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Colonisation process in the littoral zone of a dynamic Arctic marine environment

PhD Thesis

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Abstract

The long-time atmospheric data series proves that the climate has been continuously warming for several decades now. The same trends are also recognised in the ocean. The Arctic is a hot spot of climate change, with warming proceeding approximately four times faster there than anywhere in the world. The warming itself drives several other factors that can directly and indirectly affect the Arctic ecosystem. Those include: the loss of sea ice, increased turbidity due to the growing presence of suspended material carried by rivers and from melting glaciers, freshening of surface waters exacerbating the issue of stratification, increasing acidification due to the intake of CO_2, etc. All of the mentioned forcings can vary considerably on a spatial, bathymetrical and temporal scales.

Because the benthos in the Arctic is so abundant and species-diverse, it is a key component of marine food webs. It plays an important role in the ecosystem, supporting the circulation of matter and the exchange of energy known as benthic-pelagic coupling. Benthic fauna can be divided into soft-bottom and hard-bottom benthos; the former is frequently described, while the latter has received less attention. This disparity in research can stem from the difficulty associated with sampling of rocky habitats, which often require the involvement of highly experienced SCUBA divers. In the presented study, they assisted with the installation of experimental constructions holding exchangeable settlement plates. The use of plastic plates of a specified size allows the acquisition of standardised results that can be compared between various studies. This methodology has been used since at least the 1920s (although a different material was used for the plates), but has been improved since then.

Hard-bottom benthos encompasses many organisms growing on rocky substrates, including fauna and flora, but it could also include species that bore into rocks or mobile fauna associated with the habitat. The main focus in this study was placed on sessile fauna inhabiting the shallow coastal zone of the high-Arctic fjord (Isfjorden, Svalbard Archipelago). These so-called lithophiles can

grow on the natural (e.g. rocks, kelp) or anthropogenic substrate (e.g. pillars, port structures). They include barnacles, bryozoans, tubiculous polychaete worms, sponges and ascidians, etc.

There are a number of environmental factors that shape the settlement and diversity of hard-bottom fauna, which can be divided into abiotic and biotic categories. The abiotic factors include the availability of the substrate itself with preferred texture, orientation, and mineralogical composition, the hydrodynamics of the environment, such as tides and currents, and the physicochemical conditions like temperature, salinity, pH and turbidity. The biotic factors are also important to this process; they include the presence of biofilm, the occurrence of certain organisms that may support or inhibit settlement (e.g. interspecies competition), and other species interactions (e.g. predation).

The primary goal of this work was to investigate the colonisation process and factors shaping it in the changing high Arctic environmental conditions, based on a long-term field experiment.

Generally, it is expected that, as a consequence of climate warming, species from lower latitudes will expand their ranges northward. This phenomenon is called borealisation, and instances of it have already been reported from various habitats in the Arctic. Newcomer boreal taxa can compete with Arctic species, which could lead to a reduction in their numbers or even their total displacement. To reliably investigate the effects of climate warming, one or two seasonal sampling events are not enough; long-term monitoring is necessary. However, studies exceeding a decade are extremely rare. Therefore, the aim of the study was to investigate the community structure of the lithophile assemblage in the Arctic fjord (Isfjorden) shallows between two temporally distant sampling campaigns (Chapter III). The experimental constructions were first set up in the summer of 2004, and the first sample collection took place after a year in 2005. The immersion of plates was subsequently repeated in the summer of 2019, with sample collection in 2020. The obtained results showed significant differences in species diversity and density between the sampled periods. The main observation was the shift in taxonomic dominance that suggests reorganisation of the assemblage structure. For instance, in 2020, the increased density of bryozoans *Cylindroporella tubulosa*, *Microporella arctica* and *Tegella arctica* was recorded, with the simultaneous decrease of *Harmeria scutulata*. A significant influence of depth has been observed on the densities reached by taxa. The ‘depth’ factor was closely related to the presence of kelp forest (at the shallower depth), which played a significant role in shaping the environment surrounding the sampling sites and driving the higher densities of lithophiles. No new species of boreal origin were noted in the samples, therefore not supporting the assumptions about the progress of the borealisation process. It is important to note that, based on only two distant sampling campaigns, a conclusion cannot be made with certainty that the results of the investigation were directly connected to climate change.

However, climate change manifests itself not only as a gradual increase in temperature but also as a phenomenon known as heatwaves. Heatwaves are described as prolonged periods of abnormally warm conditions exceeding the typical temperatures characterising the specific area. They can occur in any season, but in the Arctic, it is expected that the anomalous conditions happening in winter months will have a greater influence on the ecosystem. In many species, even short-term warm conditions could lead to annual fluctuations in recruitment and reproductive success. Therefore, the next aim of the study was to investigate the annual variability in the structure of hard-bottom assemblages over the period of 11 years (Chapter IV). The study design closely mirrored the protocol provided for Chapter III; however, the annual exchange of settlement plates was carried out from the summer of 2009 until the summer of 2020. The annual sampling allowed for the observation of nonlinear trends in the taxonomic composition and density of lithophile assemblages in response to thermal fluctuations noted in the area. The effects were not consistent across all samples, and often responses to warm conditions were observed with a delay (lag), which is possible if the conditions were not fatal to already recruited organisms but rather affected their reproductive success. Still, no new species of boreal origin were identified. Nonetheless, the contribution of boreal organisms showed an increase following warmer years. A major observed result was the considerable decrease in the density of the endemic, opportunistic arctic bryozoan *H. scutulata* in the samples after 2013.

Another factor that influences colonisation is substrate orientation. For this study, downward-facing (horizontal), upward-facing (horizontal) and vertical orientation of artificial substrates were compared. Each of the orientations had a different degree of light exposure and ability to provide shelter from predators; therefore, the objective of Chapter V was to investigate the effect of substrate orientation and predation on the lithophile assemblage. Previous reports indicate that downward-facing substrates parallel to the sea bottom attract higher biodiversity than those oriented vertically. However, the vertical substrate was said to support relatively higher coverage of organisms due to the reduced impact of sedimentation.

The Arctic is a region with relatively low colonisation rates; therefore, predation can have a significant influence on assemblage structure, shaping the development of the initial and secondary stages. However, predatory impact can also be driven by substrate orientation. Many species of lithophiles tend to prefer shaded habitats, as shortly after settlement, they are vulnerable to predation. Consumers reported to prey on sessile organisms include gastropods, echinoids, polyplacophorans, malacostracans, asteroids, ophiuroids, pycnogonids, polychaetes and actinopterygian fishes. It was hypothesised that intense predation impact would occur on more accessible, upward-facing plates, whereas the vertical plates would have a lower amount of grazing traces. Grazing traces are a type of bioerosion. They can be a result of gastropods (radula scraping marks) and echinoids (pitted or gouged marks left by teeth from Aristotle's lantern), scraping the substrate while feeding. Knowing some grazers leave traces, the aim was to quantify the predation impact and attempt to attribute traces to specific predators known to inhabit the shallow subtidal zone of Isfjorden. The experiment examining the influence of substrate orientation and predation on the hard-bottom fauna diversity was held for two consecutive years, with annual plate submersion. The orientation of the substrate was a significant factor shaping the structure of lithophilic assemblages, with one species dominating under each design. For upward-facing plates, it was the only identified alga, *Boreolithothamnion* sp., for downward-facing plates, it was the serpulid *Circeis* sp., and for the vertical plates, the barnacle *Semibalanus balanoides* was the most abundant. Contrary to the hypothesis, the upward-facing plates did not obtain the highest predation impact; they had the lowest intensity of grazing, with no traces observed in one instance. Both the downward-facing and vertical settlement plates obtained the highest predation impact measured by the number of traces, with most traces being linked to echinoid grazing.

For the purpose of the entire study, samples from a span of 16 years were analysed, and over 200,000 individual organisms were identified. The study revealed the role of chosen factors (site, year, depth and orientation) on the structuring of lithophile assemblages in polar shallow subtidal zones. Ultimately, the obtained data set provides a vital source of baseline information for future reference, especially considering ongoing climate change. Studies of hard-bottom habitats may be scarce, but are crucial, as the organisms forming them are recognised as important sentinels of environmental change due to the sedentary nature of their adult life stage (inability to escape from adverse environmental conditions).

These findings reinforce the importance of long-term, comprehensive monitoring of diverse environmental factors and ecosystem components to reliably assess the effects of climate change.

Streszczenie

Długoterminowe serie danych atmosferycznych dowodzą, że klimat ociepla się nieprzerwanie od kilku dekad. Te same trendy obserwuje się również w oceanie. Arktyka jest traktowana jako tzw. „*hot spot*” (ang.) zmian klimatycznych, gdzie ocieplenie postępuje około cztery razy szybciej niż gdziekolwiek indziej na świecie. Samo ocieplenie napędza szereg innych czynników, które mogą bezpośrednio i pośrednio wpływać na ekosystem Arktyki. Należą do nich: utrata lodu morskiego, wzrost mętności spowodowany rosnącą dostawą zawiesiny niesionej przez rzeki i topniejące lodowce, wysładzanie wód powierzchniowych zaostrzające problem stratyfikacji, rosnące zakwaszenie wód spowodowane rozpuszczaniem CO_2 itd. Wszystkie wymienione czynniki mogą się znacznie różnić w określonych skalach przestrzennych, batymetrycznych i czasowych. Ponieważ bentos w Arktyce jest liczny i zróżnicowany gatunkowo, jest kluczowym elementem morskich sieci troficznych. Odgrywa ważną rolę w ekosystemie, wspierając cyrkulację materii i wymianę energii znane jako sprzężenie bentosowo-pelagiczne. Bentos dzieli się na bentos żyjący na miękkim i twardym dnie; pierwszy jest często badany, drugiemu zaś poświęcano znacznie mniej uwagi. Ta rozbieżność w badaniach często wynika z trudności związanych z pobieraniem próbek z siedlisk skalistych. Często wymagane jest zaangażowanie doświadczonych płetwonurków. W prezentowanym badaniu asystowali oni przy montażu konstrukcji eksperymentalnych z wymiennymi płytkami kolonizacyjnymi. Zastosowanie plastikowych płytek o określonym rozmiarze pozwala na uzyskanie ustandaryzowanych wyników, które można porównywać między różnymi badaniami. Metodyka ta jest stosowana co najmniej od lat 20. XX wieku (chociaż płytki były wykonane z innego materiału), ale od tego czasu została udoskonalona.

Bentos dna twardego obejmuje wiele organizmów żyjących na skalistych podłożach, w tym faunę i florę, ale może również obejmować gatunki drylujące w skałach lub mobilną faunę związaną z tym siedliskiem. W niniejszym badaniu główny nacisk położono na faunę osiadłą (z wyjątkiem rozdziału V, w którym uwzględniono również wapienne glony koralowe) zamieszkującą płytką

strefę przybrzeżną arktycznego fiordu (Isfjord, Archipelag Svalbard). Gatunki litofilne mogą rosnąć na podłożu naturalnym lub o pochodzeniu antropogenicznym, w tym na skałach, brunatnicach, filarach i konstrukcjach portowych. Należą do nich między innymi pąkle, mszywioły, wieloszczety osiadłe, gąbki i osłonice.

Istnieje wiele czynników środowiskowych, które kształtują kolonizację i różnorodność fauny dna twardego, i można je podzielić na abiotyczne i biotyczne. Czynniki abiotyczne obejmują dostępność samego podłoża o preferowanej teksturze, orientacji i składzie mineralogicznym, hydrodynamikę środowiska (np. obecność pływów i prądów) oraz warunki fizykochemiczne, takie jak temperatura, zasolenie, pH i mętność. Czynniki biotyczne są również istotne dla tego procesu; obejmują one obecność biofilmu na podłożu, obecność niektórych organizmów, które mogą wspierać lub hamować kolonizację (np. występowanie konkurencji międzygatunkowej) oraz inne interakcje międzygatunkowe (np. drapieżnictwo).

Głównym celem niniejszej pracy było zbadanie czynników wpływających na proces kolonizacji fauny dna twardego w zmieniających się warunkach środowiskowych Arktyki, w oparciu o długoterminowy eksperyment terenowy.

Oczekuje się, że w wyniku ocieplenia klimatu gatunki z niższych szerokości geograficznych rozszerzą swoje zasięgi na północ. Zjawisko to nazywane jest borealizacją i odnotowano już tego typu zmiany w różnych siedliskach Arktyki. Nowi przybysze mogą zacząć konkurować z lokalną fauną arktyczną, co może prowadzić do redukcji liczebności gatunków arktycznych, a nawet całkowitego ich wyparcia. Aby rzetelnie zbadać skutki zmiany klimatu, jedno lub dwa badania sezonowe nie wystarczą; konieczny jest długoterminowy monitoring. Niestety, badania trwające dłużej niż dekadę są niezwykle rzadkie w tym rejonie. Dlatego celem badania było zbadanie struktury zbiorowisk zespołu litofilów na płyciznach fiordu arktycznego (Isfjord) pomiędzy dwiema odległymi w czasie kampaniami poboru prób (rozdział III). Konstrukcje eksperymentalne po raz pierwszy zainstalowano latem 2004 r., a pierwszy pobór prób miał miejsce rok później, w 2005 r. Procedurę powtórzono następnie latem 2019 r., przy czym pobranie prób miało miejsce w 2020 r. Uzyskane wyniki wskazały istotne różnice w składzie gatunkowym i zagęszczeniu fauny między okresami pobierania prób. Główną obserwacją była zmiana dominacji taksonomicznej, która sugeruje reorganizację struktury zespołu. Na przykład w 2020 roku odnotowano wzrost zagęszczenia mszywiołów *Cylindroporella tubulosa, Microporella arctica* i *Tegella arctica*, przy jednoczesnym spadku zagęszczenia *Harmeria scutulata*. Zaobserwowano istotny wpływ głębokości na zagęszczenia osiągane przez taksony. Na płytszych głębokościach stwierdzono podwodne lasy brunatnic, które odegrały znaczącą rolę w kształtowaniu środowiska wokół miejsc poboru prób stwarzając sprzyjające warunki dla licznych litofilów. W próbach nie stwierdzono żadnych nowych gatunków pochodzenia borealnego, co nie potwierdza założeń dotyczących postępu procesu borealizacji zbiorowisk dna twardego. Jednak na podstawie zaledwie dwóch odległych kampanii poboru prób nie można z całą pewnością wyciągnąć wniosku, że wyniki badania były bezpośrednio związane ze zmianą klimatu.

Ocieplenie klimatu objawia się nie tylko stopniowym wzrostem temperatury, ale także zjawiskiem znanym jako fale upałów (ang. *heatwaves*). Fale upałów opisuje się jako przedłużające się okresy anormalnie ciepłych warunków, przekraczających typowe temperatury charakterystyczne dla danego obszaru. Mogą one występować o każdej porze roku, ale w Arktyce oczekuje się, że anomalie występujące w miesiącach zimowych będą miały większy wpływ na ekosystem. U wielu gatunków nawet krótkotrwałe ciepłe warunki mogą prowadzić do zmian w procesie rekrutacji i sukcesie reprodukcyjnym. Dlatego kolejnym celem projektu badawczego było zbadanie rocznej zmienności struktury zespołów dennych w okresie 11 lat (rozdział IV). Projekt eksperymentu ściśle odzwierciedlał protokół przedstawiony w rozdziale III; jednak coroczna wymiana płytek kolonizacyjnych miała miejsce od lata 2009 do lata 2020. Eksperyment terenowy pozwolił na obserwację nieliniowych trendów w składzie taksonomicznym i zagęszczeniu zespołów litofilnych w odpowiedzi na fluktuacje termiczne obserwowane na tym obszarze. Efekty nie były jednolite we wszystkich próbach, a reakcje na cieplejsze warunki często obserwowano z opóźnieniem, co jest możliwe, jeśli warunki te nie były śmiertelne dla już zrekrutowanych organizmów, lecz raczej wpływały na ich sukces reprodukcyjny. Również w tym badaniu nie zidentyfikowano żadnych nowych gatunków pochodzenia borealnego. Niemniej jednak udział organizmów borealnych, już obecnych w tym obszarze, wzrastał po cieplejszych latach. Głównym zaobserwowanym rezultatem był znaczny spadek zagęszczenia endemicznego, oportunistycznego arktycznego mszywioła *H. scutulata* w próbach zebranych po 2013 roku.

Innym czynnikiem wpływającym na kolonizację organizmów jest orientacja przestrzenna podłoża. W niniejszym badaniu porównano sztuczne podłoża w położeniu poziomym skierowane w dół i w górę, oraz w położeniu pionowym. Każda z orientacji charakteryzowała się innym stopniem ekspozycji na światło i zdolnością do zapewnienia schronienia przed drapieżnikami. Celem rozdziału V było zbadanie wpływu orientacji podłoża i drapieżnictwa na różnorodność zespołu litofilów. Wcześniejsze doniesienia wskazują, że podłoża skierowane w dół, równolegle do dna morskiego, przyciągają większą bioróżnorodność niż te zorientowane pionowo. Uważa się jednak, że podłoża o orientacji pionowej sprzyjają intensywnej rekrutacji bezkręgowców ze względu na mniejszy wpływ sedymentacji.

Arktyka to region o stosunkowo niskim tempie kolonizacji dna twardego, dlatego drapieżnictwo może mieć istotny wpływ na strukturę zespołu, kształtując rozwój stadiów inicjalnych i wtórnych. Jednak wpływ drapieżnictwa może być również zależny od orientacji podłoża. Wiele gatunków litofilnych preferuje siedliska ukryte, ponieważ wkrótce po zasiedleniu młode osobniki są wrażliwe na ataki drapieżników. Do konsumentów żerujących na organizmach osiadłych należą ślimaki, jeżowce, chitony, pancerzowce, rozgwiazdy, wężowidła, kikutnice, wieloszczety i ryby z rodziny promieniopłetwych. Postawiono hipotezę, że intensywna aktywność drapieżników będzie miała miejsce na łatwiej dostępnych płytkach, skierowanych ku górze, podczas gdy płytki ustawione pionowo będą miały mniej śladów żerowania. Ślady żerowania są rodzajem bioerozji. Mogą być wynikiem skrobania po podłożu przez ślimaki (ślady tarki - raduli) i jeżowce (wyżłobione ślady zębów - latarni Arystotelesa) podczas żerowania. Wiedząc, że niektóre zwierzęta pozostawiają ślady, celem było ilościowe określenie wpływu drapieżnictwa i próba przypisania śladów konkretnym drapieżnikom, o których wiadomo, że zamieszkują płytką strefę pływową Isfjordu. Oprócz podstawowego protokołu, konstrukcje eksperymentalne rozszerzono o dodatkowe poziome (skierowane ku górze) płytki kolonizacyjne i pionowe instalacje. Tak rozszerzony eksperyment przeprowadzono przez dwa kolejne lata, z corocznym zanurzaniem płytek kolonizacyjnych. Orientacja podłoża była istotnym czynnikiem kształtującym strukturę zespołów litofilnych, przy czym jeden gatunek dominował w każdym położeniu. W przypadku płytek skierowanych ku górze był to jedyny zidentyfikowany glon, *Boreolithothamnion* sp., w przypadku płytek skierowanych w dół był to wieloszczet osiadły *Circeis* sp., a wśród płyt pionowych najliczniej występowała pąkla *Semibalanus balanoides*. Wbrew hipotezie, na płytkach skierowanych ku górze nie zaobserwowano największej aktywności drapieżników; przeciwnie, odnotowano najniższą intensywność żerowania. Zarówno na płytkach kolonizacyjnych skierowanych w dół, jak i pionowych stwierdzono najwyższą aktywność drapieżników mierzoną liczbą śladów, przy czym większość śladów żerowania była związana z aktywnością jeżowców.

Na potrzeby całego projektu doktorskiego przeanalizowano próbki z okresu 16 lat i zidentyfikowano ponad 200 000 pojedynczych organizmów. Badanie ujawniło wpływ wybranych czynników (miejsca, roku, głębokości i orientacji podłoża) na strukturę zespołów litofilnych w płytkich strefach przybrzeżnych Arktyki. Uzyskany zbiór danych stanowi istotne źródło informacji referencyjnych do wykorzystania w przyszłości, zwłaszcza w kontekście trwających zmian klimatu. Badania zgrupowań dna twardego są jak dotąd nieliczne, ale mają kluczowe znaczenie, ponieważ organizmy je tworzące są uznawane za bioindykatory zmian środowiskowych ze względu na osiadły charakter ich dorosłego życia (brak możliwości ucieczki przed niekorzystnymi warunkami środowiskowymi). Wyniki te potwierdzają znaczenie długoterminowego, kompleksowego monitorowania różnych czynników środowiskowych i składników ekosystemów w celu wiarygodnej oceny skutków zmian klimatycznych.

Chapter I General introduction

Surveys of the European Arctic indicated that the great majority (over 90%) of the identified fauna species are classified as benthic invertebrates (Sirenko, 2001; Evseeva et al., 2023). Many of those inhabit coastal areas where hard and mixed substrates can be quite common, harbouring sessile organisms (lithophile or hard-bottom fauna) (Thorson, 1957; Dunlop et al., 2020). This biodiversity plays a crucial role in the circulation of matter and the exchange of energy known as benthic-pelagic coupling (Ronowicz et al., 2024). This flow is happening in both directions: pelagic activity provides food to filter feeders living on the sea bottom, and the benthic animals release larvae into the pelagic realm. After the larval stage of the life cycle, spent as meroplankton in the pelagic zone, the organisms head out on a journey to find a suitable substrate to settle on (Meadows and Campbell, 1972; Jenkins et al., 2009). A range of abiotic factors can influence the final place of recruitment, including the availability of the substrate itself with preferred texture, orientation, and mineralogical composition, the hydrodynamics of the environment, such as tides and currents, and the physicochemical conditions like temperature, salinity, pH and turbidity (Pawlik, 1992; Caley et al., 1996; Todd, 1998; Jenkins et al., 2009; Siddik et al., 2018; Ali, 2023). The biotic factors are also important to this process; those can include the presence of biofilm, the presence of certain organisms that may support or inhibit recruitment (e.g. interspecies competition), and other species interactions (e.g. predation) (Buss, 1979; Pawlik, 1992; Caley et al., 1996; Todd, 1998; Jenkins et al., 2009; Holomuzki, 2010; Barnes and Neutel, 2016). There is a wide range of abiotic and biotic factors influencing recruitment of hard-bottom fauna, and most of them are changing with depth, especially taking into account the presence of kelp forests in the shallow subtidal zone (infralittoral). Those macroalgae inhabit coastal waters penetrated by sunlight (Svendsen, 1959; Włodarska-Kowalczuk et al., 2009). Kelps are recognised habitat engineers that promote increased biodiversity by providing additional substrate, shelter, food source, and generally influencing environmental conditions within the forest, such as decreasing water movement and sedimentation (Kuklinski et al., 2006; Balazy and Kuklinski, 2017; Teagle et al., 2018; Shunatova et al., 2018b).

Studies of hard-bottom ecosystems are scarce, but vital, as the organisms forming them are significant sentinels of environmental change due to the sedentary nature of their adult life stage (inability to escape from adverse environmental conditions) (Kröncke et al., 1998; Beuchel et al., 2006; Jordà-Molina et al., 2023; Evseeva et al., 2024). Assessment of the effects of climate change poses many challenges and requires long-term, comprehensive monitoring. Most of the time, changes are gradual and hard to observe on short time scales. Constant monitoring can also provide opportunities to distinguish effects of extreme events (e.g. marine heatwaves) on the ecosystem from the general warming trend. To assess the ecosystem's response to these changes, multi-year studies are necessary (Beuchel et al., 2006; Wassmann et al., 2011; Chan et al., 2019; Jordà-Molina et al., 2023). Conducting such studies in the Arctic is quite challenging due to the prevailing conditions (including the polar night, low temperatures, changing weather conditions, frequent storms, intense wave action, strong winds, and presence of sea ice, etc.). Studying organisms associated with the hard bottom is equally challenging because they cannot be sampled using traditional tools used in benthic studies conducted on soft bottoms (i.e., van Veen grabs, box corers, and dredges) (Nicoletti et al., 2007; Renaud et al., 2007). To assess the structure of benthic communities on the hard bottom, underwater structures with replaceable settlement plates were installed in the Arctic fjord. The use of settlement panels is common in benthic research (Kuklinski and Barnes, 2005; Barnes and Kuklinski, 2005; Kuklinski et al., 2013; Meyer et al., 2017; Evseeva et al., 2023; Sowa et al., 2023). This method allows the acquisition of standardised data that can be compared between studies done by different researchers in various places (Barnes, 1996; Kennedy et al., 2017; Kuklinski et al., 2022). The panel structures were constructed to allow for the installation of plates with two orientations (downward-facing and upward-facing). Additionally, near the end of the experiment, vertical rigs were installed in proximity to the original constructions, held up by buoys. This method required the involvement of highly experienced SCUBA divers who installed the constructions and maintained the experiment on a yearly basis. This experiment was started in 2004, allowing for annual sample collection over

16 years. This time frame was expected to be sufficient to observe responses of fauna to environmental changes and recognise general trends. The specific dates correspond with the time when many changes were reported from the Arctic region (Kortsch et al., 2012; Skogseth et al., 2020), including several heatwaves in summer and winter (Beszczynska-Möller et al., 2012; Promińska et al., 2017; Skogseth et al., 2020; Mohamed et al., 2022). It is likely that the lack of lower temperatures in winters can have more profound effects on the recruitment, biodiversity of the hard-bottom fauna, interspecies competition and predation. Considering the ongoing warming of the Arctic region, expansion of boreal species is expected to occur into the Arctic waters (Renaud et al., 2015; Pinsky et al., 2020).

This research provides new insights into the status and resilience of the studied lithophile assemblage in response to ongoing environmental changes and increasingly frequent temperature anomalies in the Arctic region (Huang et al., 2021; Jordà-Molina et al., 2023). In addition to comparing long-term biological data with environmental conditions, the doctoral project describes the impact of spatial differentiation (based on experimental plates mounted in different orientations – horizontal plates oriented towards the bottom/water column, and vertical plates suspended from a buoy perpendicular to the seabed) on the structure of the studied assemblages. Previous reports and my earlier research (Kuklinski and Barnes, 2005; Barnes and Kuklinski, 2005; Kuklinski et al., 2013; Meyer et al., 2017; Sowa et al., 2023) indicate that some benthic organisms prefer to settle on substrates that allow them to "hide" from predators (plates oriented horizontally towards the bottom). Describing this data allowed for a more precise assessment of the assemblage structure associated with underwater structures of anthropogenic origin. Furthermore, based on photographic analyses of colonisation plates, a qualitative and quantitative description of predation based on traces left on the substrate surface was performed. Predation is a significant factor influencing the formation of benthic assemblages, which is difficult to observe and describe without continuous monitoring. Some predators grazing sessile organisms from the hard substrate leave characteristic traces, which can be used to determine which organisms were likely feeding on a given surface and with what intensity (Bromley, 1975; Wisshak et al., 2022; Miguez-Salas et al., 2024).

The selected study area is located in the European Arctic on the west coast of Spitsbergen. This area is influenced by the West Spitsbergen Current, which carries warmer and more saline Atlantic water deep into the Arctic (Nilsen et al., 2008; Fraser et al., 2018; Bloshkina et al., 2021). Changing physicochemical conditions in the fjord may, over time, lead to changes in the structure of benthic species communities (as already reported by Kortsch et al., 2012). As the Arctic has been continuously warming at a rate about four times faster than the rest of the globe (Rantanen et al., 2022), it is essential to build a reliable baseline knowledge of the colonisation process in the shallow coastal waters (Wassmann et al., 2011). Those areas are more exposed to warming than the deep waters, as well as other indirect processes induced or intensified by climate change (Friedlander et al., 2023). Those indirect factors include, but are not limited to, loss of sea ice, increased freshwater runoff and suspended material carried by rivers and from melting glaciers, freshening of surface waters, increasing acidification due to intake of CO_2, etc. (Brown et al., 2020; Jones et al., 2021; Vonnahme et al., 2023). The increased presence of suspended matter and the eventual sedimentation can lead to suffocation of filter feeders and other sessile organisms (Sahade et al., 2015). The freshening of surface waters could exacerbate the issue of stratification, influencing benthic-pelagic coupling (Ronowicz et al., 2024) and affecting osmoregulation (Podbielski et al., 2022). Furthermore, increasing seawater acidification may lead to a growing struggle of organisms to build their calcium carbonate shells and skeletons (Goethel et al., 2017). Besides the ongoing increase in temperatures, the higher frequency and severity of warm anomalies have been observed (Beszczynska-Möller et al., 2012; Cullather et al., 2016; Overland and Wang, 2016; Promińska et al., 2017; Skogseth et al., 2020; Mohamed et al., 2022). Therefore, due to the intense changes taking place in the Arctic, continuous monitoring is necessary to uncover trends in the future.

Purpose of Research

The overall goal of the research project was to investigate the colonisation process and factors shaping it in the high Arctic based on a long-term field experiment. The chosen research subject was explored in three interconnected approaches with the following objectives:

1. Investigation into the community structure of the lithophile assemblage in the Arctic fjord (Isfjorden) shallows between two temporally distant sampling campaigns (conducted in 2005 and 2020) under changing environmental conditions (with focus on the temperature) at two different depths, and estimation of the impact of these changes on the species composition and dominance of hard-bottom fauna.
2. Investigation of the annual variability in the hard-bottom assemblages structure over the period of 11 years, with inclusion of the impact from warm water anomalies and estimation of possible range expansion of boreal species.
3. Investigation into the effect of substrate orientation (horizontal and vertical) and predation on the recruitment and structure of the lithophile assemblage.

Chapter II Study area and general protocol

II.1 Study area

Located on the west coast of Spitsbergen, Isfjorden is the largest fjord of the Svalbard archipelago (Nilsen et al., 2008; Fig. 1). It is under the influence of two main water masses – warm Atlantic water transported by the West Spitsbergen Current ($\Theta > 3$°C, $35.1 < S_A < 35.4$ g/kg) and cold Arctic water transported by the East Spitsbergen Current ($\Theta < 1$°C, $34.5 < S_A < 35$ g/kg; continuing along the west Spitsbergen as the Spitsbergen Polar Current) (Θ – conservative temperature, representing more accurately the heat content of seawater (McDougall, 2003); S_A – absolute salinity; Fraser et al., 2018; Fig. 1), which can penetrate and mix freely within the fiord basins due to the lack of a sill at the mouth (Nilsen et al., 2008; Fraser et al., 2018).

The field experiment was deployed on the southern bank of Isfjorden proper, west of Longyearbyen, at two study sites, S1 (78.21292°N, 15.23556° E) and S2 (78.1883° N, 15.1447° E). The experimental constructions were submerged within the subtidal zone, in the infralittoral (7±1 m) and upper circalittoral zone (14±1 m). The natural substrate was mainly characterised by hard bedrock, including rocks and boulders, with pockets of sand or mud at both locations. Within the subtidal zone, two zones - the infralittoral (depth <10 m), which was vegetated by dense kelp forests and other macroalgae (JNCC, 2022), and the shallow circalittoral (depth >10 m), which was mostly barren (or with very little vegetation present) (Balazy and Kuklinski, 2017).

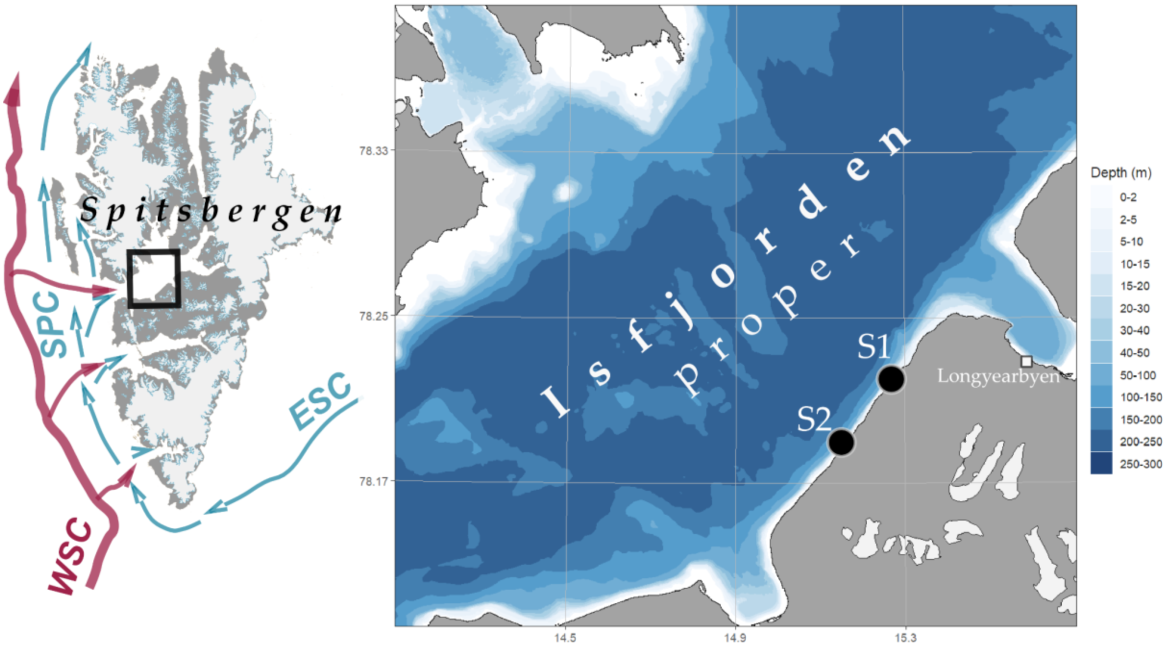


Fig. II.1 Location of the sampling sites in southern Isfjorden proper S1 (N78.213, E15.2339) and S2 (N78.1883, E15.1447) on the southern bank of Isfjorden (Svalbard, North East Atlantic Ocean). Each sampling site included constructions at the infralittoral (7±1 m) and upper circalittoral zone (14±1 m). The map includes currents: the warm West Spitsbergen Current (WSC), and the cold East Spitsbergen Current (ESC) that continues as the Spitsbergen Polar Current (SPC) along west Spitsbergen (Skogseth et al., 2020). Maps were created using the PlotSvalbard R package (Vihtakari, 2020). Adapted from Moreno et al. (2024).

Dense kelp forests were present at both study sites (S1 and S2) and reached down to about 12 and 8 meters, respectively (personal communications). They were mainly formed by *Laminaria solidungula*, *Saccorhiza dermatodea*, *Alaria esculenta*, *Saccharina latissimi*, *Laminaria digitata* and *Laminaria hyperborea* (Assis et al., 2017). Their environmental importance stems from their ability to act as significant habitat-forming organisms that are known to support diverse assemblages by providing substrate and a food source (Shunatova et al., 2018b). The circalittoral zone starts below the algae-dominated infralittoral zone, and some sparse kelps or macroalgae can be present, but the habitat is dominated by the barren seabed. The lower limit spans down to about 200 meters, so the end of the continental shelf (JNCC, 2022). The average slope between the infralittoral and upper circalittoral zones was 13.5° (24%) and 8° (14%) for S1 and S2, respectively (Moreno et al., in press). The southern bank of Isfjorden lacks any tidewater glaciers, however, a few rivers are present.

II.2 Protocol

The field investigation into benthic assemblage structure was conducted using experimental constructions (Fig. II.2). The experimental constructions consisted of a horizontal, metal frame ballasted and secured on the sea bottom with coarse cobbles and fine boulders (128–512 mm) collected from the nearby environment. The frames held exchangeable panels with black settlement plates with one mattified side (15 cm × 15 cm; 3 mm thick, made of High Impact Polystyrene), three per side of the panel. The plates were fastened to the metal frame with cable ties. The space between the experimental plates and the sea bottom was approximately 50 mm, ensuring that they would not be scratched by the gravelly substrate. However, this arrangement did not exclude macro-predators (personal communication; see Barnes et al., 2025 and references therein). The experimental construction was prepared according to the protocol described by Todd and Turner (1986) and further modified by Kuklinski et al. (2022).

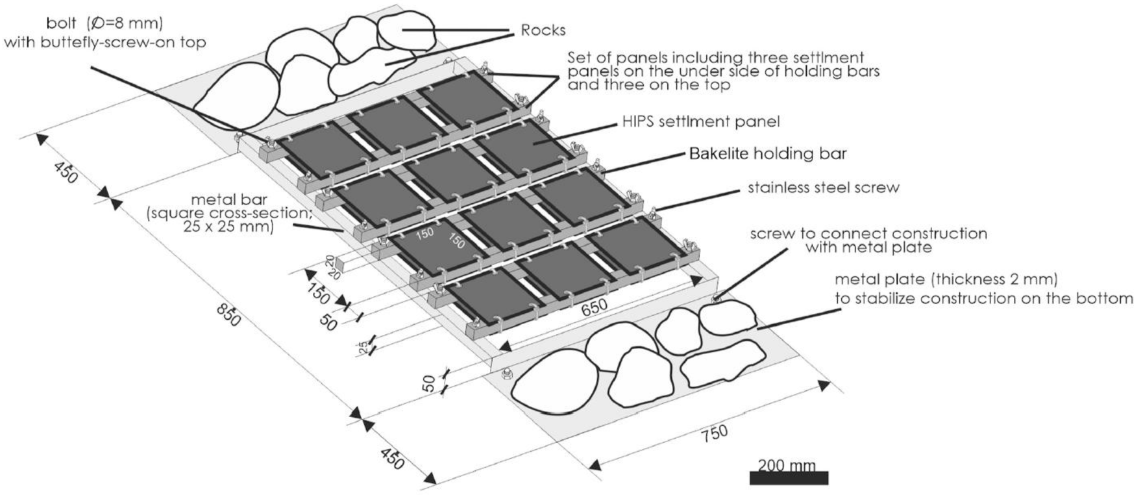


Fig. II.2 The scheme of the experimental construction. Adapted from Kuklinski et al. (2022).

At each study site, three replicate settlement plates were collected after a year of immersion. A full description of the constructions can be found in Kuklinski et al. (2022). The first settlement plates were submerged in the summer of 2004 and retrieved a year later in 2005. The protocol was then re-established in 2009, and the procedure of submersion and collection was conducted annually up to 2020. All fieldwork operations were conducted at the turn of July and August by the SCUBA divers from the IO PAN Scientific Diving Team (Fig. II.3), transported, and assigned a description (site, orientation and year of collection), and stored dry at the Institute of Oceanology, Polish Academy of Sciences (IOPAN) in Sopot, Poland.

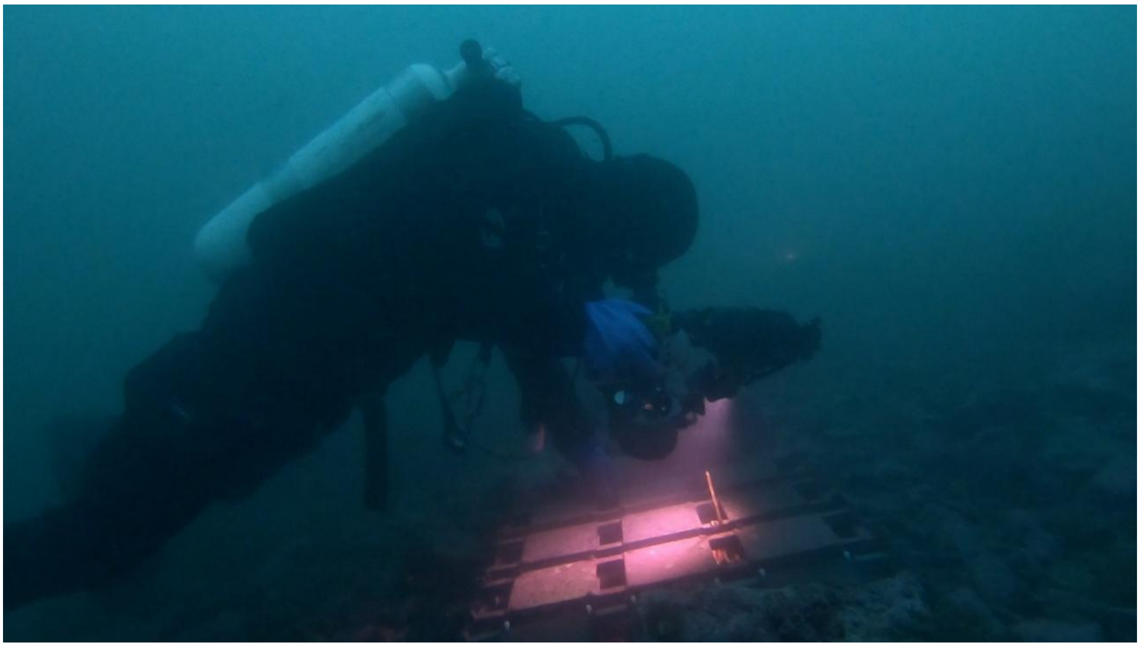


Fig. II.3 SCUBA diver from the IO PAN Scientific Diving Team in the process of photographing the settlement plates still attached to the experimental construction underwater (photo: B. Moreno).

II.3 Sample analysis

The dried panels with colonists were analysed under a stereoscopic microscope Leica M205C, with a focus on the central area of the plates (10 cm × 10 cm; region of interest - ROI) to minimise the 'edge effect' as recommended by Harris (1988). The edge of the plate acts as a boundary between the studied area and the surrounding environment and, therefore, could be considered unrepresentative of the studied assemblage structure (Harris, 1988; Kuklinski et al., 2022).

A specially designed metal frame with a 1 cm × 1 cm grid was used to eliminate the plate's unrepresentative edge during the analysis (Fig. II.4).

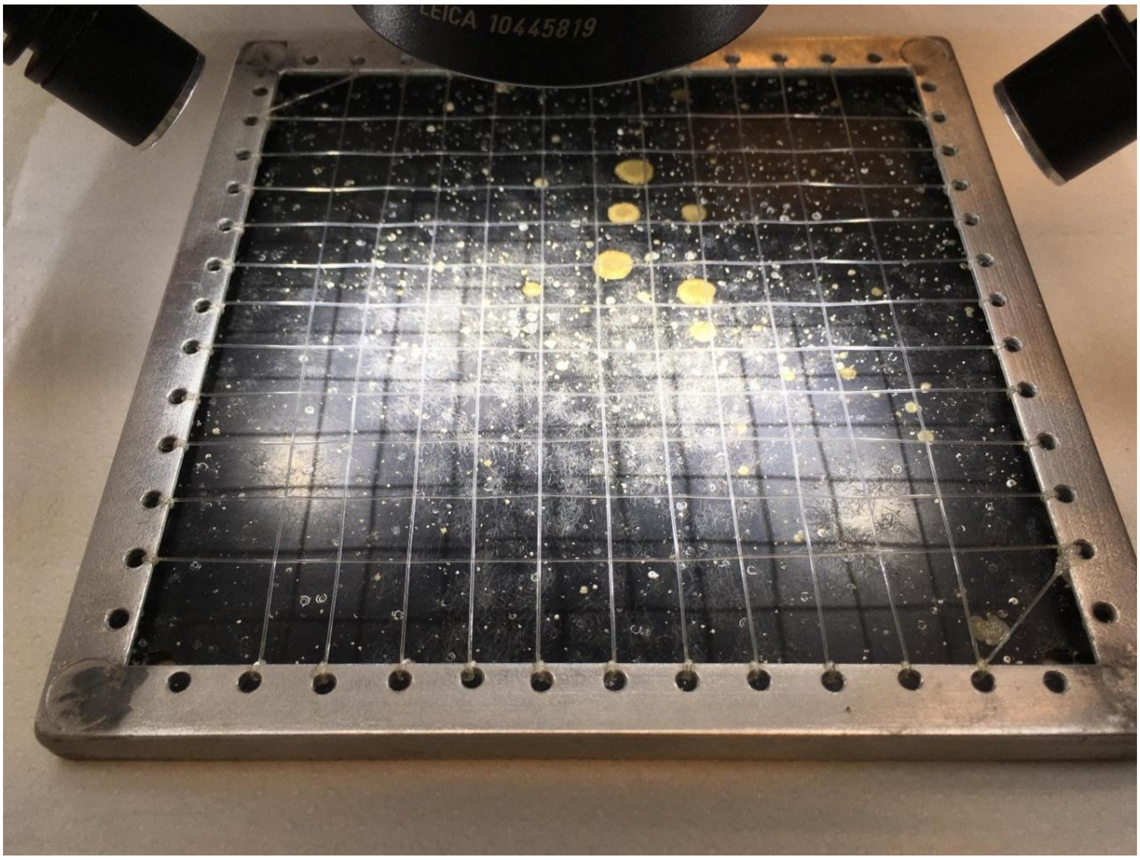


Fig. II.4 Special metal frame with 1 cm × 1 cm grid over the central region of interest (ROI, 10 cm × 10 cm) and boundary for the edge excluded from the analysis.

The encrusting fauna was identified to the lowest possible taxonomic level using taxonomic keys for bryozoans (Kluge, 1975; Shunatova et al., 2018a), calcareous tubeworms (Rzhavsky et al., 2014; Ippolitov and Rzhavsky, 2015), and cirripeds (Klekowski and Weslawski, 1991; Vassilenko and Petryashov, 2009). All organisms in the central area were counted to obtain a total and taxa density (ind./100 cm^2) of recruits. In the case of colonial organisms, a colony was counted as a single recruit. The colonies never overgrew the plates entirely due to the rather short time of submersion (a year) and the relatively slow growth rate of arctic lithophiles (e.g. see Barnes and Kuklinski, 2005). To indicate the level of overgrowth of the settlement plates, relative coverage expressed as a percentage was calculated by overlaying 100 randomised points over photographs of the central areas of the settlement plates in CPCe 4.1 software (Kohler and Gill, 2006). Then, the presence or absence of lithophiles was manually determined and noted. Based on the information from those 100 points, a percentage value of coverage was obtained.

II.4 Statistical analysis

If not stated otherwise in the next chapters, the analysis of samples followed the same protocol.

Data preparation, statistical analysis and visualisation were performed using Statistica software (StatSoft, Inc., 2007) and Primer v.7 (Clarke et al., 2008). In each chapter, the PERMANOVA (permutational analysis of variance) analysis was performed in Primer v.7 (Clarke et al., 2008) to test the impact of three factors on the number of taxa, density and assemblage structure (understood as taxonomic composition with included abundances of each taxa) on settlement plates. Additional post-hoc pair-wise comparison tests for levels of each factor were performed. To overcome the zero-inflation and high value dispersal within the dataset, the raw data were square-root transformed.

Data from the replicates (three plates from each sampling station) were averaged for further analysis and preparation of graphs. The point and whisker plots were prepared to display the overall structure of the studied assemblages or the influence of the most significant factors on the number of taxa and density. To further investigate the structure of the assemblages, the LINKTREE analysis was performed, which groups samples based on SIMPROF similarity profile tests. At each division level, a set of taxa that differentiated the samples was identified at each level of division, with values of densities characterising each branch of the split.

Further specific analysis has been described in the following chapters.

Chapter III Comparison of lithophile assemblage in a high Arctic fjord between 2005 and 2020

III.1. Introduction

Most of the Arctic has experienced sustained intense warming for decades (Rantanen et al., 2022). This intensity and magnitude of sustained changes could push the ecosystems beyond tipping points. Most of the organisms found in the Arctic waters are adapted to lower temperatures, and many of them have narrow thermal tolerance, which makes them particularly sensitive (Wassmann et al., 2011; Wassmann, 2018; Semenov, 2021; Rantanen et al., 2022). Shallow coastal areas, besides having highly unstable physical conditions (Balazy and Kuklinski, 2017; Beuchel et al., 2006), are especially predisposed to climate change influences (Friedlander et al., 2023). The continued rise in temperature leads to increasing calving and, consequently, ice scour (Conlan and Kvitek, 2005). On the other hand, seasonal sea ice in the coastal areas acts as a buffer from storm-driven erosion. With diminishing sea ice and growing intensity and frequency of storm activity, many shores will be exposed to greater deterioration (Lantuit et al., 2012). Besides the continuous warming trends, the Arctic is also experiencing increasing frequency and severity of atmospheric (Overland and Wang, 2016; Cullather et al., 2016) and marine (Beszczynska-Möller et al., 2012; Promińska et al., 2017; Skogseth et al., 2020; Mohamed et al., 2022) heatwaves. Heatwaves are characterised as prolonged periods of abnormally warm conditions in comparison with typical temperatures characterising the specific area and season (Jordà-Molina et al., 2023). With these changes superimposed over increasing turbidity and sedimentation, freshening, sea level rise and acidification (Brown et al., 2020; Jones et al., 2021; Vonnahme et al., 2023), it is crucial to perform consistent monitoring of ecological responses across ecosystems, rather than focusing (as many studies do) on a few large, charismatic species, whose responses may not represent those of wider biodiversity (Kovacs et al., 2024; Wang, 2024). When it comes to the Arctic assemblages, a main stumbling block for evaluation of the impacts of climate change impacts is the lack of established baseline information (Beuchel et al., 2006;

Wassmann et al., 2011; Renaud et al., 2015; Chan et al., 2019; Jordà-Molina et al., 2023). The Arctic has already been under the influence of ongoing and accelerating warming for about five decades, potentially leading to shifts in many ecosystem elements long before they become a focus of research studies (Friedlander et al., 2023). Future assessments of climate-change-driven alterations, such as the northward shift in ranges for boreal species from lower latitudes (Renaud et al., 2015; Górska et al., 2022), will be much more powerful if this gap in baseline knowledge is filled.

In the European Arctic, most of the studies conducted in this region focus on the organisms living on and in the soft sediment, however, the hard-bottom habitats reportedly sustain the highest biodiversity (Dunn and Halpin, 2009). Many of the benthic invertebrates (such as sponges, cnidarians, bryozoans, and ascidians) inhabit coastal areas where hard and mixed substrates (of solid rocks or loose boulders) are quite common, harbouring sessile organisms (Thorson, 1957; Dunlop et al., 2020). Benthic assemblages of species that predominantly lead a sedentary or sessile lifestyle in the subtidal are thought to be important indicators of environmental change. If they settle, survive and reproduce, it can be presumed that the conditions did not exceed their thermal tolerance range (Kröncke et al., 1998; Beuchel et al., 2006; Jordà-Molina et al., 2023; Evseeva et al., 2024). Previous studies on benthic response to environmental forcing revealed that benthic groups can display delayed feedback due to consequent lags connected to altered diet, feeding rates and eventually the reproductive rates and/or success (Beuchel et al., 2006). This could be true even when no direct influence on a given sessile organism has been exerted (Gray and Christie, 1983). With severe changes in the environment, responses of sessile (as adults) fauna could be more drastic, especially for species with narrow tolerances, for example, to temperature (Renaud et al., 2019). Studies conducted on habitats with limited available space for sessile assemblages could provide powerful evidence in the investigations of non-indigenous species extending their natural domains (Beshai et al., 2022). Borealisation is a phenomenon understood as a shift happening within the Arctic ecosystem, which is affecting biodiversity and a gradual switch to more boreal characteristics (Husson et al., 2024). This phenomenon, originally known, under the name ‘atlantification’, was first introduced by Wassmann et al. (2004) when describing biological shifts in the Barents Sea. It is expected that more species of boreal origin may extend the northern edge of their range into Svalbard waters as a result of regional warming, to maintain their thermal window (Renaud et al., 2015; Górska et al., 2022). A notable example heralding this process is the return of the thermophilous blue mussel (*Mytilus edulis*) into the Svalbard region after 1000 years since the last record of presence (Berge et al., 2005; Kotwicki et al., 2021). Furthermore, several domain expansions of boreal species have already occurred, as in the case of *Calanus finmarchicus*, with the simultaneous retreat of Arctic species *C. glacialis* and *C. hyperboreus* (Dalpadado et al., 2012), as well as a northward shift of the Atlantic cod and haddock stock (Renaud et al., 2012; Fossheim et al., 2015) into the Barents Sea region, were reported as early as 2004. Other researchers have reported changes in the structure of phytoplanktonic assemblages, with a major dominance of *Synechococcus* in the Arctic waters where it had not been previously commonly found (Paulsen et al., 2016), and northward expansion of the coccolithophore *Gephyrocapsa huxleyi* (Oziel et al., 2020). In the benthic realm, the expansion of *Gammarus oceanicus* has been observed to be coincident with the warming of Spitsbergen shores (Weslawski et al., 2010). Likewise, Górska et al. (2022) reported increased presence of cosmopolitan (e.g. *Maldane sarsi*) and arctic-boreal (e.g. *Galathowanie oculata* and *Prionospio cirrifera*) polychaetes in the deep Fram Strait. In the intertidal zone of the eastern Kola Peninsula region, new records of a bryozoan have been reported – *Valkeria uva*, a species of boreal origin previously known from the area to the west of Kola Bay (Evseeva et al., 2022). In another study focusing on Franz Josef Land, Evseeva and Dvoretsky (2024) identified 22 new records of species in the study region, with 7 having boreal origins. In both cases, the establishment of the new records was attributed to the increasing temperatures, although transport vectors have increased and many other stressors (freshening, sea level rise, acidification, etc.) were altered as well. Accumulation of these changes in the biodiversity over time could lead to cascading effects over the whole ecosystem structure (Kortsch et al., 2015). As the Svalbard region is under the intense influence of warm Atlantic waters carried by the West Spitsbergen Current, we expect to see changes in epibenthic assemblage structure there.

Up to this point in time, there are no long-time series of data specifically considering year-by-year changes in the recruitment on the hard substrate in the shallows of the Arctic. Previous studies of the hard-bottom assemblages in the Arctic tend to focus on one-year snapshots (Barnes and Kuklinski, 2005; Kuklinski and Barnes, 2005; Voronkov et al., 2016; Evseeva et al., 2023) or seasonal aspects of recruitment (Kuklinski et al., 2013; Meyer et al., 2017; Sowa et al., 2023). One-year snapshots have allowed comparisons in macro-space (Barnes, 2015) but rarely in time (but see Watson and Barnes, 2004). A 2-3 year study in deeper water found little effect of a sampling year, but these years were close together (2017-2019, see Souster et al., 2024). Nevertheless, basic information is still insufficient, especially in remote areas characterised by extreme environmental conditions.

The use of experimental constructions that can be removed from the environment at the end of the project and have limited lasting influence on the natural ecosystem aligns well with the increasing efforts to employ less invasive means of studying the ecosystem (Bowden et al., 2006; Kuklinski et al., 2022). The use of artificial substrates to research the colonisation, recruitment and development on hard bottoms was implemented a long time ago (use of this protocol: Todd and Turner, 1986; first found mention of using artificial metal plates: Parker, 1924). The uniformity of such artificial substrata and associated methodology aids comparability of replicates and results of studies performed by other researchers (Barnes, 1996; Kennedy et al., 2017; Kuklinski et al., 2022) and minimises unquantified or unknown physical differences that may characterise the natural substrate (Glasby and Connell, 2001). Furthermore, settlement plates made from black, homogenous plastic – HIPS (High Impact Polystyrene) have been used in many studies in the Arctic region and beyond, and all supported the settlement of zoo- and phytobenthos (e.g. Barnes and Kuklinski, 2005; Meyer et al., 2017; Sowa et al., 2023). Kennedy et al. (2017) reported that plastic materials accurately approximate natural coralline algae assemblages. Additionally, they uniquely preserve both the taxonomical composition and the spatial organisation of the lithophile assemblages for analysis.

Evidently, the chosen area is difficult to access, and the structure of the hard-bottom assemblages is poorly known in the Arctic. For those reasons, the goals were to 1) provide basic data on the taxonomic composition of Arctic fjordic epifaunal assemblages. Furthermore, given the intense climate forced changes already described in the Arctic, it was intended to 2) investigate whether in two temporally distant sampling campaigns the taxonomic composition, proportions of taxa and their abundance have significantly changed. It was hypothesised that the change between sampling campaigns would be significant. Lastly, as earlier reports by other researchers report that with climate change, an expansion of boreal species to the north associated with the displacement of Arctic species has been observed for other groups, the aim was to 3) examine the assemblage for the presence of newly detected species of boreal origin.

III.2. Materials & methods

III.2.1 Protocol

The protocol followed the general description provided in Chapter II. For the purpose of this study, two campaigns were held with identical methodology.

The experimental construction was first set up in the summer (in late July and early August) of 2004 with the first settlement plates by the IOPAN Scientific Diving Team. The first set of plates was collected after a year of immersion in 2005. The field experiment was then repeated in 2019 with the second set of plates and collected a year later in 2020.

III.2.2 Data analysis

In order to provide an overall description of the lithophile assemblage state, a point and whisker plot was prepared displaying mean values based on three replicates with singular standard deviation bars encompassing all factors. The Shannon–Wiener species diversity index (ln-based; H') and Pielou evenness index (J') diversity indices were calculated (Ludwig and Reynolds, 1998; Clarke and Warwick, 2001). A bar plot to display the most abundant taxa (chosen based on the mean number of individuals being equal to or higher than 100 in any sample) was prepared to investigate changes in their density over sampling periods. The ANOSIM analysis was used to test for differences between abundances of selected species as a function of the ‘year’ factor. Three-way PERMANOVA was used to test the differences in the number of taxa, abundance and taxonomic composition on plates among three factors (year, site, depth; all fixed and with two levels each) and their interactions. Additional post-hoc pair-wise comparison tests for levels of each factor were performed.

The point and whisker plots were prepared to display the influence of the most significant factors on a number of taxa and density (mean ± 95% confidence interval of ind. per 100 cm^2). A shadeplot was prepared to show the relative abundances of all the identified taxa between years. To test the structure of the assemblages, we applied the LINKTREE analysis, which groups samples based on SIMPROF similarity profile tests. At each division level, a set of taxa that differentiated the samples was identified, and cut-off values were given. The conditions that provided the best results were as follows: minimum group size = 1, minimum split size = 3, and minimum split R = 0.5.

III.2.3 Environmental conditions around the study location

To provide an environmental context, we obtained satellite data for the Isfjorden region for the time period of both sampling campaigns. These data were provided by the Danish Meteorological Institute and the Copernicus CMEMS project (Original Dataset: cmems_obs_si_arc_phy_my_L4-DMIOI_P1D-m; Translation Date: 2022-10-03). From the dataset, surface temperature (which includes data recorded by satellite over water and ice surface) and sea ice fraction (the fraction of the ocean covered with sea ice) were acquired. The geospatial coordinates limits used were 76.5° - 79.5° N and 10.97° - 17.47° E, with a resolution of 0.05°. The original data (daily measurements) were averaged monthly for two sampling periods: from July 2004 to July 2005 and from July 2019 to July 2020. Figures also include error bars that display 95% confidence intervals. Additionally, the Mann-Whitney U test was performed comparing the two sampling periods. All the operations on the data were performed using Python in the Google Colaboratory environment.

III.3. Results

III.3.1 Environmental background

Access to satellite data provided the background context for the field experiment results. The measurements obtained through the CMEMS project described surface, not near-seabottom, conditions. However, the study sites chosen for this research were relatively shallow (not exceeding 15 m). They, therefore, could still be under the direct and indirect influence of the surface temperature (affecting species with narrower thermal ranges) and sea ice presence (limiting sunlight penetration and/or phytoplankton blooms). Environmental parameters differed between the two study periods (Fig. III.5). 2019/2020 was warmer than 2004/2005, especially during the winter months (January to April). The biggest differences (13.88 °C between average values) in March could be attributed to the presence of sea ice in the fjord that influenced the measurements of surface temperature over the Isfjorden area. The Mann-Whitney U test revealed statistically significant differences in the surface temperature measurements ($p < 0.001$). No differences were found in the sea ice fraction ($p = 0.4635$), which is not that surprising as, for most of the time in both sampling periods, it equalled 0. Although Isfjorden has been largely ice-free since 2006 (Muckenhuber et al., 2016), some presence of ice was recorded during the winter of 2020.

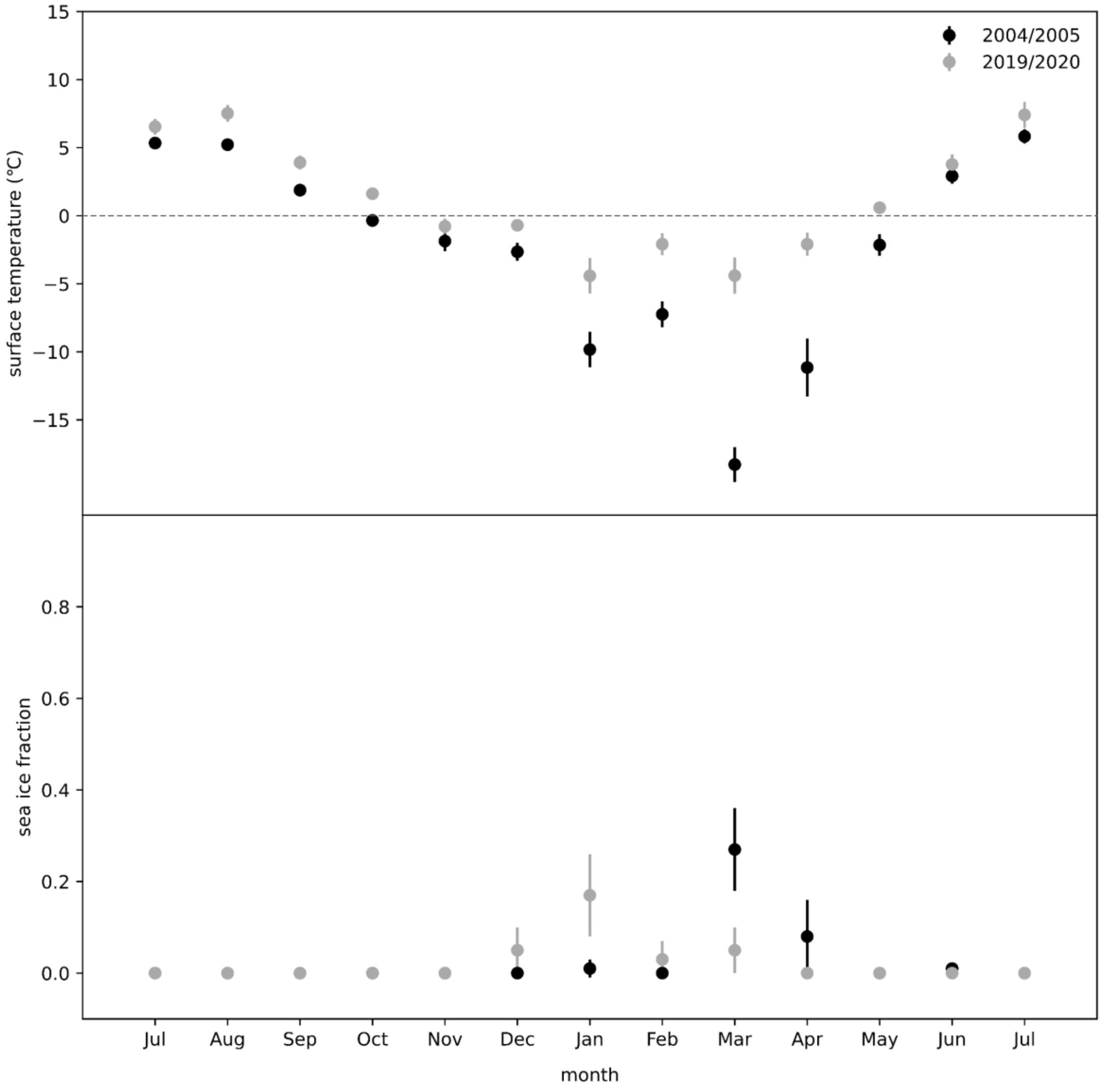


Fig. III.5 Monthly mean surface temperature (includes data recorded by satellite over water and ice surface) and sea ice concentration (fractional coverage of the grid cell, in this case, 5 km × 5 km that was covered by the sea ice) for the two periods (2004/2005 and 2019/2020) of sample submersion (from July to July) with error bars indicating 95 % confidence intervals.

III.3.2 Lithophile assemblage description

In total, over 20,000 individuals were identified combined on the 24 experimental settlement plates recovered from 7±1 and 14±1 m at two sites. The total abundance in 2005 (7,547) and 2020 (13,111) differed by >5000, while the mean densities (ind./100 cm^2) were, respectively, 1092.6±350.4 (2005) and 628.9±333.2 (2020) (mean±SD). Across all replicates, 47 taxa were identified to the lowest determinal taxonomic level (27 to species level) and represented three phyla: Bryozoa (38 taxa), Annelida (7 taxa) and Arthropoda (2 taxa). In samples from 2005, 39 taxa were identified (18.4±7.0), compared with 42 (22.7±3.3) occurring on the plates in 2020 (Supplementary Information 1).

Apart from S2 8 m, a visual increase in the mean number of taxa and abundance per plate (Fig.III.6; Table III.2) in 2020 was observed at both stations and depths. The number of taxa and abundance were the most variable at S1 (13 m) in 2020. The highest number of taxa was reached at the S2 infralittoral (8 m) station in 2005. The highest density was noted at S1 infralittoral in 2020. Also at this station, the biggest difference (more than double) in total density (ind./100 cm^2) between 2005 (693.7) and 2020 (1545.7) was observed.

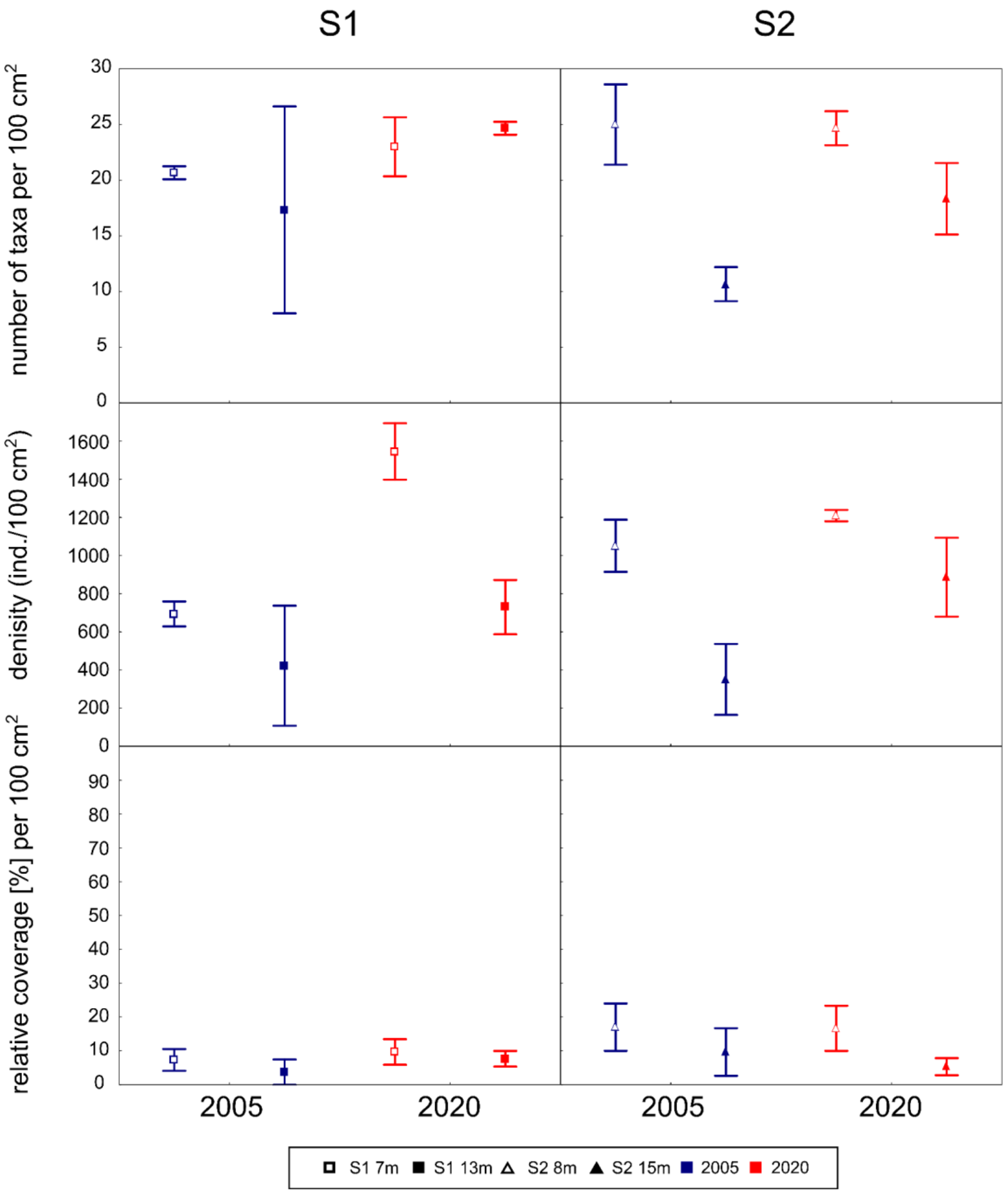


Fig. III.6 Average values (calculated from 3 replicates) of number of taxa, density (ind./100 cm^2) and relative coverage [%] in 2005 (blue) and 2020 (red) at two study sites and depths. Whiskers represent the singular standard deviation (SD). Study site S1 is displayed in squares (on the left) and S2 in triangles (on the right). Unfilled symbols were assigned to infralittoral study sites (7 m and 8 m), and filled symbols to the circalittoral sites (13 m and 15 m).

The sample from S2 at 15 m in 2005 had the lowest value of the Pielou (0.77) index (Table III.1). Those replicates were highly dominated by *Semibalanus balanoides* individuals (Fig. III.7; Supplementary Information 1). Samples from S1 (13 m) collected in 2020 reached the highest values of the Shannon-Wiener diversity index (3.03).

Table III.1 Pielou's (J') and Shannon-Wiener's diversity (H') indices for averaged data from three replicate samples, the lowest values marked in bold.

	S1				S2			
	7 m		13 m		8 m		15 m	
	2005	2020	2005	2020	2005	2020	2005	2020
J'	0.85	0.83	0.87	0.86	0.87	0.85	**0.77**	0.84
H'	2.78	2.80	2.88	3.03	2.99	2.87	**2.04**	2.70

III.3.3 Looking for borealisation evidence

The Cheilostomate bryozoans *Arctonula arctica*, *Callopora lata*, *Dendrobeania* sp., *Schizoporella obesa* and other schizoporellids that recruited on the experimental plates in 2005 were not identified in 2020. Eight taxa were recorded only on the panels recovered in 2020 (not seen in 2005): *Doryporella spathulifera*, *Diplosolen arctica*, *Tricellaria arctica*, *Tricellaria gracilis*, *Stomacrustula cruenta*, *Spirorbis tridentatus*, a dark type of *Tegella* sp. and Scrupocellidae individuals (Supplementary Information 1). Besides the mentioned taxa that differentiated results from 2005 and 2020, there were 34 taxa identified that were common for both years. In 2020, *Harmeria scutulata* (ANOSIM between years R=0.44; p=0.034) and *Semibalanus balanoides* (R=0.82; p=0.0002) were less abundant, whilst cyclostome and cheilostome ancestrulae (R=0.72; p=0.0008 and R=0.57; p=0.003, respectively), *Microporella arctica* (R=0.54; p=0.002), *Tegella arctica* (R=0.63; p=0.003), and *Circeis* sp. (R=0.73; p=0.0002) were more abundant than in 2005.

In 2005, ancestrula of Cyclostomata, *S. balanoides*, *Circeis* sp. and *P. vitrea* had the highest density (ind./100 cm^2) at S1 7 m, while *H. scutulata*, *S. balanoides*, *Circeis* sp. and *P. vitrea* at S2 infralittoral. In 2020, at the infralittoral study sites, two taxa with the overall highest density (ind./100 cm^2) were recorded: for *P. vitrea* at S1 and for *Circeis* sp. at S2 (Fig. III.7). All species densities are given in the supplementary materials (Supplementary Information 1).

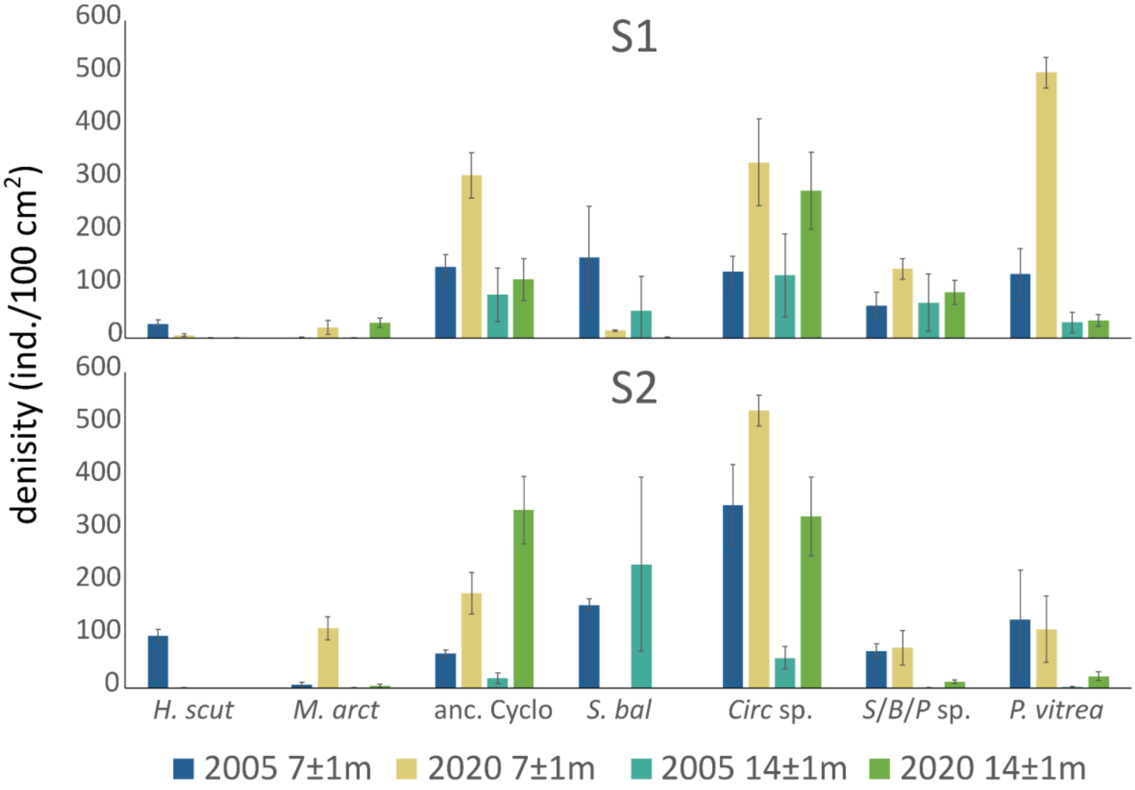


Fig. III.7 Mean density (ind./100 cm^2) with standard deviation bars on plates collated in two years, stations, and depths for the seven most abundant taxa (with a mean ≥ 100 in any replicate) *Harmeria scutulata* (*H. scut*), *Microporella arctica* (*M. arc*), ancestrula of Cyclostomata (anc. Cyclo), *Semibalanus balanoides* (*S. bal*), *Circeis* sp. (*Circ* sp.), *Spirorbis* sp./*Bushiella* sp./*Pilleolaria* sp. complex (S/B/P sp.) and *Paradexiospira vitrea* (*P. vitrea*).

The PERMANOVA analysis identified significant differences between 2005 and 2020 in the number of taxa, density and assemblage structure (Table III.2). The 'year' was the most influential factor differentiating the structure of the assemblage (CV = 28.54 %; Fig. III.9, Fig. III.10). Whereas for the number of taxa and abundance the ‘depth’ factor described most of the variability between samples (19.85 % and 30.12 %, respectively; Fig. III.8) and for both of them ‘site’ was not statistically significant. In both cases, the post-hoc pair-wise test revealed no differences between levels of the ‘site’ factor (p = 0.35 and p = 0.74, respectively). In all other cases, there were significant differences within factor levels. Only in the case of the assemblage structure, all of the study factors had a significant influence.

Table III.2 Three-way PERMANOVA analysis for differences among sites, years and depths based on the number of taxa, density (ind./100 cm^2) and assemblage structure. Raw data were square-root transformed. Significant values mean $p < 0.05$.

	number of taxa			density			assemblage structure		
factors	Pseudo-F	p	CV [%]	Pseudo-F	p	CV [%]	Pseudo-F	p	CV [%]
site	0.99	0.389	0.00	0.22	0.737	1.58	4.88	0.000	4.33
year	6.78	0.010	12.12	13.02	0.001	24.24	26.58	0.000	28.54
depth	10.47	0.003	19.85	15.93	0.004	30.12	13.16	0.000	13.57
site × year	0.02	0.948	4.10	0.27	0.688	2.96	3.92	0.000	6.51
site × depth	4.88	0.038	16.26	0.05	0.917	3.83	6.40	0.001	12.05
year × depth	4.70	0.035	15.52	2.51	0.125	6.11	3.91	0.005	6.50
site × year × depth	0.17	0.746	6.99	1.86	0.164	6.95	4.39	0.001	15.12

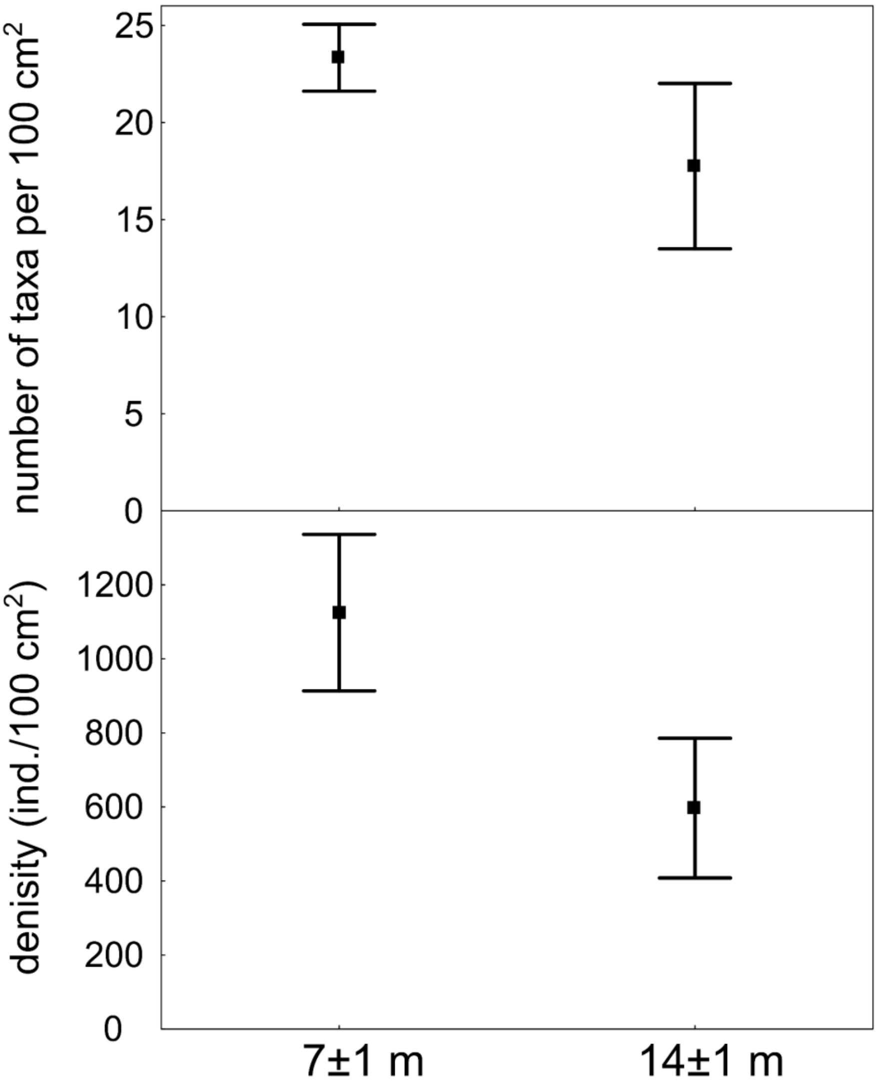


Fig. III.8 Mean values of the number of taxa and density (ind./100 cm^2) calculated from 12 replicates each (combined replicates from sites and years), displaying the effect of the factor with the highest influence on variability between samples. Whiskers represent 95 % confidence intervals.

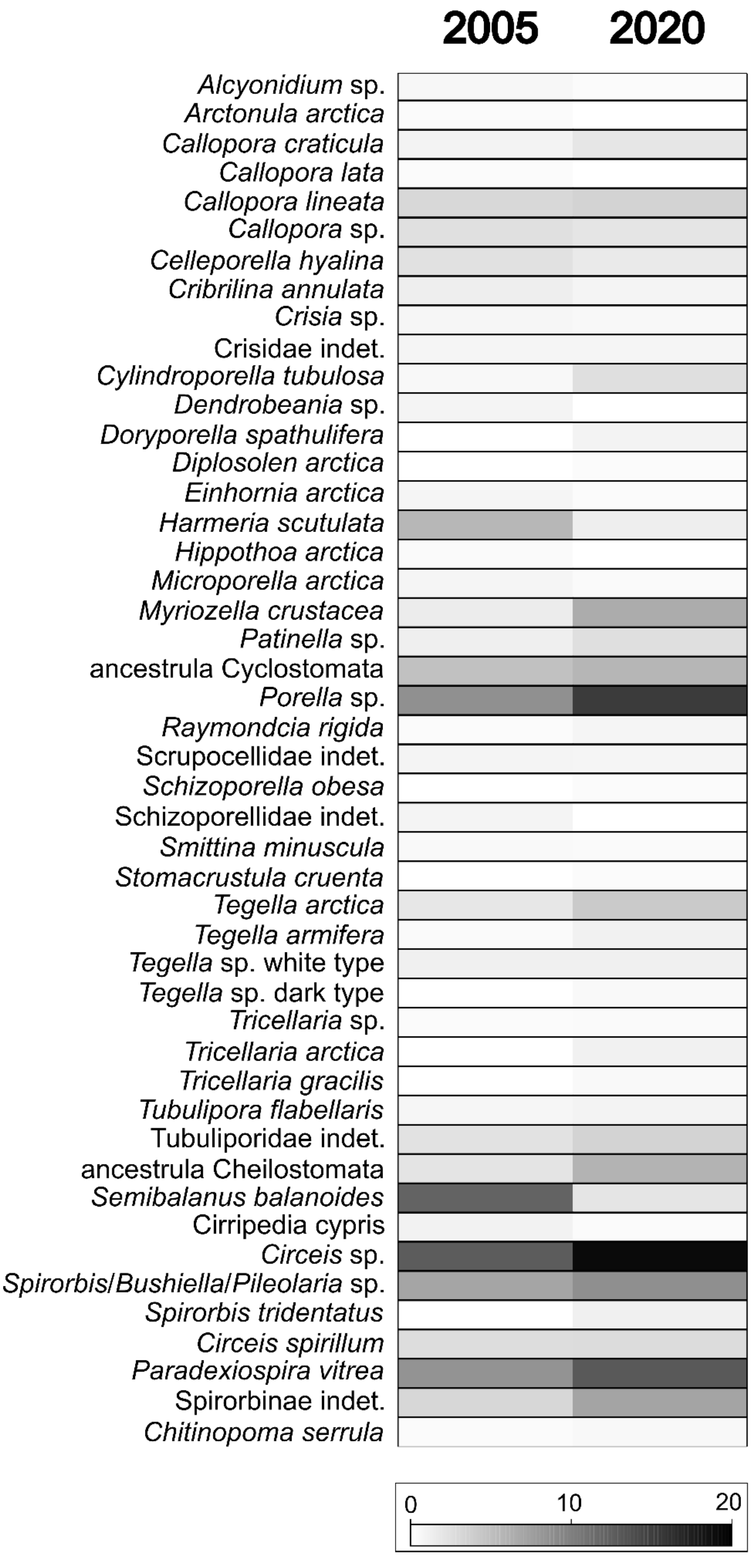


Fig. III.9 Shadeplot displaying the average densities (ind./100 cm^2) of identified taxa per plate (100 cm^2) from 2005 and 2020 sampling. Abundances were square-root transformed. All values are given in Supplementary Information 1.

The underlying structure of the epibenthic assemblage overgrowing the settlement plates was also investigated using LINKTREE analysis (Fig. III.10). The splits in the cluster were based on the densities of taxa differentiating the samples (cut-off values added in brackets). Two of the five splits were significant. The first split (A) was based on the levels of density (ind./100 cm^2) of several taxa – *Einhornia arctica* (>2.67 <0.333), *S. balanoides* (>235 <157), Tubuliporidae indet. (<0 >3.67), ancestrula Cyclostomatida (<18.7 >65.7), *Circeis* sp. (<57.3 >119), *Callopora lineata* (<0 >3.67), Spirorbinae indet. (<1 >9) or *Spirorbis* sp./*Bushiella* sp./*Pilleolaria* sp. complex (<0.667 >12.3), *Circeis spirillum* (<0 >2), *Callopora* sp. (<1.33 >2.33), *P. vitrea* (<2 >22.3), ancestrula Cheilostomatida (<1 >3.33) or *Myriozella crustacea* (<0.333 >0.667), and it differentiated the sample from S2 (15 m) collected in 2005 from the remaining samples. The next significant split (B) differentiated two groups. This split was based on the density of a few taxa – *Cylindroporella tubulosa* (<0.667 >4.67), Spirorbinae indet. (<19.3 >33.7), ancestrula Cheilostomatida (<8.67 >17.7) or *S. balanoides* (>51.7 <15). Split C grouped the rest of the samples from 2005. All samples collected in 2020 were under the splits D and E. Besides the one outlier, the rest were clearly divided by the ‘year’ factor.

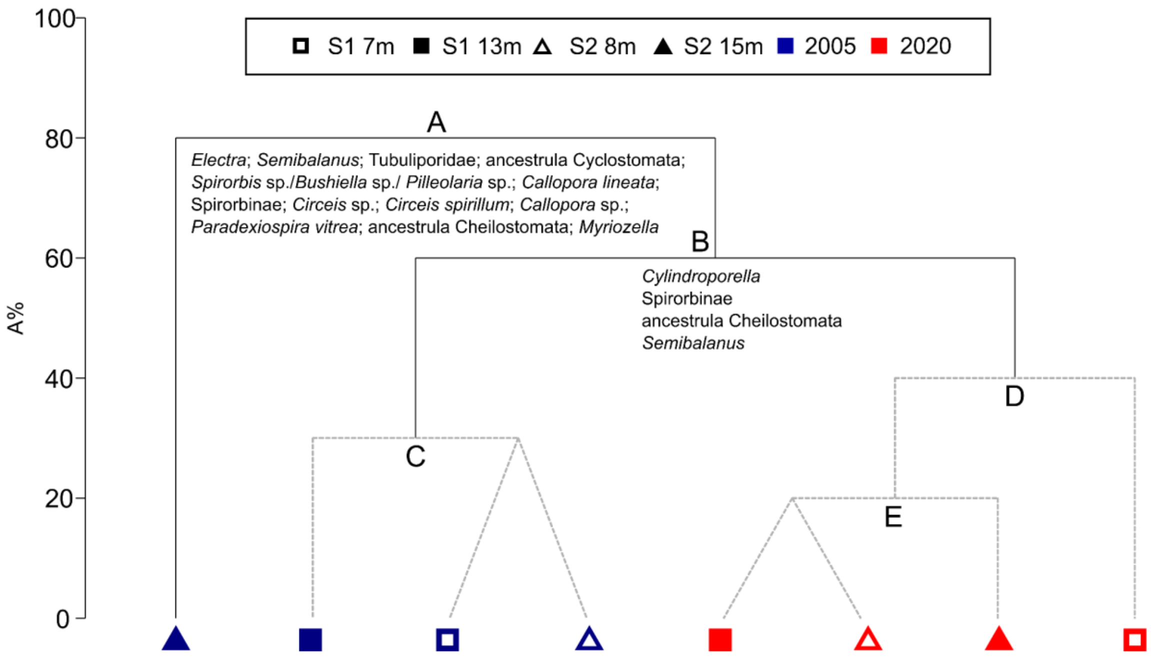


Fig. III.10 Linkage tree analysis (LINKTREE) showing the partitioning of samples obtained by the five splits (A–E). Black, solid lines represent statistically significant splits, according to the SIMPROF tests performed on averaged data from the replicates; grey, dotted lines imply splits without statistical significance in this analysis. A% scale (y axis) indicates equi-step divisions.

Overall, the results showed significant differences between samples collected in 2005 and 2020. Although there were 5 lost and 8 gained taxa in 2020, none of those significantly differentiated the samples in the cluster (apart from the outlying sample from S2 at 15 m in 2005). The 'year' factor had a significant influence on assemblage composition within samples, as indicated in the PERMANOVA analysis for assemblage structure.

III.4. Discussion

Despite holding the highest contribution to the Arctic biodiversity and being key vulnerable marine environment indicators, benthos is difficult to robustly and repeatedly sample at remote, high-latitude locations (Nicoletti et al., 2007; Renaud et al., 2007). Revisiting the same Spitsbergen study area after 16 years with the exact methodology enabled detection of changes in the structure of lithophile assemblages, mostly realised in a shift within the species dominance. Five taxa found in 2005 did not reappear in samples from 2020, but eight new ones were identified in the same samples. There are a few instances of comparable revisits using similar apparatus, protocols, site and target taxa (but e.g. for Antarctica see Dayton (1989) or Souster (2018)). Due to natural variability, detection of some biota differences across samples in space and/or time is expected, so untangling the extent of differences and what their drivers are is of key importance. Environmental differences revealed by satellite data were supported by other studies undertaken in the Isfjorden region (e.g. Pavlov et al., 2013; Skogseth et al., 2020; Bloshkina et al., 2021). Therefore, an argument can be made that the shift in the structure of the epibenthic assemblage reported in this study is likely to be connected to the changes in the temperature conditions within the fjord and other parameters driven by climate change (e.g. increasing melting of glaciers, increasing turbidity, freshening, acidification, etc.).

III.4.1 Environmental conditions of the study site area

Under the comparison of both experimental periods, monthly surface temperatures in the Isfjorden area (including temperatures of water and ice, if it was present) have significantly increased over the whole year, but especially within the winter months (Fig. III.5). The most drastic change in surface temperature over Isfjorden was recorded in March with mean values in 2005 of -18.3 °C compared to -4.4 °C in 2020. However, the temperature near the shallow seabed tended to be less variable, as reported by Moreno et al. (2024) from the same study site over the period starting in the summer of 2006 and running until the summer of 2022. The summer of 2019 was relatively warm, with maximal temperatures at the seabed reaching almost 10.0 °C at a depth of 7 meters, but also a relatively cold winter with averages in March of 2020 around -1.9 °C (Moreno et al., 2024). There have been reports of pronounced warming detected within the fjord, with a growing inflow of Atlantic water also in the bottom layers with temperatures above 3 °C starting from 2013 onwards (Bloshkina et al., 2021). In the summer of 2014, water temperatures in Isfjorden were especially high (Skogseth et al., 2020), and Atlantic water was recorded as far as in Billefjorden (Bloshkina et al., 2021). There were detectable temperature differences between years and signs of marine heatwaves occurring in the Arctic with increasing frequency (Beszczynska-Möller et al., 2012; Promińska et al., 2017; Skogseth et al., 2020; Huang et al., 2021; Mohamed et al., 2022). Aside from the rising temperatures, the Arctic is also dealing with decreased seasonal sea ice, with a loss of approximately 10 % per decade especially in winters since 1979 (Onarheim et al., 2014; Muckenhuber et al., 2016) and glaciers, with ice mass loss of 401 ± 24 kg m^{-2} a^{-1} (a indicating annual loss) over entire Svalbard between 2010 and 2017 (Tepes et al., 2021). A significant decline in the presence of sea ice cover in Isfjorden has been observed since the beginning of this century, with substantial strengthening of this trend since 2006 (Muckenhuber et al., 2016). As a result of this process, more sea surface becomes accessible for phytoplankton blooms and therefore the net primary production in the Arctic region is reportedly continuing to increase (Arrigo and van Dijken, 2015; Frey et al., 2021). However, simultaneously increased melting of sea ice is driving the freshening of upper layers of the sea (Brown et al., 2020) as well as increased turbidity and sedimentation as a result of runoff from melting glaciers and rivers (Vonnahme et al., 2023). Under such environmental forcing, it was expected that the local ecosystem would have undergone measurable changes.

III.4.2 Differences in assemblage structure

This study documents a clear difference in the structure of the hard-bottom encrusting community between 2005 and 2020, as the ‘year’ factor had the most significant effect on the variability of the assemblage structure. Considerable interannual differences between species recruitment to settlement plates have been recorded at temperate (Watson and Barnes, 2004) and polar sites (Bowden et al., 2006). However, neither was as profound as the one in the current study. Repeat visits to a polar fjord in Antarctica detected both a directional assemblage shift and identified sedimentation as a main driver of it (Sahade et al., 2015). In the Arctic, several distinct changes have already been observed within other biotic components of marine ecosystems. An overall shift in hard-bottom benthic composition was already reported by Kortsch et al. (2012) around the end of the last century in Kongsfjorden. Their 30-year-long study found an abrupt increase in macroalgae (a shift from the dominance of red calcareous algae *Lithothamnion* sp. to brown algae

Saccorhiza dermatodea) and a concurrent increase in diversity and major change of invertebrate assemblage (shift from the dominance of sea anemones to sea urchins). Weslawski et al. (2010) in a study of intertidal zones in Sorkappland and Hornsund (southern Svalbard) reported an increase in macrobenthos diversity from 19 to 43 taxa between 1988 and 2008 (using 20 cm × 20 cm frames at low tide). The species newly recorded in that study were mostly of boreal and arctic-boreal origin. In the results presented in this study, after 15 years, similar significant differences were found in the 2020 assemblage compared to 2005. All taxa sampled in both years and identified to species level have previously been reported in the Svalbard area (Table III.3). However, in the early stages of the sample analysis, obvious shifts in the abundances of a few dominant taxa were observed. This included a major drop in the density (ind./100 cm^2) of *Harmeria scutulata* and *Semibalanus balanoides* between 2005 and 2020 and a simultaneous increase in the number of individuals of *Circeis* sp., Spirorbinae indet. and cheilostome and cyclostome ancestrulae. From both groups – bryozoans and serpulids – many species are described as opportunistic and reported to be amongst the pioneer colonisers of a newly available hard substrate (Barnes, 1996; Kuklinski et al., 2013; Wisshak et al., 2022). *Harmeria scutulata* was reportedly an important species within the shallow coastal Arctic assemblages at the beginning of the century, often accounting for more than 50 % of bryozoan colonies in studied communities (Barnes and Kuklinski, 2005; Kuklinski and Taylor, 2006). In the current study, the maximum contribution of *H. scutulata* to the bryozoan assemblage on the experimental plates reached 33 % in 2005 at the S2 infralittoral (8 m) station and was below 1 % at the same station in 2020. However, in the 2014/2015 period, it was still one of the most frequently recorded pioneers collected in Gronfjorden (the outmost inlet of Isfjorden) (Evseeva and Dvoretsky, 2023) and in the eastern area of the Kola Peninsula (Evseeva et al., 2022). On the south bank of Isfjorden *H. scutulata* was also very abundant until 2014 but has become more scarce since (Chapter IV). Like most pioneers, this species is a poor spatial competitor for space, losing around 70 % of interspecies interactions (Barnes and Kuklinski, 2003). Its distribution has been reported to be circumpolar and reaches at most down to Kodiak Island in Alaska (Kuklinski and Taylor, 2006).

The acorn barnacle *S. balanoides* reportedly has a wide boreo-arctic distribution in the North Atlantic, with an established population in the Svalbard waters. It has been accepted as a sentinel of climate change as its biogeographic range and reproductive success are tightly linked to temperature (Herrera et al., 2019; Walczyńska et al., 2019). Studies held in the European intertidal zones have already indicated a shrinkage in the southern extent of this species distribution range by 300 km and drops in abundance in areas with warm winters (>10 °C) due to inhibited reproduction (Barnes, 1963; Wethey and Woodin, 2008; Rognstad and Hilbish, 2014). Jones et al. (2012) reported a contraction of the southern distribution extent by 350 km on the eastern coast of the United States, but concluded it to be driven by summer heat death rather than winter cold limitation of reproduction as suggested by Wethey and Woodin (2008) on the other side of the Atlantic. Short-term warm conditions (i.e. marine heatwaves) can also influence the abundance of barnacles, as their temperature sensitivity leads to significant annual fluctuations in recruitment (Rognstad and Hilbish, 2014; Walczynska et al., 2019). Also, barnacles, as long-lived species, may not reproduce every year (Walczyńska et al., 2019). Overall, it has been documented that increased heat stress pushes southern range limits to higher latitudes while reduced cold stress driven by warming allows expansion of northern range limits (Pinsky et al., 2020).

A few of the noted taxa displayed an increase in density (ind./100 cm^2) between the 2005 and 2020 samples. Three bryozoan species were reported to have reached higher densities (ind./100 cm^2) – *Cylindroporella tubulosa*, *Microporella arctica* and *Tegella arctica*, all typical for the Svalbard area and noted in the region previously on both natural and artificial substrates (Table III.3). This could be explained by the simultaneous decrease in the presence of *H. scutulata*, leaving more available space for other taxa. On the other hand, those species may display better resilience to changes in the environment in comparison to (the previously abundant) *H. scutulata*. Notably, there was a large number of juveniles (organisms younger than three months) of both bryozoans and serpulids (personal observations based on Sowa et al., 2023). That could be an indication of greater reproductive success in the spring and summer of 2020, or a potential change in the timing of larval release or the length of the pelagic life stage. Coincidentally, in 2020, high cumulative intensity and duration of marine heatwaves were observed throughout the Barents Sea (Mohamed et al., 2022), which is likely to have consequently influenced levels of primary production. However, serpulids release non-feeding larvae (lecithotrophic), which allows them to be independent from primary production peaks (Ushakova, 2003; Kuklinski et al., 2013). In the study conducted by Kuklinski et al. (2013), polychaete larvae were identified in the water column throughout spring and summer. However, recruitment on experimental plates has been reported to occur throughout the whole year (Kuklinski et al., 2013; Meyer et al., 2017; Sowa et al., 2023). Silberberger et al. (2016) reported the presence of bryozoan larvae throughout spring and summer in the sub-Arctic area (northern Norway). In the study of Kuklinski et al. (2013) in Adventfjorden (an Isfjorden inlet), peaks of bryozoan larvae occurred between April and June with delayed recruitment on the experimental plates. Both lecitotrophic and planktotrophic larvae can be found within the Bryozoa phylum, depending on the species (Stübner et al., 2016). The duration of their presence in the water column ranges from about two months for the feeding larvae, to even just a few hours for the non-feeding larvae, which usually remain close to the sea bottom and settle much faster and thus are rarely identified in plankton samples (Kluge, 1975; McKinney and Jackson, 1991; Temkin and Zimmer, 2002; Kuklinski et al., 2013). Larval release is driven by a variety of factors. For some lecithotrophic larvae, the main cue is light intensity (i.e. being released at dawn), although this might be very different in the Arctic region with the presence of polar day and polar night. The larvae also initially display photopositive behaviour, which may aid with better dispersal in that short window of time (Temkin and Zimmer, 2002). Increased turbidity driven by ongoing warming in the Arctic could affect larval stages (Włodarska-Kowalczuk et al., 2012). Consequently, increased sedimentation could become a limiting factor for epibenthic species by covering the hard substrate, suffocating the filter feeders, and/or burying the living lithophiles already occupying the substrate (Włodarska-Kowalczuk et al., 2005, 2012; Schönberg, 2016).

In the summer of 2019, the highest maximal bottom water temperatures in the shallow subtidal zone (7±1 m and 14±1 m) were noted (from a period between August 2006 and July 2022), as well as a wide range of logged temperatures in winter (between 2 °C in December 2019 and down to -1.7 °C until April 2020; see Moreno et al., 2024). In 2020, intense marine heatwaves were noted in the Barents Sea region (Mohamed et al., 2022). This could possibly influence the early onset of larval release in the summer of 2020, which had enough time to recruit by the time of retrieval of the experimental plates. There is prior evidence that increasing temperatures in the Arctic region could result in shortening of larval development and quicker settlement (O'Connor et al., 2007).

However, importantly, based on only two distant sampling campaigns, it cannot be concluded with certainty that the results of the investigation were directly connected to the changing climate in the Arctic. Furthermore, it cannot be ruled out that the composition of the lithophile assemblage could also be a result of natural variability stemming from the presence of different larvae at the first stages of recruitment, influencing the later observed structure, as species interactions are not yet fully understood (Cifuentes et al., 2010; Meyer et al., 2017). However, the influence of the ongoing climate warming together with the related effects (e.g. melting glaciers, water freshening, acidification, increased turbidity, etc.) seems to be the most likely factor shaping the observed changes in the assemblage structure.

III.4.3 Evidence of borealisation

The handful of new taxa were identified on the plates from the 2020 campaign and were comprised of four Arctic species – *Doryporella spathulifera*, *Diplosolen arctica*, *Tricellaria arctica*, and *Tricellaria gracilis* (with thermal ranges of: -1.23 – 3.5, -1.8 – 4.78, -1.61 – 3.2, -1.96 – 4.75 [°C] respectively; Kluge, 1975), one Arctic-boreal – *Stomacrustula cruenta* (Kluge, 1975), one polychaete with a wider distribution, recorded as far south as Spain – *Spirorbis tridentatus* (Rzhavsky et al., 2014), but previously recorded with particularly high abundance in Isfjorden in 2002 (Barnes and Kuklinski, 2005) and 2010 (Balazy and Kuklinski, 2017). Interestingly, the Arctic-boreal species of bryozoan (*Stomacrustula cruenta*) that was recorded only in 2020 has the narrowest thermal range, spanning from -1.64 to 2.7 °C (Kluge, 1975).

Furthermore, we found one family and one genus previously recorded in the Svalbard area - Scrupocellidae and *Tegella* sp. subcategorised by us as dark type (Kuklinski et al., 2013; Meyer et al., 2017). Of the above-mentioned taxa, all were identified in Svalbard fjords either before 2005 or between 2005 and 2020 in various reports (Table III.3). Based on these data, a conclusion can be made that although the composition of the assemblage was significantly different in 2020, the assemblage structure was still representative of that hitherto described for the Svalbard region. Some of the species, *D. spathulifera*, *S. cruenta* and *T. gracilis,* were reported in the samples collected by Evseeva and Dvoretsky (2024) around Franz Josef Land between 2006 and 2008, but were low in biomass. Their absence in our samples from 2005 could be a result of natural fluctuations (for example, see a 5-year-long, monthly record of species fluctuations at the same site by Watson and Barnes, 2004).

III.4.4 Structure under factors

In this study, when testing the effects of different factors, beyond investigating the influence of time (‘year’), factors related to depth and geographical location were also included (‘site’ and ‘depth’; Table III.2). Considering the overall assemblage structure, all of the factors and their interactions were statistically significant. The ‘year’ factor was the most influential, explaining most of the differentiation between samples (28.5 %). However, for the number of taxa and density (ind./100 cm^2), not all factors were significant, and the ‘depth’ factor was the most important for both, whereas the ‘site’ was not statistically relevant. The insignificance of the ‘site’ factor could be explained by the short distances between study sites, which were approximately two nautical miles apart. Although the depth difference was not large (approximately 7 m between strata) the key difference was the presence of dense kelp forests around the shallower study sites (infralittoral). The presence of kelp in this study corresponded closely with the ‘depth’ factor, as the macroalgae only occurred on the stations located in the infralittoral zone (7±1 m). The kelp could have acted as a stabiliser for the overall conditions by limiting the water movement, but also provided an additional source of food (Balazy and Kuklinski, 2017), and increased the habitat complexity. The kelps themselves are also predicted to experience range shifts under the changing climate. Assis et al. (2018) projected the potential loss of *Laminaria solidungula*, an endemic, stenothermic species (Lebrun et al., 2022) in the southwest area of Svalbard with simultaneous expansion of several other species (*Laminaria hyperborea*, *L. digitata* and *Saccorhiza dermatodea*) around parts of the archipelago (two other species of kelp – *Alaria esculenta* and *Saccharina latissima* remaining stable). An increase of biomass up to four times has already been recorded for *L. digitate* (Lebrun et al., 2022). Although the predictions are rather optimistic for the kelps in the Arctic in the sense of biomass and distribution range increase, the composition of species will experience a change that will most likely have a cascading effect on the associated fauna (Lebrun et al., 2022). The number of taxa was similar between the depths at the same sites (besides samples from S2 in 2005, which had very low recruitment), but the average density (ind./100 cm^2) of individual recruits was higher in samples from the infralittoral (7±1 m), which is presumed to be the result of more stable conditions within the kelp forest.

III.5 Conclusions

The obtained results showed significant differences between assemblages over the 16 years, supporting the hypothesis of the study. The most influential changes observed were the shifts in dominance, suggesting a reorganisation of the assemblage structure rather than a directional change in the taxonomic pool. This agrees with the nature of the shift previously observed for hard-bottom macrofauna by Kortsch et al. (2012) in Spitsbergen fjords. On the other hand, the Arctic has reportedly been under climate change forcing long before the start of our experiment in 2004. Beszczynska-Möller et al. (2012) observed a warm anomaly in the Fram Strait in 1999/2000, and Bloshkina et al. (2021) described increasing proportions and further extension of Atlantic waters in the bottom layers within Isfjorden from 2003 onwards. Within almost a century (1912 - 2009), Isfjorden experienced 1.9 °C of overall warming (Pavlov et al., 2013). Thus, the results obtained in this study may represent the already altered state of the hard-bottom assemblage. Nonetheless, they indicate the possible direction of ongoing change and provide a crucial reference point for comparison in the future. To sum up, no new boreal species to the area of Svalbard were observed within this study, although some changes in the taxonomic compositions between sampling campaigns were noted. Therefore, no significant borealisation of the assemblage could be proved.

Table III.3 Species identified in this study compared to the species lists from other studies conducted in the Svalbard area.

time/area	up to 2000 Svalbard	2002 Kongsfjord	2002 Hornsund	2002 Isfjorden	2007 Adventfjorden	2014/2015 Gronefjorden	2015 Svalbard	2017 Isfjorden
substrate type	natural	natural	natural	artificial	artificial	natural	artificial	artificial
source	Palerud et al. (2004)	Kuklinski and Barnes (2005)		Barnes and Kuklinski (2005)	Kuklinski et al. (2013)	Evseeva et al. (2023)	Meyer et al. (2017)	Sowa et al. (2023)
Arctonula arctica	X	X	X				X	
Callopora craticula	X	X	X	X	X	X	X	X
Callopora lata	X	X	X			X		
Callopora lineata	X	X	X			X		X
Celleporella hyalina	X	X	X	X	X	X	X	X
Cribrilina annulata	X	X	X	X	X		X	X
Cylindroporella tubulosa	X	X	X	X		X		X
Doryporella spathulifera	X	X	X			X		
Diplosolen arctica								X
Electra arctica	X	X	X				X	
Harmeria scutulata	X	X	X	X	X	X	X	X
Hippodiplosia obesa		X		X				X
Hippothoa arctica		X						
Microporella arctica						X	X	
Myriozella crustacea	X	X	X					
Raymondcia rigida		X	X	X				
Smittina minuscula	X	X	X			X		

time/area	up to 2000 Svalbard	2002 Kongsfjord	2002 Hornsund	2002 Isfjorden	2007 Adventfjorden	2014/2015 Gronefjorden	2015 Svalbard	2017 Isfjorden
substrate type	natural	natural	natural	artificial	artificial	natural	artificial	artificial
source	Palerud et al. (2004)	Kuklinski and Barnes (2005)		Barnes and Kuklinski (2005)	Kuklinski et al. (2013)	Evseeva et al. (2023)	Meyer et al. (2017)	Sowa et al. (2023)
Stomacrustula cruenta	X	X	X			X		
Tegella arctica	X	X	X	X	X	X	X	
Tegella armifera	X	X	X		X	X		
Tricellaria arctica		X			X			
Tricellaria gracilis	X					X		
Tubulipora flabellaris	X	X		X		X	X	
Semibalanus balanoides	X	not included	not included		X	not included	X	X
Spirorbis tridenatus				X				
Circeis spirillum	X				X		X	
Paradexiospira vitrea	X						X	
Chitinopoma serrula	X							

Chapter IV Decadal monitoring of lithophile assemblage structure (2010 - 2020)

IV.1. Introduction

Much of the Arctic has been the strongest warming region for decades (Rantanen et al., 2022). The intensity and magnitude of changes could push the ecosystem beyond tipping points, especially Arctic marine communities adapted to more constant conditions, making them particularly sensitive (Wassmann et al., 2011; Wassmann, 2018; Semenov, 2021; Rantanen et al., 2022). Besides ongoing gradual warming, the Arctic has also been experiencing more frequent heatwaves (Beszczynska-Möller et al., 2012; Overland and Wang, 2016; Cullather et al., 2016; Promińska et al., 2017; Skogseth et al., 2020; Mohamed et al., 2022). Heatwaves have often been reported during Arctic winters, and in Isfjorden (a west Spitsbergen fjord), the warmest recorded winters to date were observed in 2006, 2012, 2014 and 2016 (Skogseth et al., 2020). Furthermore, the most extreme heatwaves to date occurred during both summer and winter of 2016 in the Barents Sea waters (Mohamed et al., 2022) and were also identified around Svalbard (Skogseth et al., 2020).

The shallow subtidal zones around Svalbard are typically composed of hard or mixed substrates (Dunlop et al., 2020); however, this does not guarantee an available surface for colonisation (Konar, 2007). Proceeding warming conditions can make more substrate accessible along polar coasts for colonisation by marine fauna through increasing marine-terminating ice retreat (Vermeij and Roopnarine, 2008; Renaud et al., 2015). However, other environmental conditions changing as a result of the warming and related consequences would have to be taken into consideration before judging the final effect on the ecosystem. The faunal biodiversity of the Arctic is mostly comprised of benthic taxa (Sirenko, 2001; Renaud et al., 2015; Evseeva et al., 2023), but the endemism is considerably lower than in the Antarctic (SCARMarBIN). Generally, both polar regions hold intermediary species richness of benthos (Piepenburg et al., 2005; Clarke and Crame, 2010) when compared to temperate areas, where marine diversity reaches its peak (Tittensor et al., 2010; García Molinos et al., 2015). Many organisms associated with hard substrata are sessile as adults, recruiting to and growing directly on the natural and anthropogenic substrate, including rocks, kelps, pillars, and port structures. Some examples would include barnacles, bryozoans, tubiculous polychaete worms, sponges and ascidians. Some fauna and flora growing on hard substrate act as environmental engineers (sometimes termed bio-constructors) that provide niches for secondary colonisers or mobile taxa (Balazy and Kuklinski, 2013; Schoenrock et al., 2018). Due to their immobility in adult life stages and, in some cases, longevity, epibenthos can act as an important sentinel of environmental forcing (Piepenburg et al., 2005; Renaud et al., 2008; Jordà-Molina et al., 2023). They can display some of the most evident responses to long-term environmental changes (Hawkins et al., 2008; Kortsch et al., 2012; Balazy and Kuklinski, 2019). Hard substrates accommodating sessile organisms, in places strongly limited by available space, can act as powerful experimental sites for investigating invasions of non-indigenous species (Beshai et al., 2022). Newly freed substrate by e.g. glacial retreat along the shore in combination with increasing water temperatures could lead to easier establishment and spread of boreal species from lower latitudes (Pinsky et al., 2020; Renaud et al., 2015).

So far, to our knowledge, long-time series of data are lacking, especially examining changes in the recruitment on the hard substrate in the shallows of the Arctic. Especially rare are the studies that exceed a decade. However, multi-year, long-term research studies held by Beuchel et al. (2006), Beuchel and Gulliksen (2008) and Al-Habahbeh et al. (2020) in Kongsfjorden (79°N) have yielded important insights into succession processes on natural substrate over several decades. It has been concluded that recolonisation of disturbed substrate took substantially longer across polar regions than at lower latitudes (e.g. see Zwerschke et al., 2021). Nonetheless, the taxonomic resolution provided by these studies was very different due to the samples being photographic images, which often led to under-reporting of taxonomic richness (Beisiegel et al., 2017). Other Arctic marine studies have focused on hard but mobile substrate (Balazy and Kuklinski, 2019), described rates of colonisation (e.g. Kuklinski et al., 2013) within a year, and the seasonality of that process (Meyer et al., 2017; Sowa et al., 2023; Ronowicz et al., 2024). In Chapter III, the changes between temporally distant sampling campaigns were investigated. The analysis provided information that a significant shift in species dominance has occurred, suggesting a reorganisation within the assemblage structure. In the current study, the focus was instead placed on how the number of taxa, density and assemblage structure varied across more than a decade to provide a better baseline understanding of assemblage structure dynamics in the Arctic coastal environment. In the time frame of the study, several heatwaves were recognised and reported as potentially impacting the ecosystem (Renaud et al., 2007; Kortsch et al., 2012), emphasising the importance of complex monitoring. The deficiency of appropriate hard-bottom focused studies in the Arctic causes a major problem with differentiating the impacts of climate change on the ecosystem from natural fluctuations (Wassmann et al., 2011; Azovsky and Kokarev, 2019; Denisenko, 2020; Solan et al., 2020).

The primary aim was to 1) characterise annual variability in multiple aspects of the recruitment process of epibenthic fauna in the Isfjorden shallows across 11 years. The time frame of the study was chosen due to the prolonged warming already observed in the Arctic in the 1990s, which was connected with increased input of warm Atlantic water and overlapped with the time of thermal fluctuations. Furthermore, 2) the connection between standardised anomalies that occurred during the study period and changes in species richness, total density and substrate coverage was investigated. It was hypothesised that years with significantly different standardised anomaly categories would lead to a measurable response of the benthic assemblage. The last objective was to 3) investigate the proportional contribution of Arctic species and their responses to warmer conditions. Here, it was hypothesised that in warmer conditions, an observable increase in the contribution of boreal species in the assemblage would occur.

IV.2. Methods

IV.2.1 Protocol

For the purpose of this study, the protocol followed the description provided in Chapter II. The field experiment was started in 2009 with the submersion of first set of plates and continued with annual exchange of plates until 2020, with identical methodology each year.

IV.2.2 Environmental parameters

Alongside the experimental constructions described in Chapter II, temperature loggers were deployed at each station, collecting data every 30 minutes. The logger batteries enabled year-long operation, after which they were replaced with new ones, and the data was transferred to external hard drives.

Based on the collected temperature data, standardised anomalies were calculated for all years, except for 2014 when loggers malfunctioned, resulting in a gap within the data. They were defined as the difference between the yearly average temperature and the average temperature calculated for the entire timeframe of logger data (2009 – 2020), divided by the standard deviation of the long-term average. Years were classified as 'warm' when seawater temperature > 0.5 °C, 'cold' when seawater temperature < -0.5 °C, or 'intermediate' when the standardised anomaly fell within the range of -0.5 °C and 0.5 °C (Błaszczyk et al., 2021).

IV.2.3 Laboratory and statistical analysis

To investigate the variability within the number of taxa, density (ind./100 cm^2) and assemblage composition between the samples from different years, stations, and depths (all factors fixed and with 'site' and 'depth' having two levels, and 'year' having eleven levels, i.e. years) PERMANOVA (permutational analysis of variance) analysis was performed in Primer v.7 (Clarke et al., 2008).

Data from the replicates (three plates from each sampling station) were averaged for further analysis, with error of one standard deviation provided when displayed on graphs and listed in the text (mean±SD). Principal coordinates analysis (PCO) analysis based on a resemblance matrix calculated using Euclidean distance was used to display differences in assemblage structures of the collected samples. The structure of the assemblages was further investigated by applying the LINKTREE analysis, which divides samples into groups based on a series of SIMPROF similarity tests. At each level of division, one or a set of taxa that differentiates the sample groups was indicated. The conditions applied to the analysis were as follows: minimum group size = 3, minimum split size = 3, and minimum split R = 0.5. A relative percentage coverage was calculated to illustrate the extent of overgrowth on the experimental plates.

Additionally, changes in the contribution of taxa classified by their range of distribution (arctic, arctic-boreal, boreal, cosmopolitan, and unclassified – all based on available literature (Kluge, 1975; Klekowski and Weslawski, 1991; Rzhavsky et al., 2014)) were investigated. The proportional contribution of the total number of individuals assigned to each group to the whole assemblage was compared.

IV.3. Results

IV.3.1 Thermal conditions at study location

The temperatures recorded with data loggers attached to experimental constructions oscillated between -2 °C and 10 °C throughout the deployment, as reported by Moreno et al. (2023). Although data did not reveal a statistically significant increasing trend ($R^2 = 0.0082$), cold and warm years were differentiated in the time series (Fig. IV.11).

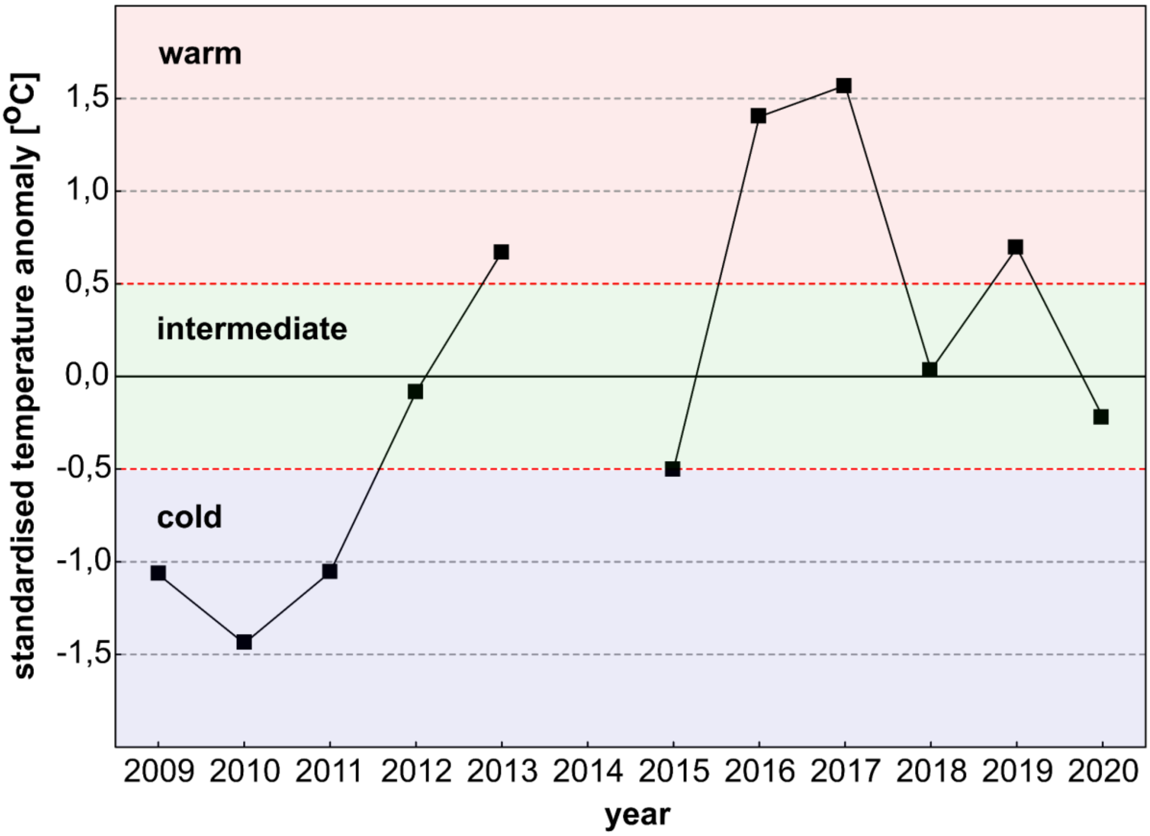


Fig. IV.11 Standardised temperature anomaly based on the temperatures logged at the study site ($R^2 = 0.37$). Lack of a data point from 2014 due to a significant gap in temperature measurements resulting from a logger malfunction. Points over 0.5 °C indicate a 'warm year', and points below -0.5 °C indicate a 'cold year' based on the method described by Błaszczyk et al. (2021).

The 'warm' and 'cold' years were qualified based on the standardised anomaly. No 'cold' years were observed after 2015 (-0.52 °C), and the negative anomaly did not exceed -1.0 °C after 2011. The 'warm' years were noted in 2013, 2016, 2017, and 2019.

IV.3.2 Epibenthic assemblage

Throughout the 11-year-long time series, 76 taxa belonging to five orders of Bryozoa, Arthropoda and Annelida were identified on the experimental plates: Ctenostomata (1 taxon), Cyclostomata (9), Cheilostomata (51), Balanomorpha (3), and Sabellida (12). Although Bryozoa and Annelida phyla were represented by different numbers of taxa, they were represented by similarly high abundances over the course of the study.

Stronger differences in the number of taxa, density (ind./100 cm^2), and relative coverage were observed between depths at the S2 study site compared to the S1 study site. The values were always higher at shallower depth at S2, while that was not the case at S1 (Fig. IV.12). At S1 the numbers of taxa and densities recorded at both depths stayed within the same range (highest-lowest average number) with values being higher either at circalittoral (13 and 15 m) or infralittoral (7 and 8 m) in different years. In the case of the abundance, the lowest values were noted in 2010 at S1 7 m (675 ind. per 100 cm^2) with a simultaneous low relative coverage (10 %) and in 2012 at S1 13 m (463 ind. per 100 cm^2) with relative coverage reaching only 6 %. The highest abundance and subsequent relative coverage at S1 7 m was reached in 2016 (1870 ind. per 100 cm^2 and 47 % respectively) and at S1 13 m in 2019 (1591 ind. per 100 cm^2).

At S2, numbers of taxa, densities (ind./100 cm^2) and relative coverages were consistently (over the years) higher in infralittoral (8 m) than in circalittoral (15 m). The highest number of taxa was reached at the infralittoral site in 2011 (34 taxa per 100 cm^2). The lowest mean value (11 taxa per 100 cm^2) and the lowest recorded number of taxa overall (7 taxa per 100 cm^2) were noted in 2016 at the circalittoral S2 study site. The highest values from the S2 15 m reached 22 taxa in both 2010 and 2014, which is 1,5 times lower than the highest values from S2 8 m. A major peak was noted in 2018 (2685 ind. per 100 cm^2), being 1.8 and 2.0 times higher values than in adjacent years. At the deeper S2 sampling site, the density (ind./100 cm^2) was lower – it did not exceed 1390 ind. per 100 cm^2 (maximal value recorded from one of the replicates in 2014). The lowest records were noted in 2012 (244 ind. per 100 cm^2) and 2016 (209 ind. per 100 cm^2). Relative coverage at S2 stayed higher at the infralittoral (8 m) site compared to the circalittoral one (15 m). At the infralittoral (8 m) site, two coverage peaks were recorded in 2011 (50 % mean, with a maximum of 73 %) and 2013 (49 %, with a maximum of 75 %), and after that, it decreased, reaching 17 % mean relative coverage in 2020.

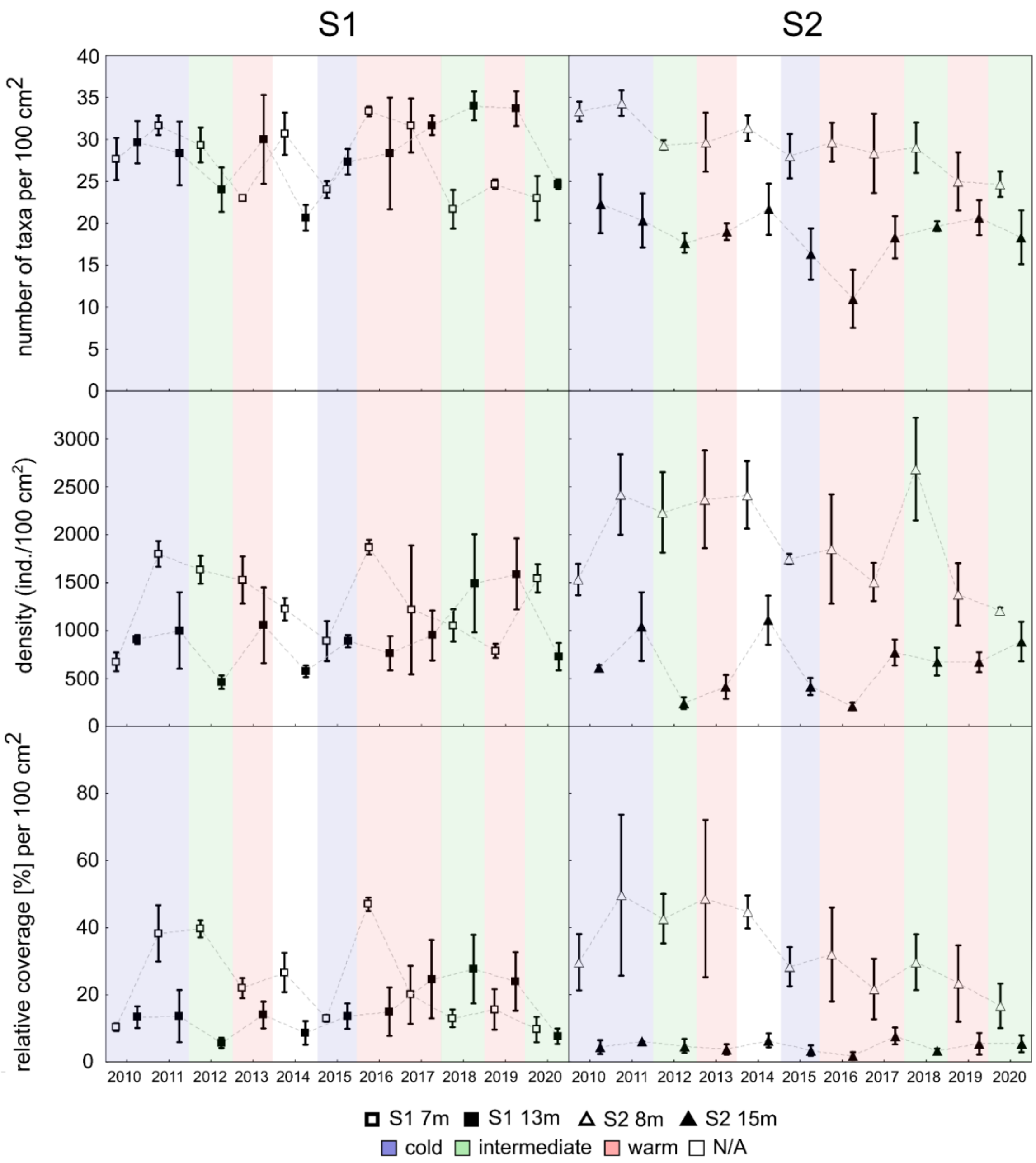


Fig. IV.12 Multiannual variability expressed as a mean value (calculated from 3 replicates) with whiskers displaying singular standard deviation of the number of taxa, density (ind./100 cm^2) and relative coverage [%]. Study site S1 is displayed in squares (on the left) and S2 in triangles (on the right). Unfilled symbols were assigned to infralittoral study sites (7 m and 8 m); filled symbols to the circalittoral sites (13 m and 15 m). Four groups based on standardised anomaly classification: cold (‘blue’), intermediate (‘green’), warm (‘red’) and N/A (no colour).

To verify the significance of each factor (site, year and depth) influence on the number of taxa, density (ind./100 cm^2), and assemblage structure, PERMANOVA analysis was performed (Table IV.4). Results show that all of the factors and their interactions were statistically significant ($p < 0.05$). The interaction of site and depth had the strongest influence on the number of taxa (CV = 39.9 %) and assemblage structure (CV = 20.6 %). Depth explained 33.6 % of the variability in the densities (ind./100 cm^2). The post-hoc pair-wise test revealed significant differences within all factors and factor levels in the case of assemblage structure. In the case of the number of taxa and density (ind./100 cm^2) levels of the 'site' and 'depth' factors were significantly different. However, not all levels of the 'year' factor showed significance (Table IV.5).

Table IV.4 Three-way PERMANOVA analysis for differences in species richness (A), density (ind./100 cm^2) (B) and assemblage structure (C) among sites, years and depths. The original data were transformed by the square root.

	A species richness			B density			C assemblage structure		
factors	Pseudo-F	p	CV [%]	Pseudo-F	p	CV [%]	Pseudo-F	p	CV [%]
site	73.54	0.0001	9.69	8.88	0.0017	0.82	43.76	0.0001	5.92
year	4.74	0.0001	2.75	7.68	0.0001	3.82	20.03	0.0001	14.51
depth	110.18	0.0001	14.58	323.51	0.0001	33.59	103.84	0.0001	14.25
site × year	5.02	0.0001	5.91	5.77	0.0001	5.46	5.43	0.0001	6.75
site × depth	150.51	0.0001	39.93	101.16	0.0001	20.86	75.31	0.0001	20.60
year × depth	8.08	0.0001	10.40	13.22	0.0001	14.00	7.56	0.0001	10.00
site × year × depth	3.70	0.0002	7.93	7.36	0.0001	14.57	7.17	0.0001	18.82

Table IV.5 Post-hoc pair-wise test results for the levels of ‘year’ factor tested in PERMANOVA analysis (Table IV.4) for the number of taxa and density (ind./100 cm^2). Significant values of p (< 0.05) are marked in bold.

		density (ind./100 cm^2)										
		2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
number of taxa	2010		**0.00**	**0.00**	**0.00**	**0.00**	0.40	**0.00**	0.12	**0.00**	**0.01**	**0.00**
	2011	0.85		**0.00**	0.05	0.08	**0.00**	**0.00**	**0.04**	0.36	**0.01**	**0.01**
	2012	**0.00**	**0.00**		**0.00**	**0.00**	**0.00**	0.41	0.01	**0.00**	**0.00**	**0.00**
	2013	**0.02**	**0.02**	0.75		0.45	**0.02**	**0.03**	0.38	0.21	0.19	0.14
	2014	**0.05**	**0.03**	0.28	0.54		**0.00**	**0.00**	0.32	0.35	0.08	0.07
	2015	**0.00**	**0.00**	0.22	0.18	**0.04**		**0.02**	0.14	**0.00**	**0.03**	**0.01**
	2016	**0.01**	**0.01**	0.26	0.22	0.12	0.44		**0.03**	**0.00**	**0.00**	**0.00**
	2017	0.38	0.33	0.06	0.14	0.32	**0.01**	0.05		0.13	0.98	0.94
	2018	**0.02**	**0.02**	0.31	0.60	0.89	0.05	0.13	0.24		**0.04**	**0.03**
	2019	**0.04**	**0.03**	0.28	0.55	0.98	**0.05**	0.12	0.30	0.88		0.84
	2020	**0.00**	**0.00**	**0.03**	**0.03**	**0.01**	0.38	0.22	**0.00**	**0.01**	**0.01**	

The epibenthic assemblage structure on experimental plates was investigated using LINKTREE (Fig. IV.13) analysis. The first split (A) in the cluster was based on the abundance of *Callopora lineata*. The second split (B) was based on the same number of Spirorbinae juveniles. Split C differentiated two further clustering groups based on the abundance of a white type of *Tegella* sp. First of the groups (splits D and E) clustered based on the numbers of *Paradexiospira (Spirorbides) vitrea*, *Juxtacribrilina annulata*, *Celleporella hyalina* and *Harmeria scutulata* (split

D), and *Semibalanus balanoides* and numbers of ancestrulas of Cyclostomata (split E). The second group under split F was again based on the number of ancestrulas of Cyclostomata (lower values than in split E). Standardised anomaly did not influence the clustering of samples.

Principal coordinates analysis (PCO) displayed similarities of the collected samples (Fig. IV.14). The first two axes explained 55.7 % of the total variation. Most of the selected taxa showed a negative relationship with the PCO2 axis, except Spirorbinae juv. and ancestrula Cyclostomata. Additionally, except for *S. balanoides,* all other taxa displayed a positive relationship with the PCO1 axis. Samples from S2 15 m appeared mostly on the left side of the graph (negative values of the PCO1 axis), whereas S2 8 m samples had a positive relationship with the same axis. Samples from years marked as ‘cold’ or ‘N/A’ exhibited only in the top part of the graph, showing mostly a positive relationship with the PCO2 axis (except samples from S1 7 m from 2015 and S1 13 m from 2010).

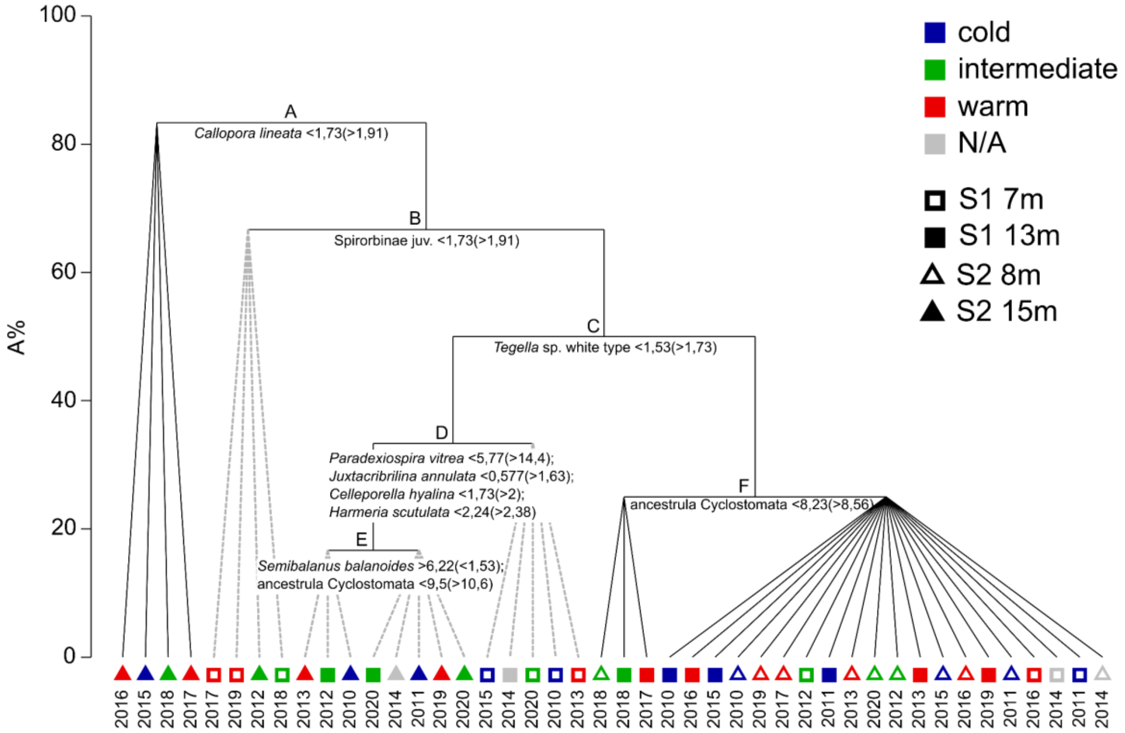


Fig. IV.13 Linkage tree analysis (LINKTREE) showing the partitioning of samples obtained by the six splits (A–F), with corresponding abundance thresholds of the most influential epibenthic taxa. Black lines represent significant splits, according to the SIMPROF tests. Study site S1 is displayed in squares and S2 in triangles. Unfilled symbols were assigned to infralittoral study sites (7 and 8 m); filled symbols to the circalittoral sites (13 m and 15 m). Four groups based on standardised anomaly classification: cold ('dark blue'), intermediate ('green'), warm ('red') and N/A ('grey').

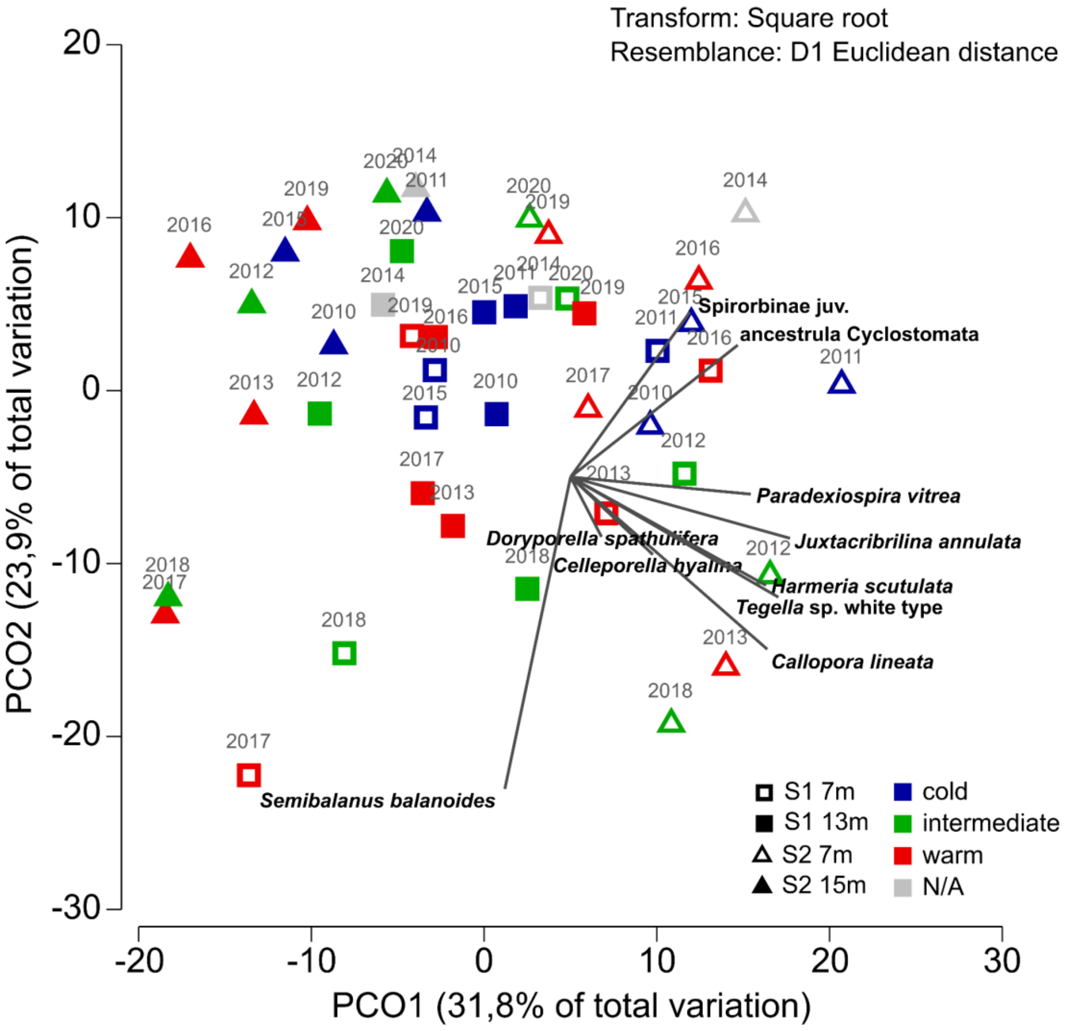


Fig. IV.14 Principal coordinates analysis (PCO) plot calculated based on Euclidean distance resemblance matrix from square-root transformed assemblage structure data showing differences between samples collected at two study locations: S1 (‘square’) and S2 (‘triangle’), two depths: 7/8 m (‘hollow shape’) and 13/15 m (‘full shape’) and in eleven years of the experiment. Years are categorised according to standardised anomaly classification as cold (‘dark blue’), intermediate (‘green’), warm (‘red’) and N/A (‘grey’).

The most abundant taxa included ancestrula Cyclostomata, *H. scutulata*, *T. arctica*, *S. balanoides*, *Circeis* sp., *Spirorbis*/*Bushiella*/*Pilleolaria* sp. and *P. vitrea* (Fig. IV.15). Overall, the highest abundance was reached by *Circeis* sp. in 2014 at the S2 7 m with 794 ind. per 100 cm^2. *Circeis* sp. also occurred in all of the analysed samples. As a result of its even occurrence, it did not have a significant influence on differentiating the samples (Fig. IV.13; Fig. IV.14). In the LINKTREE and PCO analyses, taxa that influenced the grouping of samples were appointed as *C. lineata*, *C. hyalina*, *J. annulata*, *Cylindroporella tubulosa*, *Doryporella spathulifera*, *H. scutulata*, ancestrulas of Cyclostomata, white type of *Tegella* sp., *S. balanoides*, *P. vitrea* and juveniles of Spirorbinae. A typically arctic bryozoan species, *H. scutulata*, showed a significant peak in abundance at infralittoral sites (both S1 and S2) between 2011 (‘cold’) and 2013 (‘warm’), and a subsequent decrease afterwards. It was almost absent at the circalittoral S2 site throughout the whole experiment. The highest abundances were noted at S1 in 2013 (553 ind. per 100 cm^2) and at S2 in 2012 (394 ind. per 100 cm^2). *Semibalanus balanoides* displayed a few peaks in abundance, most notable in 2018 (detected at both sites and depths, with the highest number 662 ind. per 100 cm^2 at S2 8 m). High densities of this species were also noted at S1 7 m, S2 15 m in 2017, and at S1 13 m and S2 8 m in 2013. *Paradexiospira vitrea* was a prominent species at S1 7 m throughout most of the sampling years, but at S2 8 m after high abundance in 2010 (273 ind. per 100 cm^2) and 2011 (269 ind. per 100 cm^2), a subsequent decrease was noted. The abundance of *P. vitrea* remained low at circalittoral stations, except S1 13 m in 2014, when it reached 208 ind. per 100 cm^2.

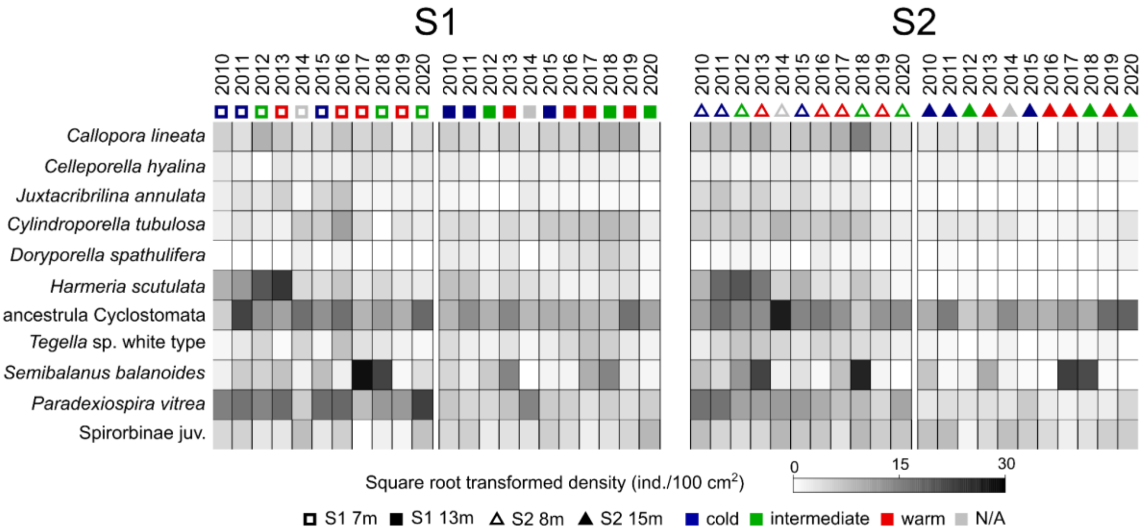


Fig. IV.15 Shadeplot displaying the densities (ind./100 cm^2) of identified taxa over the time series at two study sites (S1 – squares, S2 – triangles) and two depths (7/8 m – unfilled symbol, 13/15 m – filled symbol). Data have been transformed by the square root.

Additionally, for 43 out of 76 taxa, we identified a range of distribution (arctic, arctic-boreal, boreal, cosmopolitan or unclassified) and investigated how the overall contribution of these groups changed throughout the experiment (Fig. IV.16). The only taxon identified as boreal was *S. balanoides* and it dominated the assemblages at S1 7 m and S2 15 m in 2017 and 2018. The bursts of the abundance of the boreal group occurred with a one-year delay after ‘warm’ years noted in 2016 and 2017. Arctic taxa contributed more to the total abundance at the infralittoral S2 site than the circalittoral one, where the contribution was overall the lowest (not exceeding 10 %). The contribution of arctic taxa did not seem to follow the pattern of ‘cold’ years.

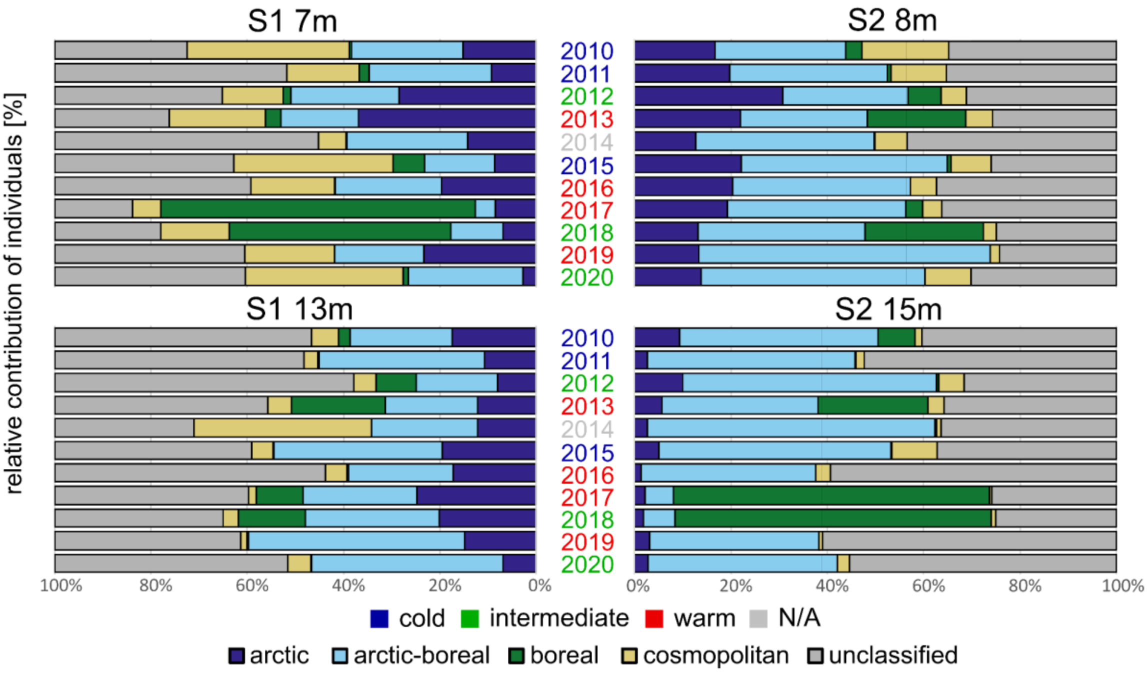


Fig. IV.16 Relative contribution of biogeographical groups (arctic, arctic-boreal, boreal, cosmopolitan and unclassified) in the total number of individuals in each group.

Overall, the results showed more of a natural annual variability without a clear pattern. Although there was an increased presence of 'boreal' species, following the 'warm' years. The PERMANOVA analysis for assemblage structure indicated that the 'year' factor had a significant influence on assemblage composition within samples.

IV.4. Discussion

IV.4.1 General observations

Characteristics of the assemblages based on the recruitment recorded on the settlement plates within a year (number of taxa, density [ind./100 cm^2] and assemblage structure – meant as the number of individuals from each taxa present) varied significantly over the 11-year-long period of the field experiment providing valuable insight into the colonisation processes of the epibenthic assemblage of Isfjorden rocky shallows. Admittedly, the differences noted were statistically significant, though no linear trend in response to the ongoing warming of the Arctic region was distinguished within the studied time frame. A major decline in the endemic Arctic species *Harmeria scutulata* was observed after 2013. This opportunistic species is adapted to habitats with high levels of disturbance (e.g. ice scour). As a poor competitor, this taxon may struggle to establish stable populations when newly disturbed habitats are not available (Kuklinski and Taylor, 2006). Regarding the contribution of Arctic taxa, their number of taxa did not drop in relation to ‘warm’ years, which could suggest no major signs of borealisation occurring yet. However, their density fluctuated over the time of the experiment. The research provided some evidence (i.e. variability in the contribution of taxa, differences in dominance) of changes in the assemblage structure potentially resulting from warming conditions.

IV.4.2 Epibenthic assemblages structure and influence of the surrounding habitat

The taxonomic resolution (the number of individual species identified within a study based on researcher's ability) acquired throughout the experiment was relatively high (maximal value of 36 taxa recorded on replicate plates) in most of the years compared with the previous studies conducted in the area following the comparable protocol (around 20 taxa in total, Barnes and Kuklinski, 2005; Kuklinski et al., 2013; Meyer et al., 2017). Identified species were typical for the studied region and overlapped with the results of previous studies undertaken using an analogous methodological framework (Barnes and Kuklinski, 2005; Kuklinski et al., 2013; Meyer et al., 2017; Evseeva et al., 2023). Consistently, bryozoans and serpulids dominated the assemblages on the settlement plates. Both groups are considered to be opportunistic as they reportedly appear first on any newly available surface (Barnes, 1996; Kuklinski et al., 2013; Wisshak et al., 2022), usually freed by habitat disturbance, or provided by freshly submerged experimental substrate.

The levels of density (ind./100 cm^2) were more unpredictable and harder to relate to other studies or processes described in the region due to the natural variability. This characteristic appears to be mostly driven by biological processes within local communities (e.g. predation). For a better understanding of the assemblage structure (densities [ind./100 cm^2] of all taxa present) and its long-term stability, it would be important to look into the influence of predation (Chapter V), especially sea urchins that can have a profound effect on the benthic communities (Kuklinski, 2005). The presence of kelp forests near study sites (within the infralittoral zone) could have influenced the communities in the area. Kelp species as ecosystem engineers promote habitat complexity that drives increased biodiversity (Teagle et al., 2018; Shunatova et al., 2018b). On the other hand, kelp forests can have a limiting effect on the water movement and consequently reduce the inflow of larvae or the food supply (Balazy and Kuklinski, 2017). At site S2, higher species richness, abundance and coverage were observed (Fig. IV.12) in the infralittoral zone (7 m), where the kelps were present in greater density than at the S1 site, and the construction itself was in closer proximity to kelps (personal communications). Therefore, an argument could be made that the kelp forest stabilised the surrounding environment, e.g., limiting the sedimentation (Kuklinski et al., 2006), and provided a habitat for sessile populations that later released their larvae in the area. Assemblages associated with circalittoral sites (13 and 15 m) were significantly different from the infralittoral (7 and 8 m) ones in most years, harbouring a lower number of taxa, density (ind./100 cm^2) and coverage. Similarly, Uribe et al. (2015) reported higher taxonomic richness of invertebrates in the kelp bed compared to barren ground on the coast of Chile. Although the protocol of that study was different, the described pattern was consistent over the course of 14 months. These reports support the opinion that the presence of kelp forests at the study sites contributes to the differences in assemblage characteristics explained by the 'depth' factor. Besides the different vicinity to the kelp forest, the constructions at S2 sites had a slightly bigger depth disparity than S1, with a steeper slope (Moreno et al., in press). Results from the S2 study site showed a clearer distinction between the assemblages from infralittoral (8 m) and circalittoral (15 m) when it comes to taxonomic composition (Fig. IV.14-17).

IV.4.3 Thermal influence on the assemblages

Marine Heatwaves and Warm Water Anomalies have become more frequent and severe in recent decades in the Arctic region (Huang et al., 2021), and this trend is predicted to continue increasing within the next century (Mohamed et al., 2022). The strongest event in the Barents Sea was observed in the summer of 2016, and the longest one occurred in the winter of the same year (Mohamed et al., 2022). The warmest winters specifically in Isfjorden were noted in 2012, 2014 and 2016 (Skogseth et al., 2020). The warmest summers in the fjord were observed in 2014 and 2017 (Skogseth et al., 2020). Major warm events were also reported by others in those years around the Arctic (Beszczynska-Möller et al., 2012; Cullather et al., 2016; Overland and Wang, 2016; Promińska et al., 2017). Using the temperature data logged at the experimental constructions at the same study sites (Moreno et al., 2024), 'warm' years could be distinguished based on the calculated standardised anomaly: 2013, 2016, 2017 and 2019. The results at least partially overlapped with reports of extremely warm events reported from Isfjorden. Not enough data was obtained to calculate the standardised anomaly for 2014, nonetheless, considering reports of both the warmest winters and summers in 2014, it could be assumed as another 'warm' year.

Assemblage responses to the varying temperature conditions were not consistent. Warm anomalies can persist through different spans of time, once or multiple times a year, or during a whole season, and their effect would differ depending on the current life cycles of organisms (i.e. larval release of different taxa occurs at different times of the year; e.g. see Kuklinski et al., 2013). For instance, the highest numbers of identified taxa and density (ind./100 cm^2) were reported at S1 infralittoral and circalittoral in 'warm' years (2016 and 2019). On the other hand, peaks of identified taxa at S2 occurred in 2011 for infralittoral and 2010 for circalittoral, both years qualifying as 'cold' according to the calculated standardised anomaly. However, it is important to note that at S2 circalittoral, a peak number of taxa was repeated in 2014, which is assumed to have been a 'warm' year, with the highest abundance noted for this study site. Interestingly, the lowest values also predominantly occurred in 'warm' years, with some appearing in 2012, which was identified in the study as 'intermediate', but other reports showed it had one of the warmest winters in Isfjorden (Skogseth et al., 2020). High temperatures in winter months could have led to lower reproductive success (measured by fertilisation and brooding) as reported for the barnacle *S. balanoides* (Crickenberger and Wethey, 2018). Then again, the highest density of *S. balanoides* occurred commonly after ‘warm’ years with an apparent one-year lag (Fig. IV.15). As this species is considered boreal, it could be adapted to higher temperatures than other taxa occurring in this region. Still, its distribution range has been experiencing retreat of the southern limit, especially in regions experiencing warmer winters (>10°C) (Barnes, 1963; Wethey and Woodin, 2008; Rhiannon and Hilbish, 2014; Crickenberger and Wethey, 2018). Appearance of such lag has been described on land by Menendez et al. (2006). It is also important to note that standardised anomalies for the purpose of this study were calculated based on calendar years, whereas submersion periods of settlement plates lasted between summer seasons. In the case of endemic bryozoan *Harmeria scutulata*, peaks of density (ind./100 cm^2) occurred at infralittoral sites in 2012 and 2013 and experienced an acute drop afterwards following the first ‘warm’ year recorded by our study in 2013, as well as the previously mentioned warm winter in 2012. Another abundant species that influenced the differentiation of samples was *Paradexiospira vitrea*. Its abundance did not directly follow thermal changes. Two drops were noted in 2014 and 2017 at S1 7 m (infralittoral), which could have possibly been connected with ‘warm’ years either directly or with the previously mentioned ‘lag’. When it came to S2 infralittoral, the density (ind./100 cm^2) fell after the first two years of sampling, which were marked as ‘cold’. Those results are somewhat surprising as *P. vitrea* is considered a cosmopolitan species and can reproduce all year round (Reitzel et al., 2004).

IV.4.4 Fluctuations in the contribution of taxa differing in distribution ranges

Benthic communities usually display shifts in response to long-term changes and not short-term fluctuations (Loeng and Drinkwater, 2007). However, major warm events could potentially have a negative impact on the ecosystem adapted to rather stable thermal conditions (Huang et al., 2021). Overall, the structure of the assemblages based on the ranges of distribution appears rather stable throughout the experiment. However, some discrepancies occur in the case of density which fluctuated more evidently. Noticeably, ‘boreal’ individuals dominated S1 infralittoral (7 m) and S2 circalittoral (15 m) in 2017-2018 following the strong heatwaves in 2016 (Mohamed et al., 2022). Importantly, due to sample collection in summer (turn of July and August), the winter heatwave of 2016 (from September until December) would influence the assemblages on exchanged settlement plates (2017 samples). In 2016, the year of a major warm event, almost no ‘boreal’ individuals were identified. On the other hand, rather unexpectedly, the contribution of ‘arctic’ taxa stayed rather consistent with the previous year (or even increased slightly at infralittoral sites). Previous studies from the Arctic and beyond showcased increased resilience and recovery of benthic communities exposed to subsequent heatwaves (Pansch et al., 2018; Brown et al., 2019; Fox et al., 2021; Jordà-Molina et al., 2023). However, borealisation has already been reported within the Arctic ecosystem: among fish communities (Fossheim et al., 2015), zooplankton communities (Møller and Nielsen, 2020), seabird communities (Descamps and Strøm, 2021), and benthic communities (Kortsch et al., 2012). Nonetheless, the results did not reveal evidence of newly arriving species of boreal or cosmopolitan origin.

IV.5 Conclusions

The field experiment allowed for the observation of changes in the structure of the lithophile assemblage inhabiting the rocky shallows of Isfjorden over 11 years. Throughout the study, nonlinear trends in the taxonomic composition and density of epibenthic assemblages were observed in response to noted thermal fluctuations. Further, on the settlement plates deployed annually for over a decade, no new species to the Svalbard region were identified. That contradicts the predictions of the massive range expansions northward of boreal taxa in response to continuous warming. As hypothesised, warm anomalies had some varied influence on the organisms. The effects were not consistent across samples or years, and often the suspected response to warm conditions displayed a lag, which is possible if the conditions were not fatal to already settled organisms but rather influenced their reproductive success that could be detected the following year. However, the influence of changing conditions is expected to become more evident over time. Still many fluctuations were most likely driven by other local processes (e.g. predation, interspecies competition). At the same time, as initially expected contribution to the overall assemblage of species classifies as boreal was increasing during or following years with warmer conditions. Undeniably, a major result coming from the provided observations was a distinct drop in the density (ind./100 cm^2) of the endemic, opportunistic arctic bryozoan *Harmeria scutulata* after 2013. Ultimately, the obtained data set supplies an important source of baseline information for future reference, especially considering sparse documentation on hard-bottom habitats in the high Arctic. The up-to-date knowledge provided by our study is necessary to approach the conservation of the hard-bottom ecosystems adequately in the future.

Chapter V Impact of substrate orientation and predation on assemblage structure

V.1. Introduction

Hard bottom habitats are influenced by many factors, which include, among others, water currents, light regimes, sedimentation rates (abiotic) (Siddik et al., 2018; Ali, 2023); food availability, predation, and interspecies competition (biotic) (Buss, 1979; Holomuzki, 2010; Barnes and Neutel, 2016). From the mentioned list, two factors are fundamental to the establishment of benthic assemblages: the availability of larvae and a suitable substrate with accommodating environmental conditions (Todd, 1998; Konar, 2007).

The most desirable settlement locations are primarily determined by the degree of light exposure and substrate orientation (horizontal vs. vertical), which together indicate the level of protection from predators that the location can offer to new settlers. In natural settings, those conditions are found under rock overhangs, crevices, and undersurfaces, but can also be found with anthropogenic constructions. Marine lithophiles (or epilithobionts as categorised by Taylor and Wilson, 2022) often exhibit a striking preference towards shaded habitats, as shortly after settlement, and often later in life, they remain vulnerable to predation by common grazers, such as echinoids, gastropods, and polyplacophorans. Therefore, substrate orientation, natural or artificial, is crucial in shaping the successful recruitment and lithophilic assemblage structure (Knott et al., 2004; Balazy et al., 2017; Siddik et al., 2018). Previous studies, not restricted to Arctic locations, showed preference of many taxonomic groups toward shaded micro-habitats, including bryozoans, serpulids and barnacles (Glasby, 1999a, 1999b; Glasby and Connell, 2001; Bowden et al., 2006; Ronowicz et al., 2014; Sokołowski et al., 2017; Sowa et al., 2023). It has been commonly observed that meroplankton (larvae of benthos) exhibit negative phototropism during the settlement (Thorson, 1964), which drives them to more shaded places (Miller and Etter, 2008). It has been previously reported that downward-facing surfaces parallel to the substrate attract more diverse assemblages than those oriented vertically to the sea bottom (Glasby and

Connell, 2001). However, vertical substrate was reported to yield relatively higher overgrowth of lithophiles due to reduced sedimentation impact (Knott et al., 2004). Interestingly, the studies on pier pilings (vertical substrate) with different levels of shading from light also showed benthic species having similar preferences as the studies using horizontal setups with colonial bryozoans, serpulids, sponges and solitary ascidians, thus reaching greater space occupation (percentage of cover) under shaded conditions (Glasby, 1999a). Similar conclusions were reached from the study done on vertically mounted settlement plates with differing levels of shading, also conducted by Glasby (1999b). The substrate orientation can limit, to some extent, the predatory pressure on the encrusting assemblages and simultaneously interact with other environmental drivers (i.e. sedimentation, wave activity, scouring, light availability) (Włodarska-Kowalczuk et al., 2005). Many sessile organisms show a preference for rocky overhangs (subvertical walls) since these terrain features are less susceptible to accumulation of sediment (Siddik et al., 2018), which can lead to suffocation of filtrators and, in general, to burial of taxa with encrusting growth forms if it occurs after settlement (Ronowicz et al., 2014).

Further, environmental conditions and the recruitment intensity are not the only factors shaping the assemblage structure, but also the interspecies interactions, which include predation impact (Osman and Whitlatch, 2004; Yakovis and Artemieva, 2015; Oricchio et al., 2016; Vieira et al., 2016) and grazing (that can be lethal or sublethal) (Anderson and Underwood, 1997).

Especially in the regions with relatively low rates of colonisation, such as the Arctic (Barnes and Kuklinski, 2005), predation is a significant factor influencing assemblage structure (Osman and Whitlatch, 2004; Yakovis and Artemieva, 2015; Oriccho et al., 2016; Vieira et al., 2016). It was reported that in Svalbard fjords, recovery following a disturbance could take over a decade in the absence of grazers (Al-Habahbeh et al., 2020). It is difficult to observe and describe predatory forcing without continuous monitoring, as most of the predators do not attach to the substrate (excluding polyplacophorans, which were occasionally present on the settlement plates during the laboratory analysis; personal observations). Consumers known to prey on sessile assemblages include gastropods (mainly nudibranchs), echinoids, polyplacophorans, malacostracans, asteroids, ophiuroids, pycnogonids, polychaetes and actinopterygian fishes (Gordon, 1972; Lidgard, 2008; Oricchio et al., 2016; Dietz et al., 2018). Predation plays an important role in shaping the development of the initial assemblages and secondary succession (Valiela and Valiela, 1995; Anderson and Underwood, 1997). The removal of lithophiles by grazers can also aid new recruits in areas with very limited available substrate (Todd, 1998). Some predators grazing on sessile organisms on the hard substrate can leave characteristic traces, which can then be used to determine which organisms were possibly feeding on a given surface and with what intensity.

As a result of ongoing climate change in the Arctic region (Skogseth et al., 2020; Rantanen et al., 2022), declining sea ice cover and warming may lower grazers' populations (Gauzens et al., 2024), leading to less checked algal growth, followed by altered successional trajectories, and eventually reduced functional diversity (Gradinger and Bluhm, 2010; Al-Habahbeh et al., 2020). The Arctic has and is going through major shifts (Kortsch et al., 2012), and many boreal taxa are expanding their ranges of distribution further north following the increasing sea temperatures (Pinsky et al., 2020). Therefore, the monitoring of grazer dynamics is crucial for better predictions of benthic assemblage responses to ongoing Arctic change in the future.

The German term ‘lebensspuren’ literally translates to ‘life traces’. In the fields of marine biology, sedimentology and ichnology, it describes the physical traces left by the activities of organisms, especially on or in marine substrates (Bromley, 1975; Miguez-Salas et al., 2024). Several trace types can be classified on hard substrata. Boring traces (bioerosion) are a result of drilling or boring into submerged rocks, but also man-made concrete or steel surfaces done by organisms (Warme, 1975; Ekdale, 1984; Wisshak and Tapanila, 2008). In contrast, attachment etchings and encrustation traces (biofouling) are a result of the activity of sessile organisms attaching themselves to hard substrates, often involving excreting glue-like substances (Glasby, 2000; Wisshak et al., 2022). For instance, barnacles possessing cement bases can leave circular marks after detachment, and tubeworms can leave remains of calcareous tubes, often in spiralled shapes (Wisshak et al., 2022). These traces are referred to using a conceptual framework known as ichnotaxonomy (Wisshak et al., 2019), and although it applies mostly to trace fossils, these terms can be applied to describe traces of current living organisms. Grazing traces are a different type of bioerosion and can be a result of, for instance, gastropods and echinoids scraping the substrate surface while feeding. These traces can originate from the activity of gastropods (radula scraping marks; short parallel scratches identified in ichnology as *Radulichnus inopinatus*; de Gilbert et al., 2007) and echinoids leaving pitted or gouged marks (five distinctive, regular stellate groupings of rectilinear grooves; pentaradiate scratches belonging to the ichnotaxon *Gnathichnus pentax*; Bromley, 1975; Wisshak et al., 2022) from Aristotle's lantern (Bromley, 1975; Taylor and Wilson, 2003).

The study aimed to explore the effects of substrate orientation (horizontal: downward-facing and upward-facing, and vertical) on recruitment and the levels of predatory forcing in Arctic coastal hard-bottom benthic assemblages. It was expected that the observed lithophilic assemblage would significantly differ among the three substrate orientations. It was hypothesised that intense grazing would occur on upward-facing plates, whereas on the vertical plates, a lower impact from predators was expected. Furthermore, distinct types of grazing traces were identified on the settlement plates and attributed to specific predators known to inhabit hard-bottom substrates in the shallow subtidal zone of the high-Arctic Isfjorden.

V.2. Methods

V.2.1 Protocol

The experimental constructions followed the description in Chapter II. However, for the purpose of this study, additional vertical frame rigs were anchored to the sea bottom and held up by a buoy approximately 50 cm above the substrate.

The first set of experimental settlement plates was deployed in the summer of 2018, in late July and early August, by the IOPAN Scientific Diving Team. In 2019, the first set was collected after a year of immersion. The second set was deployed in 2019 and collected a year later in 2020.

V.2.2 Analysis

The colonies never overgrew the artificial substrate entirely due to the relatively short time of submersion (a year) and the relatively slow growth rate of arctic ectotherms (e.g. see Barnes and Kuklinski, 2005). To help quantify the area covered, digital photographs of the dried settlement plates (photoplates) were taken. The relative area covered by lithophiles was calculated based on a hundred random points laid over pictures of the ROI of each photoplate using the CPCe 4.1 software (Coral Point Count with Excel extensions; Kohler and Gill, 2006). It was manually determined whether an epibiont, a grazing trace, or a bare plate was present under each point, and those data were reported as space occupation in relative values (percentage cover).

The variability in the number of taxa, density (ind./100 cm^2) and assemblage composition between samples was investigated under three fixed factors – ‘site’ (two levels: S1 and S2), ‘orientation’ (three levels: down, up and vertical), and ‘year’ (two levels: 2019 and 2020) were tested with PERMANOVA (permutational analysis of variance) analysis performed in Primer v.7 (Clarke et al., 2008). To deal with zero inflation and high value dispersal within the dataset, the raw data were square-root transformed. Additionally, post-hoc pair-wise tests were performed between all levels of each factor. The data from replicates (three settlement plates for each combination of factors) were averaged. The graphs (mean ± 0.95 confidence intervals) displaying data variability under the most influential factors or factor interactions chosen based on the results of PERMANOVA analysis (the highest values of components variation, CV) were prepared in Statistica software (StatSoft, Inc., 2007). To visualise the assemblage structure, LINKTREE analysis was done, providing division of the samples based on a SIMPROF similarity test from which the differentiating taxa were provided at each level of division, with values of densities characterising each branch of the split. For the best result, the following conditions were applied: minimum group size = 4, minimum split size = 3, and minimum split of R = 0.5. To present the variability among collected samples, a principal coordinates analysis (PCO) was used. It was based on a resemblance matrix calculated using Euclidean distance from standardised (the sample values were divided by the total for that sample) and square-root transformed data. Two vector overlays were added, showing the main taxa driving the dissimilarity between samples (based on SIMPER analysis) as well as the distribution of grazing trace types. The relative grazing intensity and the contribution of identified trace types were presented alongside relative (%) coverage using cumulative bar graphs.

V.2.3 Grazing bioerosion trace types

During the analysis of the settlement plates photographs (photoplates), five types of grazing traces were visually differentiated: deep lines, patches of thin lines, star lines, slight lines and straight lines (Fig. V.17). Following the data analysis, they were related to ichnotaxa mentioned in the literature (Bromley, 1975; de Gilbert et al., 2007; Wisshak et al., 2022). The density of each trace type was obtained by counting instances of grazing from the ROI (100 cm^2).

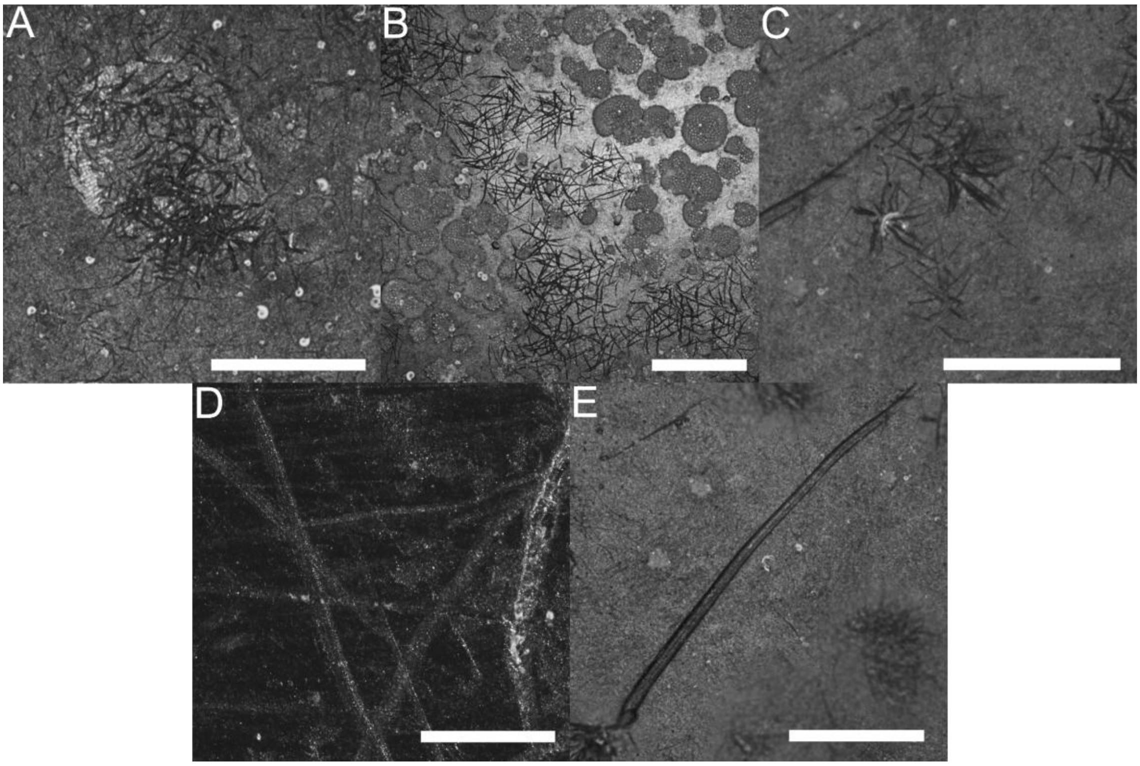


Fig. V.17 The five differentiated grazing trace types identified on the settlement plates: deep lines (A), patch of thin lines (B), star lines (C), slight lines (D), and straight line (E) with size bars indicating 500 µm (D) and 1 cm (A, B, C, E). Source: photographs of the settlement plates.

V.3. Results

On the 36 experimental settlement plates analysed (orientation (3) × site (2) × year (2); three replicates each), 59 different taxa were identified, including bryozoans (44), serpulids (12), cirripeds (adults and juveniles counted separately), and non-geniculate calcareous coralline algae (CCA). Each variation of the plate orientation was dominated by different taxa. For the upward-facing plates, *Boreolithothamnion* sp. had the highest density, the downward-facing plates were dominated by *Circeis* sp., whereas the vertical substrate had the highest number of *Semibalanus balanoides* individuals.

The PERMANOVA analysis revealed that the orientation factor was significant in all investigated aspects (assemblage structure, density, and number of taxa) (Table V.6). The orientation was also the most influential in the case of assemblage structure (66.94 %) and number of taxa (63.08 %), while density was mainly influenced by the interaction of year and orientation factors (ye×or = 20.41 %).

Table V.6 Results of the three-way PERMANOVA analysis for differences among sites (si), years (ye) and orientations (or) based on the assemblage structure, number of taxa, and density (ind./100 cm^2). Significant values were those in which $p < 0.05$. The most influential factors or factor interactions (the highest component of variation, CV) are marked in bold.

	assemblage structure			number of taxa			density		
Factor	pseudo-F	p	CV [%]	pseudo-F	p	CV [%]	pseudo-F	p	CV [%]
si	19.18	<0.01	5.49	28.43	<0.01	16.14	10.69	<0.01	8.07
ye	7.10	<0.01	1.84	2.43	0.11	0.84	12.64	<0.01	9.70
or	**148.73**	**<0.01**	**66.94**	**72.47**	**<0.01**	**63.08**	14.93	<0.01	17.41
si×ye	6.00	<0.01	3.02	1.17	0.30	0.20	7.28	0.01	10.47
si×or	6.58	<0.01	5.06	2.71	0.05	3.01	3.05	0.05	5.13
ye×or	6.93	<0.01	5.38	3.87	0.02	5.06	**9.16**	**<0.01**	**20.41**
si×ye×or	4.77	<0.01	6.83	1.30	0.28	1.07	3.76	0.02	13.80

The post-hoc pair-wise tests revealed that all factor levels were significantly different ($p < 0.05$) considering assemblage structure. In the case of density, the two levels of the orientation factor were not significantly different ($p > 0.05$) when comparing the down and vertical facing. 'Year' (factor) also showed no significant differences ($p > 0.05$) in the number of colonising taxa.

Following the results of PERMANOVA showing the significance of orientation factor on the number of taxa, means, and a 95 % confidence intervals plot was prepared (Fig. V.18), which displayed clear differentiation between the grouped up, down and vertical assemblages.

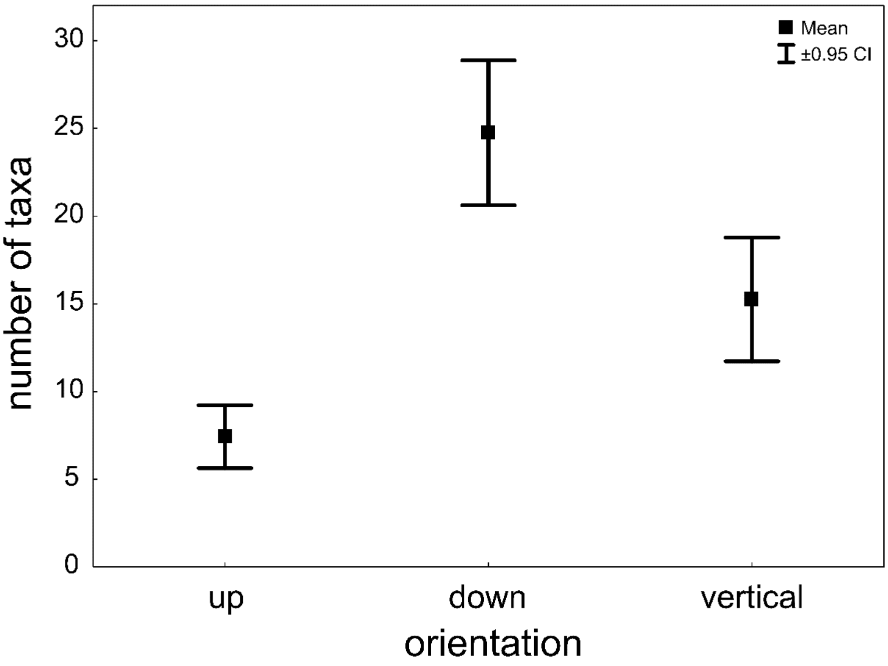
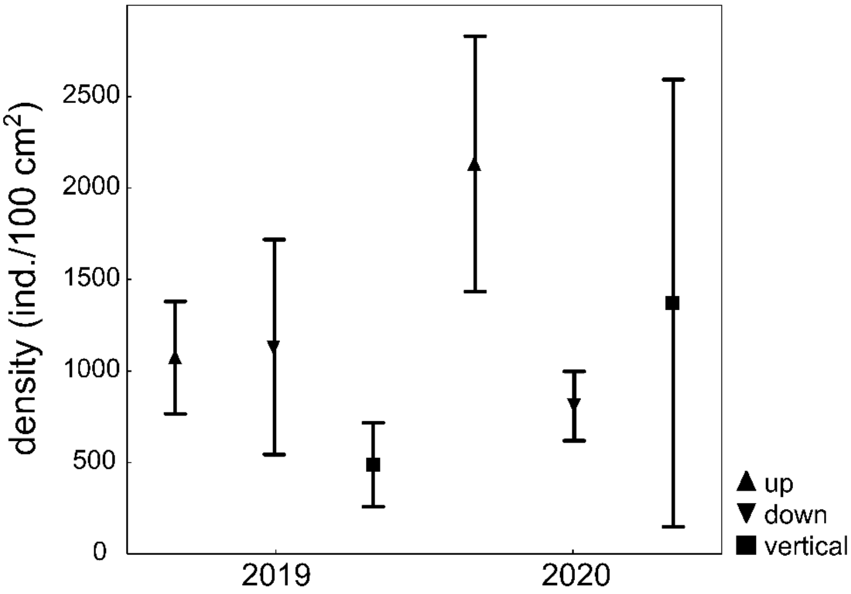


Fig. V.18 Mean values of the number of taxa calculated from 12 replicates each from combined replicates (sites and years), displaying the effect of the factor with the highest influence on variability between samples (orientation). Whiskers represent 95 % confidence intervals.

As suggested by PERMANOVA results, the 'depth' factor alone did not drive the differences between samples. However, when considering it in the interaction with the 'site' factor, differences among groups were found. The results between depths at the S1 site showed overlap in the 95 % confidence intervals. Significant separation of results was apparent at the S2 site (Fig. V.19).



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The LINKTREE analysis revealed clear differentiation of samples based on the orientation factor (Fig. V.20). The additional SIMPROF test indicated the taxa, which influenced the grouping shown on the cluster. Both splits were significant. The split A divided all upward-facing plates from the rest of the samples based on the density of the non-geniculate calcareous coralline algae *Boreolithothamnion* sp. (>28.4 <7.16), the cyclostome *Patinella* sp. (<0.58 >2.16), the cheilostome *Tegella arctica* (<0 >1) or the spirorbid *Circeis* sp. (<4.04 >4.43). The B split differentiated vertical settlement plates from the remaining downward-facing samples based on several taxa: cheilostome *Myriozella crustacea* (<0 >1), spirorbid *Paradexiospira (Spirorbides) vitrea* (<0.58 >2.08), *Semibalanus balanoides* (>12.2 <2.52), bryozoan ancestrula (<2.52 >4.24), *Cylindroporella tubulosa* (<0.58 >1.63), *Callopora craticula* (<1 >1.91), Spirorbinae juv. (<3.96 >2.24), Tubuliporidae indet (<1.41 >1.91), *Microporella arctica* (<1.63 >2.24), *Circeis* sp. (<13.4 >14.8) and *Boreolithothamnion* sp. (>1.83 <0).

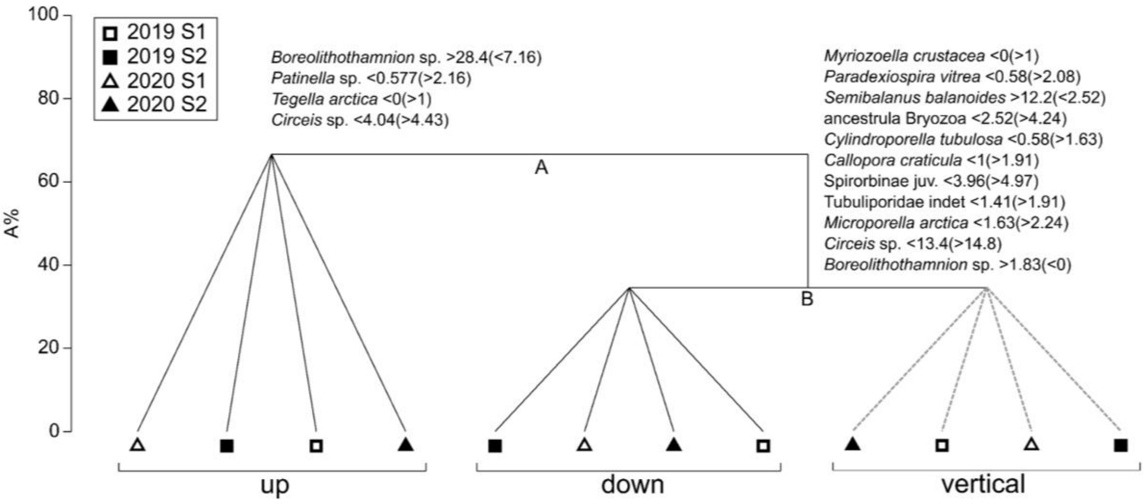


Fig. V.20 Linkage tree analysis (LINKTREE) showing the partitioning of samples obtained by the two splits (A, B) creating three groupings/clusters, with corresponding density (ind./100 cm^2) thresholds (in the brackets) of the most influential epibenthic taxa, according to the SIMPROF tests. Black lines represent significant splits. Study site S1 is displayed with an unfilled symbol, and S2 with a filled symbol. Years are differentiated by shape, 2019 in squares and 2020 in triangles.

The principal coordinates analysis (PCO; Fig. V.21) displayed a similar grouping of the samples as indicated in the LINKTREE analysis (Fig. V.20). The first two axes combined explained 89.8 % of the total variation. Two overlays were added to the graph. One showing the main taxa driving the differentiation based on SIMPER analysis. The second overlay was added to investigate the impact of predation by displaying the grazing trace types. As shown on this graph and confirmed by the combined bar plot (Fig. V.22), grazing was the most prevalent on the downward-facing and vertical plates. In some cases, it exceeded the overgrowth (the relative coverage of substrate by lithophiles).

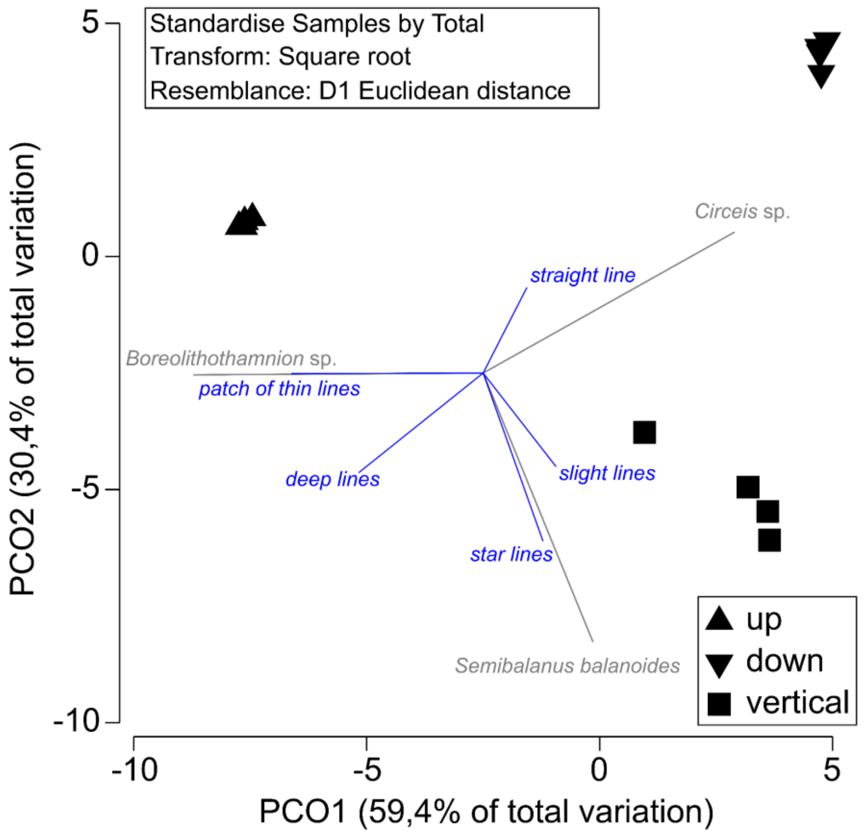


Fig. V.21 Principal Coordinates Analysis (PCO) with vectors (grey) based on SIMPER analysis results, highlighting three main taxa differentiating the samples with added vectors (blue) showcasing types of grazing traces found on the surface of the settlement plates.

The general contribution of grazing impact was the lowest on the upward-facing plates compared with other treatments. However, traces were absent in 2020 at S1 site (Fig. V.22; Fig. V.23). The majority of identified traces belonged to the type ‘slight lines’, followed by a similar category ‘patch of thin lines’ (Fig. V.17; Fig. V.23). The grazing traces contribution was higher on vertical plates at S1 sites but plates from S2 had the highest number of traces (Fig. V.22).

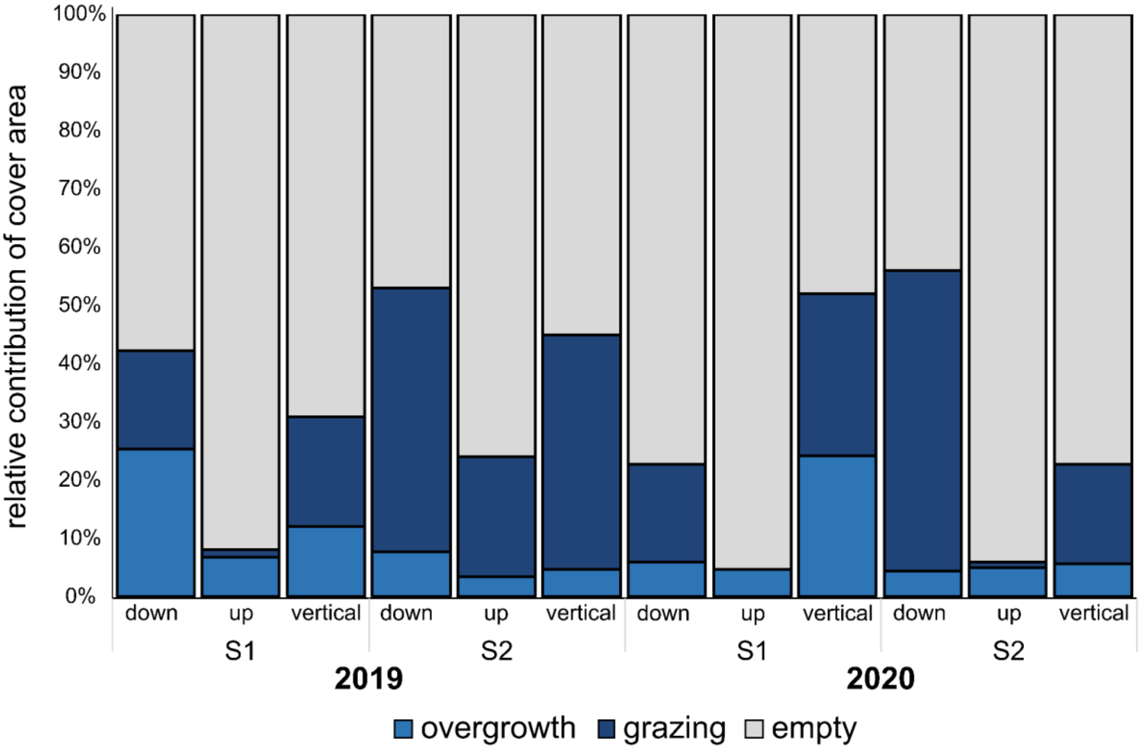
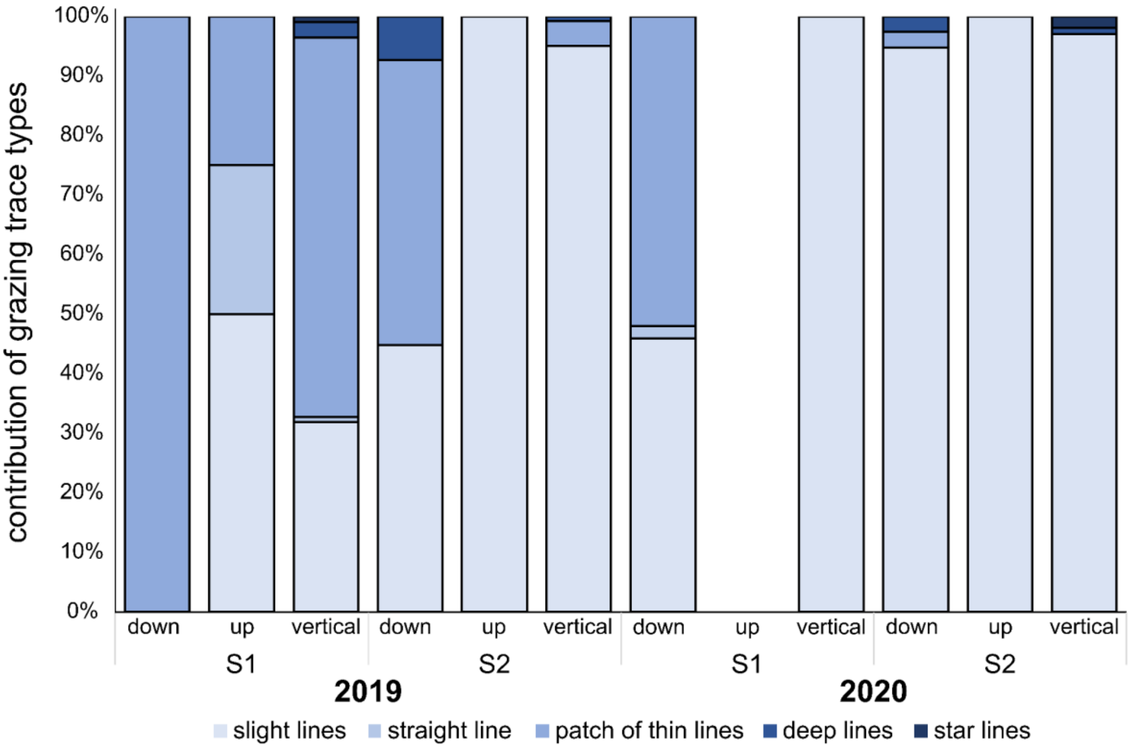


Fig. V.23 Relative overgrowth of lithophiles and grazing activity on the settlement plates under each combination of chosen factors (‘year’, ‘site’ and ‘orientation’).



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V.4. Discussion

V.4.1 General observations

The richness, abundance and relative importance of colonising taxa in the current Arctic study were all very similar to those on panels immersed for the same time period in the Antarctic, despite the major biodiversity differences between the regions (Barnes et al., 2025). Lithophile assemblages in Isfjorden shallows displayed clear differentiation between the three studied substrate orientations (downward-facing, upward-facing and vertical). The general impact of predation measured by the contribution of grazing traces was lowest on the upward-facing plates, even if those surfaces would have been the most accessible contrary to the vertical ones, as found by Miller and Etter (2008). Alongside colonisation, grazing traces were investigated, and five types were visually classified. However, four out of five were presumed to have been left by echinoids grazing with various intensities (because of visual similarities to literature echinoid grazing imagery, see Bromley (1975), de Gilbert et al. (2007), Wisshak et al. (2022)).

V.4.2 Influence of substrate orientation on colonisation and recruitment

Globally, the orientation of substrate has been reported as having one of the greatest impacts on the structure of lithophile assemblages (Glasby and Connell, 2001; Knott et al., 2004; Siddik et al., 2018). In this study, plate orientation was the most important factor driving biodiversity, with the highest number of taxa occurring on downward-facing plates (Table V.6; Fig. V.18). This trend was consistent with previous investigations of the orientation impact on early stages of recruitment in Isfjorden (Sowa et al., 2023). Comparing downward and upward-facing substrates, the results were also compatible with those observed in different marine regions: the west Antarctic Peninsula (67°S, Bowden et al., 2006), the NE Atlantic (51°N, Ronowicz et al., 2014), and the southern Baltic proper (54°N, Sokołowski et al., 2017). The upward-facing substrate differed the most from the other treatments, with the calcareous coralline algae (CCA) *Boreolithothamnion* sp. having the largest influence on the differentiation (Fig. V.20-21). Algae require light availability, although in the Arctic, CCAs are well adapted to limited access during the polar night (Schoenrock et al., 2018). They are pioneering species in arctic lithophilic assemblages, appearing in early stages of colonisation (Bonsell and Dunton, 2021). Upward-facing plates also sustained the lowest levels of relative coverage when compared to other orientations at the combination of the two other factors (year and site) (Fig. V.22). Low recruitment of substrate facing the water column could be explained by the behaviour of the settling larvae (preference for shaded habitat) or possible influence of sedimentation that could suffocate and/or bury sessile lithophiles (Thorson, 1964; Ronowicz et al., 2014; Siddik et al., 2018; Bonsell and Dunton, 2021). High turbidity can also limit the recruitment and survival of CCA propagules, thus driving down the overgrowth of upward-facing substrates (Bonsell and Dunton, 2021). Contrary to the report of Knott et al. (2004) from natural and artificial reefs around Sydney (Australia), vertical plates did not support more overgrowth than downward-facing plates.

In their study, the higher coverage on vertical surfaces was driven mostly by several species of sponges, ascidians, followed by barnacles, bryozoans, oysters and vermetid gastropods. However, they harboured the highest densities of the barnacle (*Semibalanus balanoides*), which have been reported to follow chemical cues that lead them to settle in proximity to conspecifics, the so-called gregarious behaviour (Mauck and Harkless, 2001; Ellrich et al., 2015). This behaviour is presumed to aid the establishment of populations in the most favourable locations for successful recruitment (Ellrich et al., 2015), but it can also lead to the domination of a single species in that area. On the other hand, Glasby and Connell (2001) reported more diverse assemblages on plate undersides (serpulids, barnacles, and some bryozoans) compared to those on vertical ones (algae, some bryozoans), similarly to the results observed in this study (Fig. V.18, Supplementary Information 2).

V.4.3 Predation impact assessment

In polar regions, where colonisation and recruitment tend to be lower and slower compared to temperate and tropical latitudes (Barnes and Kuklinski, 2005), predation can greatly impact the structure of lithophile assemblages (Harper and Peck, 2016) and further drive the differentiation between distinctly oriented substrates (Knott et al., 2004; Field et al., 2007). The preliminary data on the predation impact based on the traces left on the surface of the settlement plates revealed quite a high relative contribution of grazing compared with the overgrowth by the recruits, especially on the downward-facing and vertical plates (Fig. V.22). Predation was lowest or not observed at all on the upward-facing surfaces of the current study. Those plates were also characterised by very low organismal coverage (below 10 %), consistent with the low recruitment described in the previous section. This major disparity was most likely driven by predators' preference for specific prey, as the grazing traces were more prevalent on less accessible surfaces (undersides and vertical plates above the sea floor), as is known in some nudibranch molluscs (Barnes and Bullough, 1996). However, Lambert and Harris (2000) reported high settlement of echinoid (*Strongylocentrotus droebachiensis*, the species occurring in Spitsbergen waters) on coralline algae encrusted plates. They stated that this behaviour could be driven by a chemical cue produced by CCAs that induces metamorphosis of echinoids. Although they also reported that the greatest settlement of echinoids occurred at depths less than 10 m, which is shallower than the experimental construction used for the purpose of this study.

Predation impact assessments are not straightforward, especially for bryozoans, as they can be subjected to sublethal damage or feeding through the removal of soft tissue from individual zooids (for example, by pycnogonans), which does not leave traces on dried specimens (the conservation method used in this study) (Lidgard, 2008). The presence of predators in the vicinity of the substrate can also reportedly impose nonconsumptive effects on the recruits' behaviour (Ellrich et al., 2015).

Macropredator-exclusion experiments using cages have been attempted on the study sites; however, the results showed unforeseen indirect impact of metal cages on encrusting fauna due to the silting effect or overgrowth of macroalgae on the cages themselves, limiting access to the substrate by larvae (see Sowa et al., 2023 and references therein).

V.4.4 Potential predators

Many benthic predators have been recognised as preying on bryozoans, serpulids and barnacles; however, the traces identified in our study mainly indicate echinoid activity. Of the five types of traces differentiated, three (‘deep lines’, ‘patch of thin lines’, ‘star lines’; Fig. V.17) visually match with the distinctive convergent grooves left by Aristotle's lantern of sea urchins classified in ichnology as *Gnathichnus pentax* (Bromley, 1975). As mentioned by de Gilbert et al. (2007), traces left by grazers, including echinoids, rarely occur as a singular star shape. More often, they overlap in bigger patches. The ‘slight lines’ (Fig. V.17) were also suspected as marks left by sea urchins from less intense grazing activity. They did not fit the descriptions of traces left by radulas of polyplacophorans or other gastropods as depicted by de Gilbert et al. (2007) or Wisshak et al. (2022). Echinoids graze indiscriminately, but sublethally, on lithophiles; their presence (or absence) influences which representatives of said assemblage dominate (McKinney et al., 2003). Interestingly, none of the identified traces could be linked to polyplacophorans (ichnotaxon

Radulichnus transversus, Lopes and Pereira, 2019), which are considered generalist grazers (Lidgard, 2008) and have been observed in underwater images of a similar long-term succession experiment deployed at the study sites (Moreno, 2024; Moreno et al., in press), and removed directly from some of the settlement plates during the laboratory analysis (personal observations). However, the lack of visible traces does not entirely exclude the impact of specific predators on the studied assemblages.

The ‘straight line’ (Fig. V.17) posed the most difficulty in identifying the potential source. It was not a commonly occurring trace, but was identified on plates in all orientations (upward, downward and vertical). The groove was distinctive, long and quite deep, comparable with the deep gauges left by echinoids. Based on the possible predators mentioned in the literature (McKinney, 2003; Osman and Whitlatch, 2004; Lidgard, 2008; Oricchio et al., 2016), some fishes and decapod crustaceans that also prey on lithophiles could have been responsible for this particular trace. However, the trace alone could not be confidently linked to either group. Another possibility for the occurrence of this specific groove would be anthropogenic; potentially, it could have been accidentally made by a SCUBA diver during the installation or collection of the settlement plates, or transpired during transportation.

V.5. Conclusions

The substrate orientation was found to be the strongest factor shaping the structure of lithophilic assemblages, with one species dominating on each orientation treatment. For upward-facing plates, it was the only identified alga, *Boreolithothamnion* sp., for downward-facing plates, it was the serpulid *Circeis* sp. And the vertical plates were mostly overgrown by the barnacle *Semibalanus balanoides*. Contrary to predictions, the upward-facing plates were not the most grazed upon; they had the lowest intensity of grazing when compared to other treatments. Although it was expected that the vertical plates would have a lower predation impact due to the distance to the seabed, they obtained a comparable number of traces as the downward-facing plates. From all classified trace types, three were confidently related to echinoid grazing activity, identified in ichnology as *Gnathichnus pentax* (Bromley, 1975). No traces were linked to polyplacophoran or gastropod grazing. The groove classified as a straight line was hypothesised to have been made by a fish or decapod, but the possibility that it was man-made cannot be fully dismissed.

Hard-bottom assemblages are important and accessible ecological subsystems that can serve as early detection and evaluation of responses to environmental change. Devising experimental approaches to test hypotheses rigorously defined is of fundamental importance to understand responses to specific pressures rather than reactions to cumulative stressors (Loke and Chisholm, 2023). Biological interactions, notably competition and predation (including grazing), are strong forces shaping the structure of the assemblages, and therefore deserve dedicated research effort and thoroughly designed experiments. The study reveals some underlying mechanisms behind the structuring of lithophilic assemblages, highlighting the importance of biological interactions in polar shallow subtidal zones. Revisiting old theoretical frameworks such as assemblage succession paradigms, supply-side ecology, and the intertwined effects of exploitative and spatial interference competition will help decipher the mechanisms of struggle for existence in rapidly changing marine systems.

Chapter VI General conclusions

The applied study design provided many interesting findings.

1. For the entire study, over 200,000 organisms were identified.
2. Over the 15 years, observable shifts in taxonomical dominance occurred within the structure of the lithophile assemblage.
3. No new species of boreal origin were observed over the course of the study, therefore not indicating major borealisation. However, the contribution of boreal organisms to the overall assemblage was higher following warmer years.
4. A distinct drop in the density of the endemic, opportunistic arctic bryozoan *Harmeria scutulata* after 2013 was observed.
5. Throughout 11 years of annual sampling, significant differences in the structure of the assemblage were noted, including fluctuations in the contribution of boreal species to the overall assemblage. However, the response sometimes showed a ‘lag’ following the ‘warm’ standardised anomalies.
6. The ‘depth’ factor in the presented study design represented the presence and influence of kelp on the assemblage structure. The densities of taxa reached higher levels in the samples from the experimental constructions located within the kelp forest.
7. When applied, the orientation of the artificial substrate was the significant factor shaping the lithopile assemblage structure. The upward-facing plates obtained the lowest level of settlement as well as the number of traces, when compared to downward-facing and vertical plates.
8. The downward-facing and vertical settlement plates obtained the highest number of traces, indicating high predation impact, with most grazing traces being linked to echinoid activity.

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Supplementary Information 1 List of identified taxa with mean densities (ind./100 cm^2) at each sampling station.

	2005				2020			
	infralittoral		circalittoral		infralittoral		circalittoral	
	S1	S2	S1	S2	S1	S2	S1	S2
Alcyonidium sp.	1.33	0.00	0.00	0.00	0.33	0.00	0.00	0.00
Arctonula arctica	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Callopora craticula	0.00	2.00	1.67	0.00	1.33	5.00	3.67	4.67
Callopora lata	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Callopora lineata	3.67	29.67	4.33	0.00	18.00	13.33	3.67	11.67
Callopora sp.	4.33	15.33	3.00	1.33	6.00	3.67	2.33	5.00
Celleporella hyalina	9.67	11.67	0.00	1.00	5.33	3.67	1.33	0.33
Cribrilina annulata	2.67	4.67	0.00	0.00	2.67	0.33	0.00	0.00
Crisia sp.	1.67	0.33	0.00	0.00	0.33	0.67	0.33	0.00
Crisidae indet.	1.00	0.67	1.00	0.00	0.33	0.00	2.00	0.00
Cylindroporella tubulosa	0.00	0.67	0.67	0.00	5.67	4.67	5.33	9.67
Dendrobeania sp.	0.00	2.67	0.33	0.00	0.00	0.00	0.00	0.00
Doryporella spathulifera	0.00	0.00	0.00	0.00	0.00	0.67	0.67	2.00
Diplosolen arctica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Einhornia arctica	0.00	0.00	0.00	2.67	0.00	0.00	0.33	0.00
Harmeria scutulata	27.00	100.00	0.33	0.00	5.67	0.67	0.67	0.00
Hippodiplosia obesa	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00
Hippothoa arctica	1.33	0.00	1.33	0.00	0.33	0.00	0.33	0.00
Microporella arctica	1.00	7.33	0.33	0.33	20.67	113.33	29.00	5.00
Myriozella crustacea	2.00	3.33	0.67	0.33	5.33	6.67	10.33	2.67
Patinella sp.	9.67	37.33	18.00	27.67	24.33	18.33	39.67	47.00
ancestrula Cyclostomata	134.33	65.67	82.33	18.67	307.67	180.00	111.33	338.00
Porella sp.	0.33	0.00	0.00	0.00	0.00	2.00	0.67	0.00
Raymondcia rigida	0.00	2.33	0.67	0.00	0.00	1.33	0.67	0.33
Scrupocellidae indet.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Schizoporellidae indet.	1.33	1.67	0.00	0.00	0.00	0.00	0.00	0.00
Smittina minuscula	0.00	0.00	1.00	0.00	0.00	0.00	0.67	0.00
Stomacrustula cruenta	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Tegella arctica	0.00	10.33	4.00	0.00	10.67	45.67	5.33	5.67
Tegella armifera	0.00	0.67	0.00	0.00	0.67	1.00	1.33	1.67
Tegella sp. white type	0.00	4.00	1.67	0.00	0.67	3.00	2.00	0.00
Tegella sp. dark type	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.67
Tricellaria sp.	0.33	0.00	0.00	0.00	0.33	0.00	0.33	0.00
Tricellaria arctica	0.00	0.00	0.00	0.00	0.00	0.00	4.67	0.00
Tricellaria gracilis	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Tubulipora flabellaris	0.33	0.00	1.67	0.00	0.00	1.00	1.33	1.33
Tubuliporidae indet	5.33	3.67	11.00	0.00	17.00	8.67	9.33	13.00
ancestrula Cheilostomata	3.33	8.67	4.33	1.00	66.67	19.67	17.67	38.33
Semibalanus balanoides	153.00	157.33	51.67	235.33	15.00	0.00	1.00	0.00
Cirripedia cypris	0.33	0.67	2.33	1.00	0.33	0.00	0.00	0.00
Circeis sp.	125.33	346.67	119.00	57.33	332.33	527.00	278.67	326.00
Spirorbis/*Bushiella*/*Pileolaria* sp.	62.00	70.00	67.00	0.67	131.33	76.67	86.33	12.33
Spirorbis tridentatus	0.00	0.00	0.00	0.00	0.00	4.67	0.67	0.00
Circeis spirillum	2.00	22.33	4.33	0.00	13.33	10.00	2.67	4.00
Paradexiospira vitrea	121.00	130.00	30.00	2.00	502.00	111.67	33.33	22.33
Spirorbinae indet.	19.33	10.00	9.00	1.00	51.00	44.67	70.67	33.67
Chitinopoma serrula	0.00	0.00	0.33	0.00	0.00	1.00	0.00	0.33

Supplementary Information 2 Shadeplot displaying densities of identified taxa under all treatments.