



ORIGINAL RESEARCH ARTICLE

# Ecosystem maturation follows the warming of the Arctic fjords

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**Summary** Two fjords in West Spitsbergen (Hornsund 77°N and Kongsfjorden 79°N) differ with regard to their exposure towards increasingly warm Atlantic water inflow. Hornsund remains in many respects cooler than Kongsfjorden (on average 2°C SST in summer) and is less influenced by warmer and more saline Atlantic waters. Reported changes in the physical environment (temperature rise, freshwater inflow, salinity drop, turbidity, fast-ice reduction, coastal change) are discussed in the context of biological observations in the pelagic and benthic realms with special reference to krill (Euphausiacea). We conclude that well-documented changes in the physical environment have had little effect on the fjord biota and that both organisms and their ecological functions in the fjords are well adapted to the scale of ongoing change. The observed changes fit the definition of ecosystem maturation, with greater diversity, a more complex food web and dispersed energy flow at the warmer site.

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## 1. Introduction

Currently observed environmental changes – specifically those in the marine ecosystem reported in the last [IPCC document \(2014\)](#) – are well documented, yet their predicted consequences are a matter for debate. We selected two Svalbard fjords as a case study, since they are among the best studied Arctic regions ([Hop et al., 2002](#); [Svendsen et al., 2002](#)), and because the archipelago lies in the centre of reported environmental change ([ACIA, 2004](#); [Pavlov et al.,](#)

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2013; Walczowski and Piechura, 2006). Public concern about Arctic change is understandable, as the visible element – ice, disappears before our eyes (Duarte et al., 2012). When traditional marine biogeography came into being (Ekman, 1953), the Arctic was given the status of a fully “independent province”, owing to the obvious ice cover and its cold character, not because of its faunistic or functional uniqueness. This stands in stark contrast to the other polar area, the Antarctic, which is a hydrologically separate entity with a rich endemic fauna and long evolutionary history (McIntyre, 2010).

The Svalbard archipelago has most often been placed at the boundary between the High Arctic and Arctic or the Arctic and Sub-Arctic, with the borderline along the west coast of the island of Spitsbergen (Backus, 1986; Ekman, 1953; Sherman et al., 1990). Some authors have used the more general expression “temperate and cold waters of the Northern Hemisphere” (Golikov et al., 1990). The present paper summarizes and reviews data recently acquired within the GAME (Growing of Arctic Marine Ecosystem) project. We are going to demonstrate that most of the changes to the fjord ecosystem, reported from Spitsbergen, are in fact shifts within one large system. The changes resemble the process of ecosystem maturation as described by Odum (1969), namely, the development of more complex and balanced food webs and a higher level of carbon metabolism.

## 2. Material and methods

The data discussed below were collected from *r/v Oceania* during late July–early August surveys in 2013–2015, in the central basins of Hornsund (77°N) and Kongsfjorden (79°N), on a flat, even seabed of 100 m depth as part of the GAME project. There, an array of multidisciplinary observations were gathered from the water column and seabed, relating to hydrography, water column optics, water chemistry, plankton (from piko- to macroplankton), fish, as well as

sediment biogeochemistry, bacteria, and meio- and macrofaunal assessments. The oxygen consumptions of the sediment and dominant taxa were also measured. In order to ensure the best possible comparability of the data, the same group of people made the observations, within a short time window, using the same equipment and measuring techniques. The specific methodologies are described in separate papers. Archival hydrographic data, collected in the two fjords between 2000 and 2015, were also used as background to give the fresh data a long-term environmental perspective (specific data are cited in the paper). All the data are accessible on the project's website and an illustrated summary can be found at <http://www.iopan.gda.pl/projects/Game/deliverables.html>.

To place the above-mentioned observations in a wider perspective, we took the case study of the expansion of Euphausiacea to the Spitsbergen fjords, studied by the second author (literature cited in the text).

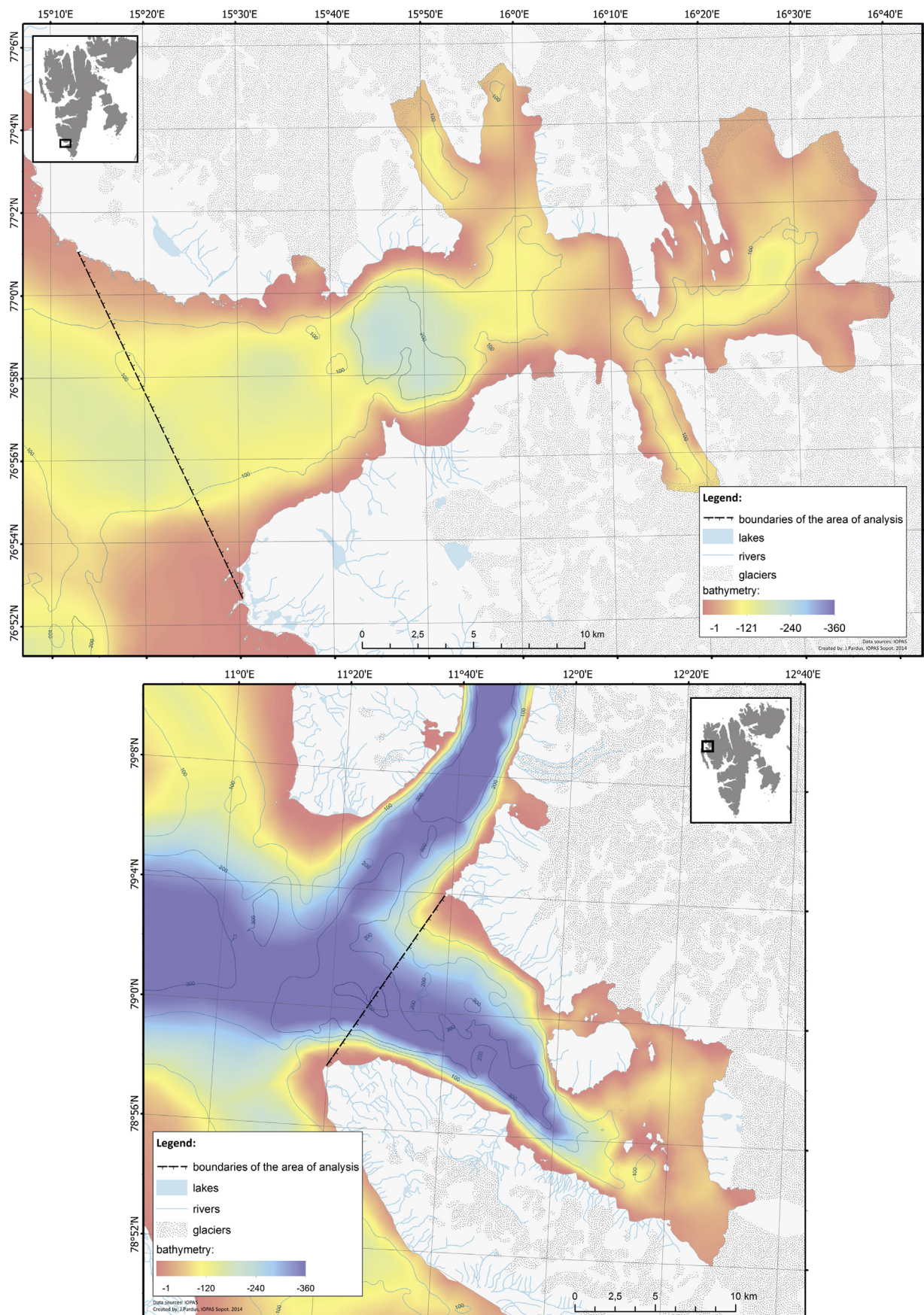
## 3. Results and discussion

### 3.1. Environmental drivers

Table 1 shows that the two fjords (Hornsund at 77°N and Kongsfjorden at 79°N) are similar in size (300 and 210 km<sup>2</sup> respectively), volume (25 km<sup>3</sup>) and shape with semi-separated inner fjord branches (Fig. 1) <http://www.iopan.gda.pl/projects/Visual/index.html>. The general circulation pattern is also similar, with shelf waters entering the fjord along the southern shore and flowing back out along the northern (Jakacki et al., 2017; Svendsen et al., 2002). Both fjords lack a sill at their entrances, yet depth is the important difference: Hornsund is shallower (max. depth 220 m) with a flat bottom profile, whereas Kongsfjorden is deep (max. depth 350 m) with a V-shaped bottom profile. Kongsfjorden's bathymetry links it directly to the outer shelf and slope via the Kongsfjordenna (Włodarska-Kowalczyk, 2007). Hornsund is

**Table 1** Observed physical differences between “cold” Hornsund and “warm” Kongsfjorden; data from cruises of *r/v Oceania* in 2010–2013 and Urbański et al. (1980), Swerpel (1985), Beszczynska-Möller et al. (1997), Błaszczuk et al. (2013), Drewnik et al. (2016), GAME project web page <http://www.iopan.gda.pl/projects/Visual/index.html>.

Factor	Hornsund	Kongsfjorden
Average near-bottom temperature in summer at 100 m depth (°C)	2	4
Average summer surface temperature	4	6
Fast ice: % of fjord area	20–25%	5–10%
Fast ice duration	3–5 months	1–3 months
Freshwater (glacial melt) volume in summer	0.7 km <sup>3</sup>	0.3 km <sup>3</sup>
Coastal change (new areas uncovered by glaciers between 1936 and 2000)	8% increase in sea bed shallower than 50 m	13% increase in sea bed shallower than 50 m
Winter cooled water retention in summer, volume	Always, usually 0.2–0.45 km <sup>3</sup>	Seldom, 0–0.02 km <sup>3</sup> at best
Wind pattern	High percentage of local easterly winds driving freshwater out of the fjord	High percentage of westerly winds driving shelf water into the fjord
Atlantic core water inflow from shelf	Rare, outer part of fjord only	Regular in summer, deep into the fjord
Fjord topography	Shallow (max. depth 220 m)	Deep (max. depth 350 m)
Fjord area	300 km <sup>2</sup>	210 km <sup>2</sup>



**Figure 1** The bathymetry and topography of two fjords upper Hornsund, lower Kongsfjord, compared in the paper, modified after <http://www.iopan.gda.pl/projects/Visual/index.html>.

colder, fresher and less influenced by Atlantic shelf waters than Kongsfjorden (Table 1). The wind pattern is slightly different, with a more local, easterly circulation in Hornsund and more often westerly, open sea winds in Kongsfjorden (Table 1).

Kongsfjorden is treated here as an example of an already warmed system, whereas Hornsund remains relatively cold. The long-term hydrographic monitoring show that along the west coast of Spitsbergen, the sea surface temperature and volume of Atlantic waters, though variable, are steadily increasing (Walczowski, 2014). It is difficult to separate a local sea temperature rise from the general temperature increase of Atlantic waters, as the two most often go together. There have been specific situations, as in 2004, when during a strong inflow of Atlantic water, easterly winds moved cold, freshened water with sea ice from east Svalbard over the top of the warm saline waters flowing along the west coast, then in “warm year” we have got cold water and sea ice (Promińska et al., 2017). Another important environmental driver is the vertical partitioning of the fjord waters. The dynamics of the thin, freshened layer at the surface with its turbid glacial outflow is controlled mainly by the wind pattern and is highly changeable. In contrast, the near-bottom waters, especially in the inner fjord basins, are more stable, slow-moving, and respond to changes at the surface after a time lag (Drewnik et al., 2016). The intermediate water column also shows a different pattern in the two fjords: the deep canyon of the Kongsfjordrenna easily directs Atlantic waters from the outer shelf deep into the fjord, whereas this happens only rarely in the shallower Hornsund (Table 1, Węstawski et al., 2016).

In contrast to the increasing numbers of krill in the Arctic (Eriksen et al., 2016), the truly polar Antarctic krill, *Euphausia superba*, is diminishing dramatically (Atkinson et al., 2004). Only a few krill species have managed to adapt to the polar environment over the last 20 my, meaning that they are irreplaceable, not even by the “ice-krill”, *E. crystallophias*, because this is eco-physiologically completely bound to the ice edge. Instead, *E. superba* is being replaced by herbivorous tunicate *Salpa thompsoni*, which prefer warmer waters (Pakhomov et al., 2002). Antarctic krill stocks are thought to have been reduced to one third during the last two decades. The reason for this is an ice-effect: with the sea ice around the Antarctic strongly receding, krill is losing an essential habitat, particularly for overwintering. Here we have a clear response to global warming, evidently associated with ice retreat. This is very unlike what we are seeing in the Arctic and in Northern Hemisphere krill.

An interesting chapter in (Arctic-) ocean warming and the associated faunal changes is the history of krill in Kongsfjorden. There are now five euphausiid species regularly present in the pelagic fauna instead of the original two; this change took place at some time before the turn of the last century. In contrast, the colder Hornsund is still at the two-species level (Buchholz et al., 2010). First of all, we would like to take a rather more global perspective by comparing and trying to predict what may happen to the zooplankton community and its associated flora and fauna in Kongsfjorden. Then, we propose to consider physiological traits in the species, because, quite obviously, their specific adaptive capacity determines their ability to persist in new regions. Thirdly, euphausiids make good water body indicators, partly because they are good swimmers and can maintain their position within a specific water mass following favourable trophic

and abiotic gradients; in other words, they are micronekton rather than zooplankton.

The first question to clear up is that there is no such thing as the “Arctic” krill. The two krill species *Thysanoessa inermis* and *Thysanoessa raschii* are non-reproducing expatriates from the Barents Sea, which are regularly carried by the remnants of the North Atlantic Current along western Spitsbergen into Kongsfjorden and beyond. However, *T. raschii* was found spawning there recently and a complete reproductive cycle can be expected soon, as the temperature increases further and the trophic environment improves, which will better match the environmental conditions of their boreal-subarctic origin. In fact, though non-Arctic, both species are definitely cold-stenothermal: they do have an upper thermal limit in terms of respiration efficiency and a heat-shock protection repertoire (Huenerlage, 2014). Indeed, their southern survival limit has already shifted northwards: in Canadian waters their numbers have fallen off dramatically (Obradovich et al., 2014) and they seem to have disappeared altogether from the warming Kattegat and the nearby Gullmarn Fjord in south-western Sweden (Buchholz and Saborowski, unpublished). It appears that they have to move to the north, evading warming waters and following the cold. We can expect them to play an increasing role in the Arctic environment as more and more of them arrive with advecting Atlantic water masses. Strangely enough, although both species thrive during the spring plankton bloom in Kongsfjorden, they then regress during summer in terms of reproduction and growth. This implies that there must be some factor either present in the water or missing from it that does not suit them, underlining that environmental improvement is a multifactorial process: not only thermal but also trophic conditions count.

Our studies of another *Euphausia* species may be helpful in understanding adaptive capacity in krill: *E. hanseni* is like its Antarctic congener – equally bound to a specific ecological situation, namely, to the upwelling regions off the West African coast on both sides of the equator and nowhere else (Huenerlage and Buchholz, 2013). The associated physiological trait is the smallest capacity for storing lipids as reserves so far found in euphausiids: only 5% of its dry weight. This means that the “upwelling-krill” depends completely on a constant food supply that is provided within one of the most productive zones of the world all the year round. This trait is found when the animals are experimentally starved: they reduce their metabolism immediately by 70%, thereby saving energy. The opposite extreme in starvation capacity as well as associated lipid storage is our “fjord-krill”: *T. inermis* can go with no food for three weeks without any reduction in respiratory metabolism: it makes use of the huge lipid store that fills most of the carapace (the lipid body constitutes a lipid reserve of at least 40% of a specimen’s dry weight). So, here we have a perfect example of cold water adaptation that allows survival over most of the productionless boreal-subarctic winter.

The three Atlantic invaders *Thysanoessa longicaudata*, *Meganyctiphanes norvegica* and *Nematoscelis megalops* are all showing an increasing trend in Kongsfjorden. First of all, they underline the “Atlantification” taking place (Huenerlage et al., 2014). Secondly, they will have a different impact in Kongsfjorden, both as consumers and competitors within the regional food web. The rather small *T. longicaudata*,

though truly oceanic and therefore a suitable indicator of immediate Atlantic influx, is probably ecologically the least important. This may not be the case with the strongly carnivorous *N. megalops*, a bi-hemispheric species of subtropical to cold temperate origin, but which seems to thrive, i.e. feeds, moults and exhibits reproductive traits, in the Arctic environment during summer. We have not tested this yet, but judging from physiological experience it may be its extraordinary hypoxia-tolerance in warm waters (Werner et al., 2012) that is responsible for its unexpected cold-tolerance. In the end, a critical cold temperature leads to cellular hypoxia, which can be counteracted by a switch of the cell metabolism to anaerobiosis, as happens in any case under external oxygen depletion. Be that as it may, this species has to be taken seriously in view of the changing food web. The greatest impact, however, will be exerted by *M. norvegica*, often called the Northern krill which, like the previous species, has a very widespread distribution and seems to be expanding everywhere, in the Mediterranean as well as in the St. Lawrence River or Georges Bank and lately in the Norwegian and Barents seas (Eriksen and Dalpadado, 2011; Link et al., 2009). In Canada this species is even being considered for commercial harvesting, with the aim of using it in natural products, e.g. medical additives (Winkler, Gesche, ref. Natural Sci. Res. Council, Canada). We have physiologically compared Northern krill from the cool north-eastern Atlantic and the warm Mediterranean (Buchholz and Saborowski, 2000): its pronounced expansive capacity is due to a combination of its very high thermal tolerance in terms of phenotypic adaptability and its being the greatest opportunist as regards food selection. Consequently, this offers the greatest opportunity to expand, always provided this happens along with the occurrence of their food. So far, we have observed *M. norvegica* feeding very well in Kongsfjorden, better than *T. inermis* (fullness of stomachs compared); the swarms of juveniles also present merely serve to underline the trend (Huenerlage et al., 2014).

Accordingly, it is quite likely that *T. inermis* and *T. raschii* will have to compete with the Atlantic newcomers. And it looks as if the latter are already doing better in terms of food choice or selective feeding. The former species are apparently more narrowly oriented, meaning that in fact they will only thrive when their matching trophic environment moves northwards and becomes established in Arctic waters. Because of their thermal upper limit they may even have to abandon the southern parts of their range. What then? In contrast to the Antarctic, the “Arctic” krill species are numerous and in terms of quantity may compensate losses and possibly improve food web quality as a whole. However, the trump card held by the *Thysanoessa* species in the Arctic environment is their huge lipid store: this trait will always be advantageous to their survival. The other species have much smaller amounts of lipids and also of poorer quality because they store other lipid types, e.g. energy rich wax esters vs. rather poor TAGs (Tri Acyl Glycerols). In the context of food web functioning, the loss of high quality lipids vs. gain in quantity through increasing krill numbers should be considered seriously – a nice task for ecosystem modellers! At any rate, the study of the interplay of different species of one (small) crustacean family may be considered as an interesting natural experiment in climatic adaptation.

### 3.2. Ecosystem response – species change

In general the biomass and biodiversity of Kongsfjorden are distinctly higher in both the water column and the sediment (Ormanczyk et al., 2017; Zaborska et al., 2016). The number of species is not very different, however, with Crustacea, for instance, represented by 120 species in Hornsund and 130 in Kongsfjorden (Legeżyńska et al., 2017). There are similar small differences among other taxonomic groups like Bryozoa (Gontar et al., 2001; Kuklinski et al., 2005), Mollusca (Włodarska-Kowalczyk, 2007), Polychaeta (Kędra et al., 2015) and various groups of marine algae (Smota et al., 2017b).

The marine species distribution shifts observed in the two fjords (Table 2) can be attributed to different phenomena (and to the data deficit as well). Species often occur naturally over a large area, yet only a part of their distribution range is actually known, so new findings are interpreted as a distribution change – a typical situation in difficult taxonomic groups (e.g. meiobenthic Nematoda – Grzelak, pers. comm.).

Another process is the delayed reaction: a species occurs under certain physical conditions, but then disappears from part of its range as a result of, for instance, disease, overharvesting, predation pressure or breeding failure. It may attempt to return to its former range of occurrence, but is prevented from doing so by new competitors or the distance from the source population. To give an example: physical conditions favourable to blue mussel *Mytilus edulis* have existed off Svalbard since the beginning of the 20th century, yet the species did not reappear until over 100 years later (Berge et al., 2005).

Again, a species is theoretically capable of living in a certain area (habitat-related, physical–chemical limits), yet some factor prevents it from colonizing that area. Once this factor changes, however, invasion is likely to ensue. The above mentioned reappearance of blue mussel in Svalbard was made possible by the unusually high northward mass transport of warm Atlantic water resulting in elevated sea-surface temperatures (Berge et al., 2005). Another example, it is the mechanical ice scouring that prevents a number of intertidal species from occurring along the shores of east Spitsbergen, but in areas where the ice cover has receded, colonization has been rapid (Wesławski et al., 2010).

A common phenomenon is dispersal: expatriates of large, long-lived species are transported passively or may swim actively far away from their natural range of distribution. This has been demonstrated for ice amphipods (*Gammarus wilkitzkii*, *Apherusa glacialis*) expatriated south with the East Greenland Current (Duris and Wesławski, 1995; Lonne and Gulliksen, 1989). See also the krill case study below.

In general, we believe that the explanation for the phenomena listed in Table 2 is the common species pool over a large area. Conditions for several of these species may be suboptimal around its edges, hence they are rare on the peripheries, even though they are supplied from an extensive area and can move their distribution back and forth. For instance, only seven Polychaeta species are dominant sublittoral benthic dwellers from central Europe to the European Arctic (Wesławski et al., 2012). The dominance of particular species may vary from year to year, yet the species pool remains the same (Beuchel et al., 2006; Renaud et al., 2007).

**Table 2** Observed changes in species occurrence in Hornsund and Kongsfjorden and adjacent shelf waters.

Species	Remarks	References
<b>New arrivals</b>		
<i>Meganyctiphanes norvegica</i>	Range extension, limit to temperature tolerance for breeding	Buchholz et al., 2010
<i>Nematoscelis megalops</i>	Range extension, high tolerance to temperature and hypoxia	Buchholz et al., 2010
Mackerel, Herring, Atlantic cod	Advection of Atlantic waters	Own observations
<i>Themisto compressa</i>	Advection of Atlantic waters	Kraft et al., 2013
<i>Mytilus edulis</i>	Local environmental change	Berge et al., 2005
<i>Limacina retroversa</i>	Advection of Atlantic waters	Weslawski et al., 2009
<b>Local species loss</b>		
<i>Gammarus wilkitzki</i>	Able to live intertidally, with at least two closely related species	Weslawski, 1994
<i>Apherusa glacialis</i>	Able to live in shallow littoral with a number of closely related species	
<b>Local species range extension</b>		
<i>Gammarus oceanicus</i>	Expansion towards inner fjords and along the coast	Weslawski et al., 2010
<i>Fucus</i> sp. and macroalgae	Expansion towards upper littoral and newly de-iced areas	
<i>Calanus finmarchicus</i>	Expansion towards inner fjords	Kwaśniewski et al., 2010

### 3.3. The ecosystem response – functional change

Serious functional alteration is usually connected to climate change or attributed to fishery collapse (Mollmann et al., 2015) or other forms of human ecosystem usage, what can lead to regime shifts (Carstensen and Weydmann, 2012). The large-scale occurrence of Atlantic cod off Svalbard, not to mention capelin, mackerel and herring, was reported recently and is likely to induce changes in the food web (Renaud et al., 2012). Boreal pelagic fish are turning up along with their food (advection of Atlantic water with plankton), but so far no perceptible changes have been reported in the benthos (Kędra et al., 2015) and the Atlantic cod in Kongsfjorden feeds mainly on krill (Węstawski et al., 2016).

The specific functions associated with sea ice are likely to be lost in warmed-up fjords, as the ice cover has retreated markedly in recent years (Table 1). However, the sea ice habitat in fjords (fast ice) adds relatively little to the benthic realm (Weslawski et al., 1993), although it is still important for the zooplankton community, which feeds on ice algal bloom as the first source of food after polar winter (Søreide et al., 2010; Weydmann et al., 2013) and acts as a breeding habitat for ringed seals (Lydersen and Ryg, 1991). As ice scouring has decreased, there are certainly more macroalgae on the coast (Weslawski et al., 2010), and consequently macro-algal detritus is recorded in the food of the deep sublittoral benthos (Legeżyńska et al., 2014; Renaud et al., 2011).

Energy flow redirection as a functional change was envisaged by Hopner-Petersen and Curtis (1980), as strong pelago-benthic coupling is believed to be typical of Arctic waters, whereas a stronger pelagic energy flow is a sign of a boreal system. Comparison of organic carbon sedimentation

rates (Table 3) reveals a higher level of carbon sedimentation in Kongsfjorden, associated with a higher level of carbon metabolism in the sediments. As a large part of the organic carbon in Hornsund is of terrestrial origin (Koziorowska et al., 2016; Zaborska et al., 2016), the marine organic matter in Kongsfjorden is being recycled whereas the terrestrial matter is being buried (Zaborska et al., 2016). The pelagic energy flow is certainly stronger in Kongsfjorden than in Hornsund as a consequence of the larger biomass and greater diversity of grazers and micropredators (Ormanczyk et al., 2017).

Another fjord function is the production of winter cooled water (in Svalbard its temperature is below  $-1.5^{\circ}\text{C}$  and the salinity over 34) and its retention through the summer. This process is almost defunct in Kongsfjorden but still occurs in Hornsund (Table 1). Basins with cold, dense waters are apparently refugia for cold-water species (Drewnik et al., 2016b), but such a function may persist even in warmer sites, as exemplified by the presence of glacial relicts in the innermost fjord basins in the much warmer present-day temperatures in continental Norway and in the Baltic (Segerstråle, 1982).

An important function that is likely to differ between the two fjords is microbial loop activity, namely, a higher level of bacterial production and biomass in a warmer Kongsfjorden than in Hornsund (Ameryk et al., 2017; Kalinowska et al., 2015). The temperature-related bacterial processes and sediment carbon burial in fjords will most likely result in biogeochemical changes (sulphur cycle and alkalinity) to the sediments, as was demonstrated in two Greenland fjords by Rysgaard and Glud (2007). The microbial-dominated sediment oxygen uptake expressed per  $\text{gC m}^{-2}$  is not statistically different between the two fjords; the higher oxygen consumption and deeper oxygen penetration in Kongsfjorden is associated with the higher biomass and the more complex benthic community there (Kotwicki et al., 2016).

**Table 3** Examples of functional changes in the fjords.

Change	Hornsund	Kongsfjord	Function change
Primary production [ $\text{gC m}^{-2} \text{ year}^{-1}$ ]	71	42	Higher proportion of macrophytes in KGF (Smola et al., 2017a)
Carbon mineralization in sediments (% of acc.)	26%	46%	Higher proportion of marine carbon in KGF (Zaborska et al., 2016)
Energy transfer to top predators (4th TL [ $\text{gC m}^{-2} \text{ year}^{-1}$ ])	0.7	0.6	More energy to top predators in Hornsund
Carbon accumulation in sediment [ $\text{g m}^{-2} \text{ year}^{-1}$ ]	90	47	Larger carbon sink in Hornsund (Zaborska et al., 2016)
Carbon demand in sediment [ $\text{g m}^{-2} \text{ year}^{-1}$ ]	51.6	85.5	Biomass and metabolic levels higher in KGF (Kotwicki et al., 2016)
Carbon demand in water column			
Microbial production in sediments [ $\mu\text{g C kg}^{-1} \text{ h}^{-1}$ ]	0.3	0.5	More microbial production and biomass in KGF sediment, less in KGF water column (Ameryk et al., 2017)
Meiofauna size structure (length to width ratio, <12)	4%	12%	Nematoda short and stout in Hornsund, long and slender in KGF (Grzelak et al., 2016)

### 3.4. The alteration of a whole system

This is a rare event in the natural environment, e.g. a change in the Bering Sea food web (Grebmeier et al., 2006) or the large-scale disappearance of sea ice and its consequences for the Central Arctic sympagic biota (Berge et al., 2012).

Some papers discussing large-scale environmental change predict mass extinctions of species in sea waters (Worm et al., 2006), yet there are very few documented cases of such extinctions (Dulvy et al., 2003). Flessa and Jablonski (1995) published an extensive biogeographical analysis discussing the extinction probabilities of different bivalve fauna. They demonstrated that because there is no endemism, Arctic bivalves are so widespread that the threat of regional extinction is unlikely. The cosmopolitan nature of distribution and the natural variability of the Spitsbergen fjord environment (from fresh to marine, and from frozen to warm) prevent the colonization of stenotopic species and the consequent threats to their existence.

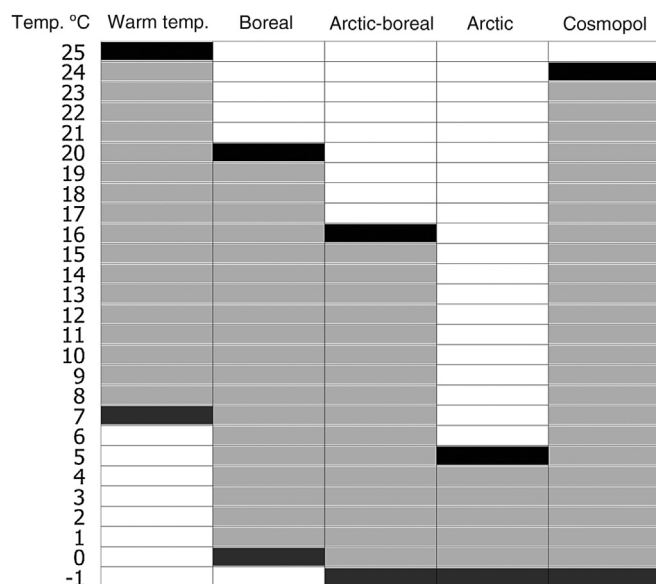
## 4. Conclusions

At a large scale, because of recent glaciation, the uniqueness of the Arctic marine fauna has just begun to be formed but has not yet had enough time to generate a new, independent ecosystem (Wares and Cunningham, 2001). Now, with increasing Atlantic water inflow and atmospheric warming of the coasts, the peripheries of the Atlantic Ocean are going to become more similar to its source, with little change in function. For the coastal marine Arctic, the sea ice is an inversed sea bottom, the habitat of a very few species that can leave the littoral for the sea ice in winter and move back to their original benthic habitat in summer (Weslawski, 1994). In general, and in contrast to the old paradigm (Beaugrand et al., 2002; Blacker, 1957), closely related species are not really replacing each other. What is currently taking place is that newcomers are arriving from warmer waters, thereby creating a richer species pool with the

original, local cold water species still present. For example, Atlantic zooplankter *Calanus finmarchicus* is not expelling the Arctic *Calanus glacialis*, although changes in species proportions are observed (Kwaśniewski et al., 2010; Weydmann et al., 2014), *Gammarus setosus* shares space with *Gammarus oceanicus* (Weslawski et al., 2010), and echinoderms are widely distributed across previously well-delimited zoogeographical boundaries (Deja et al., 2016).

Similar observations have been made in the Baltic Sea, where recently settled species add to the species pool and cause the meltdown of former zoogeographical borders (Lepakoski and Olenin, 2001).

As a consequence, observed and predicted changes in the west Spitsbergen fjords are happening within the boundaries of one, large North Atlantic biogeographical province (Sherman et al., 1990). In fact, there is not a single species from the known species lists published for the two fjords that would not be recorded in continental Norway or the Murman Coast/Kola Peninsula (see Kędra et al., 2010; Prestrud et al., 2004). The little-known biogeographical concept of Golikov et al. (1990) is based on the temperature span between extreme warm seasons in the south and extreme cold seasons in the northern range of a species' distribution (Fig. 2). This shows how large the potential space is for changes in species distribution. The differences between the colder, Arctic fjord (Hornsund) and the warmer, more open Kongsfjord are unlikely to be close to "tipping points" – irreversible change of structure and function of the system (Duarte et al., 2012), or "regime shifts" – replacement of the local ecosystem structure and function with such from the neighbouring boreal area (ACIA, 2004); it is rather a case that is fulfilling the definition of ecosystem maturation as described by Odum (1969) and Saint-Beat et al. (2015). The key phenomena observed are increases in biomass, species richness and functional group diversity, a more evenly-balanced and effective food web, and a higher proportion of organic matter metabolized within the system compared to deposited carbon, with little change in species distribution or their functions.



**Figure 2** General scheme of temperature tolerance span among different marine zoogeographical regions: range from extreme cold (winter in northern distribution limit) to extreme warm (summer at southern distribution limit); modified after Golikov et al. (1990), temperature data after Levitus (2006).

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