the interplay between sedimentation, substrate type, and hydrodynamics is critical in shaping macroalgal distribution. Fjord systems with steep slopes, rocky substrates and strong currents may experience less sediment settlement, creating favourable conditions for macroalgal growth. In contrast, fjords with gentle slopes and stagnant waters may see higher sediment deposition hindering macroalgal establishment. While warming temperatures and newly available substrates from glacier retreat provide opportunities for macroalgal expansion, increased melting rates and higher sedimentation associated with climate change may limit this growth. For example, models have predicted significant northward expansions of macroalgae in the Arctic (Assis et al., 2022; Krause-Jensen & Duarte, 2014), but these predictions may overestimate the scale of this expansion. While increased macroalgal biomass has been observed in Svalbard (Bartsch et al., 2016; Weslawski et al., 2010), field observations in other regions, such as subarctic Canada and the northwest Atlantic, have shown relatively stable kelp abundance over decades despite warming temperatures (Adey & Hayek, 2011; Merzouk & Johnson, 2011). This discrepancy suggests that local environmental conditions and topography, which influence turbidity and light penetration, likely play a more significant role than changes in temperature in driving macroalgal settlement and growth.

5.2 Shifts in pelagic density following glacier retreat

Building on the findings of **Paper I**, **Paper II** investigated pelagic density and vertical distribution of fish and zooplankton along a gradient of glacier retreat in Billefjorden. The study revealed that pelagic density was lowest near the land-terminating glacier front and highest at the site with minimal glacial input, where dense macroalgal beds supported a rich benthic and demersal habitat. BRUV footage and complementary ROV surveys revealed dense macroalgal cover and a rich benthic and demersal habitat at the site furthest from the glacier and river bays, with numerous fish, crabs, and mysid shrimps observed, contrasting with the sparse presence of organisms at the glacier and river sites.

While the marine-terminating glacier front was not sampled in this study due to logistical constraints, the transition process from marine- to land-terminating glaciers and the associated disappearance of subglacial upwelling has been widely studied (Carroll et al., 2015; Truffer & Motyka, 2016). Tidewater glacier fronts are foraging hotspots due to the upwelling of nutrient-rich waters and circulation of zooplankton to the surface, increasing their availability to predators such as seabirds, marine mammals, and fish (Hop et al., 2023; Lydersen et al., 2014; Urbanski et al., 2017). As glaciers retreat and transition from sea to land, this upwelling ceases, leading to declines in pelagic productivity. Such declines may disrupt energy transfer within the food web, forcing predators to shift their distribution or seek alternative feeding areas (Lydersen et al., 2014). The decrease in key foraging fish like the polar cod, already under pressure from rising temperatures, habitat loss and increased predation and competition (Geoffroy et al., 2023), could amplify these disruptions and lead to altered predator-prey dynamics.

Paper II highlights the potential for benthic and demersal habitat expansion, driven by macroalgal settlement following glacier retreat, to mitigate the loss of pelagic productivity. Macroalgal beds provide habitat and food for benthic invertebrates and demersal fish, which in turn may support higher trophic levels (Bertocci et al., 2015; Norderhaug et al., 2005; Steneck et al., 2002). However, this transition from pelagic- to benthic-driven productivity is contingent on optimal conditions for macroalgal growth, including low sedimentation and suitable substrates.

The implications of this transition extend beyond habitat provision. Primary production in Arctic seas is primarily fuelled by ice algae and phytoplankton blooms (Søreide et al., 2006), but these are highly seasonal. Macroalgae may provide a supplementary carbon source, particularly in coastal systems, where they contribute to food web stability and biodiversity (McMeans et al., 2013; Renaud et al., 2015). While higher trophic levels primarily rely on phytoplankton-driven production, macroalgae-derived carbon also plays a role in fuelling Arctic food webs and is utilised by fish and marine mammals (McMeans et al., 2013; Renaud et al., 2011). Additionally, macroalgae can subsidise deep-water food webs through detritus, further enhancing their ecological importance (Renaud et al., 2015).

A recent study examining benthic faunal communities in Billefjorden, conducted at the same sites as **Papers I and II**, found that glacier-influenced locations had lower density and faunal abundance compared to the reference site, likely due to high sedimentation rates limiting food availability near glacier outputs (van der Kamp et al., 2025). These findings align with **Paper II**, emphasising the impacts of sedimentation at retreating glacier fronts on both benthic and pelagic ecosystems, while highlighting the potential for benthic habitat expansion to support richer communities in areas with reduced glacial input.

The ability of Arctic species to utilise multiple prey types is critical in highly seasonal environments, where resource availability fluctuates dramatically. This dietary plasticity may allow higher trophic levels to acclimate to decreased zooplankton biomass resulting from the loss of glacial upwelling by shifting to benthic herbivores and detritivores that thrive in macroalgal habitats. An increase in macroalgal coverage is associated with higher biodiversity and more complex trophic pathways (Kortsch et al., 2012), and understanding the coupling between macroalgal-driven benthic systems and pelagic organisms is essential for predicting the resilience and adaptability of Arctic ecosystems to ongoing environmental changes.

5.3 Northward shift of Atlantic species into the Arctic

Paper III expanded the scope of this thesis by investigating borealization of pelagic fish communities across Svalbard during the polar night. The study revealed distinct spatial patterns in pelagic density and community composition, with western fjords exhibiting lower densities but higher species diversity compared to eastern sites, which were dominated by schooling species like herring and capelin. Despite these spatial differences, boreal species were found at nearly all sites, and similar levels of borealization were exhibited across Svalbard, suggesting that the extreme light regime of the polar night does not act as a strong seasonal barrier to borealization.

Atlantic cod and haddock have been shown to feed actively during the polar night, demonstrating their ability to forage effectively despite low-light conditions (Bengtsson et al., 2024; Larsen et al., 2023). Polar cod exhibit dietary flexibility by shifting their diet according to prey availability and seasonal changes in water masses (Cusa et al., 2019; Schaafsma et al., 2024). While there is relatively low dietary overlap between Atlantic cod, haddock, and polar cod, significant predation by Atlantic cod on polar cod has been documented (Bengtsson et al., 2024; Larsen et al., 2023; Renaud et al., 2012). This increased predation pressure is expected to impact the persistence of polar cod in Svalbard waters, potentially altering predator-prey dynamics and further stressing Arctic ecosystems already under pressure from climate change.

Paper III revealed catch peaks of Atlantic herring and capelin in eastern Svalbard sites. While capelin are commonly found in the Barents Sea, herring are generally associated with warmer Atlantic waters and are expected to increase their presence in northern latitudes as Atlantic water inflow intensifies (Hollowed et al., 2013). These forage fish are integral components of the marine food web, playing crucial roles in energy transfer to higher trophic levels (Dolgov, 2002; Eriksen et al., 2017). The northward expansion of forage fish like herring may provide alternative prey for predators that rely on polar cod and capelin, potentially mitigating some of the trophic effects of polar cod declines. However, this will depend on the adaptability of predators, seasonal movement patterns, and differences in energy content among forage fish species. Conversely, the expansion of herring may negatively affect other fish species, as high abundances of herring in the Barents Sea have been linked to declines in capelin biomass, primarily due to recruitment failure caused by young herring preying on capelin larvae (Dalpadado et al., 2002; Eriksen et al., 2017).

Differences in the vertical distribution of pelagic density were also observed between western and eastern sites, with western fjords exhibiting a deeper centre of mass (i.e. deeper distribution of organisms in the water column). These differences are likely influenced by the geographical context, as western fjords feature more complex topography with deep basins and rich demersal habitats, while eastern sites are situated in open ocean environments that favor pelagic schooling species. The interplay between topography and water mass distribution likely shapes the observed differences in community composition and vertical distribution.

The findings and associated implications from **Papers I and II** suggest that macroalgal expansion may facilitate the northwards range shift of temperate species like the Atlantic cod and saithe (*Pollachius virens*), by providing habitat and shelter (Cote et al., 2002; Norderhaug et al., 2005). Kelp beds offer refuge and feeding grounds for various fish, which may be particularly important during the Arctic summer, allowing them to evade predators while remaining near their foraging grounds in surface waters. In **Paper II**, BRUV footage captured multiple shorthorn sculpin (*Myoxocephalus scorpius*) in kelp forests, and these fish are known to consume pelagic prey, benthic invertebrates and small demersal fish (Norderhaug et al., 2005). Similarly, Atlantic cod, which feed on benthic and demersal invertebrates during the polar night, could benefit from enhanced foraging opportunities provided by a richer benthic habitat. Consequently, species like the shorthorn sculpin and Atlantic cod may thrive with increased macroalgal abundance.

Ultimately, the ability of boreal species to acclimate to Arctic conditions in the short term and adapt over longer timescales will be crucial in determining the extent to which Atlantic species can expand into polar regions. While the polar night does not appear to act as a strong seasonal barrier to borealization, and macroalgal expansion may lessen the risk of predation during the midnight sun, the broader ecological implications of these shifts will depend on the capacity of Arctic ecosystems to adapt to increased competition, predation, and changes in trophic dynamics.

5.4 Autonomous vehicles and hydroacoustics

Hydroacoustics proved efficient for mapping macroalgal coverage and pelagic density and vertical distribution, offering high-resolution data without physically disturbing the environment, and this was highlighted by the high success rate in detecting macroalgae in **Paper I**. The integration of hydroacoustics with autonomous vehicles was central to **Papers I and II**, enabling the investigation of both benthic and pelagic ecosystems in challenging Arctic environments. These methods provided a sustainable and effective approach to data collection, particularly in shallow coastal areas and glacier fronts, which remain understudied as traditional methods face logistical and safety challenges. As **Paper III** focused on central fjord systems and offshore locations, a ship-based acoustic survey utilising a multifrequency echosounder was the optimal methodology.

There are also limitations and challenges to using autonomous vehicles and hydroacoustics. For instance, the relatively narrow beam of the split-beam echosounder used in **Papers I and II** limited area coverage, requiring multiple transects to achieve comprehensive mapping. Attempts to map macroalgal coverage in larger areas perpendicular to the shoreline encountered issues with slope shading, where steep slopes affected echo shapes and acoustic backscatter (von Szalay & McConnaughey, 2002). Ground-truthing of the acoustic data, as done in these studies through underwater cameras, is critical for accurately evaluating the data.

Moreover, small USVs like the one used in these studies are more sensitive to challenging weather conditions and waves, which can affect the collection of acoustic data and resulted in some discarded data for **Paper I**. Additionally, USVs generally lack the capability to collect biological samples, such as zooplankton and fish. While it is possible to collect these data separately, such as using nets and traps, this is challenging in extreme environments like glacier fronts and in unpredictable Arctic conditions. These cutting-edge systems often require extensive technical support and significant time for testing and troubleshooting, as was the case prior to each field season in this study.

Combining the use of autonomous vehicles with sampling from traditional research vessels can mitigate these limitations and maximise data quality and coverage. For example, while the USV was effective for small-scale studies in **Papers I and II**, the use of a research vessel in **Paper III** allowed for broader spatial comparisons. This complementary approach demonstrates the potential of integrating autonomous vehicles with traditional sampling to address both fine-scale and large-scale research questions.

6 Conclusions and future perspectives

This thesis provides novel insights into the ecological transitions occurring in Arctic marine ecosystems in response to climate change, with a focus on macroalgal expansion and shifts in pelagic systems associated with glacier retreat, and the borealization of fish communities in Svalbard. By integrating hydroacoustics and autonomous vehicles, this work also demonstrates the potential of sustainable and non-invasive research methodologies in challenging environments. Together, the findings highlight the interplay between physical and biological changes in the Arctic and their implications for ecosystem dynamics and management.

The expansion of macroalgae into newly available substrates following glacier retreat is a key finding of this thesis. Macroalgae, as ecosystem engineers, play a critical role in carbon sequestration, nutrient cycling, and habitat provision. The results from this thesis indicate that macroalgal settlement is highly dependent on local environmental conditions, such as substrate type and sedimentation rates, which are shaped by glacier retreat and fjord topography. While warming temperatures and reduced sea ice scouring create opportunities for macroalgal growth, increased sedimentation associated with glacier melting may limit this expansion. These findings highlight the need for comprehensive mapping of Arctic coastlines, incorporating factors such as substrate availability, sedimentation rates, and light penetration, to better predict macroalgal distribution under future climate scenarios. Furthermore, long-term monitoring of macroalgal colonisation and growth rates in newly exposed substrates will provide valuable insights into their role in local and global carbon dynamics, which is increasingly relevant in the context of climate change and the mitigation of carbon emissions.

Building on this, this study examines the potential for benthic habitat expansion to mitigate the loss of pelagic productivity associated with the transition from marine- to land-terminating glaciers. This study reveals that areas with dense macroalgal beds support higher pelagic density, suggesting a potential shift from pelagic- to benthic-driven productivity in certain Arctic fjords. This transition has significant implications for trophic web dynamics, as macroalgal habitats provide food and shelter for benthic invertebrates and demersal fish, which in turn support higher trophic levels. However, the extent to which Arctic species can adapt to these changes remains uncertain, emphasizing the need for further research on benthic-pelagic coupling and the resilience and plasticity of Arctic food webs.

At a broader scale, this thesis showcases that the borealization of Arctic marine ecosystems may not be constrained by the extreme light regime of the polar night. Boreal species, such as Atlantic cod, herring and haddock, were found across multiple sites across Svalbard, indicating their ability to persist under Arctic winter conditions. These findings challenge the assumption that the polar night acts as a seasonal barrier to borealization and highlight the potential for increased competition and predation pressures on endemic Arctic species. As key endemic Arctic forage fish like polar cod face population declines, the ability of higher trophic levels to adapt by feeding on boreal newcomers will be pivotal to shaping ecosystem resilience and stability of Arctic food webs.

The implications of these findings extend beyond ecological understanding to inform conservation and management strategies. The northward expansion of commercially valuable species presents both opportunities and challenges for fisheries. As Arctic ecosystems face multiple stressors, including climate change and increased anthropogenic activity associated with easier accessibility into polar areas, adaptive management strategies will be essential to balance economic interests with conservation goals. Long-term monitoring and research programs will play a critical role in tracking these changes and ensuring the sustainable use of Arctic marine resources.

Moreover, this thesis highlights the value of integrating hydroacoustics with autonomous vehicles for studying Arctic marine ecosystems. These methods provide a sustainable and efficient approach to data collection, particularly in understudied environments like glacier fronts and shallow coastal areas, which are difficult to access. While challenges remain, such as the sensitivity of autonomous vehicles to weather conditions and the limitations in collecting biological data, the successful application of these technologies in this work demonstrates their potential to advance Arctic research. By reducing the environmental footprint of scientific activities, these methods align with the principles of sustainability and offer a promising way forward to studying and managing ecosystems in a rapidly changing world.

To conclude, this thesis emphasizes the complexity of ecological transitions in Arctic marine ecosystems and the importance of interdisciplinary approaches to understanding and managing these changes. By linking localized processes, such as macroalgal expansion and pelagic-benthic shifts, with broader regional patterns of borealization, this work provides a comprehensive perspective on the impacts of climate change in the Arctic. As the region continues to warm at an unprecedented rate, the insights and methodologies developed in this thesis will contribute to the ongoing efforts to monitor, understand, and protect Arctic marine ecosystems.

References

Adey, W. H., & Hayek, L.-A. C. (2011). Elucidating Marine Biogeography with Macrophytes: Quantitative Analysis of the North Atlantic Supports the Thermogeographic Model and Demonstrates a Distinct Subarctic Region in the Northwestern Atlantic. *Northeastern Naturalist*, *18*(mo8), 1–128. https://doi.org/10.1656/045.018.m801

Allan, B. J. M., Browman, H. I., Shema, S., Skiftesvik, A.-B., Folkvord, A., Durif, C. M. F., & Kjesbu, O. S. (2022). Increasing temperature and prey availability affect the growth and swimming kinematics of Atlantic herring (Clupea harengus) larvae. *Journal of Plankton Research*, *44*(3), 401–413. https://doi.org/10.1093/plankt/fbac014

Assis, J., Serrão, E. A., Duarte, C. M., Fragkopoulou, E., & Krause-Jensen, D. (2022). Major Expansion of Marine Forests in a Warmer Arctic. *Frontiers in Marine Science*, *9*, 850368. https://doi.org/10.3389/fmars.2022.850368

Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H., & Wiencke, C. (2016). Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biology*, *39*(11), 2021–2036. https://doi.org/10.1007/s00300-015-1870-1

Bengtsson, O., Lydersen, C., Kovacs, K. M., & Lindström, U. (2020). Ringed seal (Pusa hispida) diet on the west coast of Spitsbergen, Svalbard, Norway: During a time of ecosystem change. *Polar Biology*, *43*(7), 773–788. https://doi.org/10.1007/s00300-020-02684-5

Bengtsson, O., Lydersen, C., Węsławski, J., Berge, J., & Kovacs, K. (2024). Summer and polar night diets of polar cod Boreogadus saida and Atlantic cod Gadus morhua in Kongsfjorden, Svalbard, Norway. *Marine Ecology Progress Series*, *747*, 117–132. https://doi.org/10.3354/meps14700

Benoit, D., Simard, Y., Gagné, J., Geoffroy, M., & Fortier, L. (2010). From polar night to midnight sun: Photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean. *Polar Biology*, *33*(11), 1505–1520. https://doi.org/10.1007/s00300-010-0840-x

Berge, J., Geoffroy, M., Daase, M., Cottier, F., Priou, P., Cohen, J. H., Johnsen, G., McKee, D., Kostakis, I., Renaud, P. E., Vogedes, D., Anderson, P., Last, K. S., & Gauthier, S. (2020). Artificial light during the polar night disrupts Arctic fish and zooplankton behaviour down to 200 m depth. *Communications Biology*, *3*(1), 102. https://doi.org/10.1038/s42003-020-0807-6

Bertocci, I., Araújo, R., Oliveira, P., & Sousa-Pinto, I. (2015). REVIEW: Potential effects of kelp species on local fisheries. *Journal of Applied Ecology*, *52*(5), 1216–1226. https://doi.org/10.1111/1365-2664.12483

Bhatia, M. P., Kujawinski, E. B., Das, S. B., Breier, C. F., Henderson, P. B., & Charette, M. A. (2013). Greenland meltwater as a significant and potentially bioavailable source of iron to the ocean. *Nature Geoscience*, *6*(4), 274–278. https://doi.org/10.1038/ngeo1746

Blaxter, J. H. S., & Hunter, J. R. (1982). The Biology of the Clupeoid Fishes. In J. H. S. Blaxter, F. S. Russell, & M. Yonge (Eds.), *Advances in Marine Biology* (Vol. 20, pp. 1–223). Academic Press. https://doi.org/10.1016/S0065-2881(08)60140-6

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F.-J. W., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V. E., Walsh, J. E., Overland, J. E., Wang, M., Corell, R. W., Meier, W. N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., & Olsen, M. S. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, *14*(4), 045010. https://doi.org/10.1088/1748-9326/aafc1b

Brown, C. J., Smith, S. J., Lawton, P., & Anderson, J. T. (2011). Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuarine, Coastal and Shelf Science*, *92*(3), 502–520. https://doi.org/10.1016/j.ecss.2011.02.007

Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., Brown, C., Bruno, J. F., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., Kiessling, W., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F. B., Sydeman, W. J., & Richardson, A. J. (2011). The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science*, *334*(6056), 652–655. https://doi.org/10.1126/science.1210288

Carroll, D., Sutherland, D. A., Shroyer, E. L., Nash, J. D., Catania, G. A., & Stearns, L. A. (2015). *Modeling Turbulent Subglacial Meltwater Plumes: Implications for Fjord-Scale Buoyancy-Driven Circulation*. https://doi.org/10.1175/JPO-D-15-0033.1

Carscadden, J. E., & Vilhjálmsson, H. (2002). Introduction. *ICES Journal of Marine Science*, *59*(5), 863–869. https://doi.org/10.1006/jmsc.2002.1283

Cote, D., Ollerhead, L. M. N., Gregory, R. S., Scruton, D. A., & McKinley, R. S. (2002). Activity patterns of juvenile Atlantic cod (Gadus morhua) in Buckley Cove, Newfoundland. *Hydrobiologia*, *483*(1), 121–127. https://doi.org/10.1023/A:1021367225993

Crozier, L. G., & Hutchings, J. A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, *7*(1), 68–87. https://doi.org/10.1111/eva.12135

Cusa, M., Berge, J., & Varpe, Ø. (2019). Seasonal shifts in feeding patterns: Individual and population realized specialization in a high Arctic fish. *Ecology and Evolution*, *9*(19), 11112–11121. https://doi.org/10.1002/ece3.5615

Dalpadado, P., Arrigo, K. R., Hjøllo, S. S., Rey, F., Ingvaldsen, R. B., Sperfeld, E., Dijken, G. L. van, Stige, L. C., Olsen, A., & Ottersen, G. (2014). Productivity in the Barents Sea—

Response to Recent Climate Variability. *PLOS ONE*, *9*(5), e95273. https://doi.org/10.1371/journal.pone.0095273

Dalpadado, P., Bogstad, B., Gjøsæter, H., Mehl, S., & Skjoldal, H. R. (2002). 9 Zooplankton-fish interactions in the Barents Sea. In K. Sherman & H. R. Skjoldal (Eds.), *Large Marine Ecosystems* (Vol. 10, pp. 269–291). Elsevier. https://doi.org/10.1016/S1570-0461(02)80061-1

Dayton, P. K. (1985). Ecology of Kelp Communities. *Annual Review of Ecology, Evolution, and Systematics*, *16*(Volume 16,), 215–245. https://doi.org/10.1146/annurev.es.16.110185.001243

Demer, D. A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., Domokos, R., Dunford, A., Fassler, S., Gauthier, S., Hufnagle, L. T., Jech, J. M., Bouffant, N., Lebourges-Dhaussy, A., Lurton, X., Macaulay, G. J., Perrot, Y., Ryan, T., Parker-Stetter, S., … Williamson, N. (2015). *Calibration of acoustic instruments.* [Report]. International Council for the Exploration of the Sea (ICES). https://doi.org/10.25607/OBP-185

Deregibus, D., Campana, G. L., Neder, C., Barnes, D. K. A., Zacher, K., Piscicelli, J. M., Jerosch, K., & Quartino, M. L. (2023). Potential macroalgal expansion and blue carbon gains with northern Antarctic Peninsula glacial retreat. *Marine Environmental Research*, *189*, 106056. https://doi.org/10.1016/j.marenvres.2023.106056

Dolgov, A. V. (2002). The role of capelin (Mallotus villosus) in the foodweb of the Barents Sea. *ICES Journal of Marine Science*, *59*(5), 1034–1045. https://doi.org/10.1006/jmsc.2002.1237

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science*, *4*(Volume 4, 2012), 11–37. https://doi.org/10.1146/annurev-marine-041911-111611

Drinkwater, K. F. (2005). The response of Atlantic cod (Gadus morhua) to future climate change. *ICES Journal of Marine Science*, *62*(7), 1327–1337. https://doi.org/10.1016/j.icesjms.2005.05.015

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, *3*(11), 961–968. https://doi.org/10.1038/nclimate1970

Duarte, C. M., Middelburg, J. J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, *2*(1), 1–8. https://doi.org/10.5194/bg-2-1-2005

Duggins, D. O., Simenstad, C. A., & Estes, J. A. (1989). Magnification of Secondary Production by Kelp Detritus in Coastal Marine Ecosystems. *Science*, *245*(4914), 170–173. https://doi.org/10.1126/science.245.4914.170

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Dupont, N., Durant, J. M., Langangen, Ø., & Christian Stige, L. (2024). Changes in prey-predator interactions in an Arctic food web under climate change. *Progress in Oceanography*, *229*, 103380. https://doi.org/10.1016/j.pocean.2024.103380

Düsedau, L., Fredriksen, S., Brand, M., Fischer, P., Karsten, U., Bischof, K., Savoie, A., & Bartsch, I. (2024). Kelp forest community structure and demography in Kongsfjorden (Svalbard) across 25 years of Arctic warming. *Ecology and Evolution*, *14*(6), e11606. https://doi.org/10.1002/ece3.11606

Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, *430*(7002), 881–884. https://doi.org/10.1038/nature02808

Eriksen, E., Husson, B., Skaret, G., Ingvaldsen, R. B., Dalpadado, P., Johannesen, E., Jørgensen, L. L., Bogstad, B., Dolgov, A. V., Prozorkevich, D. V., Prokhorova, T. A., Russkikh, A. A., Strelkova, N. A., Trofimov, A. G., Prokopchuk, I. P., & Filin, A. A. (2025). The living Barents Sea response to peak-warming and subsequent cooling. *Scientific Reports*, *15*(1), 13008. https://doi.org/10.1038/s41598-025-96964-x

Eriksen, E., Skjoldal, H. R., Gjøsæter, H., & Primicerio, R. (2017). Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Progress in Oceanography*, *151*, 206–226. https://doi.org/10.1016/j.pocean.2016.12.009

ESRI. (2011). *ArcGIS Pro. Version 3.1.* [Computer software].

Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M., & Pedersen, M. F. (2019). Arctic kelp forests: Diversity, resilience and future. *Global and Planetary Change*, *172*, 1–14. https://doi.org/10.1016/j.gloplacha.2018.09.005

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*(7), 673–677. https://doi.org/10.1038/nclimate2647

Fraser, C. (2012). Is bull-kelp kelp? The role of common names in science. *New Zealand Journal of Marine and Freshwater Research*, *46*(2), 279–284. https://doi.org/10.1080/00288330.2011.621130

Fredriksen, S. (2003). Food web studies in a Norwegian kelp forest based on stable isotope (δ13C and δ15N) analysis. *Marine Ecology Progress Series*, *260*, 71–81. https://doi.org/10.3354/meps260071

Fredriksen, S., Gabrielsen, T. M., Kile, M. R., & Sivertsen, K. (2015). Benthic algal vegetation in Isfjorden, Svalbard. *Polar Research*, *34*(1), 25994. https://doi.org/10.3402/polar.v34.25994

Gardner, A. S., Moholdt, G., Cogley, J. G., Wouters, B., Arendt, A. A., Wahr, J., Berthier, E., Hock, R., Pfeffer, W. T., Kaser, G., Ligtenberg, S. R. M., Bolch, T., Sharp, M. J., Hagen, J. O., van den Broeke, M. R., & Paul, F. (2013). A Reconciled Estimate of Glacier Contributions to Sea Level Rise: 2003 to 2009. *Science*, *340*(6134), 852–857. https://doi.org/10.1126/science.1234532

Geoffroy, M., Bouchard, C., Flores, H., Robert, D., Gjøsæter, H., Hoover, C., Hop, H., Hussey, N. E., Nahrgang, J., Steiner, N., Bender, M., Berge, J., Castellani, G., Chernova, N., Copeman, L., David, C. L., Deary, A., Divoky, G., Dolgov, A. V., … Walkusz, W. (2023). The circumpolar impacts of climate change and anthropogenic stressors on Arctic cod (*Boreogadus saida*) and its ecosystem. *Elem Sci Anth*, *11*(1), 00097. https://doi.org/10.1525/elementa.2022.00097

Gjøsæter, H. (1998). The population biology and exploitation of capelin (Mallotus villosus) in the barents sea. *Sarsia*. https://www.tandfonline.com/doi/abs/10.1080/00364827.1998.10420445

Gotceitas, V., Fraser, S., & Brown, J. A. (1995). Habitat use by juvenile Atlantic cod (Gadus morhua) in the presence of an actively foraging and non-foraging predator. *Marine Biology*, *123*(3), 421–430. https://doi.org/10.1007/BF00349220

Gordó-Vilaseca, C., Costello, M.J., Coll, M., Jüterbock, A., Reiss, H. & Stephenson, F. (2024). Future trends of marine fish biomass distributions from the North Sea to the Barents Sea. *Nat Commun* 15, 5637. https://doi.org/10.1038/s41467-024-49911-9

Handegard, N. O., De Robertis, A., Holmin, A. J., Johnsen, E., Lawrence, J., Le Bouffant, N., O'Driscoll, R., Peddie, D., Pedersen, G., Priou, P., Rogge, R., Samuelsen, M., & Demer, D. A. (2024). Uncrewed surface vehicles (USVs) as platforms for fisheries and plankton acoustics. *ICES Journal of Marine Science*, fsae130. https://doi.org/10.1093/icesjms/fsae130

Hanelt, D., Tüg, H., Bischof, K., Groß, C., Lippert, H., Sawall, T., & Wiencke, C. (2001). Light regime in an Arctic fjord: A study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. *Marine Biology*, *138*(3), 649–658. https://doi.org/10.1007/s002270000481

Hawkings, J., Wadham, J., Tranter, M., Telling, J., Bagshaw, E., Beaton, A., Simmons, S.-L., Chandler, D., Tedstone, A., & Nienow, P. (2016). The Greenland Ice Sheet as a hot spot of phosphorus weathering and export in the Arctic. *Global Biogeochemical Cycles*, *30*(2), 191–210. https://doi.org/10.1002/2015GB005237

He, Y., Shu, Q., Wang, Q., Song, Z., Zhang, M., Wang, S., Zhang, L., Bi, H., Pan, R., & Qiao, F. (2024). Arctic Amplification of marine heatwaves under global warming. *Nature Communications*, *15*(1), 8265. https://doi.org/10.1038/s41467-024-52760-1

Hollowed, A. B., Planque, B., & Loeng, H. (2013). Potential movement of fish and shellfish stocks from the sub- A rctic to the A rctic O cean. *Fisheries Oceanography*, *22*(5), 355–370. https://doi.org/10.1111/fog.12027

Hop, H., Wold, A., Vihtakari, M., Assmy, P., Kuklinski, P., Kwasniewski, S., Griffith, G. P., Pavlova, O., Duarte, P., & Steen, H. (2023). Tidewater glaciers as “climate refugia” for zooplankton-dependent food web in Kongsfjorden, Svalbard. *Frontiers in Marine Science*, *10*. https://www.frontiersin.org/articles/10.3389/fmars.2023.1161912

Hopwood, M. J., Carroll, D., Dunse, T., Hodson, A., Holding, J. M., Iriarte, J. L., Ribeiro, S., Achterberg, E. P., Cantoni, C., Carlson, D. F., Chierici, M., Clarke, J. S., Cozzi, S., Fransson, A., Juul-Pedersen, T., Winding, M. H. S., & Meire, L. (2020). Review article: How does glacier discharge affect marine biogeochemistry and primary production in the Arctic? *The Cryosphere*, *14*(4), 1347–1383. https://doi.org/10.5194/tc-14-1347-2020

Huserbråten, M. B. O., Eriksen, E., Gjøsæter, H., & Vikebø, F. (2019). Polar cod in jeopardy under the retreating Arctic sea ice. *Communications Biology*, *2*(1), 407. https://doi.org/10.1038/s42003-019-0649-2

Iida, K., Mukai, T., & Hwang, D. (1996). Relationship between acoustic backscattering strength and density of zooplankton in the sound-scattering layer. *ICES Journal of Marine Science*, *53*(2), 507–512. https://doi.org/10.1006/jmsc.1996.0073

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, *2*(12), 874–889. https://doi.org/10.1038/s43017-021-00228-x

IPCC. (2022). *The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change* (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781009157964

Jacob, T., Wahr, J., Pfeffer, W. T., & Swenson, S. (2012). Recent contributions of glaciers and ice caps to sea level rise. *Nature*, *482*(7386), 514–518. https://doi.org/10.1038/nature10847

James, N. C., & Whitfield, A. K. (2023). The role of macroalgae as nursery areas for fish species within coastal seascapes. *Cambridge Prisms: Coastal Futures*, *1*, e3. https://doi.org/10.1017/cft.2022.3

Kaser, G., Cogley, J. G., Dyurgerov, M. B., Meier, M. F., & Ohmura, A. (2006). Mass balance of glaciers and ice caps: Consensus estimates for 1961–2004. *Geophysical Research Letters*, *33*(19). https://doi.org/10.1029/2006GL027511

Kavan, J., Luláková, P., Małecki, J., & Strzelecki, M. C. (2023). Capturing the transition from marine to land-terminating glacier from the 126-year retreat history of Nordenskiöldbreen, Svalbard. *Journal of Glaciology*, 1–11. https://doi.org/10.1017/jog.2023.92

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P. E., Rodrigues, J., Lønne, O. J., & Gulliksen, B. (2012). Climate-driven regime shifts in Arctic marine benthos. *Proceedings of the National Academy of Sciences*, *109*(35), 14052–14057. https://doi.org/10.1073/pnas.1207509109

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151546. https://doi.org/10.1098/rspb.2015.1546

Krause-Jensen, D., Archambault, P., Assis, J., Bartsch, I., Bischof, K., Filbee-Dexter, K., Dunton, K. H., Maximova, O., Ragnarsdóttir, S. B., Sejr, M. K., Simakova, U., Spiridonov, V., Wegeberg, S., Winding, M. H. S., & Duarte, C. M. (2020). Imprint of Climate Change on Pan-Arctic Marine Vegetation. *Frontiers in Marine Science*, *7*, 617324. https://doi.org/10.3389/fmars.2020.617324

Krause-Jensen, D., & Duarte, C. M. (2014). Expansion of vegetated coastal ecosystems in the future Arctic. *Frontiers in Marine Science*, *1*. https://doi.org/10.3389/fmars.2014.00077

Krause-Jensen, D., & Duarte, C. M. (2016). Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience*, *9*(10), 737–742. https://doi.org/10.1038/ngeo2790

Krause-Jensen, D., Marbà, N., Olesen, B., Sejr, M. K., Christensen, P. B., Rodrigues, J., Renaud, P. E., Balsby, T. J. S., & Rysgaard, S. (2012). Seasonal sea ice cover as principal driver of spatial and temporal variation in depth extension and annual production of kelp in Greenland. *Global Change Biology*, *18*(10), 2981–2994. https://doi.org/10.1111/j.1365-2486.2012.02765.x

Krumhansl, K. A., & Scheibling, R. E. (2012). Production and fate of kelp detritus. *Marine Ecology Progress Series*, *467*, 281–302. https://doi.org/10.3354/meps09940

Kruss, A., Tęgowski, J., Tatarek, A., Wiktor, J., & Blondel, P. (2017). Spatial distribution of macroalgae along the shores of Kongsfjorden (West Spitsbergen) using acoustic imaging. *Polish Polar Research*, *38*(2), 205–229. https://doi.org/10.1515/popore-2017-0009

Langbehn, T. J., Aksnes, D. L., Kaartvedt, S., Fiksen, Ø., Ljungström, G., & Jørgensen, C. (2022). Poleward distribution of mesopelagic fishes is constrained by seasonality in light. *Global Ecology and Biogeography*, *31*(3), 546–561. https://doi.org/10.1111/geb.13446

Lantuit, H., Overduin, P. P., Couture, N., Wetterich, S., Aré, F., Atkinson, D., Brown, J., Cherkashov, G., Drozdov, D., Forbes, D. L., Graves-Gaylord, A., Grigoriev, M., Hubberten, H.-W., Jordan, J., Jorgenson, T., Ødegård, R. S., Ogorodov, S., Pollard, W. H., Rachold, V., … Vasiliev, A. (2012). The Arctic Coastal Dynamics Database: A New Classification Scheme and Statistics on Arctic Permafrost Coastlines. *Estuaries and Coasts*, *35*(2), 383–400. https://doi.org/10.1007/s12237-010-9362-6

Larsen, L.-H., Cusa, M., Eglund-Newby, S., Berge, J., Renaud, P. E., Varpe, Ø., Geoffroy, M., & Falk-Petersen, S. (2023). Diets of gadoid fish in Arctic waters of Svalbard fjords during the polar night. *Polar Biology*, *46*(8), 783–799. https://doi.org/10.1007/s00300-023-03167-z

Laurel, B. J., Copeman, L. A., Spencer, M., & Iseri, P. (2017). Temperature-dependent growth as a function of size and age in juvenile Arctic cod (Boreogadus saida). *ICES Journal of Marine Science*, *74*(6), 1614–1621. https://doi.org/10.1093/icesjms/fsx028

Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S., & Berge, J. (2011). Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Progress in Oceanography*, *90*(1), 18–32. https://doi.org/10.1016/j.pocean.2011.02.004

Ljungström, G., Langbehn, T. J., & Jørgensen, C. (2021). Light and energetics at seasonal extremes limit poleward range shifts. *Nature Climate Change*, *11*(6), 530–536. https://doi.org/10.1038/s41558-021-01045-2

Løvås, S. M., & Tørum, A. (2001). Effect of the kelp *Laminaria hyperborea* upon sand dune erosion and water particle velocities. *Coastal Engineering*, *44*(1), 37–63. https://doi.org/10.1016/S0378-3839(01)00021-7

Ludvigsen, M., Berge, J., Geoffroy, M., Cohen, J. H., De La Torre, P. R., Nornes, S. M., Singh, H., Sørensen, A. J., Daase, M., & Johnsen, G. (2018). Use of an Autonomous Surface Vehicle reveals small-scale diel vertical migrations of zooplankton and susceptibility to light pollution under low solar irradiance. *Science Advances*, *4*(1), eaap9887. https://doi.org/10.1126/sciadv.aap9887

Lydersen, C., Assmy, P., Falk-Petersen, S., Kohler, J., Kovacs, K. M., Reigstad, M., Steen, H., Strøm, H., Sundfjord, A., Varpe, Ø., Walczowski, W., Weslawski, J. M., & Zajaczkowski, M. (2014). The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. *Journal of Marine Systems*, *129*, 452–471. https://doi.org/10.1016/j.jmarsys.2013.09.006

Macreadie, P. I., Anton, A., Raven, J. A., Beaumont, N., Connolly, R. M., Friess, D. A., Kelleway, J. J., Kennedy, H., Kuwae, T., Lavery, P. S., Lovelock, C. E., Smale, D. A., Apostolaki, E. T., Atwood, T. B., Baldock, J., Bianchi, T. S., Chmura, G. L., Eyre, B. D., Fourqurean, J. W., … Duarte, C. M. (2019). The future of Blue Carbon science. *Nature Communications*, *10*(1), 3998. https://doi.org/10.1038/s41467-019-11693-w

Mcleod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., & Silliman, B. R. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Frontiers in Ecology and the Environment*, *9*(10), 552–560. https://doi.org/10.1890/110004

McMeans, B. C., Rooney, N., Arts, M. T., & Fisk, A. T. (2013). Food web structure of a coastal Arctic marine ecosystem and implications for stability. *Marine Ecology Progress Series*, *482*, 17–28. https://doi.org/10.3354/meps10278

Meire, L., Mortensen, J., Meire, P., Juul-Pedersen, T., Sejr, M. K., Rysgaard, S., Nygaard, R., Huybrechts, P., & Meysman, F. J. R. (2017). Marine-terminating glaciers sustain high productivity in Greenland fjords. *Global Change Biology*, *23*(12), 5344–5357. https://doi.org/10.1111/gcb.13801

Meire, L., Paulsen, M. L., Meire, P., Rysgaard, S., Hopwood, M. J., Sejr, M. K., Stuart-Lee, A., Sabbe, K., Stock, W., & Mortensen, J. (2023). Glacier retreat alters downstream fjord ecosystem structure and function in Greenland. *Nature Geoscience*, *16*(8), 671–674. https://doi.org/10.1038/s41561-023-01218-y

Merzouk, A., & Johnson, L. E. (2011). Kelp distribution in the northwest Atlantic Ocean under a changing climate. *Journal of Experimental Marine Biology and Ecology*, *400*(1), 90–98. https://doi.org/10.1016/j.jembe.2011.02.020

Misund, O. A., Heggland, K., Skogseth, R., Falck, E., Gjøsæter, H., Sundet, J., Watne, J., & Lønne, O. J. (2016). Norwegian fisheries in the Svalbard zone since 1980. Regulations, profitability and warming waters affect landings. *Polar Science*, *10*(3), 312–322. https://doi.org/10.1016/j.polar.2016.02.001

Mork, M. (1996). The effect of kelp in wave damping. *Sarsia*. https://www.tandfonline.com/doi/abs/10.1080/00364827.1996.10413607

Niedzwiedz, S., & Bischof, K. (2023). Glacial retreat and rising temperatures are limiting the expansion of temperate kelp species in the future Arctic. *Limnology and Oceanography*, lno.12312. https://doi.org/10.1002/lno.12312

Nilsen, F., Cottier, F., Skogseth, R., & Mattsson, S. (2008). Fjord–shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. *Continental Shelf Research*, *28*(14), 1838–1853. https://doi.org/10.1016/j.csr.2008.04.015

Nilsen, F., Skogseth, R., Vaardal-Lunde, J., & Inall, M. (2016). *A Simple Shelf Circulation Model: Intrusion of Atlantic Water on the West Spitsbergen Shelf*. https://doi.org/10.1175/JPO-D-15-0058.1

Norderhaug, K. M., Christie, H., Fosså, J. H., & Fredriksen, S. (2005). Fish–macrofauna interactions in a kelp (laminaria hyperborea) forest. *Journal of the Marine Biological Association of the United Kingdom*, *85*(5), 1279–1286. https://doi.org/10.1017/S0025315405012439

Notz, D., & Stroeve, J. (2016). Observed Arctic sea-ice loss directly follows anthropogenic CO2 emission. *Science*, *354*(6313), 747–750. https://doi.org/10.1126/science.aag2345

Onarheim, I. H., Eldevik, T., Smedsrud, L. H., & Stroeve, J. C. (2018). *Seasonal and Regional Manifestation of Arctic Sea Ice Loss*. https://doi.org/10.1175/JCLI-D-17-0427.1

Overland, J. E. (2022). Arctic Climate Extremes. *Atmosphere*, *13*(10), Article 10. https://doi.org/10.3390/atmos13101670

Overland, J. E., Wang, M., Walsh, J. E., & Stroeve, J. C. (2014). Future Arctic climate changes: Adaptation and mitigation time scales. *Earth's Future*, *2*(2), 68–74. https://doi.org/10.1002/2013EF000162

Patterson, R. G., Cronin, M. F., Swart, S., Beja, J., Edholm, J. M., McKenna, J., Palter, J. B., Parker, A., Addey, C. I., Boone, W., Bhuyan, P., Buck, J. J. H., Burger, E. F., Burris, J., Camus, L., de Young, B., du Plessis, M., Flanigan, M., Foltz, G. R., … Zhang, D. (2025). Uncrewed surface vehicles in the Global Ocean Observing System: A new frontier for observing and monitoring at the air-sea interface. *Frontiers in Marine Science*, *12*. https://doi.org/10.3389/fmars.2025.1523585

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate Change and Distribution Shifts in Marine Fishes. *Science*, *308*(5730), 1912–1915. https://doi.org/10.1126/science.1111322

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine Taxa Track Local Climate Velocities. *Science*, *341*(6151), 1239–1242. https://doi.org/10.1126/science.1239352

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919–925. https://doi.org/10.1038/nclimate1958

Polyakov, I. V., Ingvaldsen, R. B., Pnyushkov, A. V., Bhatt, U. S., Francis, J. A., Janout, M., Kwok, R., & Skagseth, Ø. (2023). Fluctuating Atlantic inflows modulate Arctic atlantification. *Science*, *381*(6661), 972–979. https://doi.org/10.1126/science.adh5158

Pueschel, C. M., & Korb, R. E. (2001). Storage of nitrogen in the form of protein bodies in the kelp Laminaria solidungula. *Marine Ecology Progress Series*, *218*, 107–114. https://doi.org/10.3354/meps218107

Quartino, M. L., Deregibus, D., Campana, G. L., Latorre, G. E. J., & Momo, F. R. (2013). Evidence of Macroalgal Colonization on Newly Ice-Free Areas following Glacial Retreat in Potter Cove (South Shetland Islands), Antarctica. *PLOS ONE*, *8*(3), e58223. https://doi.org/10.1371/journal.pone.0058223

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Radomski, P. J., & Holbrook, B. V. (2015). *A comparison of two hydroacoustic methods for estimating submerged macrophyte distribution and abundance: A cautionary note*. *53*, 151–159. Available online at: https:// apms.org/wp-content/uploads/japm-53-02-151.pdf

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 1–10. https://doi.org/10.1038/s43247-022-00498-3

Raybaut, P. (2009). *Spyder-documentation. Available Online at: Pythonhosted.org* [Computer software].

Renaud, P. E., Berge, J., Varpe, Ø., Lønne, O. J., Nahrgang, J., Ottesen, C., & Hallanger, I. (2012). Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, Boreogadus saida? *Polar Biology*, *35*(3), 401–412. https://doi.org/10.1007/s00300-011-1085-z

Renaud, P. E., Løkken, T. S., Jørgensen, L. L., Berge, J., & Johnson, B. J. (2015). Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. *Frontiers in Marine Science*, *2*. https://doi.org/10.3389/fmars.2015.00031

Renaud, P. E., Tessmann, M., Evenset, A., & Christensen, G. N. (2011). Benthic food-web structure of an Arctic fjord (Kongsfjorden, Svalbard). *Marine Biology Research*. https://doi.org/10.1080/17451001003671597

Ronowicz, M., Włodarska-Kowalczuk, M., & Kukliński, P. (2020). Glacial and depth influence on sublittoral macroalgal standing stock in a high-Arctic fjord. *Continental Shelf Research*, *194*, 104045. https://doi.org/10.1016/j.csr.2019.104045

Rose, G. A. (1993). Cod spawning on a migration highway in the north-west Atlantic. *Nature*, *366*(6454), 458–461. https://doi.org/10.1038/366458a0

Rose, G. A. (2005). On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science*, *62*(7), 1360–1374. https://doi.org/10.1016/j.icesjms.2005.05.007

Schaafsma, F. L., Flores, H., David, C. L., Castellani, G., Sakinan, S., Meijboom, A., Niehoff, B., Cornils, A., Hildebrandt, N., Schmidt, K., Snoeijs-Leijonmalm, P., Ehrlich, J., Ashjian, C. J., & Eco, the Mosa. team. (2024). Insights into the diet and feeding behavior of immature polar cod (Boreogadus saida) from the under-ice habitat of the central Arctic Ocean. *Journal of Fish Biology*, *105*(3), 907–930. https://doi.org/10.1111/jfb.15836

Simmonds, E. J., & MacLennan, D. N. (2005). *Fisheries acoustics: Theory and practice* (2nd ed). Blackwell Science.

Slotte, A., Salthaug, A., Vatnehol, S., Johnsen, E., Mousing, E. A., Høines, Å., Broms, C. T., Bjarnason, S., Homrum, E. í, Skagseth, Ø., & Stenevik, E. K. (2025). Herring spawned poleward following fishery-induced collective memory loss. *Nature*, 1–8. https://doi.org/10.1038/s41586-025-08983-3

Smale, D. A., Burrows, M. T., Moore, P., O'Connor, N., & Hawkins, S. J. (2013). Threats and knowledge gaps for ecosystem services provided by kelp forests: A northeast Atlantic perspective. *Ecology and Evolution*, *3*(11), 4016–4038. https://doi.org/10.1002/ece3.774

Søreide, J. E., Hop, H., Carroll, M. L., Falk-Petersen, S., & Hegseth, E. N. (2006). Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography*, *71*(1), 59–87. https://doi.org/10.1016/j.pocean.2006.06.001

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, *29*(4), 436–459. https://doi.org/10.1017/S0376892902000322

Straneo, F., & Cenedese, C. (2015). The Dynamics of Greenland's Glacial Fjords and Their Role in Climate. *Annual Review of Marine Science*, *7*(Volume 7, 2015), 89–112. https://doi.org/10.1146/annurev-marine-010213-135133

Stroeve, J., & Notz, D. (2018). Changing state of Arctic sea ice across all seasons. *Environmental Research Letters*, *13*(10), 103001. https://doi.org/10.1088/1748-9326/aade56

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, *2*(9), 686–690. https://doi.org/10.1038/nclimate1539

Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbæk, J. B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., & Wiencke, C. (2002). The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research*, *21*(1), Article 1. https://doi.org/10.3402/polar.v21i1.6479

Szeligowska, M., Trudnowska, E., Boehnke, R., Dąbrowska, A. M., Dragańska-Deja, K., Deja, K., Darecki, M., & Błachowiak-Samołyk, K. (2021). The interplay between plankton and particles in the Isfjorden waters influenced by marine- and land-terminating glaciers. *Science of The Total Environment*, *780*, 146491. https://doi.org/10.1016/j.scitotenv.2021.146491

Teagle, H., Hawkins, S. J., Moore, P. J., & Smale, D. A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*, *492*, 81–98. https://doi.org/10.1016/j.jembe.2017.01.017

Thomsen, M. S., Stæhr, P. A. U., & South, P. M. (2024). Fabulous but Forgotten Fucoid Forests. *Ecology and Evolution*, *14*(11), e70491. https://doi.org/10.1002/ece3.70491

Truffer, M., & Motyka, R. J. (2016). Where glaciers meet water: Subaqueous melt and its relevance to glaciers in various settings. *Reviews of Geophysics*, *54*(1), 220–239. https://doi.org/10.1002/2015RG000494

Urbanski, J. A., Stempniewicz, L., Węsławski, J. M., Dragańska-Deja, K., Wochna, A., Goc, M., & Iliszko, L. (2017). Subglacial discharges create fluctuating foraging hotspots for sea birds in tidewater glacier bays. *Scientific Reports*, *7*(1), 43999. https://doi.org/10.1038/srep43999

Urmy, S. S., Horne, J. K., & Barbee, D. H. (2012). Measuring the vertical distributional variability of pelagic fauna in Monterey Bay. *ICES Journal of Marine Science*, *69*(2), 184–196. https://doi.org/10.1093/icesjms/fsr205

van der Kamp, A. A. W., Triginer, V. G., & Sen, A. (2025). Billefjorden's benthic biodiversity: The impact of glacier retreat on faunal communities in a high Arctic fjord. *Polar Biology*, *48*(3), 71. https://doi.org/10.1007/s00300-025-03390-w von Szalay, P. G., & McConnaughey, R. A. (2002). The effect of slope and vessel speed on the performance of a single beam acoustic seabed classification system. *Fisheries Research*, *56*(1), 99–112. https://doi.org/10.1016/S0165-7836(02)00020-6

Wassmann, P., Duarte, C. M., Agustí, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*, *17*(2), 1235–1249. https://doi.org/10.1111/j.1365-2486.2010.02311.x

Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., Bennett, S., & Rousseaux, C. S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, *3*(1), 78–82. https://doi.org/10.1038/nclimate1627

Weslawski, J. M., Wiktor, J., & Kotwicki, L. (2010). Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. *Marine Biodiversity*, *40*(2), 123–130. https://doi.org/10.1007/s12526-010-0038-z

Whitehead, P. J. P., Nelson, G. J., & Wongratana, T. (1988). *FAO species catalogue. Vol.7. Clupeoid fishes of the world (Suborder Clupeoidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies, and wolf-herrings. Part 2. Engraulididae*. https://openknowledge.fao.org/items/0d303f96-1efb-43da-aac5-27cf61547b12

Wiktor, J. M., Tatarek, A., Kruss, A., Singh, R. K., Wiktor, J. M., & Søreide, J. E. (2022). Comparison of macroalgae meadows in warm Atlantic versus cold Arctic regimes in the high-Arctic Svalbard. *Frontiers in Marine Science*, *9*, 1021675. https://doi.org/10.3389/fmars.2022.1021675

Zemp, M., Frey, H., Gärtner-Roer, I., Nussbaumer, S. U., Hoelzle, M., Paul, F., Haeberli, W., Denzinger, F., Ahlstrøm, A. P., Anderson, B., Bajracharya, S., Baroni, C., Braun, L. N., Cáceres, B. E., Casassa, G., Cobos, G., Dávila, L. R., Granados, H. D., Demuth, M. N., … Vincent, C. (2015). Historically unprecedented global glacier decline in the early 21st century. *Journal of Glaciology*, *61*(228), 745–762. https://doi.org/10.3189/2015JoG15J017

Zemp, M., Huss, M., Thibert, E., Eckert, N., McNabb, R., Huber, J., Barandun, M., Machguth, H., Nussbaumer, S. U., Gärtner-Roer, I., Thomson, L., Paul, F., Maussion, F., Kutuzov, S., & Cogley, J. G. (2019). Global glacier mass changes and their contributions to sea-level rise from 1961 to 2016. *Nature*, *568*(7752), 382–386. https://doi.org/10.1038/s41586-019-1071-0

Paper I

Víctor González Triginer, Milan Beck, Arunima Sen, Kai Bischof and Børge Damsgård (2024)

Acoustic mapping reveals macroalgal settlement following glacier retreat

Frontiers in Marine Science

Frontiers in Marine Science
TYPE Original Research
PUBLISHED 10 September 2024
DOI 10.3389/fmars.2024.1438332

Acoustic mapping reveals macroalgal settlement following a retreating glacier front in the High Arctic

Victor Gonzalez Triginer[1,2]*, Milan Beck[1,3], Arunima Sen[1], Kai Bischof[3] and Børge Damsgård[1]

[1]Department of Arctic Biology, The University Centre in Svalbard, Longyearbyen, Norway, [2]Faculty of Biosciences, Fisheries and Economics, The Arctic University of Norway, Tromsø, Norway, [3]Marine Botany, University of Bremen, Bremen, Germany

OPEN ACCESS

EDITED BY
Bernardo Antonio Perez Da Gama,
Fluminense Federal University, Brazil

REVIEWED BY
Jan Marcin Weslawski,
Polish Academy of Sciences, Poland
Trine Bekkby,
Norwegian Institute for Water Research (NIVA), Norway

*CORRESPONDENCE
Victor Gonzalez Triginer
✉ victortr@unis.no

RECEIVED 25 May 2024
ACCEPTED 22 August 2024
PUBLISHED 10 September 2024

CITATION
Gonzalez Triginer V, Beck M, Sen A, Bischof K and Damsgård B (2024) Acoustic mapping reveals macroalgal settlement following a retreating glacier front in the High Arctic. *Front. Mar. Sci.* 11:1438332.
doi: 10.3389/fmars.2024.1438332

Vegetated coastal marine ecosystems are projected to expand northwards in the Arctic due to climate change, but the mechanisms for this expansion are complex and nuanced. Macroalgal biomass in the littoral areas of Svalbard has been increasing, but data at the glacier fronts are very scarce. In this study, we use hydroacoustics and video validation from an unmanned surface vehicle to survey macroalgal bed distribution along the coast of a High Arctic fjord (Billefjorden, Svalbard), including river bays and land- and sea- terminating glacier fronts, as well as oceanographic measurements to indicate physical drivers of macroalgal settlement. We found high variation of macroalgal coverage along the fjord coastline, with virtually no macroalgae in the river bays but abundant coverage in areas with little terrestrial runoff. Furthermore, the presence of kelp was found at the land-terminating glacier front which has recently retreated from the sea, which suggests the potential for rapid macroalgal establishment in newly available substrate following glacial retreat. These findings suggest large ecological implications throughout the Arctic, in which macroalgal expansion may lead to significant changes in the underwater coastal landscape and ecosystem. This study shows that the use of remote autonomous vehicles and hydroacoustic mapping with video validation has a high potential for sustainable and efficient ecological monitoring.

KEYWORDS

algae, autonomous vehicles, coastal mapping, climate change, hydroacoustics, Svalbard

1 Introduction

The High Arctic is undergoing the most severe climate change of any region in the world and consequently marine ecosystems are being affected by an increase in temperature, precipitation, melting, river discharge and sedimentation (Box et al., 2019). Representing the boundary between marine and terrestrial environments where land and glacial inflow enter the marine system, littoral areas in fjord systems are particularly vulnerable to these changes, and the loss of the cryosphere is one of the main drivers for changes in biodiversity and ecosystem function in these areas (Bring et al., 2016; Hawkins et al., 2008; Hopwood et al., 2020; IPCC, 2022). The melting of tidewater glaciers and decrease in sea-ice is affecting biogeochemical parameters such as turbidity, salinity, as well as nutrient and light availability (Henson et al., 2023; Hopwood et al., 2020), and these changes may affect community composition in coastal fjord areas (Fredriksen et al., 2014; Weslawski et al., 2010).

Macroalgae are commonly found on rocky substrate and boulders in littoral and sublittoral fjord regions in the Svalbard archipelago (Fredriksen and Røst Kile, 2012; Hop et al., 2012), where they are key primary producers and represent important feeding and nursing sites for fish and benthic fauna (Carlsen et al., 2007; Lippert et al., 2001; Włodarska-Kowalczuk et al., 2009). The macroalgal community composition on Svalbard is similar to the Norwegian mainland and other regions of the North Atlantic, with few endemic Arctic species (e.g. *Laminaria solidungula*) (Fredriksen et al., 2015). Macroalgae have been shown to dominate at the sublittoral and littoral zones (2 - 15 m depth), with fucales in the shallow areas and species such as *Saccharina latissima*, *Alaria esculenta*, and *Laminaria digitata* commonly forming dense beds deeper in the euphotic zone in Svalbard fjords (Hop et al., 2012). In the Arctic, macroalgae are commonly absent in the uppermost sublittoral zone due to ice scouring (Bartsch et al., 2016; Gutt, 2001), which has an effect down to 5 m in Svalbard (Wiktor et al., 2022). Temperature and salinity are important drivers for macroalgal growth and vary significantly over the seasons in the high Arctic (Bischof et al., 2019). Macroalgae have been shown to have a high tolerance to variations in temperature and salinity, especially in the upper sublittoral zone, but freezing of the thalli and rapid changes in salinity have been shown to inhibit photosynthetic efficiency at least transiently (Becker et al., 2009; Hop et al., 2012; Karsten, 2007). Light availability is also an important factor determining the depth distribution of macroalgae (Bartsch et al., 2016; Düsedau et al., 2024), with high amounts of radiation in the uppermost littoral zone and light limitation deeper in the water column and under sea-ice (Svendsen et al., 2002). The lower depth limit for the most abundant kelp species in Svalbard is from 15 to 20 m, and is undergoing an upward shift as a consequence of a deteriorating light climate (Borum et al., 2002; Düsedau et al., 2024; Hop et al., 2012). Furthermore, mechanical factors such as tidal conditions and wave exposure are important drivers for macroalgal occurrence and community composition (Bird et al., 2013), with species like *Laminaria digitata* thriving in exposed sites (Gilson et al., 2023) while the opposite is observed for *Saccharina latissima* (Visch et al., 2020).

Changing environmental factors such as water temperature, salinity, sedimentation and light availability may have a direct impact on the spatial distribution of macroalgae (Bischof et al., 2019), and consequently affect associated species and ultimately the community composition of Arctic coastal ecosystems (Kortsch et al., 2012; Weslawski et al., 2010). The responses of macroalgal communities to changes in the cryosphere include complex interactions between environmental factors, macroalgal growth and distribution. High sediment load in the water column affects the light regime and decreases the availability of photosynthetically available radiation (Hanelt et al., 2001; Ronowicz et al., 2020). Species richness and biomass of macroalgae subsequently tend to decrease in close proximity to glacier fronts, and community composition changes with increased turbidity from glacier run-off (Ronowicz et al., 2020). Sea-terminating or tidewater glaciers flow into the ocean and their front is exposed to the marine system, while land-terminating glaciers do not have direct contact with the sea. The transition of sea-terminating to land-terminating glaciers due to increased glacial melting is changing the biogeochemical dynamics in these coastal areas, such as acidification state (Henson et al., 2023), which may impact macroalgal communities and the associated fauna by selecting those better suited for the changing conditions (Niedzwiedz and Bischof, 2023).

Heightened sedimentation due to increased river run-off and glacier melting may result in higher concentrations of dissolved bioavailable nutrients (Vonnahme et al., 2021), which potentially favours macroalgal growth. Conversely, higher river run-off can cause an accumulation of particles such as silt, sand or clay and lead to shifts in bottom sediments towards a soft-bottom seafloor which is not suitable for the settlement of macroalgae (Mann et al., 2022). Furthermore, glacial retreat is uncovering new hard substrate where macroalgae have the potential to settle, expanding their distribution (Deregibus et al., 2023). Reduced ice-scouring following sea-ice retreat may also allow for macroalgae settling in new regions (Krause-Jensen et al., 2020; Krause-Jensen and Duarte, 2014), and a northward expansion of macroalgae is expected (Assis et al., 2022).

There has been a recorded increase in littoral macroalgal biomass in Svalbard over the last 30 years (Bartsch et al., 2016; Fredriksen et al., 2015; Weslawski et al., 2010), which may be due to a decrease in mechanical disturbances such as sea-ice scouring, new substrate for settlement and higher bioavailability of nutrients (Krause-Jensen et al., 2020; Krause-Jensen and Duarte, 2014). Overall, studies show that macrophytes are generally expanding in the Arctic (IPCC, 2022; Krause-Jensen et al., 2020), but there is little research done at glacier fronts due to high difficulty to access and sample these areas.

Direct biological sampling, such as dive surveys, offers high detail and reliability to map underwater habitats and community composition, but it is rather expensive, localized and time-consuming. Acoustic methods are emerging as efficient tools for habitat assessment and ecosystem mapping and monitoring (Anderson et al., 2008; Brown et al., 2011), as they can be automated and used at large scales. Studies have shown that macroalgal beds significantly influence the strength of acoustic backscatter by dampening the return echo signal (Brown et al., 2011; Riegl et al., 2005), and hydroacoustic methods have already been used successfully to map macroalgal coverage in Arctic fjords (Kruss et al., 2017).

Due to their high susceptibility to environmental perturbations as well as their sedentary lifestyle, macroalgae are good indicators of changing conditions (Bischof et al., 2019; Fredriksen et al., 2014). Studying the spatial abundance and distribution of macroalgae at a local scale with high spatial resolution, and in relation to changes in the cryosphere and different fjord littoral habitats (glacier front, river bays and marine conditions with minimal land runoff), will contribute to inferring effects of climate change at a larger spatial scale.

The aim of this study was to map sublittoral cover of macroalgae beds in inner Billefjorden, Svalbard, and the Nordenskiöldbreen glacier front, which has recently partly transitioned from sea- to land- terminating, and investigate the role of turbidity, temperature and salinity in macroalgal presence in these areas. These oceanographical parameters were chosen as they are known drivers of macroalgal growth and are undergoing significant shifts due to climate changes, particularly in coastal fjord areas due to glacial melting and increased land runoff (Bischof et al., 2019; IPCC, 2022). We hypothesize that macroalgal biomass will decrease with increasing proximity to the glacier front and river bays due to high sedimentation rate and low light availability. Macroalgal distribution may be limited to shallower depths in these areas, where there is still enough available light to sustain growth. Finally, there might be an optimal proximity to the glacier front that allows for macroalgal growth, where there is increased nutrient concentration from subglacial upwelling and new substrate for settlement, but where the turbidity and mechanical disturbance is not high enough to prevent macroalgal settling. This study system may be used as a model to illustrate the changes taking place broadly in the Arctic.

2 Materials and methods

2.1 Study area

Billefjorden is located in Spitsbergen, Svalbard (Figure 1), and has a shallow sill at the mouth of the fjord, so that there is a layer of winter cold water at the bottom and a warmer shallow layer of Atlantic water above that enters via offshoots of the West Spitsbergen current (Nilsen et al., 2008). The inner part of the fjord is characterized by the river bay Petuniabukta and the glacier Nordenskiöldbreen in the adjacent bay Adolfbukta. This glacier has been retreating at a rate of 12-35 m per year (Szczuciński et al., 2009) and has recently receded to where the northern side is mostly land-terminating. The river bay, Petuniabukta, lies in the northwestern end of the fjord and receives a high amount of freshwater and sediment input due to the surrounding valley glaciers and mountains (Láska et al., 2012). Outwards from the river and glacier bays (Scottvika), river and glacier influence is minimal, which means that Billefjorden functions as a natural laboratory wherein the impact of both river and glacier systems can be systematically assessed. Geomorphological mapping showed that inner Billefjorden is characterized by soft bottom substrate in Petuniabukta, and both rocky and soft bottom in the glacier bay and surrounding coastline (Søreide et al., 2021). There has been a decrease in land-fast sea ice cover in Svalbard over the last decades, but inner Billefjorden is still ice-covered during the winter and spring seasons (Urbański and Litwicka, 2022).

2.2 Coastal survey

A large-scale survey was done along the coastline of inner Billefjorden, Svalbard. Acoustic mapping was performed by split-beam echosounder (SBES) measurements mounted on an unmanned surface vehicle (USV) and the seafloor was imaged with a drop camera deployed from the USV for validation of the acoustic data. A Valeport SWiFT CTDplus with Turbidity (Valeport Ltd., Totnes, UK) was mounted on the USV to collect surface oceanographic data, which included temperature (degrees Celsius), salinity (practical salinity units; psu) and turbidity (nephelometric turbidity units; ntu).

The Otter USV (Maritime Robotics AS, Trondheim, Norway) is an electric 200 x 108 x 106 cm twin hull catamaran that can carry a variety of oceanographic sensors and cameras and was used to access very shallow areas and the glacier fronts, which cannot be sampled by traditional methods. The USV was controlled remotely via broadband communication radio (Direct link 5150 – 5875 MHz) from a nearby vessel and was equipped with a downward facing BioSonics DT-X scientific split-beam echosounder (BioSonics, Seattle, USA) mounted at the back of the vehicle. The USV's internal GNSS system was used for georeferencing the echosounder data. The DT-X echosounder was used at an operating frequency of 200 kHz, a beam angle of 6.9°x 6.9°, a ping rate of 5 Hz and a pulse duration of 0.4 ms, and the USV was driven at a speed of approximately 3 knots. Autonomous vehicles have been used in previous studies to map the seafloor and study marine ecosystems (Johnsen et al., 2016; Ludvigsen et al., 2018), and provide an effective and sustainable methodology that is capable to reach understudied areas that are difficult to access.

A total of 40 km of coastline were surveyed over three separate days in July and August 2021, and the USV was manually run at a mean bottom depth isoline of 7 m (Figure 1). In August 2022, CTD profiles were taken down to bottom depth in Petuniabukta, the Nordenskiöldbreen glacier and Scottvika as locations indicating different environmental conditions (high freshwater and sedimentation from rivers – RIV, glacier front – GLA, and control marine station – CON, respectively), to complement the surface CTD measurements taken from the USV.

2.3 Acoustic detection of macroalgae

Acoustic detection of submerged flora is based on their physical properties, which scatter the acoustic signal differently than unvegetated bottom (Carbó and Molero, 1997; Kruss et al., 2017). Hydroacoustic mapping has been used extensively to map macroalgal coverage in coastal areas (Brown et al., 2011) and scientific split-beam echosounders have been used to study macroalgal settlement in Svalbard fjords (Kruss et al., 2017; Wiktor et al., 2022). The vegetation analyses were performed in BioSonics' software Visual Aquatic v.1.0.0.12146 using an edge detection method. This method is based on analysing the strength of acoustic echoes to establish boundaries between the bottom layer, macroalgal cover and the water column. When macroalgae are present, the echogram shows a weak backscattering layer above the strong bottom signal (Figure 2).

The acoustic signal was recorded as Sv values (volume backscattering strength) and the files were inspected for noise and a threshold of -40 dB was used to determine bottom depth. The

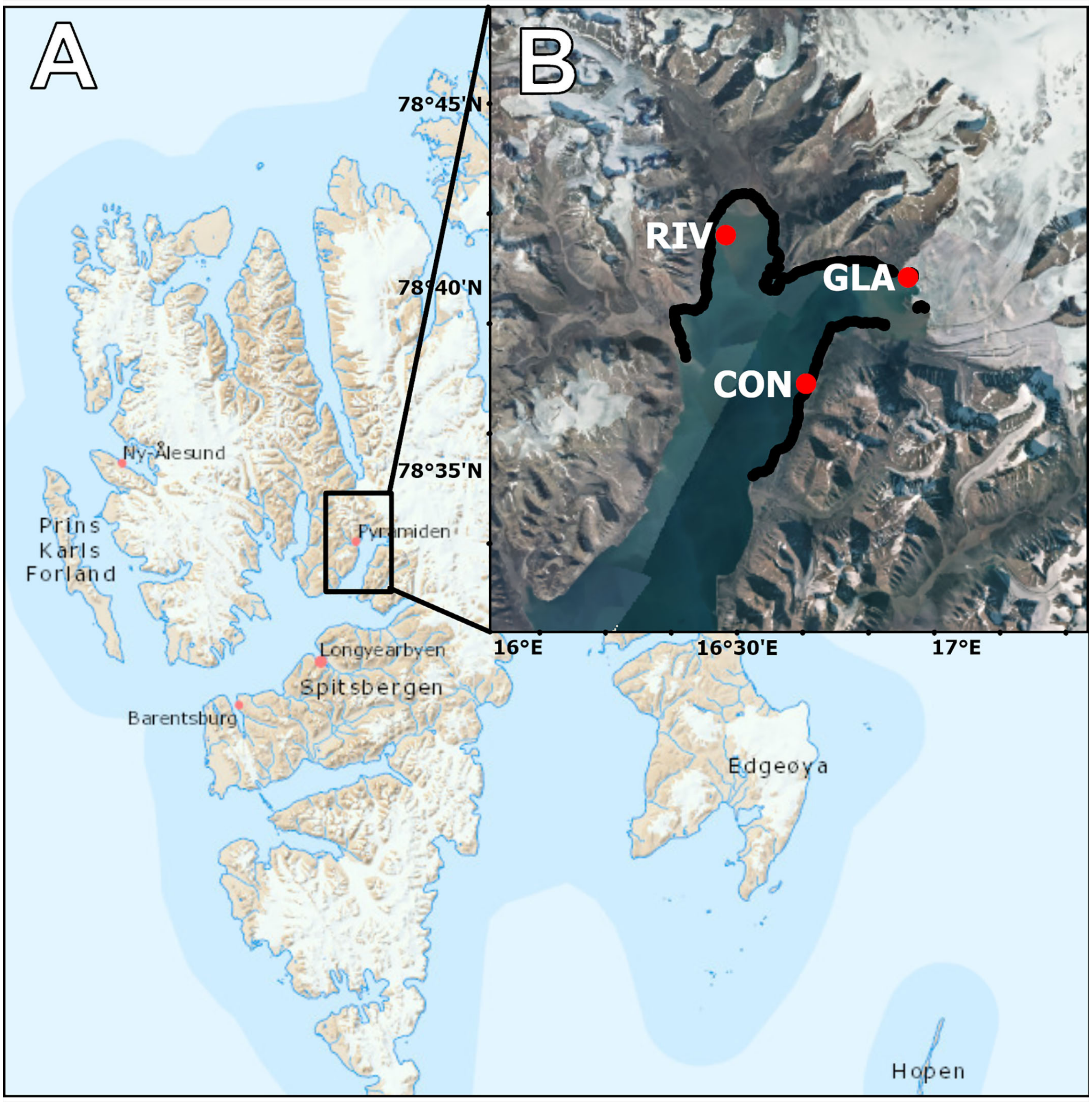


FIGURE 1
(A) Topographic map of Svalbard. **(B)** Satellite image of Billefjorden with the data transect from the coastal survey in Billefjorden (black line) and stations where CTD (Conductivity, Temperature and Density) water column profiles were done (red dots). Basemap source: Norwegian Polar Institute, Geodata AS, Kartverket, Geovekst og kommunene; Esri, USGS.

default threshold of -70 dB was used to detect presence of macroalgae. These thresholds were used based on existent literature and ground-truthing during field testing to determine the optimal values for bottom and plant acoustic boundaries (Radomski and Holbrook, 2015; Simmonds and MacLennan, 2005). A minimum detection distance of 0.3 m above the bottom was used to exclude the detection of smaller bottom structures and drift material and only include large macroalgal formations, as common macroalgae species in the Arctic can grow to >1 m in length (Diehl et al., 2023). Macroalgal detection was limited to a depth range from 1 to 20 m and minor manual editing of the bottom and vegetation lines was done to correct for noise and fish that merged with the bottom signal. The pings were clustered in groups of 50, which at a ping rate of 5 s^{-1} effectively equalled to one data point for every 10 seconds. The algorithm then detected macroalgal percentage cover of those ping clusters, and50% coverage and higher was assigned as macroalgal presence. Macroalgal presence/absence using a threshold of 50% coverage was used as a conservative approach to complement the height threshold and focus on large and established macroalgal beds and avoid over-representing macroalgal coverage by including detached and drift material and single units of macroalgae.

To ground-truth the acoustic data, a Paralenz Vaquita (Paralenz, Rødovre, Denmark) drop camera was deployed from the USV simultaneously to the echosounder recording. The camera was rigged to the USV's winch system which was linked to the echosounder and programmed to be lowered to 1.5 m from the bottom and record video of the seafloor for 10 seconds.

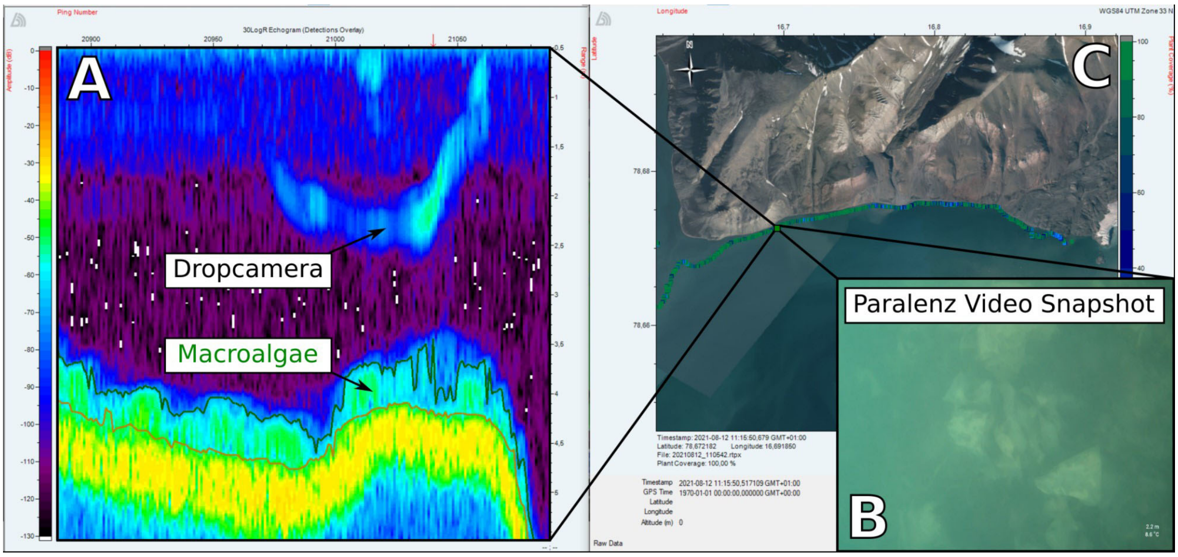


FIGURE 2
Process of validation of the acoustic data via drop camera samplings. **(A)** Echogram showing the acoustic signal from macroalgae. The signal from the drop camera is also shown. Brighter colours indicate stronger echo signal. **(B)** Video snapshot of the ocean floor at the same location. **(C)** Location of the respective sampling point.

A total of 30 drop camera deployments were used to validate the macroalgae detection algorithm. This footage was obtained at the land-terminating glacier front, along the northern coast of Adolfbukta and in Petuniabukta between 5 and 10 m bottom depth (Figure 3; Supplementary Table 1). Video that showed macroalgae covering more than 50% of the frame were assigned as indicating macroalgal presence to align with what constituted macroalgal presence in the acoustic algorithm, and this footage was cross-referenced with the acoustic data based on time stamps as well as visualizing the camera in the echogram.

2.4 Mapping and statistical analyses

In order to test the correlation between surface temperature, salinity and turbidity with macroalgal occurrence, the acoustic and CTD data were merged together by aggregating the CTD data in intervals of 10 seconds and matching the start time stamp of each acoustic cluster of 50 pings. All statistical analyses were done in RStudio v2023.03.1, and the "dplyr" and "lubridate" packages were used for the data manipulation (Grolemund and Wickham, 2011; Wickham et al., 2023).

Box plots were made using the "ggplot2" package to visualize the frequency of presence and absence of macroalgae in relation to the range values for surface temperature, salinity and turbidity. Data were analysed for normality using a Saphiro-Wilk test and checked for multicollinearity and homoscedasticity. A correlation matrix was performed to analyse the relationships between temperature, salinity and turbidity. Logistic regression (Sperandei, 2014) was used on the merged dataset to analyse the relationship between temperature, salinity and turbidity with macroalgal presence/absence, and the model output exported using the "broom" package. In addition, an inflated beta regression model (Ospina and Ferrari, 2010) was used to analyse the relationship between temperature, salinity and turbidity with macroalgal percent coverage directly using the "gamlss" package. The CTD water column profile data was analysed and plotted using the "oce" package.

Macroalgal presence/absence, percent coverage and sampling locations were mapped in ArcGIS Pro v3.1.

3 Results

3.1 Acoustic survey and image validation

The bottom depth of the acoustic survey ranged from 1 to 20 m depth, with a mean of 7.1 m. Of a total of 3481 data points, there were 1085 reports of macroalgal presence (>50% coverage) and 2396 of absence (<50% coverage). Overall, the survey revealed macroalgal coverage to be quite heterogenous along the coast of Billefjorden (Figure 4). The eastern coastline showed patchy macroalgal coverage, decreasing with proximity to the sea-terminating glacier (southern side). The sea-terminating glacier front showed no coverage, while macroalgae were present adjacent to the land-terminating front (northern side). High macroalgal coverage was observed northwest of the glacier, decreasing with proximity to the river bay and with virtually no macroalgae in the inner part of the bay. Instances with coverage increase on the western coastline and drop in front of the river bay at the end of the survey.

Out of 30 total camera drops, the echosounder correctly identified 15 cases of macroalgal presence and 13 of macroalgal absence, while 2 cases incorrectly identified macroalgal presence where the camera showed no coverage.

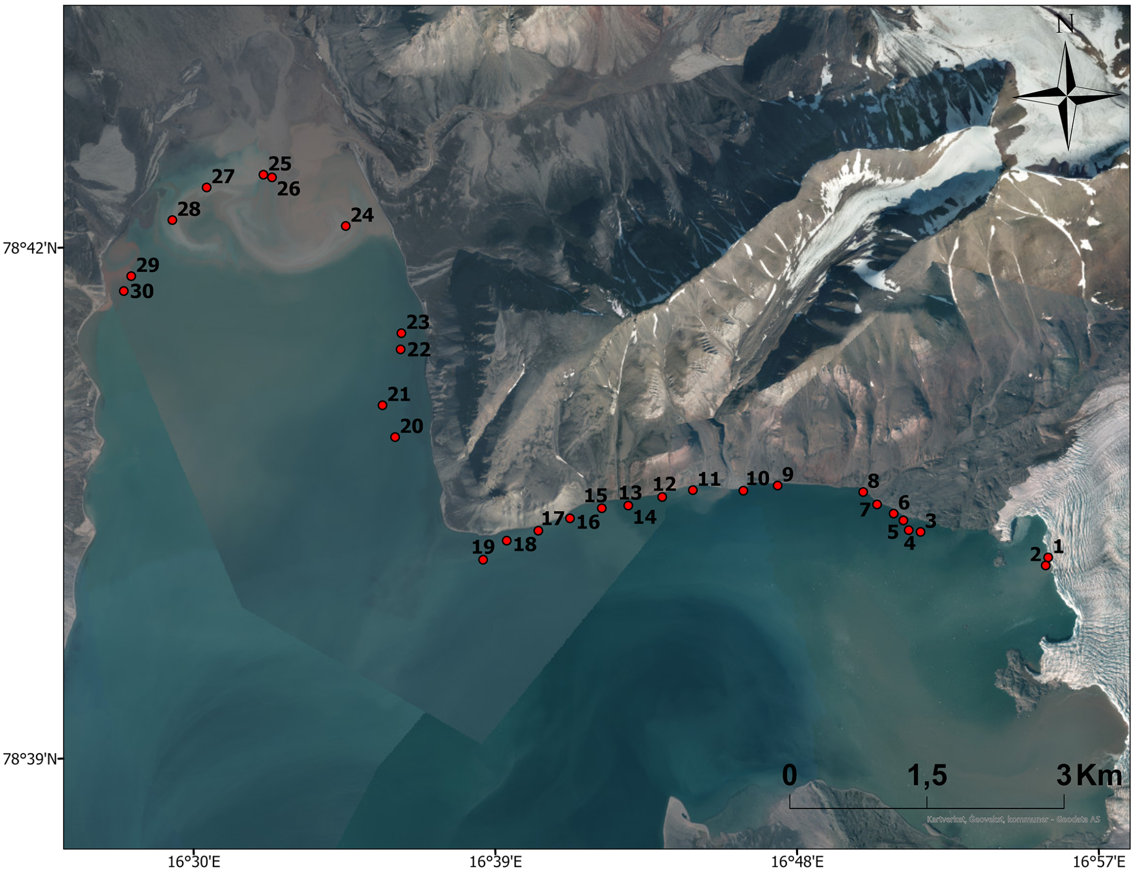


FIGURE 3
Drop camera locations along the Unmanned Surface Vehicle (USV) survey. Additional information on the environmental conditions and macroalgal coverage is presented in the Supplementary Material. Basemap: Norwegian Polar Institute, Geodata AS, Kartverket, Geovekst og kommunene; Esri, USGS.

3.2 Surface CTD measurements

CTD surface turbidity measurements from the USV survey ranged from 1.7 to 497 ntu, with a mean of 17.9 ntu, temperature ranged from 3.8 to 9.2°C with a mean of 6.4°C, and salinity ranged from 7.2 to 33.2 psu with a mean of 26.6 psu (Figure 5). The highest turbidity measurements (243 – 497 ntu) were recorded at the sea-terminating glacier front, and the highest temperature (8 – 9°C) and lowest salinity (7 – 14 psu) were recorded at the southwestern river bay. The highest salinity values (31 – 33 psu) were recorded at inner Petuniabukta and along the eastern shoreline.

3.3 CTD water column profiles

The highest surface turbidity (100 ntu) was found at the glacier station, along with the lowest salinity (below 20 psu) and lowest temperature (below 8°C; Figure 6). The control station was the most saline and least turbid station, with surface values above 25 psu and below 4 ntu respectively. The river station is the shallowest and was the only station with bottom water temperatures above 0°C.

The correlation matrix showed low correlations between turbidity and temperature and turbidity and salinity, 0.13 and -0.37 respectively, and a moderate correlation of -0.63 between temperature and salinity (Supplementary Table 2). All three predictor variables exhibited statistically significant associations with macroalgal presence in the logistic regression model (Table 1). Temperature exhibited a negative association, with a one-unit increase resulting in a 53.49% decrease in the odds of macroalgal presence, as indicated by the odds ratio (OR) of 0.465 (95% CI: 0.405, 0.535, z = -10.74, $p < 0.001$). Similarly, salinity displayed a negative association, with a one-unit increase corresponding to an 16.36% decrease in odds (OR: 0.836, 95% CI: 0.820, 0.853, z = -17.28, $p < 0.001$). Turbidity also showed a negative relationship, with a one-unit increase leading to a 3.06% decrease in odds (OR: 0.969, 95% CI: 0.961, 0.978, z =-7.19, $p < 0.001$). All predictors had highly significant p-values, indicating the robustness of these associations. A McFadden's R-squared value of 0.1 was obtained for the model. Similarly to the logistic regression, all three predictors were found to be statistically significant in the inflated beta regression model (Table 2), and all predictors exhibited negative associations with macroalgal percent coverage. A one-

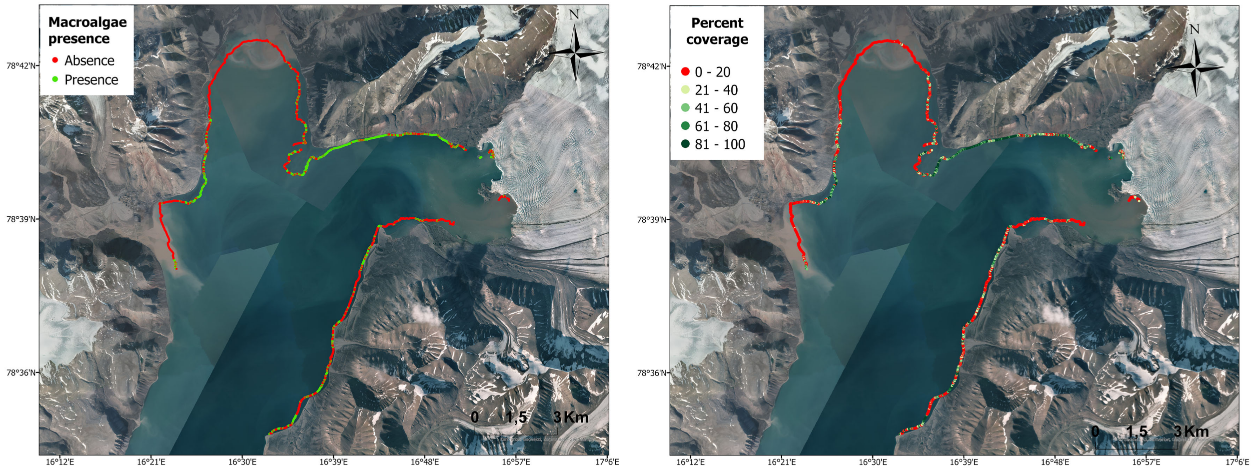


FIGURE 4
Macroalgal coverage along the inner coast of Billefjorden showing macroalgal presence (>50% coverage; green) and absence (<50% coverage; red) and percent coverage of macroalgae. Basemap source: Norwegian Polar Institute, Geodata AS, Kartverket, Geovekst og kommunene; Esri, USGS.

unit increase in temperature resulted in a decrease in the expected value of macroalgal coverage, as indicated by the estimate of -0.3903 ($t = -10.95$, $p < 0.001$). Similarly, a one-unit increase in salinity corresponded to a decrease in the expected value of coverage, with an estimate of -0.0850 ($t = -18.44$, $p < 0.001$). Turbidity also showed a negative relationship, with a one-unit increase leading to a decrease in the expected value of coverage, as indicated by the estimate of -0.0066 ($t = -10.71$, $p < 0.001$).

4 Discussion

Macroalgae-dominated coastal marine ecosystems are projected to expand northwards and become more common in the Arctic due to climate change (Krause-Jensen et al., 2020; Krause-Jensen and Duarte, 2014). Despite increasing temperatures and greater availability of substrate for macroalgal growth, higher sedimentation rates from melting glaciers and the subsequent

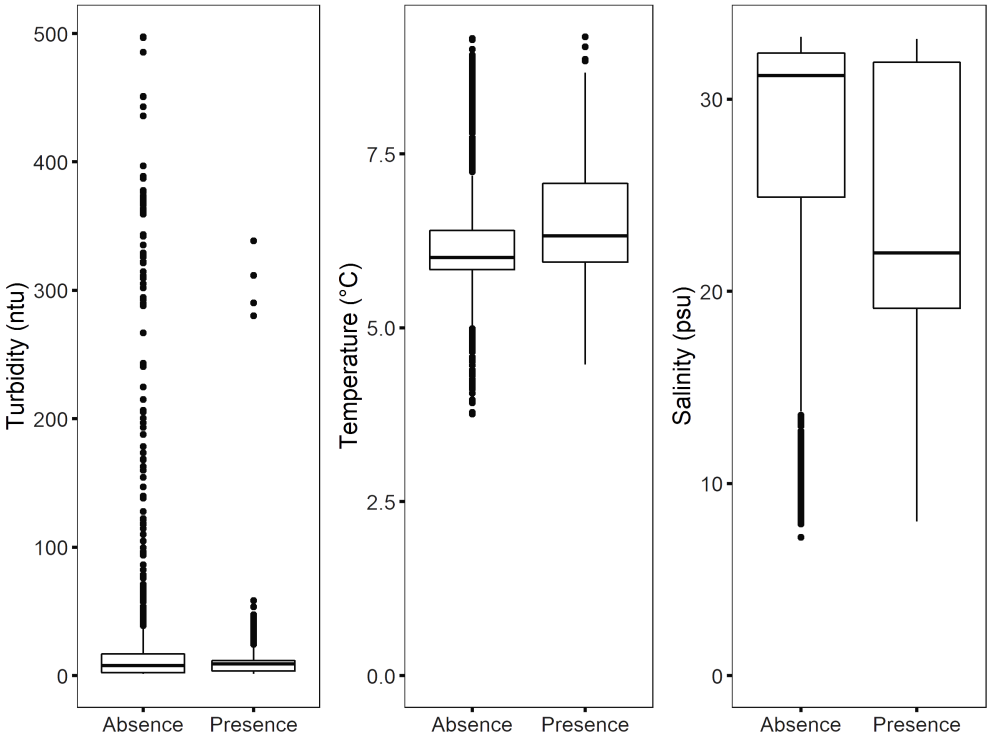


FIGURE 5
Boxplot showing the ranges of turbidity, temperature and salinity when macroalgae were present and absent. Each data point corresponds to the average values of 10-second intervals of CTD surface measurements. The box represents the interquartile range (IQR) and the line within indicates the median. The whiskers extend to the most extreme data points not considered outliers, which are represented by individual dots beyond the whiskers.

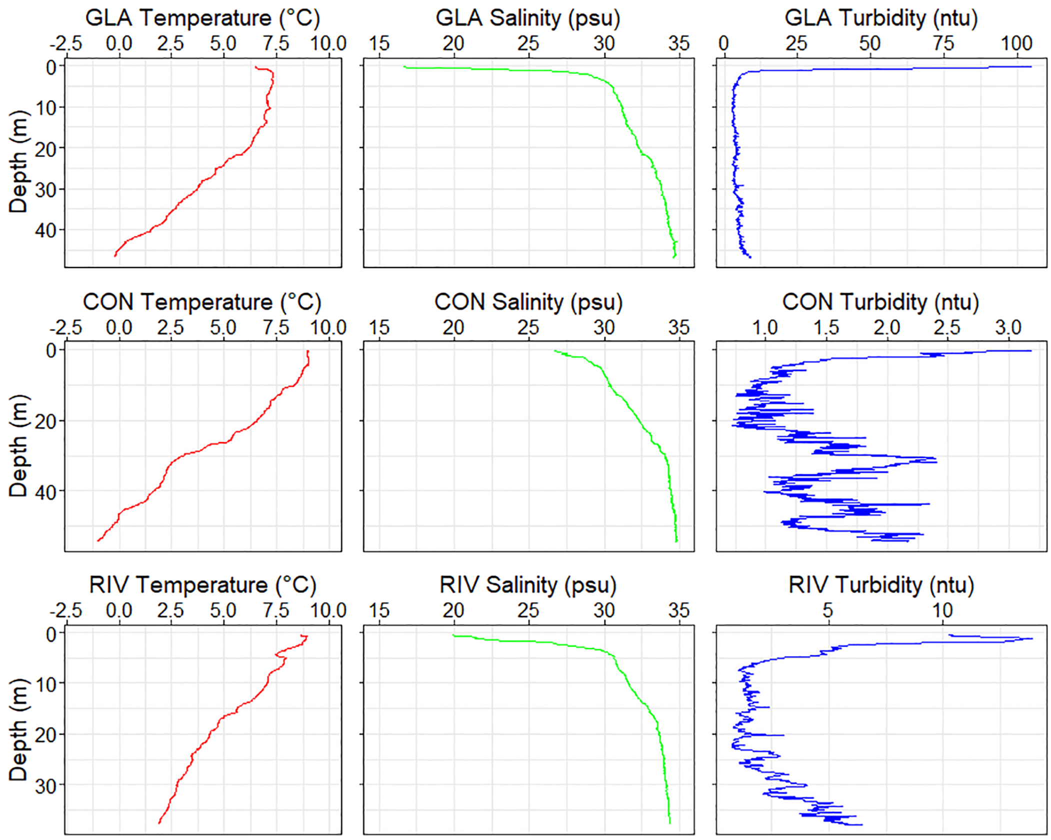


FIGURE 6
CTD depth profiles for the glacier (GLA), control (CON) and river (RIV) stations, with measures of temperature, salinity and turbidity. Turbidity scales are different between the three stations due to great variation in measurements.

changes to the light regime can limit the expansion of macroalgae in the Arctic (Assis et al., 2022). Exploring the interactions between the different changes in oceanographical conditions and their relationships with macroalgal settling and growth is crucial to understanding the new underwater landscape in littoral areas of a changing Arctic. This study focused on the shallow sublittoral area and the middle of the macroalgal depth distribution zone on Svalbard (Bartsch et al., 2016), at an average survey depth of 7 m. We aimed at exploring these relationships further and developing a sustainable monitoring protocol for surveys in shallow littoral areas and glacier fronts. We found high variation in macroalgal coverage along inner Billefjorden, with river bays such as Petuniabukta with virtually no macroalgae and the adjacent bay (Adolfbukta) with abundant biomass. Furthermore, kelp was found at the land-terminating glacier front. The image validation of the acoustic mapping of macroalgae showed a high rate of success and points at the potential of such methodology for sustainable ecological mapping.

4.1 Macroalgal coverage in relation to temperature, salinity and turbidity

The logistic and beta inflated regression models, which studied the relationships between environmental conditions and macroalgal presence/absence and percent coverage respectively, showed similar results indicating that temperature, salinity and turbidity significantly predict macroalgal presence, with increasing values

TABLE 1 Relationship between macroalgal presence and temperature, salinity and turbidity.

Variable	Estimate	Odds_Ratio	CI_Lower	CI_Upper	P_Value
(Intercept)	9.1775	9676.9293	2405.7703	38924.3151	<0.001
Temperature	-0.7654	0.4652	0.4045	0.5349	<0.001
Salinity	-0.1787	0.8364	0.8196	0.8535	<0.001
Turbidity	-0.0311	0.9694	0.9612	0.9777	<0.001

Summary of the logistic regression model. Null deviance: 4319.6 on 3480 degrees of freedom, residual deviance: 3888.1 on 3477 degrees of freedom. AIC: 3896.1.

TABLE 2 Relationship between macroalgal percent coverage and temperature, salinity and turbidity.

Component	Variable	Estimate	Std.Error	t_value	P_value
Mu	(Intercept)	4.3143	0.3352	12.87	<0.001
Mu	Temperature	-0.3903	0.0356	-10.95	<0.001
Mu	Salinity	-0.0850	0.0046	-18.44	<0.001
Mu	Turbidity	-0.0066	0.0006	-10.71	<0.001
Sigma	(Intercept)	0.2653	0.0174	15.22	<0.001
Nu	(Intercept)	-2.3748	0.0613	-38.75	<0.001
Tau	(Intercept)	-3.921	0.1283	-30.57	<0.001

Summary of the beta inflated regression model. No. of observations in the fit: 3481, Degrees of Freedom for the fit: 7, residual Degrees of Freedom: 3474. Global Deviance: 1466.295, AIC: 1480.295, SBC: 1523.381.

correlated with decreasing odds for macroalgal presence and coverage. However, the low McFadden's R-squared value indicates that the model only explains a small part of the variance, and other factors such as bottom type and nutrient availability likely play a bigger role in determining macroalgal presence. This is consistent with studies showing that macroalgae in Svalbard can thrive in wide ranges of temperature and salinity which vary seasonally (Bischof et al., 2019), and therefore these drivers are of lesser importance than substrate type and light and nutrient availability. Exposure to wave action can be a critical driver for macroalgal occurrence, but it likely does not play a major role as the coastline in inner Billefjorden is sheltered due to seasonal sea-ice cover and has low exposure to waves (Urbański and Litwicka, 2022).

Both the CTD water column profile and the drop camera footage showed high turbidity in the surface layer of the river bay Petuniabukta, which suggest high rates of run-off from the surrounding rivers. Kelp relies on rocky substrates to adhere to and grow (Steneck et al., 2002; Wulff et al., 2009) and the scarce macroalgal abundance observed in Petuniabukta may be explained by a soft bottom seafloor created by high rates of sedimentation from land, as is shown in geomorphological maps of the Billefjorden coastline (Søreide et al., 2021). Furthermore, high concentration of particles in the water and increased turbidity in the water column may have a negative effect on macroalgal growth by decreasing the available photosynthetically available radiation that reaches the bottom. Studies have shown that high sedimentation has negative effects on the germination rates of kelp by altering the recruitment of sporophytes (Traiger and Konar, 2018; Zacher et al., 2016), and the results of the acoustic survey are consistent with this area having adverse conditions for macroalgal growth. Similarly adverse conditions for macroalgal growth were expected at the glacier front, due to high sedimentation and turbidity (Szczuciński et al., 2009). The survey at the sea-terminating front was consistent with that hypothesis, as no macroalgae were detected and the surface turbidity was extremely high.

However, the hydroacoustic analyses and video validation showed considerable kelp growth on the land-terminating glacier side. This area is separated from the sea-terminating side by a small peninsula that may provide shelter from the glacial sediment plume, which combined with a rocky substrate may constitute more favourable conditions for macroalgal communities to establish. Moreover, as this section of the glacier front keeps retreating into land, there will be less mechanical disturbance from calving events. Surface turbidity measurements from the USV survey were low, while the water column profile taken further from the shore indicated more turbid surface waters, which supports that the northern, land-terminating side of the glacier may be sheltered from the sediment plume that originates at the sea-terminating side. It is of note that the drop camera footage showed a high amount of sediment on the kelp, which indicates that despite some degree of sheltering, the land-terminating side does nonetheless have appreciable sedimentation rates. The presence of macroalgae may indicate that it can thrive in areas with high sedimentation if there is enough light availability and suitable substrate. In such cases we would expect a shift in the depth range of kelp towards shallower areas, which is consistent with recent findings (Niedzwiedz and Bischof, 2023). It is important to note that environmental conditions affect macroalgae throughout the growth period, and therefore variability in temperature, salinity and turbidity over time plays a key role. Although constrained over time, the observations of oceanographic parameters in this study are representative of the summer and fall period of the year when inner Billefjorden is not ice-covered.

4.2 Ecological implications of macroalgal expansion at retreating glacier fronts

As a glacier retreats, new rocky bottom is exposed that can potentially be exploited by macroalgal communities. Furthermore, as the glacier continues to retreat and sedimentation rates and mechanical disturbances decline, the conditions will become more favourable for macroalgae and will potentially lead to higher abundance of kelp. Satellite imagery shows that the northern section of the Nordenskiöldbreen glacier became partly land-terminating in 2017-2018 (Sentinel Playground, Sinergise LTD), which implies a potential colonisation time by macrophytes of just a few years once the substrate becomes available. An acoustic survey study by Kruss et al. (2017) mapping macroalgae in Kongsfjorden, Svalbard similarly observed macroalgae close to the glacier front, and it may become common throughout the Arctic following rapid glacial retreat.

Kelp beds are important ecosystem engineers, playing a key role in nutrient cycling and energy transfer and provide shelter and substrate for many associated species (Teagle et al., 2017; Włodarska-Kowalczuk et al., 2009). Furthermore, macroalgae act as nursery areas for fish and facilitate complex interactions and trophic linkages (James and Whitfield, 2023), and play a key role in carbon cycles in coastal areas by storing CO_2 in their tissues, which is transferred through the food web (Chung et al., 2011). Glacier fronts are highly productive due to sub-glacial upwelling circulating bottom nutrient-rich water to the surface (Vonnahme et al., 2021), but this process will disappear as sea-terminating glaciers retreat into land, to be replaced by assemblages driven by the establishment of kelp as biogenic habitats. Macroalgal expansion in Arctic fjords may therefore result in an enhanced local carbon sink as well as an increase in local primary production. As this study has shown, macroalgal communities are rapidly establishing in retreating glacier fronts, and this may cause a shift from a top-down phytoplankton-dominated primary production to a bottom-up production based on kelp. Hence, as glacier fronts throughout the Arctic retreat and macroalgae settle in this new substrate, there is a potential for large scale implications and dramatic changes in the underwater landscape of Arctic fjord coastal systems.

4.3 Hydroacoustics and remote vehicles as mapping tools

Hydroacoustic mapping is highly efficient for surveying and monitoring submerged vegetation, as it can be automated and cover large areas. This methodology allows to survey very shallow areas and glacier fronts, where it is very difficult and dangerous to conduct traditional sampling. Due to this, it was possible to sample at the very edge of the glacier front, and survey these newly uncovered areas for the first time. However, image validation is essential as the acoustic properties of every site will differ according to environmental variables such as weather conditions and bottom and vessel types. Nonetheless, our results demonstrate that validating acoustic data with underwater video and performing manual corrections can result in an efficient mapping of macroalgae. The main challenge encountered was the disturbance of the acoustic signal due to waves and steep bottom slopes, which can affect echo shapes and acoustic backscatter (von Szalay and McConnaughey, 2002). Furthermore, acoustic mapping may not distinguish dead from living macroalgae, and in areas with very low macroalgal presence, such as inner Petuniabukta, the occasional incorrect reports of vegetation most likely refer to drift material, which also appeared in the validation footage. To avoid misidentification of detached kelp as macroalgal coverage, we imposed a threshold of >50% cover to determine the presence of dense kelp beds and filter out drift material. However, where macroalgae coverage was patchy and the camera showed only partial coverage, the algorithm also reflected that patchiness, which indicates that this methodology can result in high resolution mapping of macroalgae.

It's important to note that the surface CTD measurements from the USV survey offer only a snapshot of the oceanographical conditions and that this shallow water layer varies according to weather conditions and current systems in the fjord. The logistic regression model using surface CTD data in combination with the water column profiles gives a more complete picture of the conditions and how that may relate to macroalgal coverage. Moreover, this study focused on macroalgal coverage in very shallow areas and kelp may be present in deeper areas along the coast that were not covered by the acoustic beam during mapping.

This study demonstrates that macroalgal communities can rapidly establish in newly available substrate after glacial retreat, dramatically changing the coastal underwater landscape. These shifts have large scale implications as primary production and carbon cycling pathways are changing in Arctic fjords, and it is likely that these changes are taking place all throughout the Arctic. Overall, this methodology demonstrates potential for macroalgal mapping and monitoring surveys, but ground-truthing is still essential. Furthermore, such a survey is considerably more cost-efficient and sustainable than traditional methods (e.g. dredging and diving surveys) and has virtually no impact on the ecosystem. This study contributes to further understanding the links between a melting cryosphere and the expansion of macroalgae in the High Arctic, and to fill a research gap in monitoring glacier fronts and shallow littoral areas.

Data availability statement

The acoustic data generated for this study falls under confidentiality regulations of the Norwegian Mapping Authority. Requests to access the datasets should be directed to victortr@unis.no.

Author contributions

VT: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. MB: Conceptualization, Data curation, Investigation, Methodology, Software, Visualization, Writing – review & editing. AS: Project administration, Supervision, Writing – review & editing. KB: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. BD: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This study was financed through the FACE-IT project which has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 869154.

Acknowledgments

We thank the boat drivers and logistics personnel at the University Centre in Svalbard for their support during the data collection. We would also like to thank the reviewers for their valuable and helpful input.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1438332/full#supplementary-material

References

Anderson, J. T., Van Holliday, D., Kloser, R., Reid, D. G., and Simard, Y. (2008). Acoustic seabed classification: Current practice and future directions. *ICES J. Mar. Sci.* 65, 1004–1011. doi: 10.1093/icesjms/fsn061

Assis, J., Serrão, E. A., Duarte, C. M., Fragkopoulou, E., and Krause-Jensen, D. (2022). Major expansion of marine forests in a warmer arctic. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.850368

Bartsch, I., Paar, M., Fredriksen, S., Schwanitz, M., Daniel, C., Hop, H., et al. (2016). Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biol.* 39, 2021–2036. doi: 10.1007/s00300-015-1870-1

Becker, S., Walter, B., and Bischof, K. (2009). Freezing tolerance and photosynthetic performance of polar seaweeds at low temperatures. *Botanica Marina* 52, 609–616. doi: 10.1515/BOT.2009.079

Bird, C., Franklin, E., Smith, C., and Toonen, R. (2013). Between tide and wave marks: A unifying model of physical zonation on littoral shores. *PeerJ* 1, e154. doi: 10.7717/peerj.154

Bischof, K., Buschbaum, C., Fredriksen, S., Gordillo, F. J. L., Heinrich, S., Jiménez, C., et al. (2019). "Kelps and environmental changes in Kongsfjorden: stress perception and responses," in *The Ecosystem of Kongsfjorden, Svalbard*, vol. 2. Eds. H. Hop and C. Wiencke (Cham, Switzerland: Springer International Publishing), 373–422. doi: 10.1007/978-3-319-46425-1_10

Borum, J., Pedersen, M., Krause-Jensen, D., Christensen, P., and Nielsen, K. (2002). Biomass, photosynthesis and growth of Laminaria saccharina in a high-arctic fjord, NE Greenland. *Mar. Biol.* 141, 11–19. doi: 10.1007/s00227-002-0806-9

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F.-J. W., et al. (2019). Key indicators of Arctic climate change: 1971–2017. *Environ. Res. Lett.* 14, 045010. doi: 10.1088/1748-9326/aafc1b

Bring, A., Fedorova, I., Dibike, Y., Hinzman, L., Mård, J., Mernild, S. H., et al. (2016). Arctic terrestrial hydrology: A synthesis of processes, regional effects, and research challenges. *J. Geophys. Res.: Biogeosci.* 121, 621–649. doi: 10.1002/2015JG003131

Brown, C. J., Smith, S. J., Lawton, P., and Anderson, J. T. (2011). Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuar. Coast. Shelf Sci.* 92, 502–520. doi: 10.1016/j.ecss.2011.02.007

Carbó, R., and Molero, A. C. (1997). Scattering strength of a gelidium biomass bottom. *Appl. Acous.* 51, 343–351. doi: 10.1016/S0003-682X(97)00012-1

Carlsen, B. P., Johnsen, G., Berge, J., and Kuklinski, P. (2007). Biodiversity patterns of macro-epifauna on different lamina parts of Laminaria digitata and Saccharina latissima collected during spring and summer 2004 in Kongsfjorden, Svalbard. *Polar Biol.* 30, 939–943. doi: 10.1007/s00300-007-0272-4

Chung, I. K., Beardall, J., Mehta, S., Sahoo, D., and Stojkovic, S. (2011). Using marine macroalgae for carbon sequestration: A critical appraisal. *J. Appl. Phycol.* 23, 877–886. doi: 10.1007/s10811-010-9604-9

Deregibus, D., Campana, G. L., Neder, C., Barnes, D. K. A., Zacher, K., Piscicelli, J. M., et al. (2023). Potential macroalgal expansion and blue carbon gains with northern Antarctic Peninsula glacial retreat. *Mar. Environ. Res.* 189, 106056. doi: 10.1016/j.marenvres.2023.106056

Diehl, N., Steiner, N., Bischof, K., Karsten, U., and Heesch, S. (2023). Exploring intraspecific variability – biochemical and morphological traits of the sugar kelp Saccharina latissima along latitudinal and salinity gradients in Europe. *Front. Mar. Sci.* 10. doi: 10.3389/fmars.2023.995982

Düsedau, L., Fredriksen, S., Brand, M., Fischer, P., Karsten, U., Bischof, K., et al. (2024). Kelp forest community structure and demography in Kongsfjorden (Svalbard) across 25 years of Arctic warming. *Ecol. Evol.* 14, e11606. doi: 10.1002/ece3.11606

Fredriksen, S., Bartsch, I., and Wiencke, C. (2014). New additions to the benthic marine flora of Kongsfjorden, western Svalbard, and comparison between 1996/1998 and 2012/2013. *Botanica Marina* 57, 203–216. doi: 10.1515/bot-2013-0119

Fredriksen, S., Gabrielsen, T. M., Kile, M. R., and Sivertsen, K. (2015). Benthic algal vegetation in Isfjorden, Svalbard. *Polar Res.* 34, 25994. doi: 10.3402/polar.v34.25994

Fredriksen, S., and Røst Kile, M. (2012). The algal vegetation in the outer part of Isfjorden, Spitsbergen: Revisiting Per Svendsen's sites 50 years later. *Polar Res.* 31, 17538. doi: 10.3402/polar.v31i0.17538

Gilson, A. R., White, L. J., Burrows, M. T., Smale, D. A., and O'Connor, N. E. (2023). Seasonal and spatial variability in rates of primary production and detritus release by intertidal stands of Laminaria digitata and Saccharina latissima on wave-exposed shores in the northeast Atlantic. *Ecol. Evol.* 13, e10146. doi: 10.1002/ece3.10146

Grolemund, G., and Wickham, H. (2011). Dates and times made easy with lubridate. *J. Stat. Softw.* 40, 1–25. doi: 10.18637/jss.v040.i03

Gutt, J. (2001). On the direct impact of ice on marine benthic communities, a review. *Polar Biol.* 24, 553–564. doi: 10.1007/s003000100262

Hanelt, D., Tüg, H., Bischof, K., Groß, C., Lippert, H., Sawall, T., et al. (2001). Light regime in an Arctic fjord: A study related to stratospheric ozone depletion as a basis for determination of UV effects on algal growth. *Mar. Biol.* 138, 649–658. doi: 10.1007/s002270000481

Hawkins, S., Moore, P., Burrows, M., Poloczanska, E., Mieszkowska, N., Herbert, R., et al. (2008). Complex interactions in a rapidly changing world: Responses of rocky shore communities to recent climate change. *Climate Res.* 37, 123–133. doi: 10.3354/cr00768

Henson, H. C., Holding, J. M., Meire, L., Rysgaard, S., Stedmon, C. A., Stuart-Lee, A., et al. (2023). Coastal freshening drives acidification state in Greenland fjords. *Sci. Total Environ.* 855, 158962. doi: 10.1016/j.scitotenv.2022.158962

Hop, H., Wiencke, C., Vögele, B., and Kovaltchouk, N. A. (2012). Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. *Botm* 55, 399–414. doi: 10.1515/bot-2012-0097

Hopwood, M. J., Carroll, D., Dunse, T., Hodson, A., Holding, J. M., Iriarte, J. L., et al. (2020). Review article: How does glacier discharge affect marine biogeochemistry and primary production in the Arctic? *Cryosphere* 14, 1347–1383. doi: 10.5194/tc-14-1347-2020

IPCC. (2022). *The ocean and cryosphere in a changing climate: special report of the intergovernmental panel on climate change. 1st ed* (Cambridge, UK: Cambridge University Press). doi: 10.1017/9781009157964

James, N. C., and Whitfield, A. K. (2023). The role of macroalgae as nursery areas for fish species within coastal seascapes. *Cambridge Prisms: Coast. Futures* 1, e3. doi: 10.1017/cft.2022.3

Johnsen, G., Ludvigsen, M., Sørensen, A., and Aas, L. (2016). The use of underwater hyperspectral imaging deployed on remotely operated vehicles—Methods and applications. *IFAC-PapersOnLine* 49, 476–481. doi: 10.1016/j.ifacol.2016.10.451

Karsten, U. (2007). Research note: Salinity tolerance of Arctic kelps from Spitsbergen. *Phycol. Res.* 55, 257–262. doi: 10.1111/j.1440-1835.2007.00468.x

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P. E., Rodrigues, J., Lønne, O. J., et al. (2012). Climate-driven regime shifts in Arctic marine benthos. *Proc. Natl. Acad. Sci.* 109, 14052–14057. doi: 10.1073/pnas.1207509109

Krause-Jensen, D., Archambault, P., Assis, J., Bartsch, I., Bischof, K., Filbee-Dexter, K., et al. (2020). Imprint of climate change on pan-arctic marine vegetation. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.617324

Krause-Jensen, D., and Duarte, C. M. (2014). Expansion of vegetated coastal ecosystems in the future Arctic. *Front. Mar. Sci.* 1. doi: 10.3389/fmars.2014.00077

Kruss, A., Tęgowski, J., Tatarek, A., Wiktor, J., and Blondel, P. (2017). Spatial distribution of macroalgae along the shores of Kongsfjorden (West Spitsbergen) using acoustic imaging. *Polish Polar Res.* 38, 205–229. doi: 10.1515/popore-2017-0009

Láska, K., Witoszová, D., and Prošek, P. (2012). Weather patterns of the coastal zone of Petuniabukta, central Spitsbergen in the period 2008–2010. *Polish Polar Res.* 33, 297–318. doi: 10.2478/v10183-012-0025-0

Lippert, H., Iken, K., Rachor, E., and Wiencke, C. (2001). Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). *Polar Biol.* 24, 512–522. doi: 10.1007/s003000100250

Ludvigsen, M., Berge, J., Geoffroy, M., Cohen, J. H., de la Torre, P. R., Nornes, S. M., et al. (2018). Use of an Autonomous Surface Vehicle reveals small-scale diel vertical migrations of zooplankton and susceptibility to light pollution under low solar irradiance. *Sci. Adv.* 4, eaap9887. doi: 10.1126/sciadv.aap9887

Mann, P. J., Strauss, J., Palmtag, J., Dowdy, K., Ogneva, O., Fuchs, M., et al. (2022). Degrading permafrost river catchments and their impact on Arctic Ocean nearshore processes. *Ambio* 51, 439–455. doi: 10.1007/s13280-021-01666-z

Niedzwiedz, S., and Bischof, K. (2023). Glacial retreat and rising temperatures are limiting the expansion of temperate kelp species in the future Arctic. *Limnol. Oceanogr.* 68, 816–830. doi: 10.1002/lno.12312

Nilsen, F., Cottier, F., Skogseth, R., and Mattsson, S. (2008). Fjord–shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. *Continental Shelf Res.* 28, 1838–1853. doi: 10.1016/j.csr.2008.04.015

Ospina, R., and Ferrari, S. L. P. (2010). Inflated beta distributions. *Stat. Papers* 51, 111–126. doi: 10.1007/s00362-008-0125-4

Radomski, P. J., and Holbrook, B. V. (2015). A comparison of two hydroacoustic methods for estimating submerged macrophyte distribution and abundance: A cautionary note. *J. Aquat. Plant Manag.* 53, 151–159. Available online at: https://apms.org/wp-content/uploads/japm-53-02-151.pdf.

Riegl, B. M., Moyer, R. P., Morris, L. J., Virnstein, R. W., and Purkis, S. J. (2005). Distribution and seasonal biomass of drift macroalgae in the Indian River Lagoon (Florida, USA) estimated with acoustic seafloor classification (QTCView, Echoplus). *J. Exp. Mar. Biol. Ecol.* 326, 89–104. doi: 10.1016/j.jembe.2005.05.009

Ronowicz, M., Włodarska-Kowalczuk, M., and Kukliński, P. (2020). Glacial and depth influence on sublittoral macroalgal standing stock in a high-Arctic fjord. *Continental Shelf Res.* 194, 104045. doi: 10.1016/j.csr.2019.104045

Simmonds, E. J., and MacLennan, D. N. (2005). *Fisheries acoustics: Theory and practice. 2nd ed* (Oxford, UK: Blackwell Science).

Søreide, J., Pitusi, V., Vader, A., Damsgård, B., Nilsen, F., Skogseth, R., et al. (2021). Environmental status of Svalbard coastal waters: Coastscapes and focal ecosystem components (SvalCoast). *State. Environ. Sci. Svalbard. Rep.* 2020, 143–174. doi: 10.5281/zenodo.4293849

Sperandei, S. (2014). Understanding logistic regression analysis. *Biochem. Med.* 24, 12–18. doi: 10.11613/BM.2014.003

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., et al. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environ. Conserv.* 29, 436–459. doi: 10.1017/S0376892902000322

Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., et al. (2002). The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res.* 21, Article 1. doi: 10.3402/polar.v21i1.6479

Szczuciński, W., Zajączkowski, M., and Scholten, J. (2009). Sediment accumulation rates in subpolar fjords – Impact of post-Little Ice Age glaciers retreat, Billefjorden, Svalbard. *Estuar. Coast. Shelf Sci.* 85, 345–356. doi: 10.1016/j.ecss.2009.08.021

Teagle, H., Hawkins, S. J., Moore, P. J., and Smale, D. A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol.* 492, 81–98. doi: 10.1016/j.jembe.2017.01.017

Traiger, S. B., and Konar, B. (2018). Mature and developing kelp bed community composition in a glacial estuary. *J. Exp. Mar. Biol. Ecol.* 501, 26–35. doi: 10.1016/j.jembe.2017.12.016

Urbański, J. A., and Litwicka, D. (2022). The decline of Svalbard land-fast sea ice extent as a result of climate change. *Oceanologia* 64, 535–545. doi: 10.1016/j.oceano.2022.03.008

Visch, W., Nylund, G. M., and Pavia, H. (2020). Growth and biofouling in kelp aquaculture (Saccharina latissima): The effect of location and wave exposure. *J. Appl. Phycol.* 32, 3199–3209. doi: 10.1007/s10811-020-02201-5

Vonnahme, T. R., Persson, E., Dietrich, U., Hejdukova, E., Dybwad, C., Elster, J., et al. (2021). Early spring subglacial discharge plumes fuel under-ice primary production at a Svalbard tidewater glacier. *Cryosphere* 15, 2083–2107. doi: 10.5194/tc-15-2083-2021

von Szalay, P. G., and McConnaughey, R. A. (2002). The effect of slope and vessel speed on the performance of a single beam acoustic seabed classification system. *Fisheries Res.* 56, 99–112. doi: 10.1016/S0165-7836(02)00020-6

Weslawski, J. M., Wiktor, J., and Kotwicki, L. (2010). Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. *Mar. Biodivers.* 40, 123–130. doi: 10.1007/s12526-010-0038-z

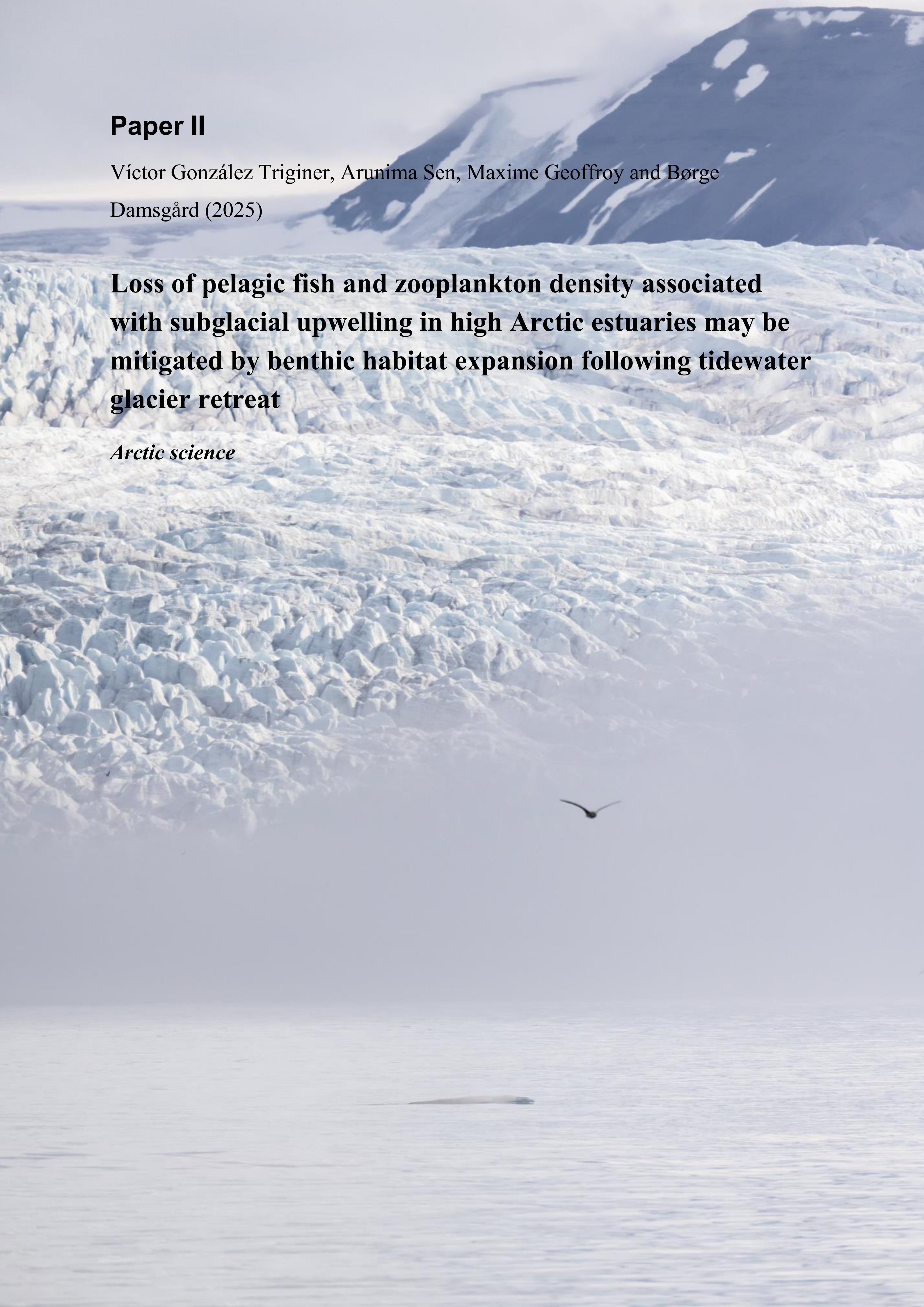
Wickham, H., François, R., Henry, L., Müller, K., and Vaughan, D. (2023).dplyr: A grammar of data manipulation. Available online at: https://dplyr.tidyverse.org. (accessed August 20, 2024).

Wiktor, J. M., Tatarek, A., Kruss, A., Singh, R. K., Wiktor, J. M., and Søreide, J. E. (2022). Comparison of macroalgae meadows in warm Atlantic versus cold Arctic regimes in the high-Arctic Svalbard. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.1021675

Włodarska-Kowalczuk, M., Kukliński, P., Ronowicz, M., Legeżyńska, J., and Gromisz, S. (2009). Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). *Polar Biol.* 32, 897–905. doi: 10.1007/s00300-009-0590-9

Wulff, A., Iken, K., Quartino, M. L., Al-Handal, A., Wiencke, C., and Clayton, M. N. (2009). Biodiversity, biogeography and zonation of marine benthic micro- and macroalgae in the Arctic and Antarctic. *Botm* 52, 491–507. doi: 10.1515/BOT.2009.072

Zacher, K., Bernard, M., Bartsch, I., and Wiencke, C. (2016). Survival of early life history stages of Arctic kelps (Kongsfjorden, Svalbard) under multifactorial global change scenarios. *Polar Biol.* 39, 2009–2020. doi: 10.1007/s00300-016-1906-1



Paper II

Víctor González Triginer, Arunima Sen, Maxime Geoffroy and Børge
Damsgård (2025)

Loss of pelagic fish and zooplankton density associated with subglacial upwelling in high Arctic estuaries may be mitigated by benthic habitat expansion following tidewater glacier retreat

Arctic science

Arctic Science

OPEN ACCESS | Research Article

Loss of pelagic fish and zooplankton density associated with subglacial upwelling in high Arctic estuaries may be mitigated by benthic habitat expansion following tidewater glacier retreat

Victor Gonzalez Triginer[a,b], **Arunima Sen**[a], **Maxime Geoffroy**[b,c], **and Børge Damsgård**[a]

[a]Department of Arctic Biology, The University Centre in Svalbard, Longyearbyen, Norway; [b]Faculty of Biosciences, Fisheries and Economics, The Arctic University of Norway, Tromsø, Norway; [c]Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial University of Newfoundland, St. John's, NL, Canada

Corresponding author: **V. Gonzalez Triginer** (email: victortr@unis.no)

Abstract

Glacier fronts are hotspots of pelagic productivity due to upwelling of nutrient-rich water. As tidewater glaciers retreat into land, this subglacial circulation will disappear and sedimentation from terrestrial runoff will increase, leading to a decrease in pelagic productivity with a decline in the abundance of fish and zooplankton. We used Billefjorden, a high Arctic fjord with a glacier recently transitioned from sea- to land-terminating as a case study to identify spatial differences and small-scale environmental drivers of density and vertical distribution of fish and zooplankton along a gradient of glacier retreat (directly in front of the land-terminating glacier front, a river bay with terrestrial input from land-terminating glaciers further inland and a location with minimal glacial input). We developed a sustainable and efficient protocol to safely sample the glacier front and shallow coastal areas using hydroacoustics and a remote autonomous vehicle combined with oceanographic measurements and baited remote cameras. Over 2 years, pelagic density was lowest at the now land-terminating glacier front and highest at the site with lowest terrestrial input. Temperature, depth, and turbidity explained less than 8% of the variation each. The site with the least glacial input had the most heterogenous bottom habitat due to the presence of kelp forests, and the richer demersal habitat likely contributed to the higher pelagic density. In shallow fjords and areas with hard bottom substrate, it is expected that sea-ice and glacial retreat will promote macroalgal settlement, and we suggest that macroalgal expansion may compensate the loss of tidewater glacier-associated density of fish and zooplankton by the increase of benthic-driven density. Arctic pelagic ecosystems could thus be more resilient to glacier retreat than initially thought, but this is highly dependent on fjord topography, sedimentation rate, and substrate type. Our developed protocol is an efficient non-invasive method to survey shallow coastal areas and glacier fronts in the Arctic.

Key words: kelp forest, fish, zooplankton, Svalbard, acoustics, climate change

1. Introduction

The impacts of global warming and climate change have been widely studied on offshore shelves and in the open ocean, but knowledge gaps persist with respect to nearshore coastal areas and within Arctic fjords and glacier fronts. The effects of retreating tidewater glaciers on fish distribution remain particularly understudied, as they are areas under rapid change and very challenging to access and monitor. The high abundance and biomass of zooplankton in glacier plumes suggest that glacier fronts may serve as refugia for zooplankton-dependent food webs (Hop et al. 2023), and are important feeding areas for key Arctic fish species such as polar cod (*Boreogadus saida*) (Renaud et al. 2012; Lydersen et al. 2014). Upwelling from tidewater glaciers, caused by subglacial freshwater discharge that rises to the surface, circulates nutrient-rich bottom waters and replenishes zooplankton and juvenile fish to the surface waters, making these areas highly productive hotspots for fish, marine mammals, and seabirds (Lydersen et al. 2014; Vonnahme et al. 2021). It has been suggested that these areas provide refugia for Arctic species due to enhanced prey availability, as access to other feeding areas such as the marginal ice zone becomes more energetically demanding as the ice edge retreats (Varpe and Gabrielsen 2022; Hop et al. 2023). As glaciers retreat, these refugia are getting fewer and smaller, but further research is needed to study how pelagic organisms will react to these changes in littoral fjord areas.

Despite a shift from tidewater glaciers to land-terminating glaciers, significant amounts of nutrients can nonetheless be brought into the sea through terrestrial runoff, groundwater discharge, and permafrost thawing (Holmes et al. 2008; Terhaar et al. 2021), which are increasing due to higher precipitation and melting rates (Nowak et al. 2021). However, the associated high sediment and freshwater input leads to higher stratification and light attenuation in the water column that inhibit primary production at a local scale (Halbach et al. 2019; Connolly et al. 2020), and hence the transition from tidewater to land-terminating glaciers is expected to negatively affect pelagic productivity in Arctic fjords (Hopwood et al. 2020). Conversely, the retreat of tidewater glaciers and sea ice is opening new areas where macroalgae can potentially settle and drive benthic primary production (Krause-Jensen and Duarte 2014; Assis et al. 2022), which may offset the loss of production from tidewater glacier retreat and associated glacial upwelling. In deep fjords and coastal areas where sediment runoff is increasing from land-terminating glaciers, macroalgal settlement may be inhibited due to low light penetration and unsuitable settling substrate, but these interactions are highly dependent on fjord topography and bottom substrate type. Macroalgae are ecosystem engineers and provide important feeding and nursing sites for fish and benthic fauna (Lippert et al. 2001; James and Whitfield 2023), and a macroalgal expansion in the Arctic is expected to provide opportunities for associated species (Włodarska-Kowalczuk et al. 2009). The interactions of glacial discharge with the marine coastal ecosystem are complex, as there are several concomitant and occasionally counteracting effects, and little empirical data exist on the transition from a rich tidewater glacier front to a land-terminating glacier system, and particularly to what extent this will affect fish and zooplankton communities in these areas.

Pelagic ecosystems at glacier fronts and shallow nearshore areas are challenging to study with traditional sampling (e.g., gillnets, trawls) due to risks from drift ice, shallow rock formations, and difficulties operating vessels close to shore. Furthermore, these techniques have inherent biases such as size and species selectivity and are invasive (e.g., bycatch and damage to the seafloor). For this reason, coastal fish communities in Arctic fjords and their responses to glacier retreat are understudied. Developing a methodology to efficiently and sustainably study fish and zooplankton dynamics in these areas may provide a valuable link between the effects of glacier retreat on marine biogeochemistry and primary production and changes in fish and zooplankton communities and distribution. Alternative methods such as autonomous vehicles and hydroacoustics are emerging as a sustainable and non-invasive method for ecological monitoring in the Arctic (e.g., Geoffroy et al. 2016; Dunn et al. 2023). Though active acoustics are often used in conjunction with net sampling to achieve higher taxonomic resolution and for ground truthing (Simmonds and MacLennan 2005), scientific echosounders can be used as a standalone tool to record acoustic backscatter as a proxy for density as well as vertical distribution patterns (Axenrot et al. 2004; Kaartvedt et al. 2009).

The aim of this study was to compare areas along a gradient of glacier retreat, from a very recently transitioned glacier front from tidewater to land-terminating, a bay heavily affected by land-terminating glaciers further inland to a site where glaciers have been absent for a long period of time. Specifically, the density and vertical distribution of fish and zooplankton were compared between the three study locations. Comparing different environmental conditions within a single fjord provided a natural laboratory from which to measure the impacts from different physical environmental parameters linked to glacier retreat and, ultimately, how it could apply to large-scale modifications to the cryosphere. We hypothesized that land and glacial runoff at the river bay and land-terminating glacier front, with high sedimentation rates and low light availability for primary producers, leads to an area with low productivity and low biomass of zooplankton and fish. Furthermore, we developed and present a protocol to study pelagic ecosystems in coastal and glacier front habitats in the Arctic using a novel, cost-efficient, and non-invasive technology.

2. Materials and methods

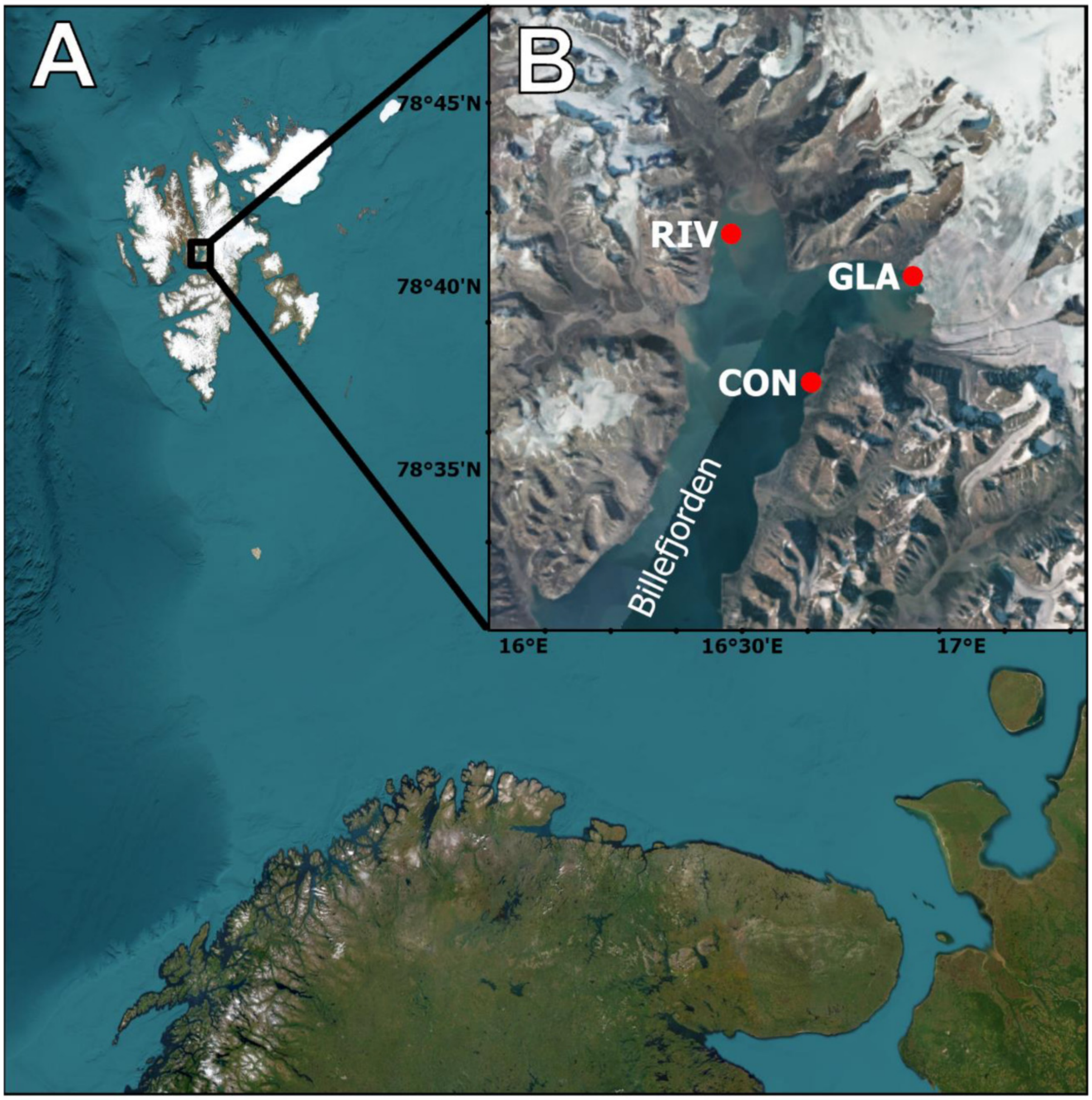
2.1. Study area

We conducted this study in Billefjorden, a high Arctic fjord located in Spitsbergen, Svalbard in September 2021, August 2022, and August 2023. Billefjorden is characterized by a shallow sill (70 m depth) at the fjord mouth, which limits the inflow of Atlantic water from the West Spitsbergen current that normally flows into the western fjords in Svalbard (Fig. 1A). This allows Billefjorden to stay colder than the surrounding fjords (Nilsen et al. 2008). Billefjorden has a heterogenous coastscape with a large river bay and the glacier Nordenskiöldbreen located at the inner part of the fjord (Fig. 1B). This originally marine-terminating glacier has been retreating rapidly and the northern side is now mostly land-terminating since 2017 (Szczuciński et al. 2009; Kavan et al. 2023). Petuniabukta, located northwest from the glacier, gathers a high amount of sediment runoff from the surrounding valleys and land-terminating glaciers through rivers (Láska et al. 2012), which creates a river bay with a large tidal flat. Glacial freshwater input from rivers and the sediment plume of the Nordenskiöldbreen glacier decrease with distance from both the river bay and the Nordenskiöldbreen glacier bay, and becomes minimal in the middle of the fjord, where the glacier front retreated 11 000 years ago (Baeten et al. 2010). This allows for a natural laboratory and the systematic comparison between the recently land-terminating glacier site (GLA), the river bay (RIV) with inland glacier-derived river input, and a site with minimal glacial input that can be considered practically as a control site for glacial influence (CON) (Fig. 1B).

2.2. Survey design

At each of the three stations (RIV, GLA, and CON), pelagic backscatter, a proxy for density of pelagic organisms, was measured via active acoustic mapping with a downward facing BioSonics DTX scientific split-beam echosounder (BioSonics, Seattle, USA) mounted to the rear of an uncrewed surface vehicle (USV). Hydroacoustics is commonly used as a method to study fish and zooplankton, as these organisms scatter sound due to the contrast between their morphological

Fig. 1. (A) Study area in Svalbard. (B) Satellite image of Billefjorden with the study stations (site with a recently land-terminating glacier—GLA, river bay—RIV, and site with low glacial input—CON. Map source: Earthstar Geographics and Norwegian Polar Institute.



properties (e.g., gas-filled structures and hard exoskeletons) and the surrounding water (Stanton et al. 1996; Simmonds and MacLennan 2005). Metrics of acoustic backscatter were recorded to quantify abundance and density of fish and zooplankton in the water column. We used an Otter USV (Maritime Robotics, Trondheim, Norway), an electric 200 × 108 × 106 cm vehicle, which was controlled remotely via broadband communication radio (direct link 5150–5875 MHz) from a nearby ship. The echosounder was used at an operating frequency of 200 kHz, which is commonly used to detect and study fish and zooplankton (Simmonds and MacLennan 2005), a ping rate of 5 Hz and pulse duration of 0.4 ms. Georeferencing of the acoustic data was done through the USV's internal Global Navigation Satellite System. Hydroacoustic mapping was done by running the USV in transects at an approximate speed of 3 knots perpendicular to the shoreline twice, in August 2022 and August 2023. The middle points of the transects were between 200 and 800 m away from shore and with an average of 30 m water depth at all sites, with all stations covering the minimum range of 24–42 m depth. In 2022, the transects were 17 min long covering an area of 2.8 ha and were done six times at each station (Supplementary Fig. 1). In 2023, the sampling area was increased for each station to 8.5 ha and 45 min long transects by increasing the number of transect lines and were conducted two times. Each time the transects were run is considered a replicate (six replicates in 2022 and two replicates in 2023).

To characterize the physical environment, oceanographic data were collected via a Valeport SWiFT CTDplus with Turbidity (Valeport Ltd., Totnes, UK). CTD water column deployments were conducted from the ship to record temperature (°C), salinity, and turbidity (nephelometric turbidity units; ntu) before the acoustic surveys. CTD profiles were taken for the entire water column (surface down to bottom depth) at the three stations in both years. The CTD deployments were taken at approximately 200 m from the center of the acoustic transects. These data were recorded to broadly characterize and compare the different study sites, as a high-resolution description of the oceanography of these areas would require a more comprehensive survey. Temperature and salinity profiles were also used to calculate the speed of sound and coefficients of absorption to calibrate the acoustic data.

To document the benthic habitat and bottom substrate type, baited remote underwater video (BRUV) deployments were done once at each of the stations in September 2021. The BRUV rig consisted of a metal frame with a GoPro camera and a 1 m long arm holding a mesh bag with 1 kg of polar cod (*B. saida*) as bait. The BRUV was lowered to the bottom at a depth of 10 m and recorded video for 1 h at each station. The maximum number of individuals observed at the same time at any one time on the entire video (MaxN) was used as a measure of relative abundance of taxa, which is commonly used in BRUV analyses to avoid double-counting (Osgood et al. 2019).

2.3. Hydroacoustic analyses

All raw acoustic files were extracted from the USV system and merged to create a single file for each station using Visual Acquisition v6.4.1.12747 (BioSonics, Seattle, USA). Acoustic data were subsequently processed in Echoview 13.1.121 (Echoview Software Pty Ltd, Tasmania, Australia). For each station, the file was scrutinized for noise and a bottom line was set by using the “Best bottom candidate” algorithm. A smoothing filter was applied to correct for benthic fish merging with the bottom signal, and very minor manual editing was done to correct for gaps in the bottom line when the signal momentarily dropped below the threshold. An exclusion line was added at a fixed depth of 5 m to exclude near field region noise close to the transducer, as well as a line 1 m above the bottom to exclude bottom noise, and the analyses were limited to the water column in between the exclusion lines.

To study variability in pelagic density between replicates for each station, each replicate of the 2022 data were then divided in 1 min long echointegration cells, for a total of 17 grids (as each run was 17 min long), and the integrated volume backscattering strength (Sv in the logarithmic form dB), center of mass (in m), and inertia (in m^2) for each cell were exported for further processing and analyses in the R statistical software v4.1.2 (R Core Team 2021). Volume backscattering strength (Sv) is a proxy for the density of organisms, center of mass identifies the average backscattering depth in the water column, and inertia is a measure of the spatial dispersion of scatterers around their center of mass (Urmy et al. 2012). A low inertia indicates tightly packed scatterers, while a high inertia indicates a larger spread.

The acoustic data were also exported as one file per replicate and the center of mass, inertia, and Sv in the logarithmic form (dB) were plotted to visualize dissimilarities between the stations (CON, RIV, and GLA) and years (2022 and 2023) in terms of their acoustic properties. To assess potential relationships between pelagic biomass and oceanographic conditions among stations and years, the acoustic and CTD datasets were structured in 1 m depth bins and the data merged by depth bin (CON: 5–43 m, GLA: 5–46 m, RIV: 5–37 m in 2022; CON: 5–47 m, GLA: 5–50 m, RIV: 5–34 m in 2023). A correlation matrix was done and a permutational multivariate Analysis of variance (PERMANOVA) was conducted with Sv mean in the linear form (m^2/m^3) as the response variable and temperature, turbidity, depth, year, and station as explanatory variables. A separate PERMANOVA was conducted with salinity instead of temperature as explanatory variable to avoid multicollinearity between temperature and salinity (Supplementary Fig. 2). As the top 5 m layer of the acoustic data had to be excluded due to near field noise, the analyses of the environmental data are therefore not including the top layer of the water column. As the CTD water profiles and acoustic transects had slightly different depth ranges, these analyses were performed only for the depth bins where both acoustic and CTD data were available. The “dplyr” and “vegan” packages were used in Rstudio to arrange and export the data as tables and to conduct the PERMANOVA analyses. ArcGIS Pro v.3.1 was used to map the locations of the sampling stations.

Table 1. Bottom depth (m) and descriptive statistics of the oceanographic measurements per station and year.

Station	Year	Bottom depth	Temperature range	Salinity range	Turbidity range
RIV	2022	37.6	7.1	14.5	13.1
RIV	2023	34	6.5	9.2	8.4
GLA	2022	46.4	7.6	18.2	102.5
GLA	2023	50.6	9.5	11.7	22.7
CON	2022	53.7	10	8.1	2.5
CON	2023	54.4	9.8	3.8	2.8

Note: Temperature in °C, salinity in practical salinity units, and turbidity in nephelometric turbidity units (ntu).

3. Results

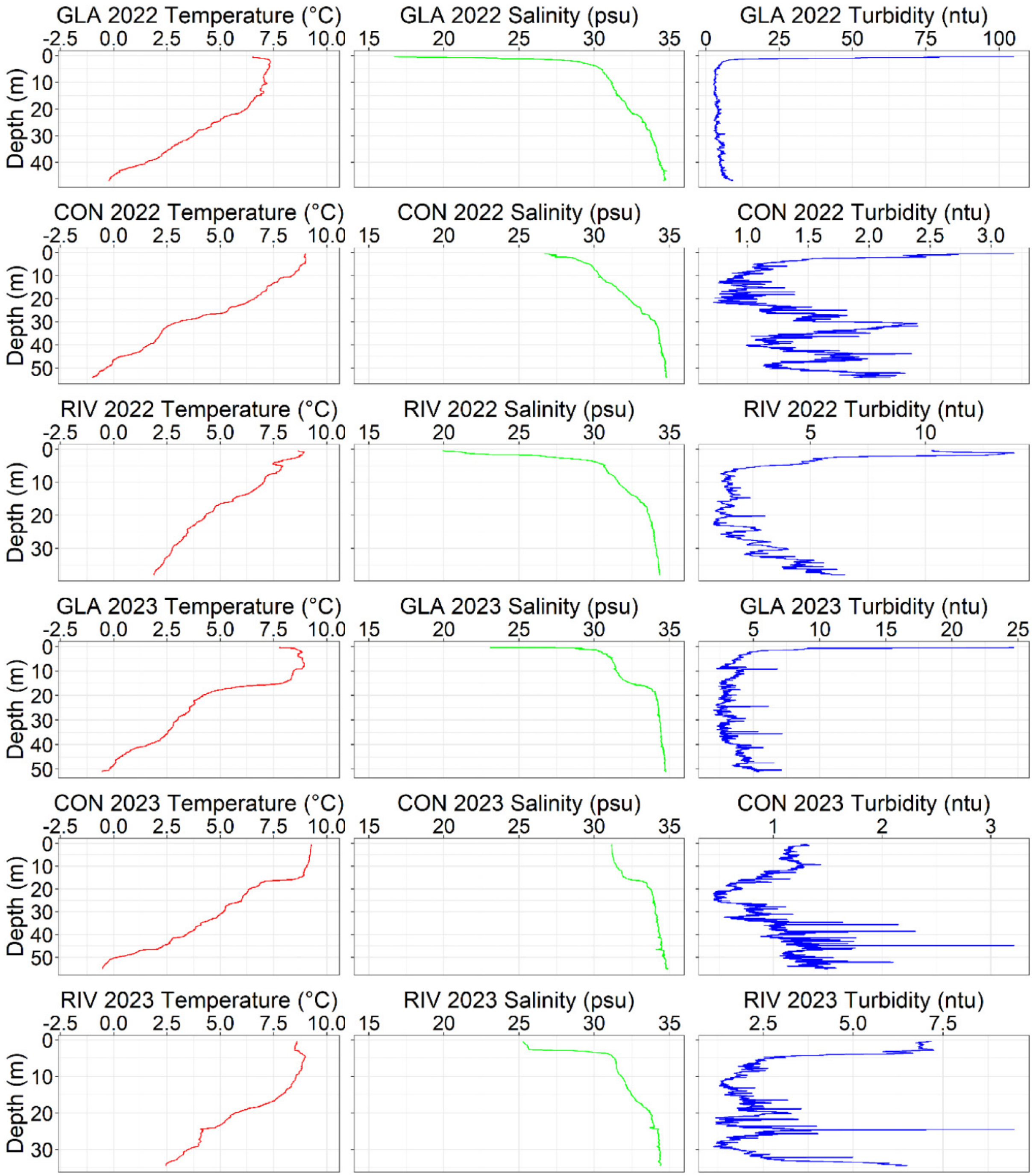
3.1. CTD water column profiles

The bottom depth at the CTD sampling stations was 37.6 and 34 m at the RIV station, 46.4 and 50.6 m at the GLA station, and 53.7 and 54.4 m at the CON station in 2022 and 2023, respectively (Table 1, Fig. 2). The ranges of temperature (max temperature–min temperature) were highest at the CON station with 10 °C and lowest at the RIV station with 6.5 °C. Salinity ranges were highest at the GLA station with 18.2 psu and lowest at the CON station with 3.8 psu. Turbidity ranges were highest at the GLA station with 102.5 ntu and lowest at the CON station with 2.5 ntu. The GLA station showed the highest surface turbidity and lowest surface salinity in both years, indicating a highly stratified surface water layer.

3.2. Pelagic density and vertical distribution

The bottom depths at the study sites during the acoustic mapping surveys ranged from 5 to 56 m (Table 2). The RIV station had a flat and homogenous bottom topography, while the GLA station had an irregular bottom with steep cliffs, and the CON station showed a gradual slope (Fig. 3).

Fig. 2. CTD water column profiles for the glacier (GLA), CON, and river station (RIV) in 2022 and 2023 with measurements of temperature, salinity, and turbidity.



In 2022, Sv values and standard deviation were two orders of magnitude higher at the CON station than at the other two stations, indicating higher pelagic density and higher variability at this station (Fig. 4, Table 2). Several large pelagic aggregations producing a strong backscatter were observed in the echogram and are likely the cause of the high variation in Sv values at the CON station (e.g., Fig. 3, right panel). Pelagic density was similar between the glacier and river stations. The glacier station had the deepest center of mass at 24.7 m and highest inertia at 147.2 m^2, which was reflected by a deep and dispersed scattering layer in the echograms from 15 m depth down to the bottom.

In 2023, the GLA and RIV stations displayed higher pelagic density than the previous year, with an increase of one and two orders of magnitude respectively. The RIV and CON stations showed an increase in center of mass, which could be linked to several strong scattering aggregations deeper in the water column at both stations (Fig. 3). The GLA station showed the lowest backscatter with one order of magnitude lower than the CON and RIV stations, and the high-

Table 2. Results from the integration of the acoustic data showing Sv mean, center of mass, inertia, and standard deviation for the means of all the replicates.

Station	Year	Bottom depth range (m)	Sv mean (m^2/m^3)	Center of mass (m)	Inertia (m^2)	Standard deviation
RIV	2022	24–42	5.3e-09	13.2	66.4	1.7e-07
RIV	2023	24–43	1.6e-07	24.8	102.6	8.5e-06
GLA	2022	10–49	7.6e-09	24.7	147.2	1.5e-07
GLA	2023	5–56	3.3e-08	22.4	169.7	1.2e-06
CON	2022	7–45	8.9e-07	17.1	44.9	2.7e-05
CON	2023	13–50	2.2e-07	31.3	97.3	6.3e-06

Fig. 3. Echogram snapshots of the RIV (left), GLA (middle), and CON (right) stations from 2023.

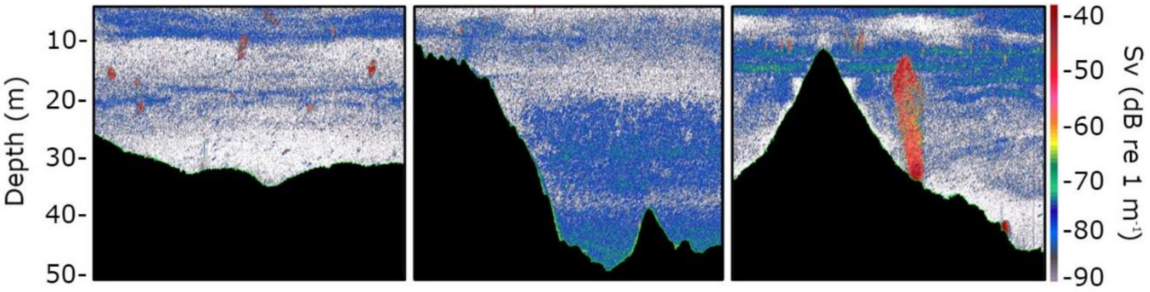


Fig. 4. Differences among stations in acoustic parameters (logarithmic Sv mean, center of mass, and inertia). Mean values for Sv, center of mass, and inertia were extracted for each transect (six replicates in 2022 and two replicates in 2023) and are presented by station and year. The box represents the interquartile range (IQR), and the line within indicates the median. The whiskers extend to the most extreme data points not considered outliers, which are represented by individual dots beyond the whiskers.

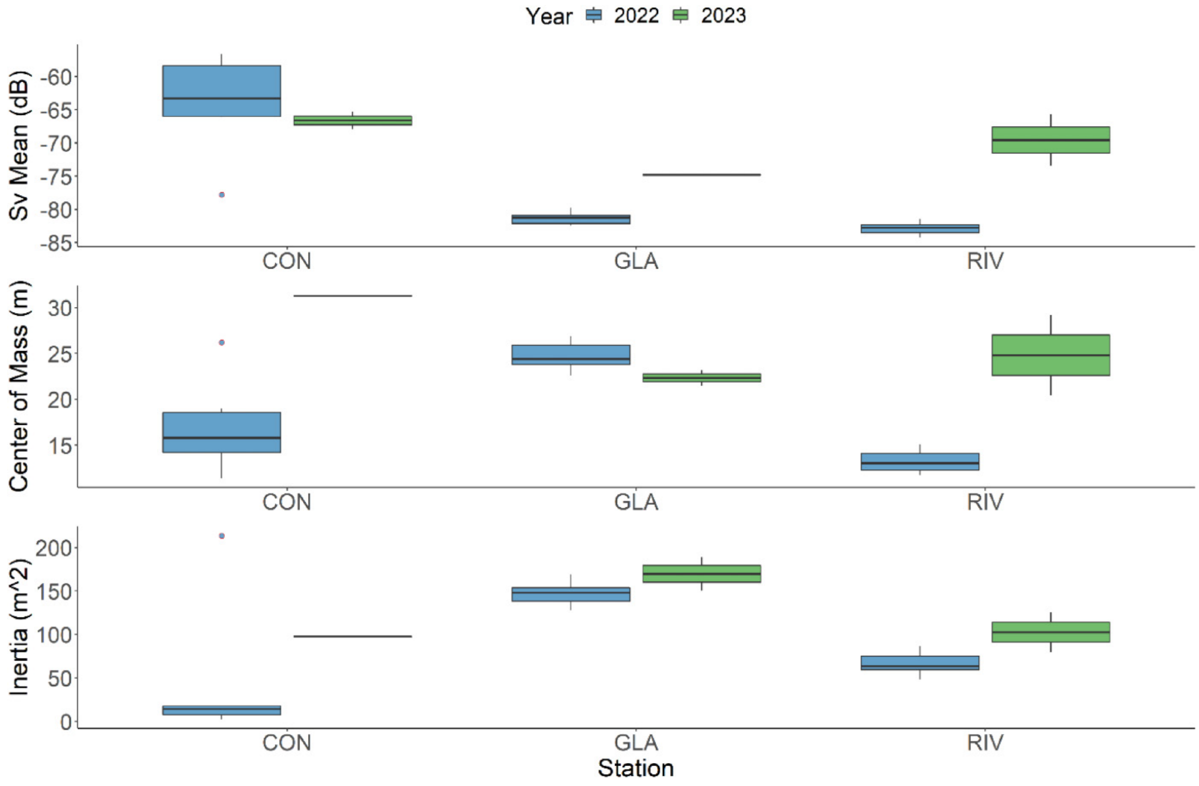


Fig. 5. Boxplots showing the ranges of Sv (dB) mean for each grid at the CON, GLA, and RIV stations in 2022.

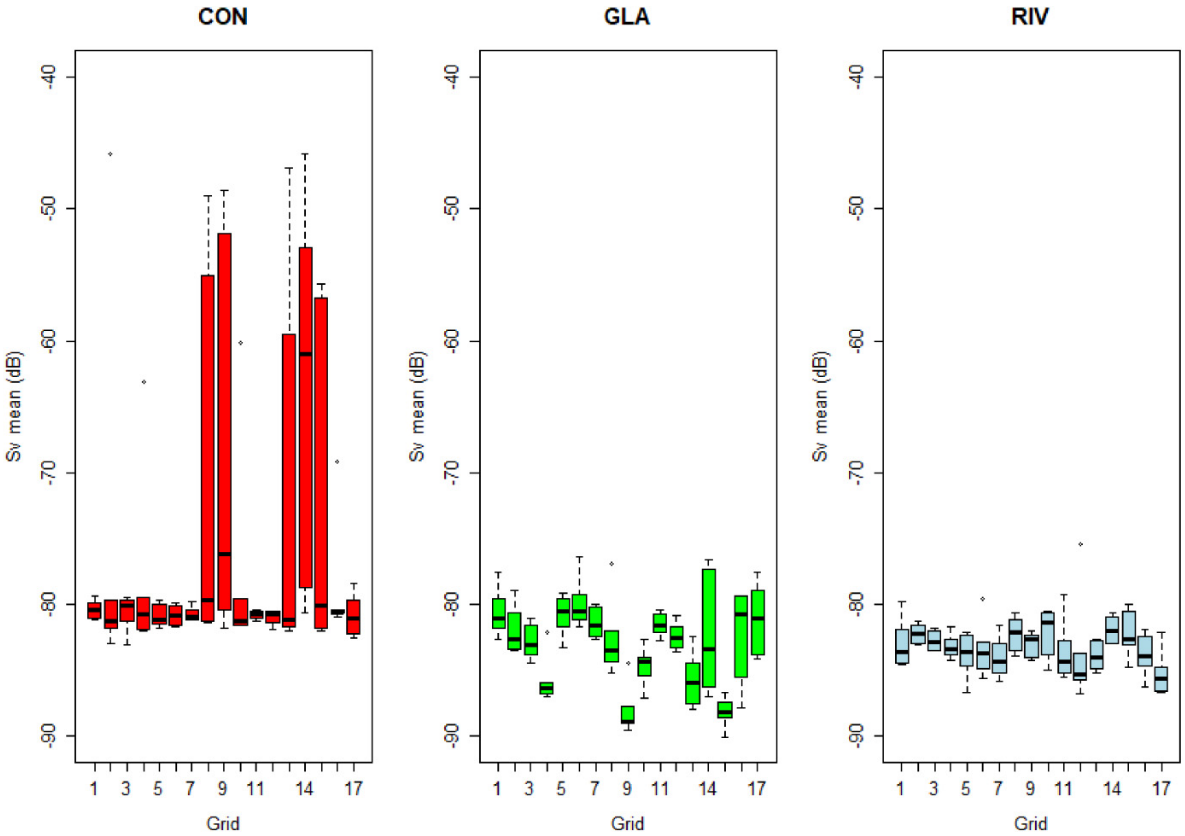


Table 3. Permutational multivariate Analysis of variance (PERMANOVA) with 999 permutations of Sv mean as the response variable and temperature, turbidity, depth bin, year, and station as explanatory variables.

	df	SumOfSqs	R2	F	Pr(>F)
Temperature	1	0.86	0.01	4.87	0.005
Turbidity	1	4.93	0.08	27.89	0.001
Year	1	10.57	0.17	59.74	0.001
Station	2	6.18	0.10	17.48	0.001
DepthBin	1	1.27	0.02	7.16	0.001
Residual	226	39.97	0.63	NA	NA
Total	232	63.79	1.00	NA	NA

Table 4. Permutational multivariate Analysis of variance (PERMANOVA) with 999 permutations of Sv mean as the response variable and salinity, turbidity, depth bin, year, and station as explanatory variables.

	df	SumOfSqs	R2	F	Pr(>F)
Salinity	1	0.25	0.00	1.40	0.236
Turbidity	1	4.91	0.08	27.55	0.001
Year	1	11.05	0.17	62.05	0.001
Station	2	6.34	0.10	17.79	0.001
DepthBin	1	0.97	0.02	5.47	0.003
Residual	226	40.26	0.63	NA	NA
Total	232	63.79	1.00	NA	NA

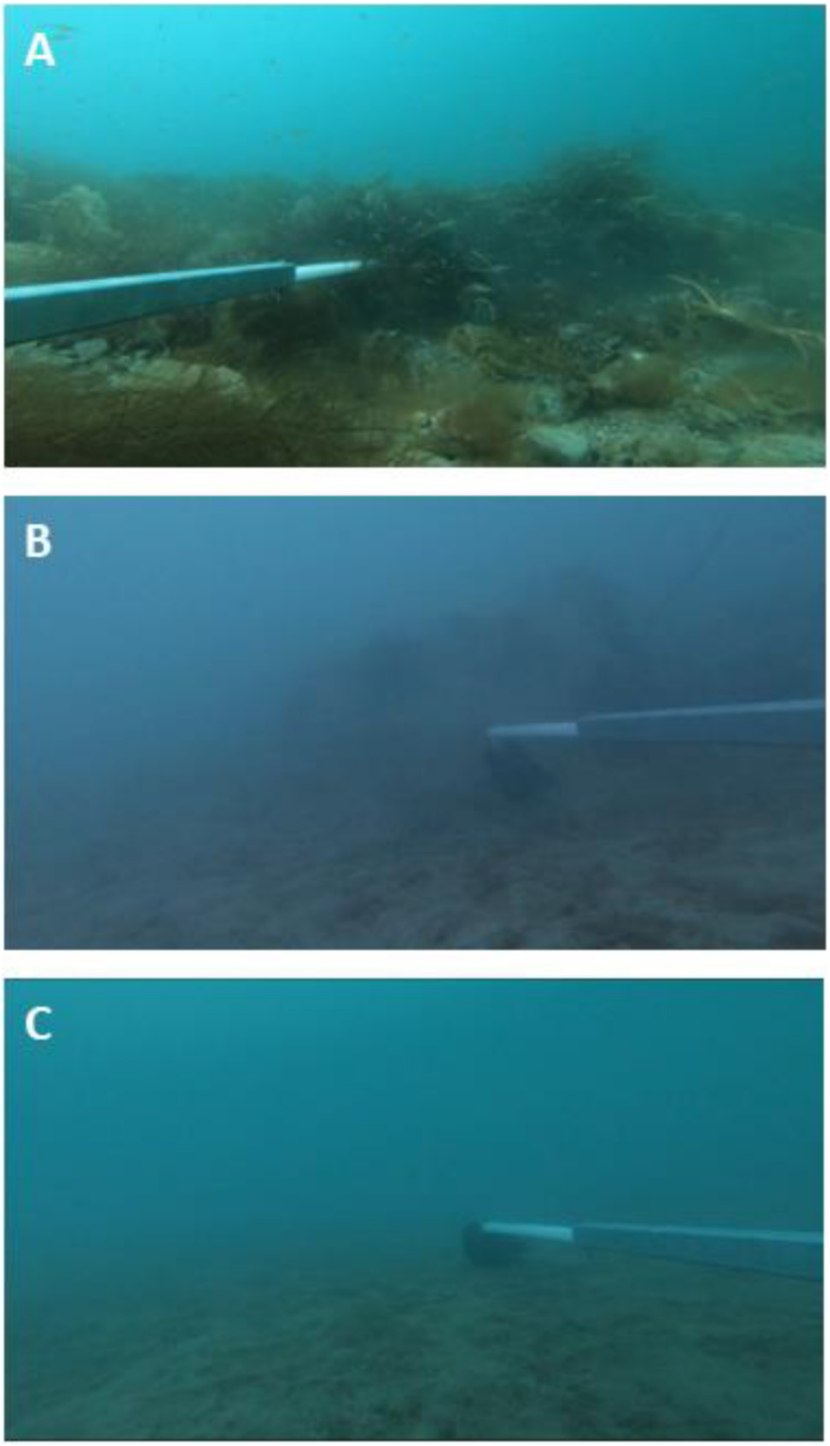
est inertia at 169.7 m^2 reflecting a disperse scattering layer. Despite the interannual differences mentioned above, the CON station consistently reflected the highest pelagic density (Fig. 4).

The variability of the logarithmic Sv values between replicates was higher at the CON station, with values ranging from −80 to −45 dB (Fig. 5). At the GLA and RIV stations, Sv values ranged between −90 and −75 dB and between −87 and −75 dB, respectively.

3.3. Acoustic backscatter and physical oceanography

The correlation matrix showed a high correlation between temperature and salinity (−0.88), and hence these variables were analyzed in separate PERMANOVAs. The PERMANOVA analysis revealed weak but significant effects ($p < 0.05$) of temperature turbidity and depth as well as station and year on the variation of pelagic density (Table 3). Of the CTD measurements, turbidity showed the strongest effect with an F value of 27.89, while year showed the strongest effect overall with an F value of 59.74. Temperature had the weakest effect on pelagic density with an F value of 4.87. However, temperature and turbidity only explained ≤8% of the variation in pelagic backscatter each, indicating the importance of other drivers. Salinity showed no significant effect on pelagic density with an F value of 1.37 and $p > 0.05$ (Table 4).

Fig. 6. Snapshots from the BRUV deployment at (A) the CON station, (B) the GLA station, and (C) the RIV station.



3.4. BRUV

The BRUV footage revealed an abundance of fish, crabs, and large zooplankton at the CON station, in which dense kelp beds could also be observed (Fig. 6A). The visibility at the glacier and river stations was low, but the BRUV showed a more homogenous landscape at these stations compared to the CON station, with almost no macroalgae. Three unidentified fish were observed at the glacier station, while no organisms were observed at the river station (Table 5).

4. Discussion

4.1. Links between cryosphere changes and pelagic density and distribution

Tidewater glacier fronts are highly productive pelagic environments due to subglacial nutrient circulation, but as these glaciers retreat onto land, the upwelling of nutrients disappears. In coastal areas with high influence of land-terminating glaciers either directly in front or due to river

Table 5. Summary of the baited remote underwater video (BRUV) deployment data and maximum observed number of a taxa in a single frame (MaxN).

Station	Latitude (°N)	Longitude (°E)	Fish MaxN	Zooplankton MaxN
CON	78°37.063	16°40.704	6	100+
GLA	78°40.062	16°55.563	3	0
RIV	78°41.054	16°27.768	0	0

Note: There were 60 observations per hour (1 min each) at every station, and all deployments were done at 10 m depth.

runoff from inland glaciers, high sedimentation rates and subsequent low light availability would lead to less productive pelagic ecosystems (Hopwood et al. 2020). Among our three study sites along a gradient of glacier influence, the acoustic data consistently showed higher pelagic density at the CON site with the lowest glacial influence, and the higher standard deviation and wider range of Sv values between the replicates at this site indicate a more productive and dynamic pelagic system at this site than at the GLA and RIV stations with higher glacial influence. Although it is difficult to identify the organisms that compose the scattering structures with a single frequency acoustic system, the large and strong scattering aggregations visible in the echogram at the CON station and large variability of Sv values within grids likely indicate large fish schools. In the absence of data indicating large fish schools, the pelagic density was consistently low, which suggests these fish schools and scattering aggregations with high Sv values drive the high pelagic density at the CON station. The echograms and acoustic analyses showed the large strong scattering aggregations to be linked to the bottom, which was consistent with the BRUV footage in which numerous crabs, benthic fish, and mysid shrimp appeared next to the bait bag and indicated a rich demersal habitat and high densities of organisms on or near the seafloor.

In contrast, the two glacier-influenced stations (RIV and GLA) showed a generally lower pelagic density over the water column, albeit with several small fish schools causing a higher acoustic backscatter at the river station in 2023. While the acoustic data showed fish schools associated to the bottom at the CON station, the scattering aggregations were dispersed across the water column at the river and glacier sites. One explanation for this difference could be due to variation in topography between the study sites. For instance, the steep cliffs at the glacier front at the GLA station likely contribute to a dispersed scattering layer and the observed higher inertia. Conversely, the flatter bottom at the river site may lead to a concentrated scattering layer. Nonetheless, the echograms show distinct patterns in that, when fish schools are present, these aggregations are small and dispersed over the water column at the river and glacier stations, while they are large and associated to the bottom at the CON station as is shown by the higher Sv values and lower inertia. The similarities in pelagic density and distribution between the glacier and river stations, particularly in 2022, may be linked to the parallels in environmental conditions between these two sites, namely the high sediment input from rivers and glaciers, which hinders the settling of benthic primary producers and favors a pelagic-associated ecosystem (Hop et al. 2023). Furthermore, the depth range of the river station was deeper than the depth distribution of macroalgae in Svalbard (Düsedau et al. 2024), but macroalgal growth would not be expected in a river bay with high sediment load. Conversely, the depth ranges at the GLA and CON stations covered shallower ranges (from 5 and 7 m depth, respectively) where macroalgae could be present. Similarly to the river bay, at the glacier front, albeit land-terminating, there is a high sediment input as shown by the high turbidity values and by the BRUV footage, and hence the low light regime may hinder macroalgal growth. At the CON station, however, the low glacial input, low turbidity, and rocky substrate facilitates macroalgal settlement as seen on the BRUV. These differences in light regime leading to a richer benthic and demersal habitat at the CON station may explain the differences in pelagic density and distribution between the sites.

The ranges in the oceanographic measurements indicated that salinity and turbidity values fluctuate more at the RIV and GLA stations compared to the CON station, particularly in the surface layer, likely due to freshwater and sediment input from the rivers and glacier. Furthermore, the high values of turbidity observed at the glacier station may be linked to sediments being brought by currents from the nearby tidewater glacier plume. The analysis of the relationship between pelagic biomass and oceanographic measurements showed only weak statistically significant effects of temperature, depth, and turbidity on the acoustic backscattering strength, and no significant effect of salinity. It should be noted that due to removing the top 5 m of the water column in the acoustic analyses to eliminate near field noise, this shallow layer was also omitted from the CTD data when merging the datasets, and therefore is not included in the statistical analyses. As the water column CTD profiles showed, the highest variability in the physical oceanography was in the top layer, likely due to the sediment plumes from the river bay and glacier. Therefore, in the top 5 m environmental conditions may be more important than at deeper depths, as high variations in salinity and temperature can drive the abundance and movement dynamics of fish and zooplankton. Differences in these environmental factors between the stations can drive the patterns of pelagic density and distribution deeper in the water column (e.g., high surface turbidity at the glacier front reduces light availability and may alter the vertical distribution of fish and zooplankton). However, as temperature, depth, salinity, and turbidity explained little of the variation, other factors must thus have a major role to drive ecosystem dynamics. As seen on the BRUV footage, there was a rich benthic and demersal ecosystem at the CON station, characterized by dense kelp beds, at least in the shallow areas that are within the depth distribution of kelp in Svalbard Conversely, little macroalgal coverage was observed at the river and glacier stations, likely due to the high sediment input, low light availability, and soft bottom substrate. The BRUV was deployed in 2021 and therefore not concurrent with the acoustic study, and hence, there are limitations in comparing these data, but the underwater footage provides a snapshot of the benthic habitat and substrate type, which is likely an important driver for pelagic density at the deeper parts of the stations. The high sedimentation at the river and glacier sites was visible in the BRUV footage, while there was more light availability and hard substrate at the site with less terrestrial runoff.

In shallow areas with hard bottom, low sedimentation input, and little mechanical disturbance, macroalgal growth can be stimulated and lead to a high associated biomass of organisms that feed on the algae or use them as shelter or nursery grounds (Lippert et al. 2001; Teagle et al. 2017; James and Whitfield 2023). Glacier and sea-ice retreat open up new areas where marine organisms can settle, and previous studies have shown that macroalgae are expanding northward (Krause-Jensen and Duarte 2014; Assis et al. 2022) and settling at retreating glacier fronts (Deregibus et al. 2023; Gonzalez Triginer et al. 2024). In shallow coastal areas, these demersal habitats can also benefit pelagic fish and zooplankton, which may explain why both the demersal habitat richness and pelagic density were consistently higher at the CON site. The effects of the expansion of these habitats in the Arctic on fjord ecosystem dynamics are complex, and conducting similar studies in other areas would aid in understanding their potential in mitigating the loss of pelagic productivity due to glacial retreat. Our results are consistent with the literature in showing that areas influenced by land-terminating glaciers and rivers may be linked to lower density of fish and zooplankton compared to areas without the influence of terrestrial runoff (Hopwood et al. 2020). In our study, the site with the highest recorded pelagic density had the lowest influence from rivers and glaciers, which potentially allowed for settlement and growth of macroalgae. It has been suggested that an enhanced demersal habitat expanding into areas previously covered by tidewater glaciers might be beneficial to both benthic and pelagic organisms, at least in shallow ecosystems. A recent study in inner Billefjorden recorded macroalgal settlement in areas that were covered by the glacier until very recently, while there was virtually no macroalgal coverage at the river bays (Gonzalez Triginer et al. 2024). However, there is limited data on the potential of macroalgal expansion to offset the loss of productivity driven by subglacial upwelling in high Arctic fjords, and it is likely closely linked to fjord topography and land runoff in coastal fjord areas, and hence highly vary between fjord systems. More research is needed to further study the expansion of rich demersal habitats following glacial retreat and their role in ecosystem dynamics and fjord productivity in the Arctic.

4.2. The potential of autonomous hydroacoustic surveys in coastal areas

The acoustic properties of the water column in shallow coastal areas can be highly dynamic and complex, and therefore, both echogram visualization and data analyses need to be taken into consideration when interpreting the results. Moreover, complementing the acoustic data with underwater video and oceanographic measurements further aids in understanding the complexity of a spatial comparison of pelagic distribution. As a measure of the average backscatter depth in the water column, the center of mass metric is sensitive to being skewed by outliers in the data such as fish aggregations. Inertia is a measure of dispersion or spread of scatterers, and it considers both the squared distances from the center of mass and their Sv values (Urmy et al. 2012). Therefore, inertia is less sensitive to outliers and can lead to a representative measure of pelagic dispersion, and a combination of center of mass and inertia are a more robust measure of the location and dispersion of the pelagic scattering layer.

The efficiency of hydroacoustics to map and assess pelagic biomass in the Arctic has been shown in multiple studies (e.g., Benoit et al. 2008; Kaartvedt et al. 2009; Geoffroy et al. 2019), but validation of acoustic data is still critical to identifying species and functional groups. Validation of such data is often done by trawl surveys (Geoffroy et al. 2019), but when working in shallow littoral areas, it is often not possible to trawl, and alternative validation methods are very limited and often biased, especially in muddy and shallow glacier front areas.

Acoustic surveys have been done in the high Arctic in the past to map macroalgae coverage (Kruss et al. 2017; Wiktor et al. 2022), and such methodology can be adapted to study the pelagic environment in these areas. The inaccessibility of glacier fronts and remote areas in the high Arctic makes it challenging to use traditional methods for marine sampling in coastal areas, and autonomous hydroacoustic and remote sensing techniques can be used to safely and efficiently study these sites, which are undergoing large changes due to climate shifts. The use of such novel methodology allowed for sampling very close to the glacier front, which would not be possible from a ship. This allowed to gain new insight on glacier fronts, which, as boundaries between the cryosphere and the marine ecosystem, are key areas to understanding the effects of climate change on marine biological processes. As rich benthic habitats such as kelp forests expand following glacier retreat, littoral fjord areas in the high Arctic may be more resilient to loss of biomass and biodiversity than previously thought.

Acknowledgements

We would like to thank Kathy Dunlop and the Institute of Marine Research for the loan of the BRUV and for helping with the setup. We also thank the technical staff at the University Centre in Svalbard for their support during long hours of fieldwork. We would like to thank the reviewers for their valuable input, which helped to improve our manuscript.

Article information

History dates

Received: 27 May 2024
Accepted: 10 October 2024
Accepted manuscript online: 23 October 2024
Version of record online: 23 January 2025

Notes

This paper is part of a collection entitled Thirty years of Earth System Science in high-Arctic Svalbard: status, trends, and future recommendations.

Copyright

Data availability

The CTD profile datasets are publicly available at https://doi.org/10.5281/zenodo.13323435. The acoustic data generated and analyzed during this study fall under confidentiality regulations of the Norwegian Mapping Authority.

Author information

Author ORCIDs

Victor Gonzalez Triginer https://orcid.org/0000-0002-9020-1599
Arunima Sen https://orcid.org/0000-0001-7847-2137
Maxime Geoffroy https://orcid.org/0000-0003-2633-5565
Børge Damsgård https://orcid.org/0000-0002-7731-0168

Author contributions

Conceptualization: VGT, AS, BD
Data curation: VGT
Formal analysis: VGT
Funding acquisition: BD
Investigation: VGT, AS
Methodology: VGT, BD
Project administration: AS, MG, BD
Software: VGT
Supervision: AS, MG, BD
Validation: VGT
Visualization: VGT
Writing – original draft: VGT
Writing – review & editing: AS, MG, BD

Competing interests

The authors declare there are no competing interests.

Funding information

This study was financed through the FACE-IT project, which has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 869154. MG acknowledges funding from the Canadian Natural Sciences and Engineering Research Council (NSERC) Discovery Grant program, and RCN-funded projects Deep Impact (#300333) and Opkrop (#343352).

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/as-2024-0040.

References

Assis, J., Serrão, E.A., Duarte, C.M., Fragkopoulou, E., and Krause-Jensen, D. 2022. Major expansion of marine forests in a warmer Arctic. Frontiers in Marine Science, **9**: 850368. doi:10.3389/fmars.2022.850368.

Axenrot, T., Didrikas, T., Danielsson, C., and Hansson, S. 2004. Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. ICES Journal of Marine Science, **61**(7): 1100–1104. doi:10.1016/j.icesjms.2004.07.006.

Baeten, N.J., Forwick, M., Vogt, C., and Vorren, T.O. 2010. Late weichselian and holocene sedimentary environments and glacial activity in Billefjorden, Svalbard. Geological Society, London, Special Publications, **344**(1): 207–223. doi:10.1144/SP344.15.

Benoit, D., Simard, Y., and Fortier, L. 2008. Hydroacoustic detection of large winter aggregations of Arctic cod (*Boreogadus saida*) at depth in ice-covered Franklin Bay (Beaufort Sea). Journal of Geophysical Research: Oceans, **113**(C6): 2007JC004276. doi:10.1029/2007JC004276.

Connolly, C.T., Cardenas, M.B., Burkart, G.A., Spencer, R.G.M., and McClelland, J.W. 2020. Groundwater as a major source of dissolved organic matter to Arctic coastal waters. Nature Communications, **11**(1): Article 1. doi:10.1038/s41467-020-15250-8.

Deregibus, D., Campana, G.L., Neder, C., Barnes, D.K.A., Zacher, K., Piscicelli, J.M., et al. 2023. Potential macroalgal expansion and blue carbon gains with northern Antarctic Peninsula glacial retreat. Marine Environmental Research, **189**: 106056. doi:10.1016/j.marenvres.2023.106056. PMID: 37385084.

Dunn, M., Pedersen, G., Basedow, S.L., Daase, M., Falk-Petersen, S., Bachelot, L., et al. 2023. Inverse method applied to autonomous broadband hydroacoustic survey detects higher densities of zooplankton in near-surface aggregations than vessel-based net survey. Canadian Journal of Fisheries and Aquatic Sciences, **80**(3): 451–467. doi:10.1139/cjfas-2022-0105.

Düsedau, L., Fredriksen, S., Brand, M., Fischer, P., Karsten, U., Bischof, K., et al. 2024. Kelp forest community structure and demography in Kongsfjorden (Svalbard) across 25 years of Arctic warming. Ecology and Evolution, **14**(6): e11606. doi:10.1002/ece3.11606. PMID: 38919650.

Geoffroy, M., Cottier, F., Berge, J., and Inall, M. 2016. AUV-based acoustic observations of the distribution and patchiness of pelagic scattering layers during midnight sun. ICES Journal of Marine Science, **74**(9): 2342–2353. doi:10.1093/icesjms/fsw158.

Geoffroy, M., Daase, M., Cusa, M., Darnis, G., Graeve, M., Santana Hernández, N., et al. 2019. Mesopelagic sound scattering layers of the High Arctic: seasonal variations in biomass, species assemblage, and trophic relationships. Frontiers in Marine Science, **6**: 364. doi:10.3389/fmars.2019.00364.

Gonzalez Triginer, V., Beck, M., Sen, A., Bischof, K., and Damsgård, B. 2024. Acoustic mapping reveals macroalgal settlement following a retreating glacier front in the High Arctic. Frontiers in Marine Science, **11**: 1438332. doi:10.3389/fmars.2024.1438332.

Halbach, L., Vihtakari, M., Duarte, P., Everett, A., Granskog, M.A., Hop, H., et al. 2019. Tidewater glaciers and bedrock characteristics control the phytoplankton growth environment in a fjord in the Arctic. Frontiers in Marine Science, **6**: 254. doi:10.3389/fmars.2019.00254.

Holmes, R.M., McClelland, J.W., Raymond, P.A., Frazer, B.B., Peterson, B.J., and Stieglitz, M. 2008. Lability of DOC transported by Alaskan rivers to the Arctic Ocean. Geophysical Research Letters, **35**(3). doi:10.1029/2007GL032837. PMID: 24347740.

Hop, H., Wold, A., Vihtakari, M., Assmy, P., Kuklinski, P., Kwasniewski, S., et al. 2023. Tidewater glaciers as "climate refugia" for zooplankton-dependent food web in Kongsfjorden, Svalbard. Frontiers in Marine Science, **10**. doi:10.3389/fmars.2023.1161912.

Hopwood, M.J., Carroll, D., Dunse, T., Hodson, A., Holding, J.M., Iriarte, J.L., et al. 2020. Review article: how does glacier discharge affect marine biogeochemistry and primary production in the Arctic? The Cryosphere, **14**(4): 1347–1383. doi:10.5194/tc-14-1347-2020.

James, N.C., and Whitfield, A.K. 2023. The role of macroalgae as nursery areas for fish species within coastal seascapes. Cambridge Prisms: Coastal Futures, **1**: e3. doi:10.1017/cft.2022.3.

Kaartvedt, S., Røstad, A., Klevjer, T.A., and Staby, A. 2009. Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. Marine Ecology Progress Series, **395**: 109–118. doi:10.3354/meps08174.

Kavan, J., Luláková, P., Małecki, J., and Strzelecki, M.C. 2023. Capturing the transition from marine to land-terminating glacier from the 126-year retreat history of Nordenskiöldbreen, Svalbard. Journal of Glaciology, 1–11. doi:10.1017/jog.2023.92.

Krause-Jensen, D., and Duarte, C.M. 2014. Expansion of vegetated coastal ecosystems in the future Arctic. Frontiers in Marine Science, **1**. doi:10.3389/fmars.2014.00077. PMID: 27785452.

Kruss, A., Tęgowski, J., Tatarek, A., Wiktor, J., and Blondel, P. 2017. Spatial distribution of macroalgae along the shores of Kongsfjorden (West Spitsbergen) using acoustic imaging. Polish Polar Research, **38**(2): 205–229. doi:10.1515/popore-2017-0009.

Láska, K., Witoszová, D., and Prošek, P. 2012. Weather patterns of the coastal zone of Petuniabukta, central Spitsbergen in the period 2008–2010. Polish Polar Research, **33**(4): 297–318. doi:10.2478/v10183-012-0025-0.

Lippert, H., Iken, K., Rachor, E., and Wiencke, C. 2001. Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biology, **24**(7): 512–522. doi:10.1007/s003000100250.

Lydersen, C., Assmy, P., Falk-Petersen, S., Kohler, J., Kovacs, K.M., Reigstad, M., et al. 2014. The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. Journal of Marine Systems, **129**: 452–471. doi:10.1016/j.jmarsys.2013.09.006.

Nilsen, F., Cottier, F., Skogseth, R., and Mattsson, S. 2008. Fjord–shelf exchanges controlled by ice and brine production: the interannual variation of Atlantic Water in Isfjorden, Svalbard. Continental Shelf Research, **28**(14): 1838–1853. doi:10.1016/j.csr.2008.04.015.

Nowak, A., Hodgkins, R., Nikulina, A., Osuch, M., Wawrzyniak, T., Kavan, J., et al. 2021. From land to fjords: the review of Svalbard hydrology from 1970 to 2019 (SvalHydro). Svalbard Integrated Arctic Earth Observing System. doi:10.5281/zenodo.4294063.

Osgood, G.J., McCord, M.E., and Baum, J.K. 2019. Using baited remote underwater videos (BRUVs) to characterize chondrichthyan communities in a global biodiversity hotspot. PLoS ONE, **14**(12): e0225859. doi:10.1371/journal.pone.0225859. PMID: 31800602.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from https://www.R-project.org/ [accessed 25 May 2024].

Renaud, P.E., Berge, J., Varpe, Ø., Lønne, O.J., Nahrgang, J., Ottesen, C., and Hallanger, I. 2012. Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, Boreogadus saida? Polar Biology, **35**(3): 401–412. doi:10.1007/s00300-011-1085-z.

Simmonds, E.J., and MacLennan, D.N. 2005. Fisheries acoustics: theory and practice. 2nd ed. Blackwell Science.

Stanton, T.K., Chu, D., and Wiebe, P.H. 1996. Acoustic scattering characteristics of several zooplankton groups. ICES Journal of Marine Science, **53**(2): 289–295. doi:10.1006/jmsc.1996.0037.

Szczuciński, W., Zajączkowski, M., and Scholten, J. 2009. Sediment accumulation rates in subpolar fjords—Impact of post-little Ice Age glaciers retreat, Billefjorden, Svalbard. Estuarine, Coastal and Shelf Science, **85**(3): 345–356. doi:10.1016/j.ecss.2009.08.021.

Teagle, H., Hawkins, S.J., Moore, P.J., and Smale, D.A. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology, **492**: 81–98. doi:10.1016/j.jembe.2017.01.017.

Terhaar, J., Lauerwald, R., Regnier, P., Gruber, N., and Bopp, L. 2021. Around one third of current Arctic Ocean primary production sustained by rivers and coastal erosion. Nature Communications, **12**(1): 169. doi:10.1038/s41467-020-20470-z. PMID: 33420093.

Urmy, S.S., Horne, J.K., and Barbee, D.H. 2012. Measuring the vertical distributional variability of pelagic fauna in Monterey Bay. ICES Journal of Marine Science, **69**(2): 184–196. doi:10.1093/icesjms/fsr205.

Varpe, Ø., and Gabrielsen, G.W. 2022. Aggregations of foraging black guillemots (Cepphus grylle) at a sea-ice edge in front of a tidewater glacier. Polar Research, **41**. doi:10.33265/polar.v41.7141.

Vonnahme, T.R., Persson, E., Dietrich, U., Hejdukova, E., Dybwad, C., Elster, J., et al. 2021. Early spring subglacial discharge plumes fuel under-ice primary production at a Svalbard tidewater glacier. The Cryosphere, **15**(4): 2083–2107. doi:10.5194/tc-15-2083-2021.

Wiktor, J.M., Tatarek, A., Kruss, A., Singh, R.K., Wiktor, J.M., and Søreide, J.E. 2022. Comparison of macroalgae meadows in warm Atlantic versus cold Arctic regimes in the high-Arctic Svalbard. Frontiers in Marine Science, **9**: 1021675. doi:10.3389/fmars.2022.1021675.

Włodarska-Kowalczuk, M., Kukliński, P., Ronowicz, M., Legeżyńska, J., and Gromisz, S. 2009. Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). Polar Biology, **32**(6): 897–905. doi:10.1007/s00300-009-0590-9.

Paper III

Víctor González Triginer, Maxime Geoffroy, Elena Eriksen, Børge Damsgård
and Arunima Sen (2025)

Borealization of pelagic fish communities in the high Arctic during the polar night

In review at Estuarine, Coastal and Shelf Science

Borealization of pelagic fish communities in the high Arctic during the polar night

Victor Gonzalez Triginer [a,b], Maxime Geoffroy [b,c], Elena Eriksen [d], Børge Damsgård [a], Arunima Sen [a]

[a]Department of Arctic Biology, The University Centre in Svalbard, Longyearbyen, Norway

[b]Faculty of Biosciences, Fisheries and Economics, The Arctic University of Norway, Tromsø, Norway

[c]Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial University of Newfoundland, St. John's, NL, Canada

[d]Ecosystem Processes Research Group, Institute of Marine Research, Bergen, Norway

Corresponding author: Victor Gonzalez Triginer, victortr@unis.no

Abstract

The northward range expansion of Atlantic species into Arctic waters poses challenges for management and increases competition and predation pressures within Arctic ecosystems. In the Svalbard area, there has been a clear increase in borealization, a higher occurrence and abundance of Atlantic species during recent decades. Studies regarding fish communities during the polar night are scarce. Understanding how Arctic winter conditions may restrict the northward shift of temperate species is key to identifying barriers for borealization. This study targets this knowledge gap and investigates fish community composition and pelagic fish distribution across Svalbard during the polar night. Acoustic-trawl surveys and oceanographic measurements were conducted in four locations in western Svalbard and at six locations in eastern Svalbard. We observed distinct spatial patterns in the density and community composition of pelagic fish, with western, Atlantic-influenced fjords exhibiting lower fish densities but higher species diversity compared to eastern, Arctic-influenced sites. The fish were distributed deeper in western fjords than in the eastern part of Svalbard. However, notably, borealization was as pronounced in the eastern, more Arctic Svalbard region, where Norwegian spring-spawning (NVG) herring (*Clupea harengus*) and capelin (*Mallotus villosus*) dominated, as in the western, more Atlantic fjords. This suggests that the entire Svalbard region is

now borealized, including during the polar night, and that Atlantic species can persist under the extreme light regime of the high Arctic. This may have consequences for fisheries and management as commercially valuable species move further north.

Keywords: Svalbard, Arctic ecosystems, Climate change, Acoustics, Species distribution, Biodiversity

1. Introduction

Climate change is leading to unprecedented and complex changes in the Arctic region, with significant implications for marine ecosystems (IPCC, 2022). The warming climate has led to changes in sea ice cover, increased sea surface temperature, glacier retreat and higher influx from land to the sea (Box et al., 2019). Furthermore, as there is strong seasonality in Arctic ecosystem processes, environmental changes are affecting the phenology of key mechanisms such as the match between the proliferation of sea-ice algae and phytoplankton with zooplankton grazing activity (Leu et al., 2011; Søreide et al., 2010), which has significant impacts for the pelagic food web. The Arctic serves as a critical indicator of climate change impacts as shifts are happening at a faster rate than the rest of the globe (Rantanen et al., 2022), and changes in species distributions and ecosystem dynamics highlight broader environmental trends for both local communities and the global environment.

As temperatures increase and sea ice retreats, the Arctic is becoming more accessible to boreal fish species (Fossheim et al., 2015; Kortsch et al., 2015). This phenomenon, known as borealization, is characterized by the northward expansion of temperate fish species into Arctic waters (Husson et al., 2024). The influx of boreal species can impact food web structures in the Arctic, as these newcomers compete with endemic Arctic species for resources and potentially introduce new predation pressures (Kortsch et al., 2015; Renaud et al., 2012). Some species like polar cod (*Boreogadus saida*) are of key importance in the Arctic food web and highly associated with Arctic features such as sea ice, and are threatened by an increase in predation and competition from Atlantic species like the Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Bengtsson et al., 2024; Geoffroy et al., 2023). Subsequently, the relative abundance of polar cod and other Arctic species will decrease at the expense of boreal species at the southern part of their distribution range (Christiansen et al., 2014). In addition to predatory and high trophic level species, species like the Norwegian spring-spawning (NVG) herring (*Clupea harengus*) and capelin (*Mallotus villosus*) are expanding their distribution as well and are now commonly found across Svalbard, particularly in areas that are more exposed to Atlantic water masses (Hollowed et al., 2013; Rose, 2005). These fish species are of key importance for the trophic web and are common prey items for several species of other fish, seabirds and marine mammals. Furthermore, both predatory and prey species whose numbers are increasing are of commercial interest and their expansion into Svalbard fjords may have associated implications for fisheries and management (Jørgensen et al., 2020). While commercial fisheries in Svalbard are not currently a major industry compared to other Arctic regions, they may grow in importance due to the northward expansion of commercially valuable fish species.

Most models that project species' poleward shifts are based on thermal niche tracking, i.e. tracking species' preferred temperatures as climate warms. These predictions often overlook other significant factors that contribute to species redistributions, e.g. the light regime (Ljungström et al., 2021). Fish species respond to seasonal differences in light availability through various strategies, including vertical migration and changes in their spatial distribution in order to maximize foraging and minimize the risk of predation (Baker, 2021; Levine et al., 2023). For example, research has shown that species like polar cod exhibit diel vertical migrations even during the polar night, likely driven by predator-prey interactions, which suggests that species can be adapted to deal with Arctic light regimes (Benoit et al., 2010). Therefore, studies have suggested that light acts as a constraint for the poleward shift of boreal fish species (Kaartvedt, 2008; Langbehn et al., 2022; Ljungström et al., 2021). Despite this, the dynamics of Arctic pelagic fish communities during the winter months are understudied. There has been research done on the diet and feeding patterns of fish during the polar night (Cusa et al., 2019; Geoffroy & Priou, 2020; Larsen et al., 2023), as well as reports on ecosystem surveys (van der Meeren et al., 2025), but there is a lack of broad spatial studies on community composition and species distribution at this time of the year.

Besides extreme seasonal changes, there can be a large spatial variation in oceanographic conditions even within a relatively small biogeographic region of the Arctic. For example, in Svalbard the west is influenced by the West Spitsbergen Current, which brings warm and saline Atlantic water, while eastern Svalbard is more influenced by colder and fresher Arctic water masses (Nilsen et al., 2016; Svendsen et al., 2002), and the front where the two converge in the Barents Sea is known as the Barents Sea polar front (Smedsrud et al., 2013). These currents and water masses significantly influence sea ice cover, with eastern Svalbard experiencing much more extensive sea ice cover due to colder Arctic influences than the western side. Recently there has been an increase in the influence of the West Spitsbergen Current (Ingvaldsen et al., 2021; Skogseth et al., 2020), which has been recorded to affect community composition across several trophic levels, from microorganisms to fish to marine mammals (Kortsch et al., 2015; Wassmann et al., 2011). One would therefore expect a higher degree of borealization of fish communities in western Svalbard than north of the polar front in eastern Svalbard.

In this study, we rely on acoustic-trawl surveys conducted to the west and east of Svalbard to investigate the composition, distribution and density of pelagic fish communities across Svalbard during the polar night. We also examine how environmental conditions may influence these patterns. More precisely, we assess whether the different oceanographical conditions prevailing in western and eastern Svalbard result in different levels of borealization and fish ecology.

2. Materials and methods

2.1 Study area

Acoustic-trawl surveys were conducted at locations in Isfjorden, Billefjorden, Nordfjorden and Kongsfjorden on the western side of Svalbard, and Storfjorden and a number of locations in southeast

Svalbard, on board R/V *G.O. Sars* from 12-18 November 2022 (Figure 1).

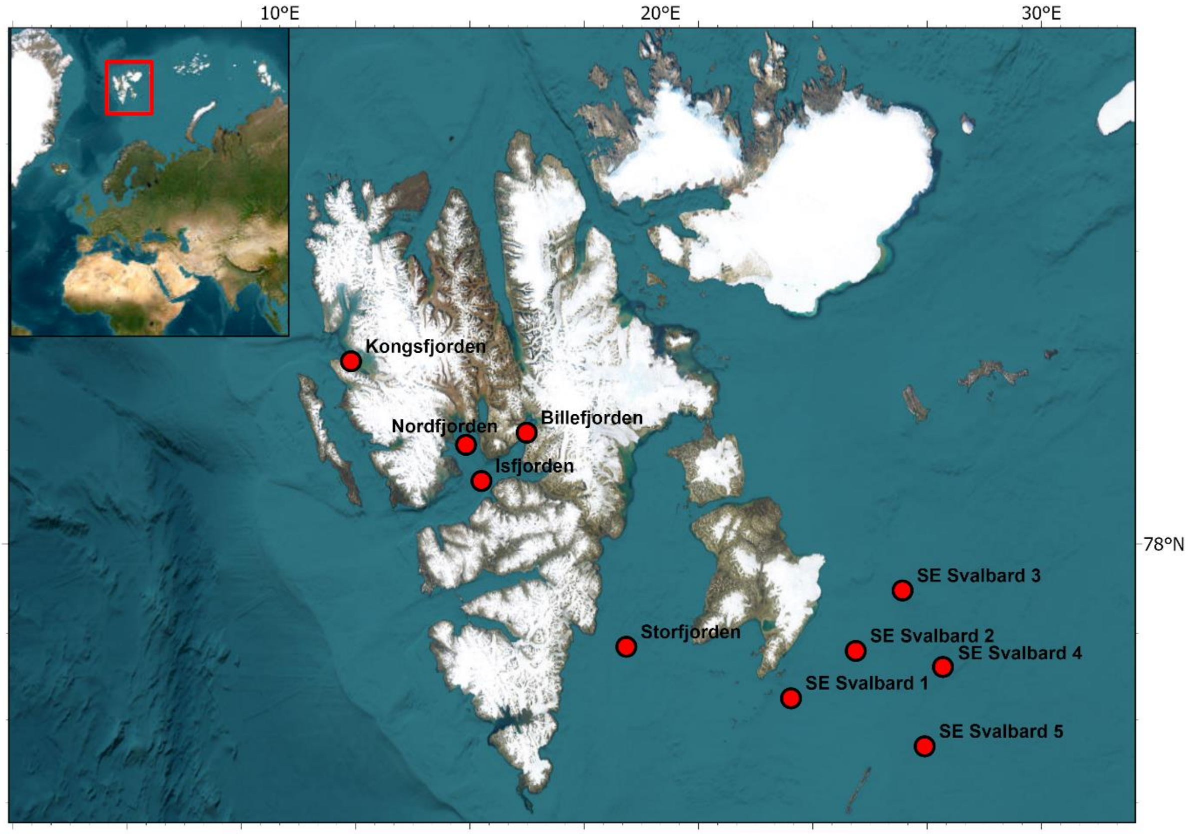


Figure 1. Map of the sampling stations. The study sites were in Isfjorden, Billefjorden, Nordfjorden, Kongsfjorden, Storfjorden and five sites in southeast (SE) Svalbard. Map source: Earthstar Geographics.

2.2 Data collection and processing

Hydroacoustics

A keel-mounted Simrad EK80 split-beam echosounder was used to record acoustic data at 18, 38, 70, 120 and 200 kHz (Supplementary table 1). The echosounder was calibrated following the standard sphere method prior to the survey (Demer et al., 2015) and acoustic data were recorded continuously throughout the cruise. A Sea-Bird SBE 9 CTD recorded temperature, salinity and sound speed at each of the sampling stations (Chierici & Husson, 2022). Sound speed measurements were extracted from the CTD data, averaged across the water column, and used to calibrate the acoustic data for each station (Mackenzie, 1981). Hydroacoustic data were processed in Echoview v13.1 (Echoview Software Pty Ltd, Tasmania, Australia). Acoustic files were standardized across stations by trimming them to comprise from 1 hour before to 1 hour after each pelagic trawl deployment. The data were processed in Python using Spyder v6.0.1 (Raybaut, 2009) and maps were produced in ArcGIS Pro v3.1.

The acoustic files were scrutinized for noise and bad data regions were set to be excluded from the analyses. A bottom line was established at the lowest frequency (18 kHz), a smoothing filter was added, and very minor manual editing was done to correct for gaps in bottom line. An exclusion line was added at a fixed depth of 10 m from the surface to exclude near-field region noise as well as a line 1 m above the bottom to exclude bottom noise, and the analyses were limited to the water column between the exclusion lines. The processed data were exported for each station. Mean volume backscattering strength (Sv in dB re m^2/m^3) was used as a proxy for pelagic backscatter and density, and centre of mass was used as a measure of the vertical distribution of pelagic density (Urmy et al., 2012). The mean centre of mass was extracted for each station at all frequencies, and the relative depth of pelagic backscatter was calculated by subtracting the mean centre of mass from the midwater depth at each station.

Trawl surveys

A Harstad pelagic trawl with an opening of 20x20 m covered the upper 50-60 meters of the water column and was towed at a speed of ca. 3 knots for 34-48 minutes (Table 1). At each station, tows were conducted at three predetermined depths, each for 0.5 nautical miles (nm), with the headline at 0 m, 20 m and 40 m except the trawl at SE Svalbard 2 which targeted the sound-scattering layer at 15-45 m depth. The organisms were identified to genus or species level onboard. Catch weight was recorded, and catch density was standardized by trawl distance (kg/nautical mile (nm)) to be compared across stations.

Table 1. Metadata and description of sampling stations.

Location	Station short name	Duration (min)	Lat (N)	Long (E)	Bottom depth (m)	Trawling depth min-max (m)
Isfjorden	ISF	48	78°20.42	15°17.75	254	0-40
Billefjorden	BLF	38	78°35.59	16°29.19	152	0-40
Nordfjorden	NRF	38	78°31.83	14°53.84	126	0-40
Kongsfjorden	KNF	38	78°57.50	11°52.72	339	0-40
Storfjorden	STF	36	77°25.47	19°06.34	173	0-40
SE Svalbard 1	SE1	40	77°07.65	23°25.85	103	0-40
SE Svalbard 2	SE2	34	77°24.08	25°07.68	82	15-45
SE Svalbard 3	SE3	40	77°44.55	26°21.40	113	0-40
SE Svalbard 4	SE4	37	77°18.59	27°24.76	206	0-40
SE Svalbard 5	SE5	41	76°50.53	26°56.39	114	0-40

A Hellinger transformation was applied to pelagic community data (Legendre & Gallagher, 2001), and an analysis of similarities (ANOSIM) was conducted on the Euclidean distances with 9999 permutations to test whether community composition differed significantly between western and eastern stations. As Billefjorden exhibited a colder hydrography and is considered a fjord with more Arctic conditions than the other western fjords in this study (Nilsen et al., 2008), the ANOSIM was conducted twice, once with Billefjorden included in the ‘west’ category and once with it included in the ‘east’ category to assess its influence on the results. Non-metric multidimensional scaling (nMDS) on these data was conducted to visualize community dissimilarities between stations and regions. The nMDS was performed in three dimensions to improve the fit of the ordination as indicated by the stress value. In order to assess species turnover between western and eastern sites, beta diversity between western and eastern regions was calculated using the Sørensen-Dice index, which measured the proportion of shared vs unique species between regions based on presence/absence data aggregated for all stations within each region.

To analyze differences in the relative abundance of boreal fish species between sites, we calculated a boreal index based on the density of boreal fish species relative to the total fish density caught at each station. Species were classified as Arctic, boreal or boreal-Arctic based on their biogeographical ranges. The biogeographical classification of each fish species was based on Fossheim et al. 2015 and Geoffroy et al. 2019 (Table 3). To assess differences in boreal levels between western and eastern sites, a Mann-Whitney U test was conducted on the index values.

3 Results

Fjord hydrography

The different stations represented a large gradient in bathymetric regimes, with Kongsfjorden reaching a depth of 323 m, while SE Svalbard 2 was the shallowest station at 70 m water depth. The hydrographic profiles showed differences in temperature and salinity, indicating diverse oceanographic conditions (Table 2, Figure 2). Western fjords (Isfjorden, Kongsfjorden and Nordfjorden) showed the highest maximum temperatures, with more than 4 °C. Billefjorden and Storfjorden exhibited the lowest minimum temperatures of -1.81 °C and -1.51 °C respectively as well as the largest temperature differences (4.73°C and 4.37°C respectively). Differences in salinity were low across all stations. A higher temperature regime indicated higher Atlantic influence in the western sites, and all fjords showed a stratified water column, but stratification was weak in SE Svalbard sites 2, 3 and 5.

Table 2. Oceanographic conditions at all stations.

Station	Temperature Max (°C)	Temperature Min (°C)	Temperature difference (°C)	Salinity Max	Salinity Min	Salinity difference	Region
Billefjorden	2.91	-1.81	4.73	34.73	33.95	0.79	West
Isfjorden	4.53	2.00	2.53	34.78	34.08	0.69	West

Kongsfjorden	5.18	1.56	3.61	34.96	33.93	1.03	West
Nordfjorden	4.17	0.60	3.57	34.64	33.67	0.97	West
Storfjorden	2.86	-1.51	4.37	35.04	33.96	1.08	East
SE Svalbard 1	3.13	0.70	2.43	34.70	34.03	0.67	East
SE Svalbard 2	0.45	0.42	0.04	34.07	34.05	0.02	East
SE Svalbard 3	0.45	-0.27	0.72	34.43	34.12	0.31	East
SE Svalbard 4	0.76	-1.29	2.05	34.84	34.13	0.71	East
SE Svalbard 5	1.42	0.26	1.17	34.27	34.04	0.22	East

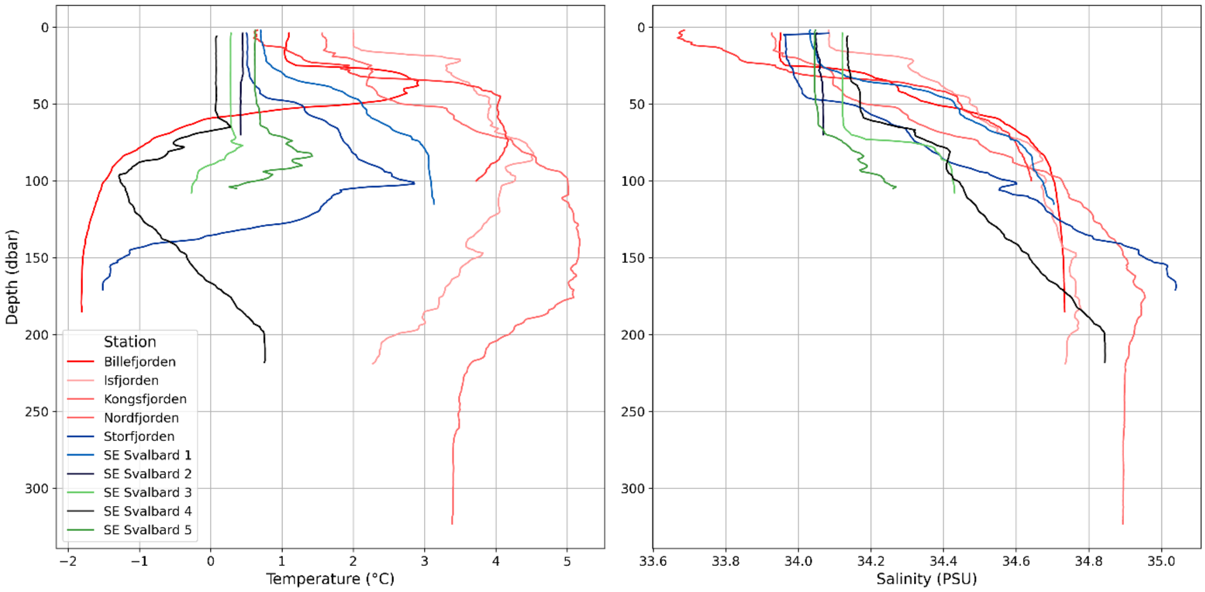


Figure 2. Temperature and salinity profiles at all stations. Shades of red represent western stations and blue, green and black represent eastern stations.

Spatial comparison of pelagic communities

The pelagic density and community composition varied across the sampling stations (Figure 3, Table 3). Western stations overall displayed lower densities but higher number of species, including catches of 174.0 kg/nm and 555.3 kg/nm of polar cod, and 648.0 kg/nm and 461.7 kg/nm of the jellyfish

Hydroidolina at Billefjorden and Isfjorden respectively. Kongsfjorden was characterized by a high density of herring at 940.0 kg/nm, while at Nordfjorden the catch consisted primarily of polar cod, cod and herring of 146.0 kg/nm, 90.0 kg/nm and 129.0 kg/nm respectively.

SE Svalbard 4 showed the highest total fish density, mainly driven by capelin (6818.3 kg/nm), while SE Svalbard 2 was dominated by herring (4251.3 kg/nm). Storfjorden and SE Svalbard stations 1, 3 and 5 were dominated by the jellyfish *Hydroidolina*.

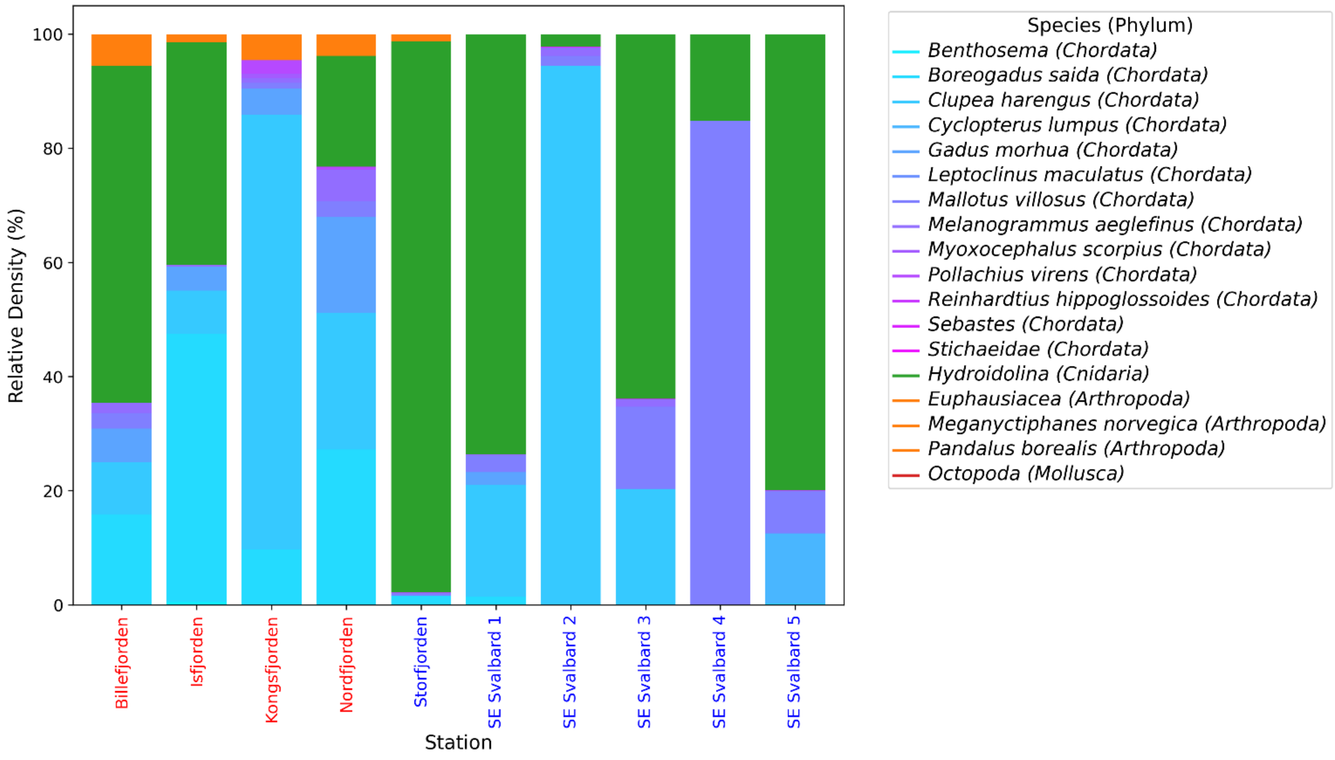


Figure 3. Pelagic community composition across stations, classified as western (red) and eastern (blue) stations.

Table 3. Details of the organisms sampled in the pelagic trawls across all stations. Station abbreviations ISF: Isfjorden, BLF: Billefjorden, KNF: Kongsfjorden, NRF: Nordfjorden, STF: Storfjorden, and the station number for the SE Svalbard stations. The biogeographic classification is based on Fossheim et al. 2015 and Geoffroy et al. 2019.

Scientific name	Phylum	Classification	Density (kg/nm)	Stations
Benthosema	Chordata	Boreal-Arctic	6.5	ISF
Boreogadus saida	Chordata	Arctic	1045.5	BLF, ISF, KNF, NRF, SE 1, SE 2, SE 3, SE 5, STF
Clupea harengus	Chordata	Boreal	5860.1	BLF, ISF, KNF, NRF, SE 1, SE 2, SE 3, SE 5, STF
Cyclopterus lumpus	Chordata	Boreal-Arctic	138.8	SE 5
Gadus morhua	Chordata	Boreal	290.3	BLF, ISF, KNF, NRF, SE 1, SE 2, SE 5, STF
Leptoclinus maculatus	Chordata	Boreal-Arctic	0.5	BLF
Mallotus villosus	Chordata	Boreal	7175.1	BLF, ISF, KNF, NRF, SE 1, SE 2, SE 3, SE 4, SE 5, STF
Melanogrammus aeglefinus	Chordata	Boreal	139.2	BLF, ISF, KNF, NRF, SE 1, SE 2, SE 3, SE 5, STF
Myoxocephalus scorpius	Chordata	Boreal-Arctic	9.5	KNF
Pollachius virens	Chordata	Boreal	33.0	KNF, NRF, STF
Reinhardtius hippoglossoides	Chordata	Arctic	0.7	NRF, SE 5
Sebastes spp	Chordata	Boreal	10.8	SE 2, SE 3, SE 5
Stichaeidae	Chordata	Boreal-Arctic	0.3	KNF, STF
Euphausiacea	Arthropoda	Boreal-Arctic	145.3	BLF, KNF, NRF, STF
Meganyctiphanes norvegica	Arthropoda	Boreal	15.9	ISF
Pandalus borealis	Arthropoda	Boreal-Arctic	18.5	KNF, STF
Hydroidolina	Cnidaria	Unclassified	6653.1	BLF, ISF, NRF, SE 1, SE 2, SE 3, SE 4, SE 5, STF
Octopoda	Mollusca	Unclassified	0.4	ISF

The nMDS provided a visualization of community composition and revealed no clear clustering across eastern and western stations (Figure 4). The stress value of 0.1452 indicates a fair representation of the data. The ANOSIM analysis based on Euclidean distances calculated from Hellinger-transformed abundance data indicates that a west vs east clustering is not significant regardless of which group Billefjorden is included in, R=0.26, p-value=0.07 when included in the west group and R=0.27, p-value=0.14 when included in the east group. Due to this, in all subsequent results comparing western and eastern sites, Billefjorden is included in its original classification among the western fjords. The Sørensen-Dice index revealed a mean dissimilarity of 0.24 between the aggregated western and eastern regions, indicating that 24.1% of the species were unique to either region and 75.9% were shared.

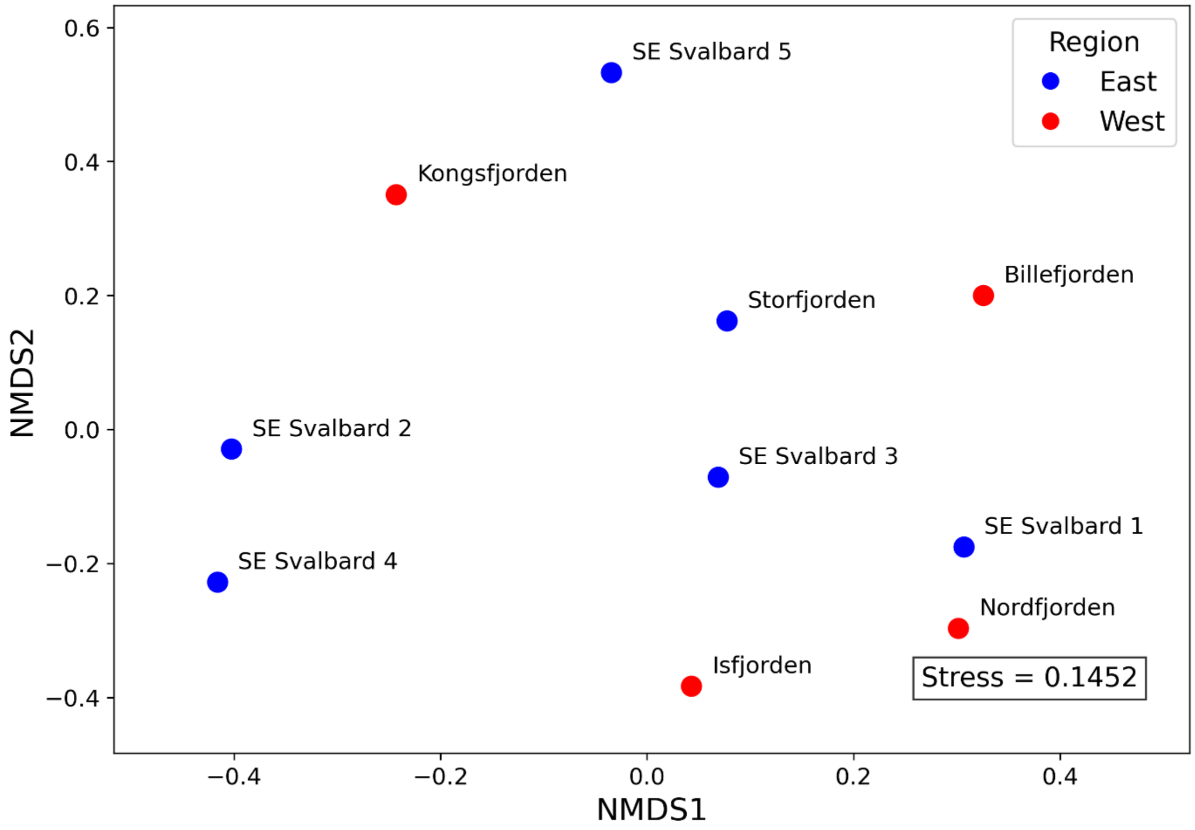


Figure 4. Non-metric multidimensional scaling (nMDS) plot performed in three dimensions. Sampling stations are colour-coded according to the classification: western (red) and eastern (blue).

The highest values of the boreal fish index were found in the SE Svalbard stations 1, 2, 3 and 4 with more than 99% (Table 4, Figure 5), resulting from large schools of a single fish species dominating the catch as well as low catch diversity. Isfjorden, Storfjorden and SE Svalbard 5 showed the lowest values with less than 40% of the catch consisting of boreal fish species. The Mann-Whitney U test resulted in a U-statistic of 6.0 and a p-value of 0.26, indicating no statistically significant differences in boreal indices between western and eastern sites.

Table 4. Boreal index calculated for each station. The index was calculated as the density of boreal fish species relative to the total fish catch at each station.

Station	Boreal Index (%)
Billefjorden	55.1
Isfjorden	22.1
Kongsfjorden	89.0
Nordfjorden	64.5
SE Svalbard 1	94.4
SE Svalbard 2	99.9
SE Svalbard 3	99.8
SE Svalbard 4	100
SE Svalbard 5	37.8
Storfjorden	28.4

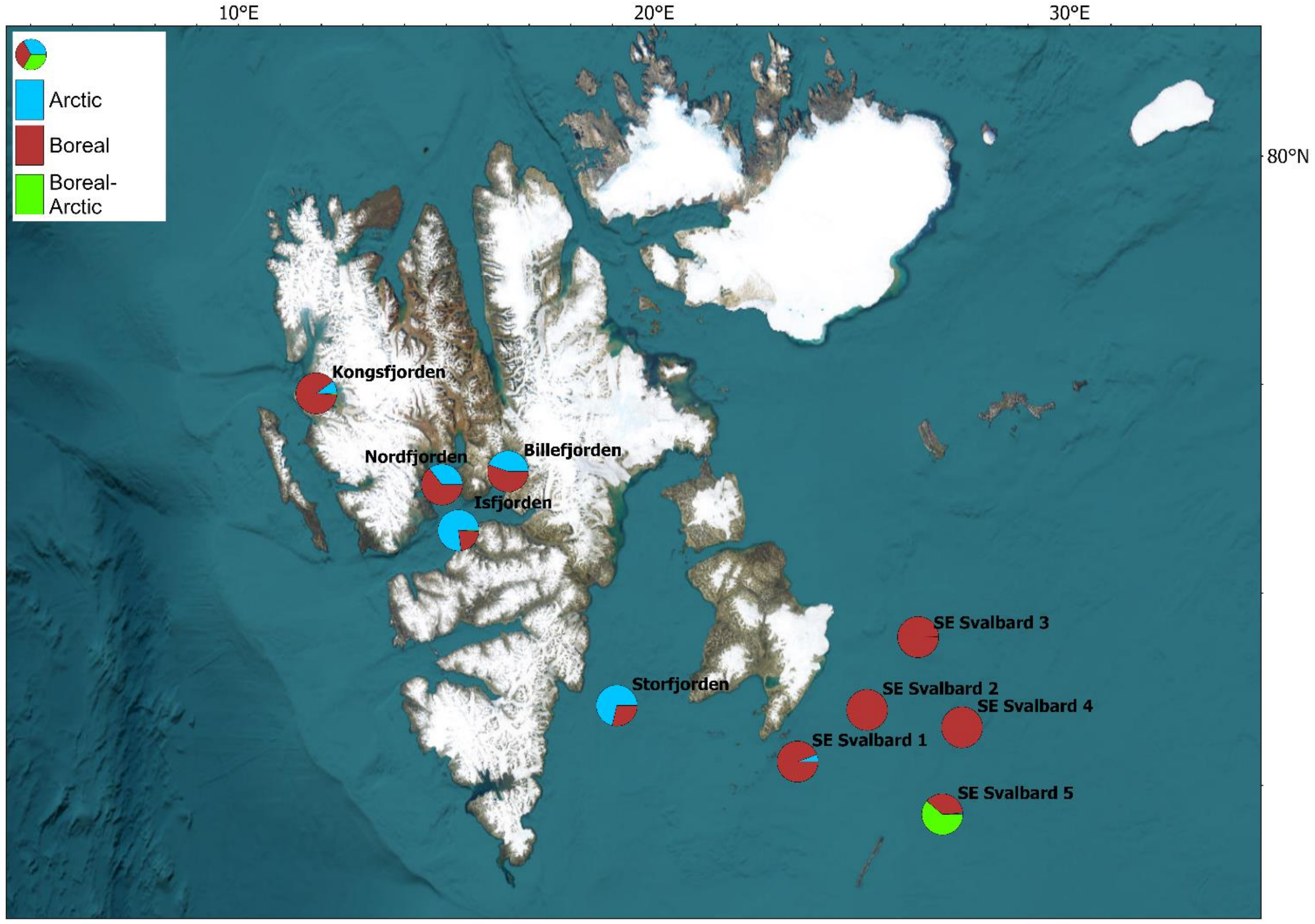


Figure 5. Spatial distribution of fish community composition across sampling stations. Pie charts represent the relative proportions of Arctic (blue), boreal (red) and boreal-Arctic (green) fish species at each station, based on fish density (kg/nm). Map source: Earthstar Geographics.

Pelagic backscatter and vertical distribution

The acoustic backscatter data showed distinct patterns of pelagic density across the sampling stations (Figure 6). SE Svalbard 4 exhibited the highest mean Sv, aligning with the substantial density of capelin caught in the trawl at that station. Similarly, SE Svalbard 2 showed high backscatter likely influenced by the high density of herring caught. At these stations, the peaks are particularly pronounced at lower frequencies (18 kHz, 38 kHz and 70 kHz), which are more sensitive to large organisms like fish. Billefjorden, Isfjorden, Kongsfjorden and SE Svalbard 5 exhibited high Sv values contrasting with low total densities of organisms caught in the pelagic trawl at these sites.

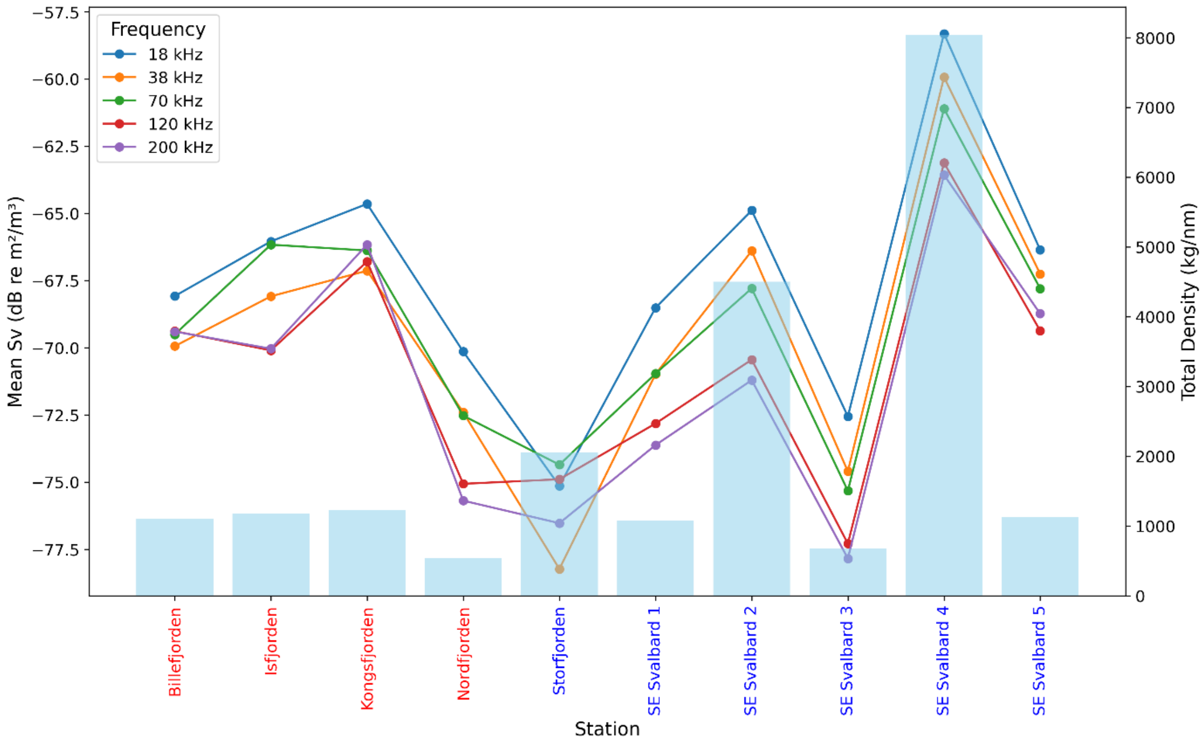


Figure 6. Mean Sv values in dB re m^2/m^3 across all frequencies and stations (lines) and total density of fish caught (kg/nm) across stations (bars).

The vertical distribution of pelagic backscatter varied across stations (Figure 7) and between western and eastern regions. Billefjorden, Isfjorden and Kongsfjorden showed a centre of mass 20 m or more deeper than the midwater depth at all frequencies, while all eastern stations except for SE Svalbard 5 showed a shallower centre of mass. Nordfjorden and SE Svalbard 1 exhibited a centre of mass close to the midwater depth.

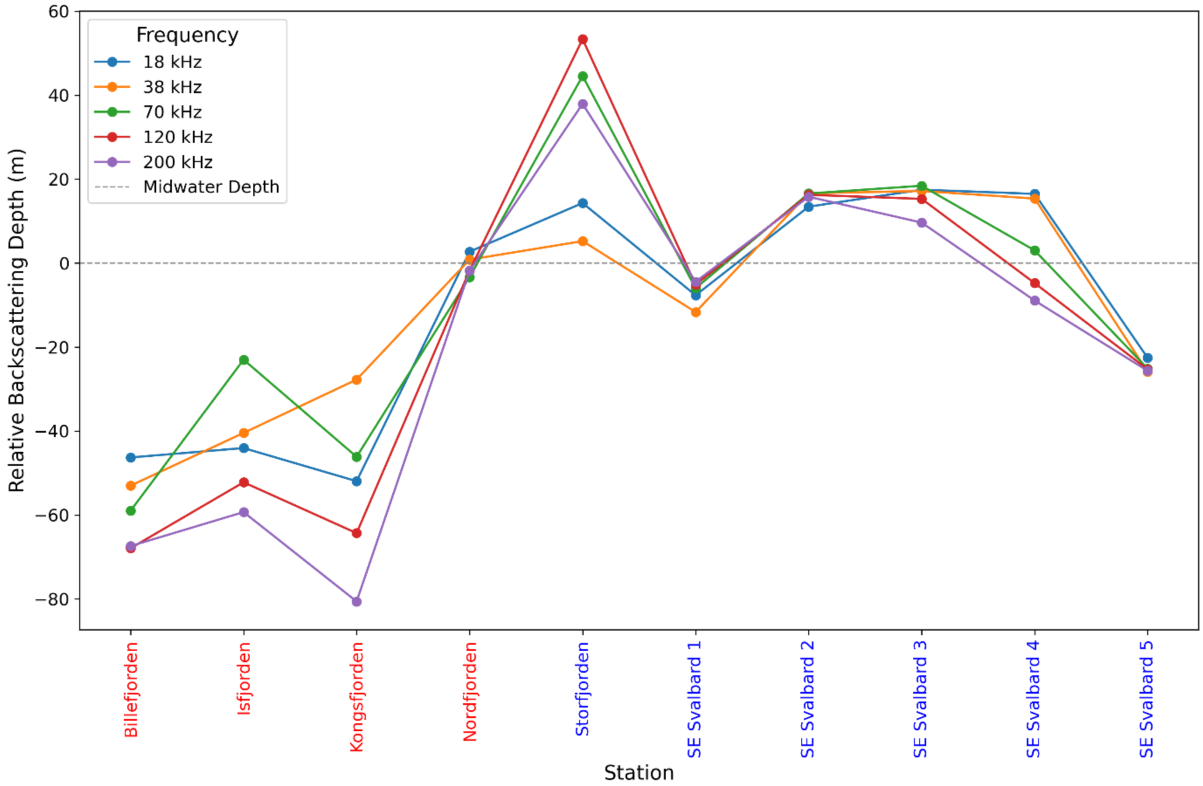


Figure 7. Relative depth of the centre of mass of pelagic backscatter across all stations and frequencies. Each line represents the difference between the midwater depth of the station and the mean centre of mass. A positive value indicates that the centre of mass is shallower than the midwater depth, while a negative value indicates that it is deeper.

4 Discussion

Fish borealization across Svalbard

Cold temperatures, sea ice cover, and extreme variation in light availability are some of the environmental barriers preventing boreal species from expanding into Arctic and polar waters. With climate change, cold temperature and sea ice cover, but not light, have been weakening as barriers over the last decades, which has allowed for Atlantic species to shift northward in the Svalbard region (Eriksen et al., 2025; Fossheim et al., 2015; Kuletz et al., 2024). The extreme light regime can still act as a seasonal barrier, as pelagic fish are often visual predators and their activity levels are closely tied to light availability (Langbehn et al., 2022). During the polar night, highly reduced light availability is expected to significantly impact the feeding behaviour and distribution of boreal fish. On the contrary, studies have shown that specialist Arctic species like the polar cod are able to use very slight light cues to forage (Benoit et al., 2010), which suggests that Arctic fish species are specifically adapted for the low light conditions of the Arctic polar night. Conversely, the 24 hours of daylight during the summer prevents many mesopelagic fish from safe foraging near the surface and forces them to stay in deeper and less nutrient-rich waters or risk predation by feeding near the surface (Langbehn et al., 2022). Therefore, the highly variable and extreme light regime of the Arctic may be a factor that could continue to limit fish borealization of the Arctic at a time when climate change is breaking down other physical barriers.

Our trawl and acoustic data showed differences in density, diversity and vertical distribution across stations. Fish community composition was more diverse in the western stations, while the catches in the eastern stations were dominated by single species of schooling fish such as herring and capelin, as well as high densities of jellyfish (Figure 3). However, the nMDS and ANOSIM results suggest that fish communities across western and eastern parts of Svalbard were not strongly distinct. This lack of differentiation was further supported by the beta diversity analysis, which indicated moderate species turnover and a relatively high percentage of shared species between western and eastern locations. Overall, we expected to observe mainly Arctic fish species in our study during the polar night, and even a dominance of them in eastern sites where Arctic water masses dominate. Contrary to our expectations, we observed a high degree of boreal species and Arctic species only constituted the majority of the catch at two locations. Additionally, we did not observe significantly different levels of borealization between western and eastern stations, and boreal species were captured at virtually all stations irrespective of their hydrography. Furthermore, eastern stations displayed the highest boreal indices, which is due to these stations being dominated by a single boreal species. Western fjords exhibited more Arctic species, likely due to a more diverse catch, but this could also be explained by fjord topography offering refugia for Arctic species, e.g. in deep cold basins that are more sheltered from Atlantic water influence (Nilsen et al., 2008). Overall, although minor differentiation was seen, pelagic communities were not significantly different between western and eastern sites, and boreal fish species were not only present, but highly prevalent across all our study sites.

Our findings show that Atlantic species are present in the low light conditions and cold temperatures of both east and west Svalbard waters during the polar night and suggest that the whole of Svalbard is now borealized, even during the polar night. The presence and even abundance of Atlantic species during this time of the year suggests that they are able to thrive in the challenging conditions of the polar night. This tolerance for the darkness of the polar night may be driven by a combination of physiological and behavioural plasticity that allows these species to exploit available resources even in low-light conditions, and indeed, previous studies have shown that boreal gadoids such as the Atlantic cod and haddock are able to feed efficiently during the polar night (Larsen et al., 2023). Moreover, studies have reported a northward shift in herring spawning sites and high biomass of herring in the Svalbard area in recent years (Eriksen et al., 2025; Slotte et al., 2025). The presence of these species during the polar night may alter the dynamics of local ecosystems. For example, it could mean that the increased competition and predation pressure on Arctic species by generalist boreal species may be taking place year-round, therefore light or the lack thereof, is not a seasonal barrier that strongly limits the northward expansion of Atlantic species in Svalbard. The polar night, therefore, does not provide Arctic species with a period of respite from Atlantic species. However, it should be kept in mind that species range shifts, including the expansion northward of temperate species, are highly dependent on a number of other environmental conditions. For instance, the availability of suitable spawning grounds and nursery habitats is crucial for the successful establishment of temperate species into the Arctic (Drinkwater, 2005; Perry et al., 2005; Sundby & Nakken, 2008). Additionally, prey abundance during critical life stages, such as larval and juvenile development, and mismatches between the timing of prey availability and life history requirements may act as a bottleneck for the northward expansion of boreal species (Hollowed et al., 2013; Leu et al., 2011). Furthermore, while boreal species may be able to thrive during the polar night light regime, extremely low temperatures and high sea ice cover may still constrain borealization in regions with stronger Arctic water influence. Significant borealization might thus not be possible in other regions of the Arctic where more Arctic-like conditions still prevail.

Arctic species are already under heightened stress due to environmental changes, such as habitat loss, rising temperatures and extreme weather events driven by climate change (Leu et al., 2011; Wassmann et al., 2011). The presence of boreal species during the polar night, a critical period of reduced energy intake and low productivity conditions, may further accentuate the effects of increased predation and competition pressures on Arctic species, and this may be a key process in determining their vulnerability to climate change. Furthermore, the expansion of species of commercial interest such as cod, haddock and herring further north has important implications for fisheries and management. While large-scale commercial fishing is not currently as major in Svalbard waters as it is in other Arctic areas, the increased presence of these species raises the question of whether this region will become a new frontier for fisheries in the near future (Misund et al., 2016). The retreat of sea ice and thus increased accessibility to Arctic waters, combined with the increasing presence of commercially valuable species, may incentivize the development of fisheries in areas that were previously inaccessible or unprofitable (Cheung et al., 2010; Jørgensen et al., 2020; Perry et al., 2005). There is a need for adaptive measures that consider the ecological consequences of expanding human activity further north in an already vulnerable ecosystem, and effective management strategies will need to be prioritized (Eriksen et al., 2021; Jørgensen et al., 2020).

Pelagic vertical distribution across regions

In the western sites, organisms were distributed deeper in the water column, which suggests a demersal-dominated system where organisms are more closely associated with the seafloor or deeper water layers. In contrast, the eastern sites exhibited a shallower vertical distribution of pelagic organisms, with acoustic backscatter concentrated in the upper water column. This pattern aligns with the dominance of schooling fish such as herring and capelin, which were abundant in eastern sites, and are known to occupy pelagic habitats and form dense aggregations in shallow layers. The trawl catches with the highest densities were at two SE Svalbard sites, and this was consistent with high acoustic backscatter peaks in the lower frequencies at these sites, which are more sensitive to large organisms like fish (Simmonds & MacLennan, 2005). In contrast, there was a decoupling between catch densities and backscatter strength at the western sites of Billefjorden, Isfjorden and Kongsfjorden, where the trawl catch densities were low but the acoustics showed high backscatter. This may be explained by the differences in vertical distribution between regions, as western fjords exhibited a deeper centre of mass than the midwater depth and hence the low fish density captured by the trawl at these sites may be due to organisms inhabiting deeper layers than the sampling depths.

This contrast, between a more pelagic and a more demersal fish community in the eastern and western stations respectively, may be linked to differences in site topography. In the west, complex fjord systems, which include deep basins and sills, provide stable environments and rich foraging grounds for species that utilize both the demersal and pelagic environments, such as the Atlantic cod and polar cod (Brand et al., 2023; Gonzalez Triginer et al., 2025; Mérillet et al., 2022). Conversely, the eastern sites are situated further offshore and favour pelagic species due to open water conditions that support schooling fish like herring and capelin (Gjøsæter, 1998; Hop & Gjøsæter, 2013). Ultimately, while boreal species were similarly found at virtually all sites, the observed differences in community composition and vertical distribution between western and eastern sites highlight the importance of local environmental and topographical conditions in shaping fish communities, in addition to water masses. These findings suggest that, even as borealization progresses across Svalbard, regional differences in habitat structure and oceanographic conditions may mediate how fish communities respond to climate-driven changes. For example, in silled fjord systems, inner areas and deep basins that are sheltered from Atlantic water influence may act as refugia for Arctic species. In contrast, the pelagic-dominated systems in open waters may be more susceptible to rapid shifts in community composition, as schooling boreal species like herring and capelin potentially outcompete

Arctic specialists. This highlights the need to consider regional and topographical variability when predicting the ecological impacts of borealization and assessing Arctic ecosystem resilience.

This study provides new insights into the composition, distribution and density of pelagic fish communities across Svalbard during the polar night, a typically understudied period. Our findings suggest that borealization is taking place across both western and eastern parts of Svalbard, with boreal species thriving even under the extreme light and temperature conditions of the polar night. This suggests that the seasonal light barrier may not effectively limit the northward expansion of Atlantic species, and that the associated predation and competition pressures are taking place all year round. While this study provides relevant information on the borealization of Svalbard waters, there is a need for long-term monitoring of the borealization of Arctic food webs, and to better understand the potential of boreal species to establish stable and thriving populations in these northern areas.

Acknowledgements

We would like to thank Bérengère Husson, Melissa Chierici and the Norwegian Institute of Marine Research for collecting the fish trawl and CTD data, and the crew members of R/V. *G.O. Sars.*

Author contributions

Victor Gonzalez Triginer (Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Software, Validation, Visualization, Writing-original draft), Maxime Geoffroy (Supervision, Writing- review and editing), Elena Eriksen (Data curation, Investigation, Resources, Writing-review and editing), Børge Damsgård (Supervision, Writing-review and editing), Arunima Sen (Conceptualization, Investigation, Supervision, Writing-review and editing)

Conflict of interest

The authors declare no conflict of interest.

Funding

This study was funded through several projects including the Nansen Legacy project which received funding from the Research Council of Norway (RCN # 276730) and the FACE-IT project, which received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 869154.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

References

Baker, M. R. (2021). Contrast of warm and cold phases in the Bering Sea to understand spatial distributions of Arctic and sub-Arctic gadids. *Polar Biology*, *44*(6), 1083–1105. https://doi.org/10.1007/s00300-021-02856-x

Bengtsson, O., Lydersen, C., Węsławski, J., Berge, J., & Kovacs, K. (2024). Summer and polar night diets of polar cod Boreogadus saida and Atlantic cod Gadus morhua in Kongsfjorden, Svalbard, Norway. *Marine Ecology Progress Series*, *747*, 117–132. https://doi.org/10.3354/meps14700

Benoit, D., Simard, Y., Gagné, J., Geoffroy, M., & Fortier, L. (2010). From polar night to midnight sun: Photoperiod, seal predation, and the diel vertical migrations of polar cod (Boreogadus saida) under landfast ice in the Arctic Ocean. *Polar Biology*, *33*(11), 1505–1520. https://doi.org/10.1007/s00300-010-0840-x

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F.-J. W., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V. E., Walsh, J. E., Overland, J. E., Wang, M., Corell, R. W., Meier, W. N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., & Olsen, M. S. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, *14*(4), 045010. https://doi.org/10.1088/1748-9326/aafc1b

Brand, M., Spotowitz, L., Mark, F. C., Berge, J., Langhelle, E. L., Węsławski, J. M., Godiksen, J. A., & Fischer, P. (2023). Age class composition and growth of Atlantic cod (Gadus morhua) in the shallow water zone of Kongsfjorden, Svalbard. *Polar Biology*, *46*(1), 53–65. https://doi.org/10.1007/s00300-022-03098-1

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., & Pauly, D. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, *16*(1), 24–35. https://doi.org/10.1111/j.1365-2486.2009.01995.x

Chierici, M., & Husson, B. (2022). *Unpublished Conductivity-Temperature-Depth (Pressure)-CTD data from NANSEN LEGACY cruise 2022114 onboard RV G.O. Sars in Svalbard waters in November 2022* [Dataset].

Christiansen, J. S., Mecklenburg, C. W., & Karamushko, O. V. (2014). Arctic marine fishes and their fisheries in light of global change. *Global Change Biology*, *20*(2), 352–359. https://doi.org/10.1111/gcb.12395

Cusa, M., Berge, J., & Varpe, Ø. (2019). Seasonal shifts in feeding patterns: Individual and population realized specialization in a high Arctic fish. *Ecology and Evolution*, *9*(19), 11112–11121. https://doi.org/10.1002/ece3.5615

Demer, D. A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., Domokos, R., Dunford, A., Fassler, S., Gauthier, S., Hufnagle, L. T., Jech, J. M., Bouffant, N., Lebourges-Dhaussy, A., Lurton, X., Macaulay, G. J., Perrot, Y., Ryan, T., Parker-Stetter, S., … Williamson, N. (2015). *Calibration of acoustic instruments.* [Report]. International Council for the Exploration of the Sea (ICES). https://doi.org/10.25607/OBP-185

Drinkwater, K. F. (2005). The response of Atlantic cod (Gadus morhua) to future climate change. *ICES Journal of Marine Science*, *62*(7), 1327–1337. https://doi.org/10.1016/j.icesjms.2005.05.015

Eriksen, E., Husson, B., Skaret, G., Ingvaldsen, R. B., Dalpadado, P., Johannesen, E., Jørgensen, L. L., Bogstad, B., Dolgov, A. V., Prozorkevich, D. V., Prokhorova, T. A., Russkikh, A. A., Strelkova, N. A., Trofimov, A. G., Prokopchuk, I. P., & Filin, A. A. (2025). The living Barents Sea response to peak-warming and subsequent cooling. *Scientific Reports*, *15*(1), 13008. https://doi.org/10.1038/s41598-025-96964-x

Eriksen, E., van der Meeren, G., Nilsen, B., von Quillfeldt, C., & Johnsen, H. (2021). *Particularly valuable and vulnerable areas (SVO) in Norwegian seas—Environmental values* (Rapport Fra Havforskningen).

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*(7), 673–677. https://doi.org/10.1038/nclimate2647

Geoffroy, M., Bouchard, C., Flores, H., Robert, D., Gjøsæter, H., Hoover, C., Hop, H., Hussey, N. E., Nahrgang, J., Steiner, N., Bender, M., Berge, J., Castellani, G., Chernova, N., Copeman, L., David, C. L., Deary, A., Divoky, G., Dolgov, A. V., … Walkusz, W. (2023). The circumpolar impacts of climate change and anthropogenic stressors on Arctic cod (*Boreogadus saida*) and its ecosystem. *Elem Sci Anth*, *11*(1), 00097. https://doi.org/10.1525/elementa.2022.00097

Geoffroy, M., Daase, M., Cusa, M., Darnis, G., Graeve, M., Santana Hernández, N., Berge, J., Renaud, P. E., Cottier, F., & Falk-Petersen, S. (2019). Mesopelagic Sound Scattering Layers of the High Arctic: Seasonal Variations in Biomass, Species Assemblage, and Trophic Relationships. *Frontiers in Marine Science*, *6*, 364. https://doi.org/10.3389/fmars.2019.00364

Geoffroy, M., & Priou, P. (2020). Fish Ecology During the Polar Night. In J. Berge, G. Johnsen, & J. H. Cohen (Eds.), *POLAR NIGHT Marine Ecology: Life and Light in the Dead of Night* (pp. 181–216). Springer International Publishing. https://doi.org/10.1007/978-3-030-33208-2_7

Gjøsæter, H. (1998). The population biology and exploitation of capelin (Mallotus villosus) in the barents sea. *Sarsia*. https://www.tandfonline.com/doi/abs/10.1080/00364827.1998.10420445

Gonzalez Triginer, V., Sen, A., Geoffroy, M., & Damsgård, B. (2025). Loss of pelagic fish and zooplankton density associated with subglacial upwelling in high Arctic estuaries may be mitigated by benthic habitat expansion following tidewater glacier retreat. *Arctic Science*, *11*, 1–12. https://doi.org/10.1139/as-2024-0040

Hollowed, A. B., Planque, B., & Loeng, H. (2013). Potential movement of fish and shellfish stocks from the sub- A rctic to the A rctic O cean. *Fisheries Oceanography*, *22*(5), 355–370. https://doi.org/10.1111/fog.12027

Hop, H., & Gjøsæter, H. (2013). Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Marine Biology Research*, *9*(9), 878–894. https://doi.org/10.1080/17451000.2013.775458

Husson, B., Bluhm, B. A., Cyr, F., Danielson, S. L., Eriksen, E., Fossheim, M., Geoffroy, M., Hopcroft, R. R., Ingvaldsen, R. B., Jørgensen, L. L., Lovejoy, C., Meire, L., Mueter, F., Primicerio, R., & Winding, M. (2024). Borealization impacts shelf ecosystems across the Arctic. *Frontiers in Environmental Science*, *12*, 1481420. https://doi.org/10.3389/fenvs.2024.1481420

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, *2*(12), 874–889. https://doi.org/10.1038/s43017-021-00228-x

IPCC. (2022). *The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change* (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781009157964

Jørgensen, L. L., Bakke, G., & Hoel, A. H. (2020). Responding to global warming: New fisheries management measures in the Arctic. *Progress in Oceanography*, *188*, 102423. https://doi.org/10.1016/j.pocean.2020.102423

Kaartvedt, S. (2008). Photoperiod may constrain the effect of global warming in arctic marine systems. *Journal of Plankton Research*, *30*(11), 1203–1206. https://doi.org/10.1093/plankt/fbn075

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151546. https://doi.org/10.1098/rspb.2015.1546

Kuletz, K. J., Ferguson, S. H., Frederiksen, M., Gallagher, C. P., Hauser, D. D. W., Hop, H., Kovacs, K. M., Lydersen, C., Mosbech, A., & Seitz, A. C. (2024). A review of climate change impacts on migration patterns of marine vertebrates in Arctic and Subarctic ecosystems. *Frontiers in Environmental Science*, *12*, 1434549. https://doi.org/10.3389/fenvs.2024.1434549

Langbehn, T. J., Aksnes, D. L., Kaartvedt, S., Fiksen, Ø., Ljungström, G., & Jørgensen, C. (2022). Poleward distribution of mesopelagic fishes is constrained by seasonality in light. *Global Ecology and Biogeography*, *31*(3), 546–561. https://doi.org/10.1111/geb.13446

Larsen, L.-H., Cusa, M., Eglund-Newby, S., Berge, J., Renaud, P. E., Varpe, Ø., Geoffroy, M., & Falk-Petersen, S. (2023). Diets of gadoid fish in Arctic waters of Svalbard fjords during the polar night. *Polar Biology*, *46*(8), 783–799. https://doi.org/10.1007/s00300-023-03167-z

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S., & Berge, J. (2011). Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Progress in Oceanography*, *90*(1), 18–32. https://doi.org/10.1016/j.pocean.2011.02.004

Levine, R. M., De Robertis, A., Grünbaum, D., Wildes, S., Farley, E. V., Stabeno, P. J., & Wilson, C. D. (2023). Climate-driven shifts in pelagic fish distributions in a rapidly changing Pacific Arctic. *Deep Sea Research Part II: Topical Studies in Oceanography*, *208*, 105244. https://doi.org/10.1016/j.dsr2.2022.105244

Ljungström, G., Langbehn, T. J., & Jørgensen, C. (2021). Light and energetics at seasonal extremes limit poleward range shifts. *Nature Climate Change*, *11*(6), 530–536. https://doi.org/10.1038/s41558-021-01045-2

Mackenzie, K. V. (1981). Nine-term equation for sound speed in the oceans. *The Journal of the Acoustical Society of America*, *70*(3), 807–812. https://doi.org/10.1121/1.386920

Mérillet, L., Skogen, M. D., Vikebø, F., & Jørgensen, L. L. (2022). Fish Assemblages of a Sub-Arctic Fjord Show Early Signals of Climate Change Response Contrary to the Benthic Assemblages. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.822979

Misund, O. A., Heggland, K., Skogseth, R., Falck, E., Gjøsæter, H., Sundet, J., Watne, J., & Lønne, O. J. (2016). Norwegian fisheries in the Svalbard zone since 1980. Regulations, profitability and warming waters affect landings. *Polar Science*, *10*(3), 312–322. https://doi.org/10.1016/j.polar.2016.02.001

Nilsen, F., Cottier, F., Skogseth, R., & Mattsson, S. (2008). Fjord–shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. *Continental Shelf Research*, *28*(14), 1838–1853. https://doi.org/10.1016/j.csr.2008.04.015

Nilsen, F., Skogseth, R., Vaardal-Lunde, J., & Inall, M. (2016). *A Simple Shelf Circulation Model: Intrusion of Atlantic Water on the West Spitsbergen Shelf*. https://doi.org/10.1175/JPO-D-15-0058.1

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate Change and Distribution Shifts in Marine Fishes. *Science*, *308*(5730), 1912–1915. https://doi.org/10.1126/science.1111322

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 1–10. https://doi.org/10.1038/s43247-022-00498-3

Raybaut, P. (2009). *Spyder-documentation. Available Online at: Pythonhosted.org* [Computer software].

Renaud, P. E., Berge, J., Varpe, Ø., Lønne, O. J., Nahrgang, J., Ottesen, C., & Hallanger, I. (2012). Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, Boreogadus saida? *Polar Biology*, *35*(3), 401–412. https://doi.org/10.1007/s00300-011-1085-z

Rose, G. A. (2005). Capelin (Mallotus villosus) distribution and climate: A sea “canary” for marine ecosystem change. *ICES Journal of Marine Science*, *62*(7), 1524–1530. https://doi.org/10.1016/j.icesjms.2005.05.008

Simmonds, E. J., & MacLennan, D. N. (2005). *Fisheries acoustics: Theory and practice* (2nd ed). Blackwell Science.

Skogseth, R., Olivier, L. L. A., Nilsen, F., Falck, E., Fraser, N., Tverberg, V., Ledang, A. B., Vader, A., Jonassen, M. O., Søreide, J., Cottier, F., Berge, J., Ivanov, B. V., & Falk-Petersen, S. (2020). Variability and decadal trends in the Isfjorden (Svalbard) ocean climate and circulation – An indicator for climate change in the European Arctic. *Progress in Oceanography*, *187*, 102394. https://doi.org/10.1016/j.pocean.2020.102394

Slotte, A., Salthaug, A., Vatnehol, S., Johnsen, E., Mousing, E. A., Høines, Å., Broms, C. T., Bjarnason, S., Homrum, E. í, Skagseth, Ø., & Stenevik, E. K. (2025). Herring spawned poleward following fishery-induced collective memory loss. *Nature*, 1–8. https://doi.org/10.1038/s41586-025-08983-3

Smedsrud, L. H., Esau, I., Ingvaldsen, R. B., Eldevik, T., Haugan, P. M., Li, C., Lien, V. S., Olsen, A., Omar, A. M., Otterå, O. H., Risebrobakken, B., Sandø, A. B., Semenov, V. A., & Sorokina, S. A. (2013). The Role of the Barents Sea in the Arctic Climate System. *Reviews of Geophysics*, *51*(3), 415–449. https://doi.org/10.1002/rog.20017

Søreide, J. E., Leu, E., Berge, J., Graeve, M., & Falk-Petersen, S. (2010). Timing of blooms, algal food quality and Calanus glacialis reproduction and growth in a changing Arctic. *Global Change Biology*, *16*(11), 3154–3163. https://doi.org/10.1111/j.1365-2486.2010.02175.x

Sundby, S., & Nakken, O. (2008). Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, *65*(6), 953–962. https://doi.org/10.1093/icesjms/fsn085

Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbæk, J. B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., & Wiencke, C. (2002). The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research*, *21*(1), Article 1. https://doi.org/10.3402/polar.v21i1.6479

Urmy, S. S., Horne, J. K., & Barbee, D. H. (2012). Measuring the vertical distributional variability of pelagic fauna in Monterey Bay. *ICES Journal of Marine Science*, *69*(2), 184–196. https://doi.org/10.1093/icesjms/fsr205

van der Meeren, G., Prozorkevich, D. V., Eriksen, E., Karlson, S., Lerch, S. J., Mørk, H., Prokhorova, T. A., Grøsvik, B. E., Klepikovsky, R., Johannesen, E., Bogstad, B., Aune, M., Russkikh, A., Filin, A., Windsland, K., Skaret, G., Dolgov, A., Wienerroither, R., Zimmermann, F., … Fauchald, P. (2025). *Scientific report from the Norwegian and Russian Barents Sea ecosystem surveys in August-October 2024 (BESS)* (IMR-PINRO).

Wassmann, P., Duarte, C. M., Agustí, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*, *17*(2), 1235–1249. https://doi.org/10.1111/j.1365-2486.2010.02311.x

Supplementary material

Supplementary table 1. Settings for the echosounder Simrad EK80 used for the acoustic sampling.

Frequency (kHz)	Pulse duration (ms)	Transmitted power (W)	Ping rate (Hz)
18	1.024	1600	35.71
38	1.024	2000	20.83
70	1.024	600	25
120	1.024	200	31.25
200	1.024	105	41.67