



Review

Coming home - Boreal ecosystem claims Atlantic sector of the Arctic

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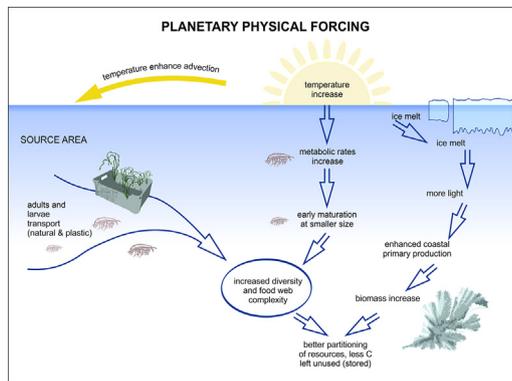
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HIGHLIGHTS

- Marine ecosystems of the European Arctic homogenise with those of the North Atlantic.
- The biological messages of the Atlantification are expressed on all trophic levels.
- The change is rather slow and quantitative towards more complicated food webs.
- Neonative taxa are reappearing at sites, from where they retreated during the LGM.
- Floating plastic debris may serve as a new way of transport for expanding boreal taxa.

GRAPHICAL ABSTRACT



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ABSTRACT

The Atlantification of the European Arctic has been an increasingly discussed topic in polar science over the past two decades. The alteration of local marine ecosystems towards a more temperate state and the appearance/range expansion of subarctic-boreal species at higher latitudes is a complex phenomenon induced mainly by the changing properties of Atlantic water (AW) transported from the south. Areas under the direct influence of AW experience biological Atlantification of their communities on all trophic levels, resulting in the growing complexity of arctic food webs. Here, besides summarising the main documented messages of biological Atlantification, we take a critical view on the threat posed on Arctic marine communities. We take into account the formation of the Arctic marine fauna, as well as the nature of (re)colonisation of Arctic sites by boreal organisms when evaluating the extent of the issue. We take a look at the history of Arctic colonisations by boreal organisms in an attempt to identify 'neonative taxa returning home'. We also highlight the role of floating plastic debris as an 'instrument from the toolbox of the Anthropocene' aiding the distribution of marine taxa.

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1. What is “Atlantification”?

Several studies in the previous decade have reported the Atlantification of the Arctic (e.g. Buchholz et al., 2012; Dalpadado et al., 2016; Kraft et al., 2013; Neukermans et al., 2018; Vihtakari et al., 2018; Wang et al., 2020). Researchers identify this phenomenon mostly as an increasing Atlantic influence in the Arctic region, initiated by global climate change - meaning that certain areas of the Arctic are becoming more similar to the North Atlantic. Obviously, the term can be interpreted differently depending on the scientific discipline. For physical oceanographers, Atlantic influence is presented by the water masses, which originate in the Atlantic Ocean and are transferred to the Arctic in the form of warm ocean currents. These masses are modified on their way north and after this transformation with time, only isotopes or microelements can tell the difference between them and local Arctic waters. On the other hand, some studies have already reported the effect of increased heat advection of Atlantic water (AW) from below, on ice melting (Polyakov et al., 2017). From the marine biology point of view, the water masses that contribute to Atlantification are those that sustain species of Atlantic origin, full marine salinity and elevated water temperature, thus maintaining optimal conditions for Atlantic organisms to live (Box 1).

Based on literature findings, areas under Atlantification are experiencing alteration of the local marine ecosystems towards a more temperate state and the appearance and range expansion of sub-arctic species (Polyakov et al., 2020). The effects are widespread, from physical and chemical parameters of water masses to the ecology, distribution and phenology of local marine organisms.

When describing such changes, one needs to consider the correct evaluation of the geographic areas, where the processes operate. Generally, we may talk about Atlantification in the case of those areas of the Arctic, which are directly exposed to AW inflow. If we consider the widely accepted division of the global shelf marine ecosystem into 66 LME (Large Marine Ecosystems) – management-biological units introduced by NOAA (<https://www.lmehub.net/#>), the geographic Arctic consists of 18 LME (Faroe Plateau, Iceland Shelf and Sea, Greenland Sea, Norwegian Sea, Barents Sea, Kara Sea, Laptev Sea, East Siberian Sea, East Bering Sea, Aleutian Islands, West Bering Sea, Northern Bering-Chukchi Seas, Central Arctic, Beaufort Sea, Canadian High Arctic-North Greenland, Canadian Eastern Arctic-West Greenland, Hudson Bay Complex, Labrador-Newfoundland) (Fig. 1A). Of those, four are under the direct influence of Pacific waters (East Bering Sea, Aleutian Islands, West Bering Sea, Northern Bering-Chukchi Seas, Beaufort Sea), three are highly isolated (Laptev Sea, East Siberian Sea and Canadian Eastern Arctic-West Greenland) and the six (Faroe Plateau, Iceland Shelf and Sea, Greenland Sea, Norwegian Sea, Barents Sea, Kara Sea) are considered as extensions of the Atlantic ocean.

It is essential to point out that not all the processes induced by climate change in the Arctic are related to Atlantification. While the former is a global phenomenon operating in polar regions with an elevated force,

Atlantification cannot necessarily be considered as a general feature of the whole Arctic. Global climate change influenced air temperatures measured in the Arctic, and its flanking regions have been showing a strong

Box 1

Formation of the Arctic marine fauna.

The biogeography of Arctic marine fauna has been described in a number of papers (see review in Bluhm et al., 2011) and while the shelf and coastal waters are well known, there is still a gap in our knowledge about the deep Arctic Ocean. As the Arctic Basin was formed in the late Cretaceous, initially the Pacific influence was equally as important, as the Atlantic. Unlike the Antarctic, where speciation has been progressing for millions of years, resulting in endemic species distinct from their closest relatives, the Arctic fauna is relatively young. It is composed of animals both Atlantic and Pacific origin (Hardy et al., 2011). Concurrently a number of Pacific species colonised the Atlantic Ocean, before the Bering Strait was closed (trans-arctic colonisation), and later became narrow and shallow (Herman, 1970). For this reason, when studying the effects of Atlantification on the distribution of animals one needs to understand the composition and the history of the Arctic marine fauna. Throughout the fluctuations of paleoclimate there have been periods of optimal conditions for residents of boreal areas to colonise habitats at higher latitudes. The climate of other eras may have forced the same species to retreat south.

The checklists of marine fauna completed for the different parts of the European Arctic (Gulliksen et al., 1999; Palerud et al., 2004; Sirenko, 2001) show the clear pattern of species number decrease from the Norwegian Sea towards east – along the diminishing inflow of Atlantic waters along the Arctic shelf. A prominent change in species richness along the Norwegian shelf has also been reported with approximately 200 species extending their northerly distribution limits into Norwegian waters since the 1990s (Narayanaswamy et al., 2010). The source area for the large sub-arctic/arctic region is the boreal part of the Atlantic (Bluhm et al., 2011). True endemic Arctic species are very few, and all belong either to the perennial sea ice habitat of Central Arctic or brackish waters of the Siberian seas (Bluhm et al., 2011). The apparent exception is large charismatic animals associated with the Arctic (e.g. polar bear (*Ursus maritimus*), walrus (*Odobenus rosmarus*), narwhal (*Monodon monoceros*) and bowhead whale (*Balaena mysticetus*)). All those species are relatively recent (e.g. polar bear evolved from brown bear about 600 kya (Hailer et al., 2012). Arctic mammals have been widely distributed in the past e.g. walrus in the North and Norwegian Sea in the Neolithic period and bowhead whales in the Mediterranean (Harington, 2008).

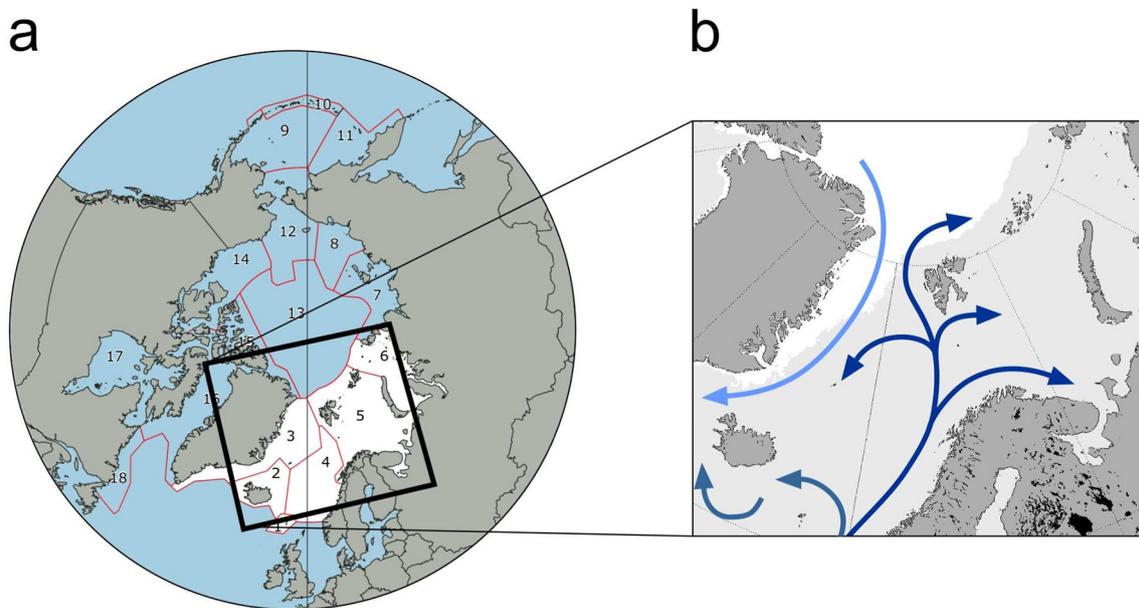


Fig. 1. a. Map showing the Arctic region with Large Marine Ecosystem (LME) boundaries indicated. LMEs coloured white are the interest areas of the present review. 1.: Faroe Plateau, 2.: Iceland Shelf and Sea, 3.: Greenland Sea, 4.: Norwegian Sea, 5.: Barents Sea, 6.: Kara Sea, 7.: Laptev Sea, 8.: East Siberian Sea, 9.: East Bering Sea, 10.: Aleutian Islands, 11.: West Bering Sea, 12.: Northern Bering-Chukchi Seas, 13.: Central Arctic, 14.: Beaufort Sea, 15.: Canadian High Arctic-North Greenland, 16.: Canadian Eastern Arctic-West Greenland, 17.: Hudson Bay Complex, 18.: Labrador-Newfoundland. b. Map of the North Atlantic – European Arctic region with main ocean currents indicated. Dark blue: warm currents, light blue: cold currents. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

warming trend. Due to the snow and ice melting and the subsequent decrease in the albedo, the fraction of the absorbed solar insolation has been significantly increasing. At the same time, contrary to the common opinion, the marine realm of the European Arctic is not “the fastest warming marine area”. Extensive study by Belkin (2009) demonstrates that net sea surface temperature increase is most pronounced in the shallow marginal seas influenced by the freshwater runoff (e.g. Baltic, Black and North Sea). As previously mentioned, large parts of the Arctic experience a sharp increase in the air temperatures (IPCC, 2014) yet not that strong in the sea surface temperatures (Belkin, 2009).

2. Concept of the review – materials and methods

To assess the threats of the Atlantification and its influence on the north Atlantic/European Arctic marine fauna this paper will focus on the contemporary changes along the Atlantic Water passage into the Arctic Ocean, including the marginal seas of the Atlantic Ocean (Greenland, Norwegian, Barents and Kara seas) (Fig. 1B). We concentrated on distribution shifts of marine organisms, and changes in the trophic structure of ecosystems of the European Arctic. Our goal was to identify and describe the messages of biological Atlantification and to define their possible interconnections. We have collected data and examined the effects on different trophic levels while focusing on a wide range of interactions and consequences. At the same time we give a critical review on the extent of the threat. In this study we focus mainly on the biological aspects of Atlantification, meaning the distribution of boreal and arctic marine species, as well as the ecology, food web complexity and functional profile of influenced communities.

The “messages of biological Atlantification” can be explained on different trophic levels and have both ecological and conservational importance. These messages include e.g. the change in the nature of phytoplankton blooms, and the subsequent shift in zooplankton species composition and energy content; the abrupt changes of Arctic intertidal communities; the increasing role of different anthropogenic vectors, such as plastic waste, in the transfer of boreal organisms to higher latitudes; the resulting shifts in pelagic fish communities; the effects reflected on higher trophic levels, such as the diet and distribution change of sea birds and mammals.

To provide this review, we conducted a comprehensive literature survey with the help of the following search engines: JSTOR, Web of Science, Google Scholar, Wiley Online Library. We used different combinations of the keywords ‘arctic’, ‘climate change’, ‘range expansion’, ‘marine’, ‘Atlantic’, ‘boreal’, ‘colonisation’, ‘Atlantification’, ‘borealization’. In consequence we gathered and overviewed a collection of 73 studies dealing with the problems and challenges of the marine realm introduced by growing Atlantic influence in the European Arctic. We also examined the accumulation of studies dealing with the aforementioned processes through the years to see if there has been any significant change in their number (Fig. 2).

3. The occurrence of Atlantification processes and awareness through the past 100 years

One important period similar in nature to today's Atlantification process occurred in the last century, in the 1920s and the 1930s. The

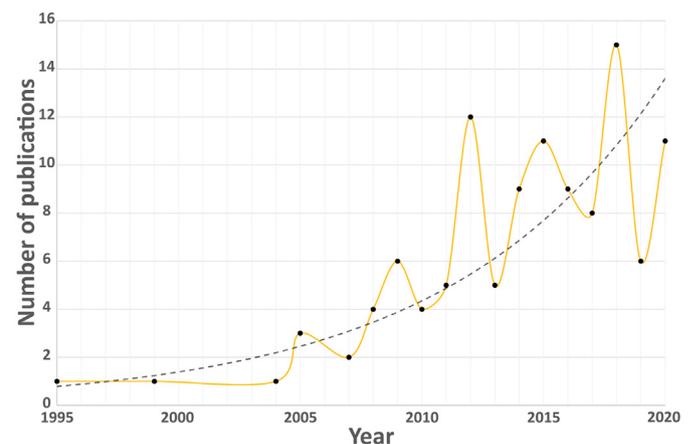


Fig. 2. Graph indicating the accumulation of studies dealing with Atlantification related processes. Studies were searched using different combinations of the keywords ‘arctic’, ‘climate change’, ‘range expansion’, ‘marine’, ‘Atlantic’, ‘boreal’, ‘colonisation’, ‘Atlantification’, ‘borealization’ in JSTOR, Web of Science, Google Scholar, Wiley Online Library.

documented regime shift in the North Atlantic included the increased ocean and air temperatures as well as reduced sub-arctic sea ice in the region. The northward expansion and increased biomass at higher latitudes of fish, such as Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*) was reported, together with the establishment of new spawning sites for these species (see Drinkwater, 2006) and references therein). The most recent period presenting such processes started in the late 1980's and reached its maximum at the beginning of the 21st century (Matishov et al., 2012). Fig. 2 shows the general growing awareness on the issue through the last 25 years reflected in the accumulation of scientific literature on the subject. Especially after 2007 a well-defined increase can be observed in the number of publications reporting different aspects of the Atlantification phenomena. This can be explained by a general increased awareness about global warming. On the other hand it has been observed that the changes in species composition, distribution and abundance of both boreal and arctic fauna usually follow the alterations of hydrological regimes by a 5 year lag (Matishov et al., 2012). This observation together with the fact that there was a period of abnormally warm years in the European Arctic between 2001 and 2006, could possibly explain the peak in the number of studies in 2012.

4. Physical attributes of Atlantification

The physical attributes of the ongoing Atlantification have been thoroughly discussed in a recent review by Polyakov et al. (2020). Thus, here we mention only briefly the main processes relevant for this study.

4.1. Atlantic water in the Arctic - temperature and salinity increase

Atlantic water enters the Arctic Ocean using the Nordic Seas as a gateway (Fig. 1B). Two main Atlantic branches provide AW supply to the Arctic Basin. The Fram Strait branch is operating through the West Spitsbergen Current. At the Fram Strait, AW submerges to the intermediate layer (150–1000 m) of the water column and joins the Arctic Ocean Boundary Current at the shelf of the Nansen Basin (Woodgate et al., 2001). The Norwegian Atlantic Slope Current is another branch transporting AW and it enters the Barents Sea Opening, and eventually enters the Arctic Ocean through the St. Anna Trough. The carried volume of AW is partly cooled down in the Barents Sea and does not advect significant amounts of heat to the Arctic Ocean. This is mainly due to atmosphere-ocean surface interaction along the shallow continental shelf, and freshwater inflow from ice melt. Through this process, heat is lost through longwave radiation to the atmosphere (Barton et al., 2018). The heat transferred by AW to the Arctic ocean was estimated to contribute 88% to the net ocean heat transport in the last century (Mulwijk et al., 2018). Pacific water transferred to the Canadian Arctic through the narrow and shallow Bering Strait is colder and less saline than the Atlantic water. Atlantic inflow into the Arctic is also unique as it brings the mesopelagic waters (between 1000 and 100 m depth) while the Pacific transport is realised through the shallow Bering Strait (50 m depth) and the waters of Siberian rivers are buoyant and influence the upper surface layer only (Aagaard and Carmack, 1989).

Water mass distribution in the Arctic is strongly affected by atmospheric processes. Generally, the properties of the AW entering the Arctic region are not steady and show annual, as well as long-term natural variability. Strong seasonal variability in the AW core temperature at the Fram Strait was recorded (Schauer et al., 2004). The minimum temperature of the AW layer, along with the highest volume of northward heat transport was recorded in the winter. Ivanov et al. (2009) demonstrated that the seasonal temperature variability of average 1.2 °C can also be observed after the AW passes the Fram Strait and submerges into the intermediate layer. While the largest amplitudes of seasonal and short term variability can be detected above 200 m depth, the interannual variability is more prominent in deeper layers. At the Barents Sea Opening at 300–400 m depth, the temperature anomaly

associated with interannual timescales exceeds the one associated with seasonal cycles (Furevik, 2001). In the past decades, several warm anomalies have been recorded in the European Arctic shelf region. The previously mentioned Barents Sea Opening experienced two warm periods (1983–84; 1990–92) and a cold one (1986–88) (Oziel et al., 2016). While the earlier warm period was associated with the increased heat of the AW inflow, the latter was suggested to be a result of the decreased heat flux to the atmosphere in the region of the Nordic Seas during these years. AW passing through the Fram Strait showed two strikingly warmer periods in the past 30 years: 1999–2000 and 2005–2007. In both cases a rising trend was detected in the core temperature of AW, arriving in this area (Beszczyńska-Möller et al., 2012). Tracking the source of such cycles is generally a difficult task, and the nature of AW temperature variability is not clear yet (Beszczyńska-Möller et al., 2012; Ivanov et al., 2009). Some studies suggest the anomalies are related to the North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation (AMO) and Arctic Oscillation (AO) (Dickson et al., 2000; Furevik, 2001; Hurrell and Deser, 2009; Oziel et al., 2016). Although the importance of these recurrent atmospheric behaviours cannot be excluded, the general long term warming trend is also becoming more and more prominent. A comprehensive study was conducted on the AW heat transport variability using hydrographic observations from the last century. The results show large decadal oscillations of ocean heat transport in the Atlantic sector as well as a consistently ongoing warming in the core temperature and increased volume of AW inflow (Mulwijk et al., 2018). This trend, of course, has been documented on smaller time scales and geographically more localised ranges. With the intensification of the North Atlantic Current, increased heat and salinity have been detected in the Nordic Seas since 1995 (Holliday et al., 2008). Since 2005, a strong warming and salinity increase trend has been described in the Barents Sea Basin, heavily affecting the position of the Polar Front (PF) (Barton et al., 2018). The PF is a water mass boundary, which separates Atlantic Water from Arctic water and is situated in the Barents Sea. On the west, it follows the topography of the sea bottom, while in the eastern part it separates into a southern temperature gradient front, and a northern salinity gradient front. This is an important transition zone, between the temperature-stratified Atlantic and salinity-stratified Arctic Ocean (Oziel et al., 2016). The northward shift of this front has drastic effects on sea ice dynamics and primary production in this area (see Section 5.1).

4.2. Ice melting

Some of the most drastic and noticeable changes in the European Arctic, induced by the Atlantification, are the loss in sea ice area, thickness and the reduced duration of seasonal ice cover (Fig. 3). A 50% decrease in the winter ice area in the Barents Sea between 1998 and 2008 has been reported as a result of increased AW inflow (Árthun et al., 2012). The AW temperature has been significantly increasing in the region since 2005, preventing sea ice from exceeding south from the PF (Barton et al., 2018). Ocean heat anomalies in the Barents Sea associated with periods of positive NAO index (Lien et al., 2017) are significantly affecting winter sea ice formation. Fast ice on the shores (ice foot) is also heavily affected by the Atlantic influence. Fast ice duration along the west coasts of Svalbard decreased from 5 months per year to <1 month per year in the past decade (Węśławski et al., 2018). The change is especially prominent in the fjords of the archipelago, which are believed to be more protected from the AW. Such processes, both on open sea and along the shores, can strongly affect not only the nature of primary production (Section 5.1) but also life forms on different trophic levels (see below).

4.3. Acidification

The primary cause of marine acidification is the increased uptake of atmospheric carbon dioxide (CO₂) by the ocean (AMAP, 2018). The

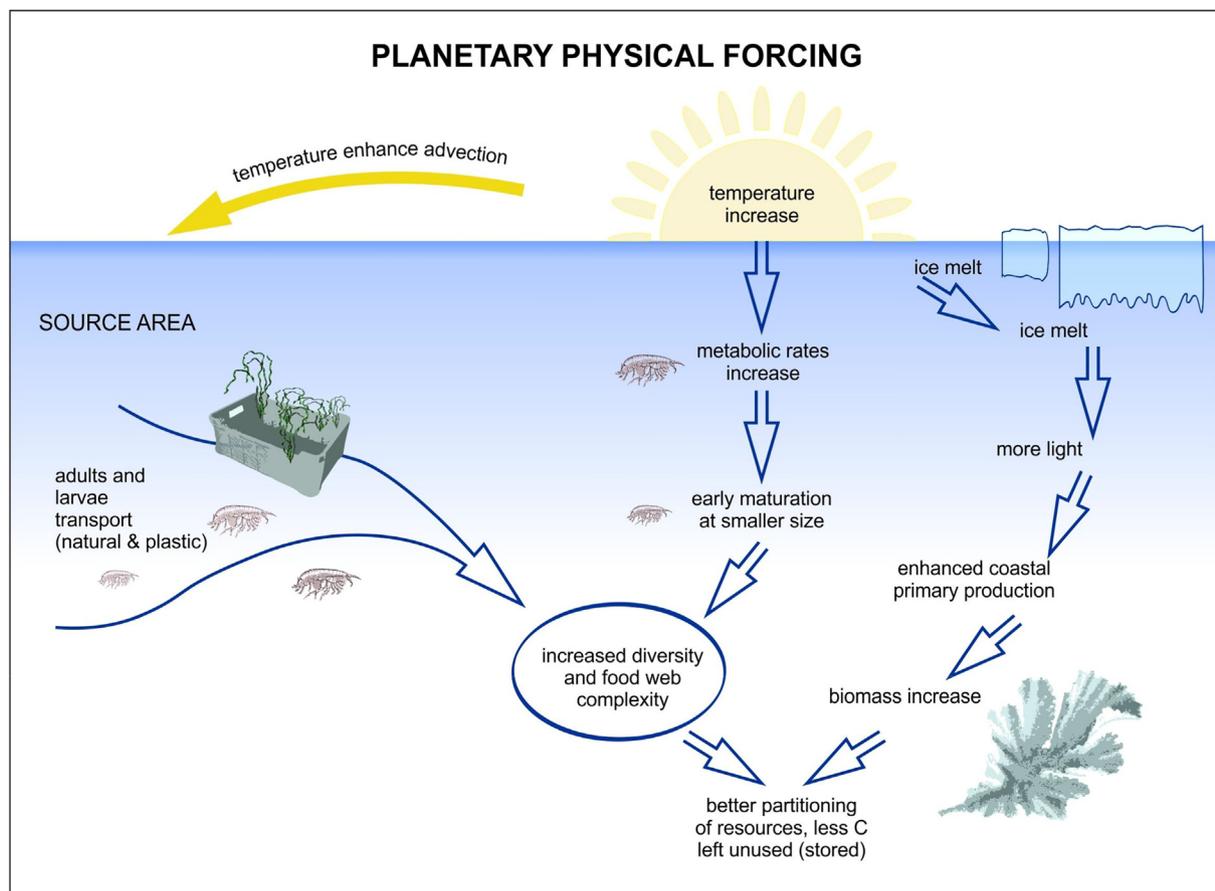


Fig. 3. Observed and predicted consequences of increased Atlantic water advection and ice melting on marine diversity, food webs and resource usage.

elevated CO_2 level is a well described aspect of global climate warming, connected to the strengthening greenhouse effect. The present epoch of the Anthropocene is characterised by human induced ocean acidification, and thus a decrease in sea water pH and carbonate mineral aragonite saturation state (IPCC, 2011; Qi et al., 2017). While the Arctic Ocean due to its low surface temperature and low alkalinity, is especially vulnerable to the increased CO_2 levels (Hoppe et al., 2018), those Arctic shelf areas, which are mainly free of sea ice (e.g. Barents Sea, Greenland Sea) are predicted to experience the smallest pH decline due to greater vertical mixing and primary production (Popova et al., 2014). Besides the direct, surface uptake of CO_2 the release of methane (CH_4) from methane hydrates stored in sediments can also contribute to ocean acidification (AMAP, 2018). The release of CH_4 from such sea bottom deposits is the most prominent along the AW passage and shallow regions directly impacted by AW (Biaśtoch et al., 2011). Ocean acidification can have a severe effect on the biogeochemical cycles of marine habitats, as well as direct and indirect physiological consequences for many marine species (Riebesell et al., 2013). Severe decrease in pH can make arctic waters corrosive for calcareous organisms in the near future (Büdenbender et al., 2011).

5. Messages of the biological Atlantification

5.1. The nature of primary production is changing in the High Arctic

Phytoplankton species, which are the foundations of marine food webs, are highly sensitive to changing physical and chemical conditions. With the geographical shifts of the ice edges and the decrease of fast ice duration along the shores, the nature of phytoplankton blooms undergoes drastic changes (Fig. 3).

With the decreasing sea ice extent, bigger areas may become favourable for pelagic phytoplankton growth, and thus for open water primary production. The shallow margins of the continental shelves contribute more than 4/5 of organic carbon production of the whole Arctic (Węśławski, 2013). In these generally open water areas, pelagic phytoplankton blooms dominate, but annual ice-edge blooms along the shrinking ice edge also significantly contribute to primary production (Perrette et al., 2010). Since sea ice cover has been gradually retreating northward, and the availability of light has increased, the elevated rate of pelagic primary production as well as a general northward shift of the production areas have been documented (Barton et al., 2016; Neukermans et al., 2018; Perrette et al., 2010). The increased open water surface area may also provide an opportunity to enhance CO_2 uptake from the atmosphere, thus to further facilitate primary production. Especially the growth of small sized phytoplankton was shown to boost under elevated CO_2 levels (Keys et al., 2018). The most prominent northward shift can be observed in the changing position of the annual spring-ice edge blooms. Ice edge blooms are occurring in seasonally ice-covered areas and are characteristically following the melting ice on the north (Perrette et al., 2010). They form narrow but long bands and are induced by freshwater input from the melting ice, which releases nutrients and trace elements into the upper ocean layer (Cherkasheva et al., 2014; Schandlmeier and Alexander, 1981). Based on chlorophyll-a and on particulate inorganic carbon concentration increase, around 30% growth in primary production was estimated in the northern and eastern Barents Sea in the period 1998–2014 (Oziel et al., 2017). Atlantic intrusion is one of the factors, which may promote the northward and eastward shift of these ice-edge blooms in the Barents Sea.

Similar processes have been described in the area of the Fram Strait. A significant increase in May chlorophyll concentration was detected

between 1998 and 2009 in the southern Fram Strait (Cherkasheva et al., 2014). The authors concluded that the described process was due to the elevated levels of warm AW inflow, increased light availability, and the decline of shelf ice around Svalbard.

Not only the spatial but also the temporal shifts of phytoplankton blooms have been more frequently discussed. Although the length of the polar night is not changing, the earlier decline of sea ice due to elevated temperatures leads to the shifts of summer blooms to earlier periods (Søreide et al., 2010). A significant shift in phytoplankton blooms to earlier periods have been recorded at different areas of the eastern Arctic region, including the Greenland Sea, the Kara Sea, the areas around Novaya Zemlya (Kahru et al., 2011).

The increasing advance of boreal/temperate phytoplankton species affects the overall species composition. The calcifying phytoplankton *Emiliana huxleyi* of temperate origin has significantly shifted its distribution northward into the Barents Sea in the past 30 years (ca. 500 km) (Hegseth and Sundfjord, 2008). The species has been expanding its blooms not only in the direction of the Barents Sea but, in 2003, it was the most dominant phytoplankton species in the AW surfacing north of Svalbard. Now the northern limit of its distribution has reached the PF (Neukermans et al., 2018). Based on a combination of historical observation and predictions, it may be concluded that a great share of the North Atlantic diatom and dinoflagellate communities shifts progressively northward and eastward (Barton et al., 2016).

5.2. Zooplankton: phenology, distribution, and community composition changes

Consequences of the Atlantification are also well reflected in the zooplankton communities of the European Arctic. Alterations in the physical environment together with the spatial and temporal shifts in phytoplankton blooms propagate changes in zooplankton phenology, distribution, community composition and thus in the overall energy content (Fig. 3). Studies have shown that the greatest changes were observed at the boundary of the Arctic shelf seas at transition zones between the Atlantic and Arctic (Gregory et al., 2009). The reduction of sea ice surface and thickness as well as of the associated algal flora in the Arctic marginal ice zone have been recorded as a potential problem for the maturation and reproduction of *Calanus glacialis*, an endemic arctic herbivorous zooplankton species (Søreide et al., 2010). *C. glacialis* makes up to 80% of the biomass in Arctic shelf seas and is a crucial component of the pelagic lipid-based food web (Feng et al., 2016). During its development, it takes advantage of both ice and pelagic phytoplankton blooms (females use the ice bloom, while offspring have access to the pelagic bloom two months later (Søreide et al., 2010)). Even a small-time lag in this fine-tuned system (i.e. earlier break-up of the ice, and thus earlier pelagic bloom) can have significant effects on food web dynamics influencing higher trophic levels. Different zooplankton species are known to be associated with different water masses (Atlantic, Arctic, mixed). Consequently grazer zooplankton taxa have been shifting their distribution in the Atlantic-Arctic, following warm water masses and phytoplankton shifts. A comprehensive study focused on the changes of nine planktonic calanoid species assemblages (a total of 108 calanoid species/taxa) in the north-eastern part of the North-Atlantic Ocean between 1958 and 2005 (Gregory et al., 2009). The authors reported an overall northward shift of several species assemblages and changes in species composition in different parts of the studied range, e.g. a decrease in the abundance of subarctic species and an increase in cold-temperate mixed water species south from Iceland since 2003. The copepod *Calanus finmarchicus*, of boreal north-Atlantic origin, has been reported several times to expand its distribution northeast into the Arctic (Chust et al., 2014). Its increased dominance compared to arctic mesozooplankton species was observed in the West Spitsbergen Current and adjacent areas (Weydmann et al., 2014), as well as in the Barents Sea (Aarflot et al., 2018). These kinds of replacements can lead to increased biodiversity of zooplankton

communities, but at the same time to a decrease in the mean size of organisms and of energy content (lipids). The available lipid content of plankton is a crucial factor in the Arctic food webs. Because of the low temperature and strong seasonality of parameters (polar day to polar night shift) arctic organisms need high quality and quantity of long-chain omega-3 fatty acids (Ackman, 1989). The loss of nutritional value induced by the community level switch to boreal zooplankton species can have widespread effects on the whole ecosystem level (see later sections). Also, due to the different life cycles of boreal and arctic zooplankton (overwintering, egg production), switches in species composition can ultimately lead to a mismatch between the peak of available lipid content and the activity of predators from higher trophic levels. On the contrary a study by Renaud et al. (2018) argued that the switch from arctic to boreal zooplankton exactly because of the aforementioned changes in generation length and population turnover might provoke a more efficient way of energy transfer in future, altered arctic food webs. The authors also point out that lipid content of zooplankton rather depends on developmental stage (therefore body size), than on the species, questioning the reliability of the species-based approach of community observations. Evidently, the average mesozooplankton biomass in the Barents Sea remained relatively stable despite the documented decrease in Arctic zooplankton following the retreat of Arctic water masses (Dalpadado et al., 2012). To that end the true consequences of community wide zooplankton composition changes for taxa on higher trophic levels remain debatable.

Arctic fjords are interesting places to observe range shifts and appearance of boreal species. The more open fjords are vulnerable for the warm Atlantic influence compared to closed fjords (Trudnowska et al., 2020). On the other hand, freshwater inflow from melting glaciers and the subsequent decrease in seawater salinity does not allow for every zooplankton organism to survive (Węstawski and Legezyńska, 1998). Macro-zooplankton euryhaline krill species are among the few which can tolerate such conditions (Buchholz et al., 2010). In 2006, the appearance of several expatriate euphausiid species was recorded in Kongsfjorden, West-Spitsbergen. These were the temperate-boreal *Meganycitophanes norvegica* and *Thysanoessa longicaudata*, as well as subtropical-temperate *Nematoscelis megalops* (Buchholz et al., 2010). The occurrence of such species suggests a strengthening Atlantic influence on this northern Arctic fjord. *Meganycitophanes norvegica* was recently found in the diet of Arctic fish in the northern Barents Sea, proving the involvement of this boreal taxa in the Arctic food web (Eriksen et al., 2020). A study reported the strikingly lower lipid content of these boreal/subtropical species compared to arctic residents. Besides lipid content the differences in energy storage patterns of these species can also propose problems when it comes to their implementation into Arctic food webs (Huenerlage et al., 2016) (Fig. 3).

In many cases, although the appearance of boreal/temperate species has been recorded on the High Arctic, the environmental conditions may not be suitable for the establishment of stable populations. Reporting the successful reproduction of these species in the High Arctic is a sign of further Atlantification of the area. *Thysanoessa raschii*, another boreal origin krill species, although had not been showing any evidence of reproduction since its first report in Kongsfjorden, was shown to spawn by (Buchholz et al., 2012). This further proves the increase of Atlantic influence. The successful reproductive activity of *Themisto compressa*, a north-Atlantic pelagic amphipod was reported in 2011 at the Fram Strait. The presence of all life developmental stages, including ovigerous females with fertilized eggs as well as recently hatched juveniles was recorded (Kraft et al., 2013).

5.3. The functional trait profile of fish communities in the Arctic seas is under change

With the disappearance of climatic barriers, the northward shifts of pelagic fish species are more common and have been reported several times through the past decades (Drinkwater, 2009; Fleischer et al.,

2007; Fossheim et al., 2015; Hollowed et al., 2013; Spies et al., 2019). Fish are capable of large scale geographical range shifts. For example, the presence of the widely distributed Atlantic snake pipefish (*Entelurus aequoreus*) was recorded as far north as the west coast of Spitsbergen, confirming a latitudinal shift of 15° from the northern edge of its regular distribution (Fleischer et al., 2007). The potential movement of fish species towards higher latitudes is influenced by a great number of factors, such as growth potential, optimal spawning conditions, spawning stock size, thermal tolerance, habitat depth, migration corridor depth, prey availability and foraging plasticity (Hollowed et al., 2013). At the same time, underlying adaptive transformations of their life history strategies are the key element in enabling rapid and large scale shifts (Nielsen et al., 2013). Pelagic long-distance migratory fish species are more likely to shift their distribution range (Fossheim et al., 2015). Another reason for big-scale range shifts can be the potential expansion of foraging areas due to the shift in the distribution of prey. This happened in the case of the Northeast Atlantic mackerel (*Scomber scombrus*) which has, in recent years, expanded its summer feeding migration significantly to the west and to the north from the Norwegian Sea (Berge et al., 2015; Pacariz et al., 2016). Northward and eastward shifts of entire fish communities have been reported in the Barents Sea (Fossheim et al., 2015). This study confirmed the poleward expansion of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), and the north-eastward shift of the beaked redfish (*Sebastes mentella*). Parallely, the advance of boreal pelagic fish species has led to the retreat of arctic benthivorous fish to deeper areas of the Barents Sea, bordering the Arctic Basin (Frainer et al., 2017). Due to such shifts, a sharp change in the functional trait profile of fish communities is evident. Larger body size, generalist diet, better swimming ability and higher growth rate have been shown to become more dominant traits of fish in the northern Barents Sea. Smaller bottom-dwelling Arctic fish species are retreating and thus the significance of these traits are declining in the communities (Frainer et al., 2017). The increase in pelagic primary production (see Section 5.1) can further enhance the shift from Arctic to boreal-like community composition, as the latter is generally more dependent on this energy pathway (Reigstad et al., 2011). The disappearance of sea-ice and associated benthic fallout of ice associated algae has led to the decreased supply of benthic secondary production. In this altered environment, the switch from benthic to pelagic energy pathways can be abrupt and can have a very serious negative effect on arctic benthic fish communities. Such changes in the functional traits of communities can influence whole ecosystems. A recent study, implementing metaweb analysis revealed increasing connectance and decreasing modularity of Arctic food webs, as a result of expanding boreal generalists (Pecuchet et al., 2020). Parallely Renaud et al. (2012) detected <40% of dietary overlap among two boreal (*Gadus morhua*, *Melanogrammus aeglefinus*) and one arctic (*Boreogadus saida*) fish. Although polar cod (*Boreogadus saida*) in pelagic habitat might not be severely affected by changing environmental conditions, young life stages of the species residing under pack ice are to a greater extent disturbed. Young polar cod have been shown to dominantly prey on *Apherusa glacialis*, an ice-associated amphipod in the Central Arctic Ocean (Kohlbach et al., 2017). Such discovery supports the assumption that polar cod is in fact strongly linked to the cryosphere during its early development. Hence the disappearing pack ice poses a significant threat for this Arctic key species, as it will likely lose the ice-associated part of its life cycle (Hop and Gjøsaeter, 2013).

The ongoing changes in zooplankton community composition influence both local Arctic, and advancing boreal fish species. The dynamics of energy transfer from lower trophic levels have been altered, and as a result food webs are undergoing complex changes. The previously described switch from Arctic *C. glacialis* to boreal *C. finharmicus* for instance may affect predators in different ways. The results of a recent study by Bouchard and Fortier, 2020 indicate that *C. glacialis* was the main carbon source for juvenile polar cod in circumpolar Arctic seas between 1993 and 2009. The habitat reduction of *Themisto libellula*, a key

arctic amphipod species has likely led to the reduced abundance of polar cod in West Spitsbergen fjords (Dalpadado et al., 2012). On the other hand areas which are under direct Atlantic influence (e.g. Norwegian Sea, Barents Sea), and have already experienced major shift in zooplankton community composition (increased mesozooplankton and krill availability), are now increasingly available for boreal generalist fish species such as the capelin (*Mallotus villosus*), the sand lance (*Ammodytes spp.*) (Bouchard and Fortier, 2020), and the Atlantic cod (*Gadus morhua*). Predators of capelin have been also benefiting from the growing abundance of this fish species. Atlantic cod has been recorded to reach record high stock of age 3+ individuals in recent years in the Barents Sea, and the underlying reason is partly the increased availability of capelin (Johannesen et al., 2016).

5.4. Intertidal and benthic communities

Within the concept of Atlantification, the distribution of organisms existing in the pelagic realm is greatly impacted by the movement of water masses with different core temperatures (see above). On the contrary, shallow coastal and intertidal habitats are more likely to be influenced by the surface water warming and its consequences (Renaud et al., 2015). At the same time, other factors, such as seafloor morphology and sediment type, can play important roles in determining the overall fate of coastal habitats (Węśławski et al., 2011).

The Arctic intertidal and shallow benthos are generally species-poor (Węśławski et al., 2011) (Box 2). However, with the changing conditions, important keystone species from boreal areas have already or are still predicted to shift northward (e.g. seaweed species). Distribution of seaweeds is strongly correlated with sea surface temperature (Jueterbock et al., 2013). In the Arctic environment, the intertidal macroalgae diversity is low, mainly because of harsh conditions on shores dominated by fast ice (Wiencke and Amsler, 2012). The disappearance of the ice foot allows macroalgae to have access to more light and to an increased area of inter- and subtidal substrate (Węśławski et al., 2011). Such processes are believed to have played a role in the extended depth range and productivity of kelp along the coast of Greenland (Krause-Jensen et al., 2012). Erect boreal macroalgae have progressively replaced calcareous algae in the fjords of western

Box 2

Dispersal ability of marine organisms.

The patchy distribution of near-shore habitats in the European Arctic raises an interesting problem when studying the dispersal of intertidal/shallow benthic animals. Given the habitat discontinuity and the generally great distances between shores suitable for inhabiting, some of these organisms may face challenges reaching remote areas, such as the Svalbard archipelago. The mode of dispersal, of course, depends on the dispersal potential, which is directly linked with life-history traits. In the case of species with highly dispersive, e.g. planktonic or free-swimming, larval life stages, the main dispersal mode is drifting with ocean currents (Fig. 3). At high latitudes, where planktonic larval stages last longer, even considering the moderate current speeds, dispersal distances can be great (Álvarez-Noriega et al., 2020). This way, if conditions are optimal, boreal species can reach the High Arctic along the routes of main ocean currents, transporting AW from south to north. In the case of animals without pelagic larvae, an effective way of dispersal can be rafting on floating substrata. Drift on wood or algae has always been a natural way of transport, but recently there has been a rapid increase in the amount of plastic - which can also serve as a surface for rafting - entering the oceans (Fig. 3; Box 3).

Box 3

The role of floating plastic debris in the dispersal of marine organisms.

The global impact of plastic debris on marine ecosystems is a serious issue, and the attention it is given is greatly justified. Several common types of plastic debris are buoyant and have been reported to be transferred by ocean currents. The floating plastic can accumulate in so-called 'convergence zones' or 'garbage patches' in sub-tropical regions of the oceans. From here it can be washed up on the shores of mid-ocean islands, or even reach distant regions of the Earth such as the Arctic or the Antarctic (Barnes and Milner, 2005). In fact, the Arctic Ocean has been reported to be the dead end for plastic transferred from Europe by the North Atlantic current (Cózar et al., 2017). Plastic debris in this region has been identified mostly as fishing equipment and household items (Węśławski and Kotwicki, 2018). The surface of such plastic items is many times exposed to biofouling by different species of bacteria and algae as well as by encrusting invertebrates such as bryozoans, barnacles, molluscs etc. (Van Sebille et al., 2016) (Fig. 3). Although the presence of these taxa on floating and washed up macroplastic has been recorded (Gil and Pfaller, 2016; Kershaw et al., 2011), the extent of the colonising effects of such organisms at their destinations has yet to be verified. At such cold water temperatures, as in the Arctic Ocean, the decomposition time of plastic waste can take longer compared to other regions in the world's oceans. In result, species which use the floating plastic as their temporary mobile home, can travel long distances, up to several thousands of kilometres (Kershaw et al., 2011). More importantly, rafting on plastic debris can be an effective way of transport for species with both high and low dispersal potential. Compared to other ways of transport, e.g. transport in the ballast water of ships, travelling on plastic is slower, giving rafting organisms more time to acclimate to changing conditions and a better chance of survival (Barnes and Milner, 2005).

Svalbard, resulting in the restructuring of entire communities (Kortsch et al., 2012). The advance of temperate seaweed species can facilitate the recruitment and growth of associated organisms. As boreal species appear and expand, the biodiversity of such habitats increases. When macrophytes colonised the inner fjords of Svalbard, the associated epifauna, such as bryozoans also advanced (Kortsch et al., 2012). The abundance of the sediment dwelling polychaetes together with meiofauna, as well as of boreal amphipods significantly increased along the High Arctic coasts in the last 30 years (Węśławski et al., 2010).

Besides the increasing temperature and the homogenisation of shallow near-shore habitats, the enhanced food supplies for pelagic larvae of boreal animals (see the aforementioned increased rates of primary production) could also lead to improved conditions for survival and growth of newly appearing species (Fig. 3).

The North Atlantic blue mussel, *Mytilus edulis*, is an indicator of milder, AW influenced marine conditions at the high Arctic (Hjort et al., 1995). The (re)appearance of the species was first recorded on Bjornoya (Węśławski et al., 1997), then a few years later in a fjord on (Berge et al., 2005), and was hypothesized to be aided by atypical weather conditions. In the year 2002, the masses of warm Atlantic water transported northward by the West Spitsbergen Current were unusually large (strong positive NAO), and the normally strong southern winds preventing the Atlantic inflow to enter the fjords of Svalbard were absent (Berge et al., 2005). The pelagic larvae of *M. edulis* could be transported by these waters, and thus the species could settle in the Arctic fjord. Now *M. edulis* is widespread and reproducing along the western shores of Spitsbergen (Leopold et al., 2019).

The amphipod crustacean *Gammarus oceanicus*, another boreal intertidal invertebrate widespread on Svalbard, started to colonise the high Arctic since the LGM. The progressive expansion of its geographical range has been well documented. While in the 1980's the species was shown to inhabit only some more Atlantic-influenced sites along the archipelago, by 2011 *G. oceanicus* was generally widespread and abundant along the whole western Svalbard (Węśławski et al., 2018). *G. oceanicus* also showed increased abundance and more dynamic demography, compared to *Gammarus setosus*, a species which prefers colder conditions and has apparently survived in the Arctic during the LGM (Grabowski et al., 2019).

With the appearance of new inhabitants, Arctic intertidal taxa also face new challenges. The retreat of resident Arctic species is believed to be to a certain extent, limited. Unlike in the case of pelagic organisms, near-shore marine species have access to a very narrow range of potential areas, which can still maintain optimal condition. Such areas could be shores influenced by cold ocean currents (e.g. the eastern part of Svalbard), or more protected, closed inner fjords. On the other hand model projections implemented by Renaud et al. (2019) actually predicted low mean % habitat loss for arctic benthic taxa under recent climate change. In the light of such results the authors question the extent of the vulnerability of these taxa considering biogeography and general physiology.

The Arctic intertidal amphipod, *Gammarus setosus*, was shown to significantly decrease in abundance on the western, warmer, shores of Svalbard and to gradually retreat to the northern and eastern parts of the archipelago, where the colder conditions still dominate (Węśławski et al., 2018). At the same time, other cold-adapted species can benefit from the milder climate conditions. The growth rates of the Arctic bivalve, *Serripes groenlandicus* was shown to be higher on the more Atlantic influenced, western parts of Spitsbergen compared to the eastern shores (Carroll et al., 2011).

5.5. The ecology and distribution changes of birds and mammals

The distribution and life history adaptation of animals at higher trophic levels are very often shaped not only by environmental conditions but also by the changing availability of their prey. Monitoring seabird gut content is one great way to track the shifts in the distribution of fish species, but also to infer the level of predator adaptation to changing prey availability. Black-legged kittiwakes (*Rissa tridactyla*), a small circumpolar surface-feeding seabird of the gull family, have been proven to be a great indicator of the Atlantification processes in western Svalbard (Vihtakari et al., 2018). The study reported a shift from Arctic prey dominance to an increased boreal prey abundance in the diet of the Svalbard populations of the species since 2007. The changing arctic food web systems and the involvement of boreal species might propose an additional threat to higher trophic levels in the form of introducing novel parasite-host interactions. As a result of the ongoing Atlantification processes, Arctic seabirds now have access to an increased number of boreal crustacean and fish species to include in their diet. Trophically transported parasites have complicated life cycles, which often include intertidal invertebrates (molluscs, crustaceans) as intermediate hosts. Birds are often not specific hosts of these parasites, but rather get infected by consuming infected fish (Kuklin et al., 2004). A 2004 study pointed out that the majority of Arctic birds of Svalbard probably got infected by boreal parasites during their annual migration to more southern nesting sites (Kuklin et al., 2004). However, with the changing conditions of local habitats, the high Arctic has now become suitable for an increasing range of helminth parasites (including trematodes, cestodes, nematodes) to complete their life cycles (Galaktionov, 2017).

An additional aspect of the shifting distribution of organisms at lower trophic levels is the change in the foraging strategies of seabirds. There is a need for such behavioural changes in order to optimize the energy budget of the organism between altered circumstances. The

ecology (especially feeding) of some polar bird species, e.g. the ivory gull (*Pagophila eburnea*), are strongly dependent on the sea ice (Descamps et al., 2017). With the repositioning of the marginal ice zone north, towards the Arctic Ocean (see Section 4.2) foraging trips of such species can be severely altered. Little auks (*Alle alle*) in Franz Josef land have switched to new foraging hotspots along the edge of melting glaciers, as the area has reportedly been free of pack ice since 2005 (Grémillet et al., 2015). On the other hand, the possibility of such a strategy shift may not be available in all areas. Seabird foraging trips thus can increase in distance, time and energy input. In such cases, other important components of fitness (e.g. reproductive success, chick mortality) can be severely impacted. In fact, the abundance of copepod zooplankton was shown to be one of the main determinants, besides atmospheric temperature, in choosing wintering locations for the little auk (*Alle alle*) in eastern Greenland (Fort et al., 2012). The energy rich *C. glacialis* copepodite stage V is known to be the main prey of little auks. The previously mentioned spatial and temporal shifts of zooplankton can introduce certain challenges for seabirds, whose foraging behaviour is connected to the distribution and abundance of arctic plankton. Increasing sea surface temperatures thus can prolong the length of foraging trips of those birds, which are dependent on Arctic prey. Birds can choose different strategies to maintain the energy balance of their diet in the face of currently occurring changes. Different colonies of little auks on Svalbard either extended their foraging trips to the distant marginal ice zone (high arctic colonies), or chose to vertically expand their foraging area and prey in deeper depths (boreo-arctic colonies) (Jakubas et al., 2017). Interestingly, despite the changing environmental conditions during studied years, the overall energy value of chick's diet and chick survival rate was not significantly altered in a Horsund colony of little auks. On the other hand maximum chick body mass in warmer years was lower (Jakubas et al., 2020).

Similar to some seabird species, the endemic arctic ringed seal (*Pusa hispida*) has also been shown to alter foraging behaviours due to shifting sea ice extent. Sub-adult individuals generally expressed an increased foraging effort, such as longer diving periods and shorter resting intervals (Hamilton et al., 2015). This behaviour could also be connected to the previously mentioned shifting prey distribution, which is of course also affected by the retreating sea ice. Other marine mammals have been hypothesized to switch their prey preferences and to include advancing Atlantic taxa in their diet. Based on changes in habitat use in the fjords of Svalbard, beluga whales (*Delphinapterus leucas*) are now hypothesized to feed increasingly on Atlantic prey (Vacquié-Garcia et al., 2018). Cetacean observation in the Atlantic-Arctic is a common practice to access information about the distribution of different species. Between 2002 and 2014 a general pattern of shifting towards higher latitudes and into coastal environments was observed in the case of cetaceans (minke whales (*Balaenoptera acutorostrata*), fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*), sperm whales (*Physeter macrocephalus*)) (Storrie et al., 2018). The presence of such shifts could be potentially dangerous, as long-distance migrating species may expand their ranges into areas, where commercial shipping is more frequent. This possibly happened in the case of the North Atlantic right whale (*Eubalaena glacialis*), with an increasing number of deaths observed parallel to the northward range shift of the species (Meyer-Gutbrod and Greene, 2018).

There has been a considerable amount of studies published, dealing with the consequences of climate alteration for the flagship species of the Arctic, the polar bear (*Ursus maritimus*). Possibly one of the most prominent issues induced by climate change coupled with the strengthening Atlantification for this top predator in the European Arctic, is the severe loss of sea ice. The decreasing area and duration of both fast and pack ice (see Section 4.2) results in a reduced access of polar bears to ice associated prey and thus increases the length of their fasting periods (Laidre et al., 2020). Fast ice areas near glacier fronts are particularly important for the survival of females and young cubs, as this habitat provides the best access to predictable prey (ringed seal pups) (Freitas

et al., 2012). The annual later arrival of sea ice to Hopen Island (Svalbard) has had a negative effect on female body mass (Derocher et al., 2011). Floating ice also serves as a general corridor for the species between their foraging and denning areas. Due to the observed decrease fewer pregnant females were reported to reach their traditional denning areas in east Svalbard (Descamps et al., 2017). As another possible result of declined ice associated foraging, adult polar bears have reportedly started to prey on the Svalbard reindeer (Iversen et al., 2013; Kavan, 2018), and even presented interspecific predation (Stirling and Ross, 2011). A monitoring study aiming to reveal demography of the polar bear population in the Norwegian Arctic showed that population size has remained stable compared to results of a 2004 survey (Aars et al., 2017). The debate is open on whether the population size is yet to follow the declining sea ice area, or the top predator of the Arctic will manage to endure the challenges proposed by Atlantification.

6. Neonatives in the Arctic: Atlantification as the latest chapter in the climatic history of the Arctic

The climatic history of the Earth is turbulent and, especially during the last 2.5 Mya, characterised by interchanging glacial and interglacial periods. The distribution of animal and plant species, as well as microorganisms, has always been affected by the changes in climate. In the marine realm, where temperature gradients are among the main restrictors of species expansions over a wide range, the role of oscillating climatic conditions is crucial in shaping spatial distributions over a long term. While a high level of population connectivity and genetic panmixia is generally associated with interglacial periods, during glacial phases populations are often structured and isolated in different glacial refugia (Jesus et al., 2006). After the end of a glacial period, expansion from such refugia, and subsequent colonisation of previously inhabitable areas were a general pattern many terrestrial and marine organisms followed in the past (Hewitt, 2004). Most evidence about glacial and interglacial dynamics of marine populations are available for the Last Glacial Maximum (LGM) (ca. 21 ky BP) and the postglacial warming from ca. 16 ky BP. During LGM, the continental 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 (Nørgaard-Pedersen et al., 2003) (Fig. 4A). However, there is some evidence for sub-Arctic or even Arctic refugia (Grabowski et al., 2019; Hardy et al., 2011) (Fig. 4A). The end of the LGM and the subsequent deglaciation period provided the opportunity for species surviving in glacial refugia to reconquer the previously uninhabitable areas (Brochmann et al., 2003; Krebs et al., 2011). The Holocene Thermal Maximum (HTM), which started ca. 12,000 BP, was characterised by a strong Atlantic influence on the Arctic (Fig. 4B). This interval created generally milder conditions in marine habitats, facilitating recolonisation (Hjort et al., 1995). Observing the past distribution of many taxa in the North Atlantic and in the European Arctic, we cannot exclude the possibility, that a certain share of boreal organisms expanding their ranges towards higher latitudes today, are in fact returning to areas where they already existed before the LGM and/or in the last climatic optimum (ca. 9500–5000 BP). For such organisms, here we use the term “neonatives”. The term has been intended to describe species, which expand their distribution ranges into previously uninhabited areas as a result of human induced environmental change (Essl et al., 2019). Upon definition the authors clarified that neonative organisms should not include species, which recolonise historically lost regions. At the same time, the study overlooks those species, which return to areas previously inhabited by them, and lost not during historical times, but earlier, due to altering glacial and interglacial cycles. Therefore we consider extending the meaning of neonative species to include such organisms also. The term indeed very well describes the nature of such (re)colonisation and the difference of these creatures from aggressively expanding invasive species. Tracking the distribution

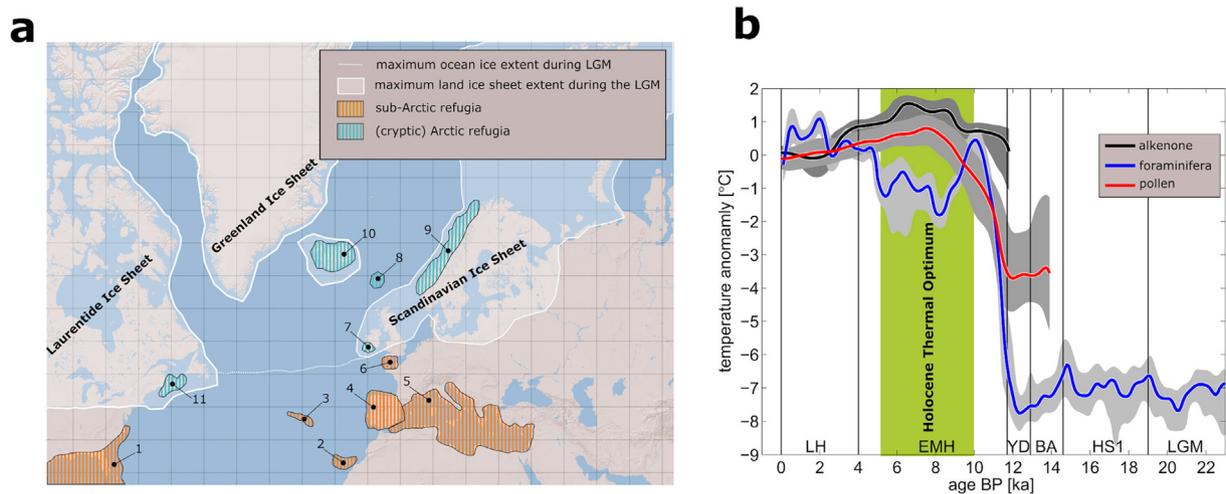


Fig. 4. a. Map of the North Atlantic region during the last glacial maximum (LGM). Maximal extent of land ice sheets and sea ice are marked. Documented sub-Arctic and (cryptic) Arctic ice age refugia for marine taxa are marked (following Maggs et al., 2008). 1: Carolinas, Florida and the Gulf of Mexico; 2: Canary Islands; 3: Azores; 4: Iberian Peninsula; 5: Mediterranean Sea; 6: Western English Channel; 7: Southwest Ireland; 8: Faroe Islands; 9: Northern Norway; 10: Iceland. b. Graph showing the reconstructed paleoclimate of the Norwegian Sea from 22 kya until present. The graph has been imported from Eldevik et al. (2014). The graph indicates the potential timeframes suitable for North Atlantic marine taxa to (re)colonise higher latitudes from ice age refugia. The Holocene Thermal Optimum (HTM) is marked on the graph as one such time period. LGM: Last Glacial Maximum; HS1: Heinrich Stadial 1; BA: Bølling-Allerød; YD: Younger Dryas; EMH: Early-Mid Holocene; LH: Late Holocene.

of neonative plants and animals can be understood as the observation of the distribution range fluctuations of some species that follow climate oscillations. On the other side of the spectrum, invasive species usually spread fast, often with abrupt appearance aided by unintentional human help. They can be characterised by fast-breeding, short generation times, and wide physiological tolerance to a variety of environmental factors (Marchetti et al., 2004). Invasive species are often globally distributed and/or cryptogenic (without known origin area). The increased number of such species in the Arctic can be connected to the growing occurrences of accidental introductions. Chan et al. (2019) identified the main factors, which promote the influx of invasive species to the Arctic. These include the ballast water of vessels, biofouling and aquaculture activities as well.

A series of phylogeographical studies have been published in the last 20 years, reporting the postglacial range shifts of different marine taxa. The recolonisation of high latitude sites by neonative organisms after the end of the LGM started from glacial refugia. Such refugia were either situated in more southern areas (e.g. Mediterranean Sea, Iberian Peninsula, Azores, Florida), or in some cases, cryptic northern refugia were also described (e.g. Faroe Islands, Iceland) (Maggs et al., 2008) (Fig. 4A). From these northern refugial areas population expansion and recolonisation of previously glaciated areas were possible. In the case of intertidal organisms, during the LGM not only the cold temperature but also the decreased access to rocky shore habitats limited the distribution of taxa. Especially on the American side of the Atlantic, with the southern margin at Long Island, rocky intertidal habitats were entirely covered by the Laurentide Ice Sheet during the LGM, and thus uninhabitable. Furthermore, southern refugia alongside the American shores (e.g. Florida) were lacking hard substrata, making it almost impossible for rocky intertidal taxa to remain in the Western Atlantic (Wares and Cunningham, 2001). A comprehensive study on the phylogeny and population structure of *Gammarus oceanicus* in the North Atlantic revealed significant demographic expansion on previously glaciated sites, as well as evidence of glacial refugia on the Faroe Islands (Grabowski et al., 2019). One of the most known cases of a neonative species returning to the Arctic is the example of the North Atlantic mussel, *Mytilus edulis*, which (re)appeared in Svalbard in the beginning of the 21st century (Berge et al., 2005). According to fossil data, the species was present on the archipelago at ca. 12–13 kya, at the beginning of the HTM (Hjort et al., 1995), and later possibly retreated due to colder climatic conditions. Another taxon, which has survived

the LGM in the North Atlantic-Arctic is the furoid seaweed, *Ascophyllum nodosum*. This important keystone species possibly had refugia both on the American and European shores of the North Atlantic Ocean (Olsen et al., 2010). From the pelagic realm, the case study of the arctic foraminifera, *Neogloboquadrina pachyderma* represents the possibility of a planktonic species getting isolated in the Arctic, even before the last glaciation (Darling et al., 2007).

There are also pelagic taxa, which have been reported to have gone through postglacial population expansion in the North Atlantic-Arctic region. For example, the study by Weydmann et al. (2018) presents the case of *Calanus glacialis*, which increased its population size by 1000-fold approximately 10,000 years BP. The authors concluded that the observed expansion could have been aided by the increasing temperature and changing ocean circulations after the LGM.

7. Conclusions

The term Atlantification covers a wide range of processes induced by the present-day climate change in the Atlantic sector of the Arctic, which ultimately shape the climate, the environment and the marine species composition to resemble that of the North Atlantic region. Due to the strong seasonality of the environment (light, temperature, nutrients, ice cover) in this region, organisms of all trophic levels had to adapt their life-history traits (e.g. reproduction, feeding, growth, phenology) to, often very narrow, time-windows of optimal conditions. By severely altering environmental conditions, and by facilitating the northward advance of boreal organisms, the increasing Atlantic influence introduces an additional threat to this fragile system. As the processes of biological Atlantification operate on many different scales and trophic factors, its messages are also widespread, but at the same time interconnected:

1. The overall rate of open water primary production increases in the Arctic shelf seas. The temporal shifts of phytoplankton blooms due to changing light availability have been documented. This event can induce severe mismatches between primary production peaks and other components of the Arctic food webs. The northward shift of boreal phytoplankton can possibly further intensify the issue.
2. The Atlantification generates changes in the distribution, species composition, and ultimately, energy content of zooplankton communities. The most affected areas in this matter are those shelf areas,

where the AW enters the Arctic Ocean (Barents Sea, Fram Strait and the fjords of western Svalbard). The warmer temperature together with the northward and eastward expanding boreal species lead to the lower energy content of zooplankton, which can have severe effects on other parts of arctic communities, which prey on these animals.

- Due to the changes on lower trophic levels, and the more frequent northward shifts of boreal fish species, the functional trait profile of Arctic fish communities has been transforming. Larger body size, generalist diet, better swimming ability and higher growth rate are replacing smaller body size and bottom-dwelling lifestyles in arctic fish communities.
- The geographical expansion of intertidal keystone species often leads to subsequent shifts of associated taxa (especially, in the case of algae species, when they serve as substratum for a variety of other organisms). Local, Arctic species retreat simultaneously, although they have limited possibilities to do so. As a result of the patchy distribution of nearshore habitats in the European Arctic, some boreal intertidal taxa with low dispersal potential may have problems dispersing northward. The increasing amount of plastic litter transported by ocean currents to the Arctic, may act as a possible 'transporter' for some species.
- Species representing higher trophic levels at the Arctic often need to change their distribution and/or ecology, based on the availability of their prey. The alteration in the diet and/or foraging strategy of arctic seabirds has already been reported as ways of resolving changing prey composition and availability. Cetacean observations confirmed northward shifts in the case of several marine mammals. The reason behind this phenomenon could possibly be the retreating sea ice edge and the northward shift of prey taxa. The Arctic top predator polar bear has been reported to encounter serious challenges in the face of declining areas of pack- and fast ice. The response of the species to its changing habitat is to this day subject of extensive research.
- Studying the climatic history and past species distribution in the Arctic region may help to understand and explain the current changes and possible trends. Several taxa can be identified as neonatives, indicating that their current northward expansion may be in fact a return to habitats from where they had to leave due to harsh climatic conditions in the past. The distinguishing of such repatriant organisms from more and more aggressively spreading alien, invasive species poses as a new important task for marine researchers

The perspective for the European Arctic in the face of Atlantification is 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. On the other side of the spectrum, change observed in the European Arctic seas so far may not be the "tipping point" nor the "regime shift" – but rather slow, quantitative change towards more complicated food webs (Renaud et al., 2019; Węśławski et al., 2017). The ongoing process may be also a manifestation of a general trend for biotic homogenisation – unification of habitats and biota on a large geographical scale (Deja et al., 2016; Olden and Rooney, 2006).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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