Summary in English

Phylogeography and population genomics of boreal marine macroinvertebrates colonising High Arctic

Several recent studies have reported the phenomenon of 'Atlantification' in the High Arctic. The alteration of the local marine ecosystems towards a more temperate state and the appearance and/or range expansion of subarctic-boreal species at higher latitudes is a complex phenomenon, mainly induced by the warming climate conditions. The process affects organisms from different taxa as well as from different trophic levels. The appearance/expansion of phyto- and zooplankton, as well as benthic invertebrates and several species of fish have been recorded. The shifts in the distribution of these organisms have also consequences for species at higher trophic levels, influencing their diet and overall fitness.

The focus area of this thesis, Svalbard lies north from continental Europe, halfway between Norway and the North Pole. The archipelago has been an attractive subject of research for several decades. The great infrastructure (international research stations, airports, ports), and the large amount of data on geography, marine ecology, climate, glacier dynamics etc., make Svalbard a suitable location to conduct climate change research in the Arctic. The archipelago is characterised by a great temperature gradient between the west and the east coastlines, as these areas are influenced by warm and cold ocean currents, respectively. At present times Svalbard is experiencing the fastest temperature increases, and the highest sea ice loss within the circumpolar Arctic. Just in the last decades fast ice duration along the coasts has decreased from over 5 months to less than 1 month per year. Throughout the history of Earth there have been several intervals, when the Arctic and Svalbard were warmer than nowadays. For instance, during the Pleistocene climate fluctuations, North Atlantic marine species expanded and contracted their occurrence ranges in accordance with the variations in temperature. In the Last Glacial Maximum (LGM), shelf areas in the Arctic were covered by extensive, thick ice sheets that strongly reduced the bioproduction rates, thus creating conditions not suitable for maintaining a rich life. The end of the LGM and the subsequent deglaciation period provided the opportunity for species surviving in glacial refugia to reconquer the previously uninhabitable Arctic. The Holocene Thermal Optimum (HTO), which started ca. 11 000 BP, was characterised by a strong Atlantic influence on the western coasts of Svalbard. This interval created generally milder conditions in marine habitats, facilitating recolonization. Although the Atlantic influence weakened for some time after

5000 BP, the repatriation processes have continued ever since and seem to strengthen due to the present-day climate conditions.

Past climate alterations could have operated in a similar way to present ones. Namely, the rising air temperature and the increased inflow of warm Atlantic water are the two main factors inducing dynamic changes in the Arctic region. The subsequent loss of sea ice is partly a self-generating process. The reduced winter ice formation is caused by the warming of the surface layer of the sea, as well as by heat advected from below by Atlantic water. Furthermore, the disappearance of sea ice and the following increase in water turbulence lead to the weakening of natural stratification of water layers with different temperature and salinity. The warming effect of the Atlantic inflow will thus further intensify. Habitats along the shores are generally more vulnerable to alterations in physical parameters. Decrease in fast ice (ice fastened to the coastline and seafloor) area, duration and thickness enhances the coastal water turbidity and wave erosion. These effects coupled with increased sedimentation due to glacier melting ultimately lead to structural changes in coastal habitats (homogenization). The increased light availability and the reduced ice stress facilitate the spread of erect macroalgae along the coasts. These conditions could favour the range expansion of intertidal species associated with this kind of habitat. Arctic coastal marine communities have been changing both in structure and function, including alteration of primary production as well as of biogeochemical cycles. Newly appearing organisms may, many times, adapt easier to such a changed environment, while the previously inhabiting species may experience population decline, disappear or contract their ranges. The distribution of marine species is highly dependent on seawater temperature. Changes in water temperature affect the density, salinity and the oxygen saturation. These parameters influence the metabolic rates, life cycles, reproduction and eventually the distribution of marine organisms. Favourable, warmer climate conditions may thus help boreal species to extend their distribution ranges northwards into the Arctic region.

The first paper in the thesis reviews in detail the ecological and biogeographical aspects of the Atlantification phenomenon. The focus area of the review is the European Arctic, more specifically five Large Marine Ecosystem (LME) areas (Fig. 1). The study is divided into subsections to describe Atlantification related processes from the lowest trophic level (primary producers) to the highest (top predators). In order to provide an extensive summary on the state of the art knowledge about the effects of Atlantification on arctic/boreal fauna and flora, we reviewed 73 studies dealing with the challenges of marine ecosystems in the studied regions. Furthermore, the review dedicates a section to the discussion of the role of

floating macro-plastic debris and its potential to aid the dispersal of marine fauna and flora and to facilitate Atlantification. Lastly, as a crucial section of this paper, we challenge the concept of contemporary, human aided Atlantification. We argue that Atlantification might be a recurring anomaly, and many of the current colonisers are in fact neo-natives returning to areas they inhabited during previous, colder climate cycles.

When it comes to studying the biogeography and population genetics in marine systems over a wide geographic range, one needs to take into consideration different factors, which may have an influence on population structure. One of those is the reproductive strategy of the study organism. This aspect is specifically important when one studies creatures without the ability of free swimming. Generally, those animal and plant species, which have life stages spent as part of the plankton are more likely to be able to disperse to long distances via passive dispersal (several hundreds or thousands of kilometres depending on pelagic larval duration). Such dispersal dynamics - if not limited by other (e.g geographical) constraints - may lead to the formation of large, panmictic populations with very minimal or no detectable genetic structure. In the opposite case, when the planktonic stage is absent from the life cycle the dispersal potential can be significantly lower. Such direct developing organisms often brood their offspring, thus those settle in the close proximity of the parent. This may lead to developing strong population structure as the level of gene flow between populations is limited. At the same time it is important to point out that direct developers may also have the possibility to disperse to long distances by other means (e.g. via drafting on natural or artificial floating substrata, or by anthropogenic aid). Thus, when assessing the present day population structure of different marine species, the above mentioned determinants need to be taken into consideration.

In the second paper of the thesis we investigated and compared the historical biogeography of three boreal macroinvertebrates potentially influenced by the Atlantification processes (Fig. 1). The study focuses on the north Atlantic and the Arctic utilising a large amount of publicly available DNA barcode data alongside newly generated DNA sequences. Our analyses, as expected, revealed different levels of population structure: stronger for the two examined direct developer species, while very weak and not geography associated for the species with pelagic larva (Fig. 2). Upon inspecting the Svalbard populations we discovered that all three species showed signals of population expansion in this area. Further investigation revealed that in all cases the population expansion was dated after the end of the LGM, but not young enough to be considered as a result of the contemporary Atlantification (Fig. 4). Thus we

concluded based on our results that the studied boreal invertebrates expanded their populations at the Arctic possibly during an earlier warm cycle.

Although DNA barcode data is still widely used in population genetic studies, when it comes to species with wide geographic distribution ranges and/or high dispersal potential (like many organisms within the marine realm), the utilisation of multiple markers leads to higher resolution inferences. With the exponentially rising availability and quality of next generation sequencing techniques, population genomic studies (where one may conduct the analysis of several hundreds, up to millions of markers) have increased in number.

In the third manuscript of the thesis we conducted high resolution population genomic analyses on one of the model species *Semibalanus balanoides*. We utilised low coverage whole genome sequencing data and genotype likelihoods to decide between two alternative hypotheses considering the origin of the species' populations on Svalbard: (1) Svalbard *S. balanoides* populations are the result of the contemporary Atlantification of the Arctic or (2) The divergence of Svalbard populations from their source is older, potentially dated after the end of the last glacial maximum. Our results unveiled the presence of a particularly strong, geography influenced population structure of the species in the studied region with individuals from Svalbard and the Bjornoya Islands forming a divergent demographic group most closely related to Scandinavian and British individuals (Fig. 1). We investigated neutrality statistics to find evidence whether a recent bottleneck event (followed by genetic drift) occurred, which could explain the divergent population still following the hypothesis of recent Atlantification (Fig. 3). Besides not finding signals of such a bottleneck event in the statistics, the results of the demographic reconstruction also confirmed that in fact the divergence of the Svalbard *S. balanoides* populations from the European ones occurred during an earlier warm period, namely during the Holocene Thermal Optimum.

Evaluating the results of this thesis invites readers to look at present day Atlantification processes from a different perspective. The overwhelming majority of the literature discusses this phenomenon in the frames of present day, human induced climate change, which ignited during the industrial revolution and has been rapidly intensifying ever since. While it is indeed crucial to study and understand these contemporary processes and their influences on Arctic ecosystems, it is equally valuable to identify potentially recurring global trends when it comes to marine species redistribution. The dynamics reviewed in the second and third chapters of the thesis support the hypothesis proposed by the first chapter, about the presence of multiple Atlantification events throughout the past interglacial and potentially even before the LGM. As Arctic ecosystems are considered young in evolutionary terms (compared to

e.g. Antarctic ones), one cannot underestimate the significance of these processes in shaping them.

Atlantification, past or present, by definition means that Arctic ecosystems are becoming more similar to those of the North Atlantic in their local climate, habitat structure and species composition. The present PhD thesis displays how this similarity is expressed in the distribution, phylogeography and population genetics of three boreal macroinvertebrates. While these findings are just small fragments in the field of Atlantification research, they still provide novelty to the discipline.

As for the perspective for the Arctic in the face of Atlantification, it remains uncertain. With the increasing influence of Atlantic water masses and the shift of species distribution boundaries towards higher latitudes, the true borders of the Arctic region may be questionable in the near future. Colonisation of Arctic habitats by newly appearing species and returning neonatives challenges the fates of current residents. The work to understand this phenomenon needs to extend way beyond the frames of this PhD thesis.