

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 CO₂, 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.