The future of Arctic benthos: Expansion, invasion, and biodiversity

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A R T I C L E   I N F O

A B S T R A C T

One of the logical predictions for a future Arctic characterized by warmer waters and reduced sea-ice is that new taxa will expand or invade Arctic seafloor habitats. Specific predictions regarding where this will occur and which taxa are most likely to become established or excluded are lacking, however. We synthesize recent studies and conduct new analyses in the context of climate forecasts and a paleontological perspective to make concrete predictions as to relevant mechanisms, regions, and functional traits contributing to future biodiversity changes. Historically, a warmer Arctic is more readily invaded or transited by boreal taxa than it is during cold periods. Oceanography of an ice-free Arctic Ocean, combined with life-history traits of invading taxa and availability of suitable habitat, determine expansion success. It is difficult to generalize as to which taxonomic groups or locations are likely to experience expansion, however, since species-specific, and perhaps population-specific autecologies, will determine success or failure. Several examples of expansion into the Arctic have been noted, and along with the results from the relatively few Arctic biological time-series suggest inflow shelves (Barents and Chukchi Seas), as well as West Greenland and the western Kara Sea, are most likely locations for expansion. Apparent temperature thresholds were identified for characteristic Arctic and boreal benthic fauna suggesting strong potential for range constrictions of Arctic, and expansions of boreal, fauna in the near future. Increasing human activities in the region could speed introductions of boreal fauna and reduce the value of a planktonic dispersal stage. Finally, shelf regions are likely to experience a greater impact, and also one with greater potential consequences, than the deep Arctic basin. Future research strategies should focus on monitoring as well as compiling basic physiological and life-history information of Arctic and boreal taxa, and integrate that with projections of human activities and likely ecosystem consequences to facilitate development of management strategies now and in the future.

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1. Rationale and objectives

It is highly likely that marine ecosystems in a future Arctic will be considerably different than those we see today (e.g. Doney et al., 2012; Michel et al., 2013). Conceptual and ecosystem models suggest dramatic changes in environmental conditions and human activities, which will affect species distributions, interactions, and functioning (ACIA, 2004). Globally, marine species are changing their distributional range in response to increasing temperatures (Poloczanska et al., 2013), but in the Arctic well-documented examples of changes are still scarce. Predictions, particularly regarding the benthos, have been largely limited to general statements about how warmer temperatures and less ice, combined with increased shipping traffic, will allow for range extensions and introductions of new species into Arctic habitats (Josefson and Mokievsky, 2013). Available data suggest that this has already begun in some areas (Berge et al., 2005; Mueter and Litzow, 2008; Drinkwater, 2009; Lambert et al., 2010; Mironov and Dilman, 2010). Current predictions, however, have failed to identify locations or taxa most likely to spread into or within the Arctic, or any specific consequences of predicted changes in biodiversity (see review of documented changes by Wassmann et al. (2011)).

The recent International Polar Year and related initiatives have helped Arctic researchers extend data series, develop improved sampling and monitoring technologies, enhance ecosystem models, and generally derive a better understanding of Arctic systems

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and the knowledge gaps existing there. Further it has united research communities across the Arctic through the goal of obtaining a true pan-Arctic perspective on how processes and change may act across the Arctic, and impact ecosystems both locally and remotely. Since biodiversity and other elements of community structure are integral to understanding ecological processes (e.g. Worm and Duffy, 2003), understanding of distributional patterns and the environmental conditions that promote them is necessary before we can describe how Arctic ecosystems function, now and in the future.

We, therefore, review newly gained understanding of Arctic biodiversity patterns obtained during the recent Arctic Ocean Diversity Census of Marine Life program, together with model predictions of ocean temperature distributions up to the year 2100, and results from relevant recent studies and existing time series, to formulate 4 research questions that can help structure Arctic benthic research for the coming years.

Question 1: What is the biodiversity status of Arctic benthos today, and the historical context that has steered its development?

Question 2: What biological and physical factors are most important in promoting or limiting changes in biogeographical boundaries of benthic species due to climate change?

Question 3: Which habitats and regions are most susceptible to exhibit biodiversity change in the coming decades, and what taxa will contribute to these changes?

Question 4: What are the most pressing research needs for understanding biodiversity changes in Arctic benthos?

2. Historical perspectives of Arctic benthic biodiversity

Today's Arctic fauna reflect the aggregated effects of millions of years of exchange across ocean basins and subsequent ecological and evolutionary change. Against this background, current climatic changes and expected expansion of faunal distributions are likely minor relative to the tectonically driven processes responsible for the establishment of current ecosystem structure. Still, insights from historical processes can point to potential mechanisms of current and future expansion, extinction, and persistence that can help us predict which taxa and regions are most likely to be important elements of change in Arctic benthos in the coming decades.

Much of the structure of today's Arctic benthic communities has its origins in the combined effects of tectonic processes and multiple glaciation periods. Since the mid-Pleistocene, approximately 3.5 Mya, the most influential process has been the lowering of the Bering land bridge and opening of the Bering Strait. This process allowed a corridor for shallow water species from the rich and highly developed North Pacific benthos (Briggs, 2003) to expand into the Arctic, and through to the North Atlantic. Through this and earlier exchanges, much of the North Atlantic benthic fauna appears to have Pacific origins (e.g. Vermeij, 1989). For example, 261 of 295 mollusc lineages determined to have taken part in trans-Arctic exchange have Pacific origins, whereas only 34 have Atlantic origins (Vermeij, 1991). Similar patterns have been found in other faunal groups, including echinoderms, fish, and barnacles (cited in Vermeij, 1991; Mironov and Dilman, 2010), although dominance of Atlantic origin was found for other taxa such as bivalves (e.g. Krylova et al., 2013). This pronounced asymmetry has been explained by presumed superior competitive ability of Pacific taxa (Briggs, 2003), but a different theory has suggested that higher 'ecological opportunity' caused by lower diversity in Atlantic communities, has led to greater potential invasibility of Atlantic communities (Vermeij, 1991). The latter theory is consistent with the concept of centers of faunal redistribution by which dispersal occurs from regions of higher to regions

of lower diversity (Mironov, 2006). It also has some support from the observation that invasion rarely leads to extinction of resident fauna (Vermeij, 1989), and from more recent evidence of how glacial history produces refugia and disjunct distributions, thus contributing to genetic structure of benthic populations and communities (Dunton, 1992; Väinölä, 2003; Rawson and Harper, 2009; Hardy et al., 2011). These mechanisms are not mutually exclusive, however, and much remains to be learned about the evolutionary and colonization history of many taxonomic groups.

The timing of faunal expansion events, and life-history strategies of the organisms involved, provide insight that is helpful in predicting patterns of modern faunal expansion. According to prevailing theory, the main waves of invasion, at 3.5 and 2.4 Mya and most recently after the last glacial maximum 18–21,000 years ago took place during warm climatic/oceanographic periods when the Arctic was seasonally, and in places perennially, ice-free (Vermeij, 1989; Rawson and Harper, 2009). Warmer temperatures *per se* may not, however, be the only mechanism determining successful invasion. Altered, more freely-flowing ocean currents, greater area of ice-free shallow-water habitat, and perhaps greater food supply in an ocean with more light penetration could all lead to enhanced transport through, and survival within, the Arctic region (Vermeij and Roopnarine, 2008). These mechanisms facilitate a 'stepping-stone' approach to long-distance transport. In addition, rafting of fauna on macroalgal detritus or other floating material (e.g. wood) may be very important for dispersal in some groups, and could be expected to proceed more quickly in a sea with little ice. Such transport mechanisms further suggest that warmer conditions promoting more rapid transport and providing greater habitat for settlement have, in geological history promoted expansion into and through the Arctic, and perhaps will in the coming decades as well.
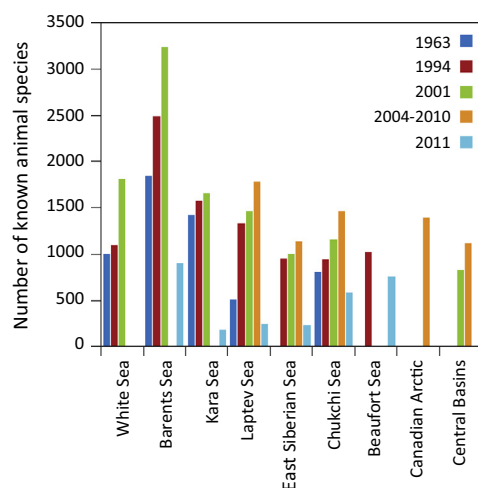
Historical species-distribution records support the idea that boreal taxa expand during times of warmer conditions in sub-Arctic regions. The classic example is the warming period in the North Atlantic during the 1930s and 1940s, which led to expansions in ranges of boreal fish and benthic communities well into traditionally Arctic regions in northern Greenland, in the Barents Sea, and around Svalbard (reviewed in Drinkwater, 2006; Renaud et al., 2008). Also modern populations of boreal species that penetrated the sub-Arctic during warmer periods 1000–5000 years ago today live in refugia in northern Norway (a chiton; Sirenko, 1998) and the East Siberian Sea (the blue mussel *Mytilus trossulus* and the cumacean *Leucon kobjakovae*: Golikov et al., 1994; Vassilenko, 1994). On the Pacific side, the position of the Bering Sea 'cold pool' fluctuates with climate due to patterns of winter ice production in the region, and has been identified as a barrier to invasion of some Pacific taxa into the Chukchi Sea, for example some commercially harvested larger fish species (Hunt et al., 2013; Hollowed et al., 2013). In recent years, northward shifts have also been observed in three species of benthic invertebrates into and within the Chukchi Sea (Sirenko and Gagaev, 2007, but see Blanchard et al., 2013), a benthic mollusc and pipefish species in the Barents Sea region (Berge et al., 2005; Fleischer et al., 2007), and the commercially important Atlantic cod (*Gadus morhua*) in the North Atlantic (Drinkwater, 2009). Trans-Arctic exchange has recently been observed in a Pacific diatom reaching the Atlantic (Reid et al., 2007) and an Atlantic ascidian appearing in the Pacific (Lambert et al., 2010), although ballast-water or ship fouling cannot be excluded as the cause for either of these species. Clearly these are relatively few examples and may represent an increase in research effort rather than an increasing trend, but more trans-Arctic exchange is expected. For example at least 77 shallow-water mollusc lineages from the northern Bering Sea have been described as being able to extend to the Atlantic via a warmer Arctic (Vermeij and Roopnarine, 2008). Increased surveillance of

these and other taxa will document faunal expansion into a warmer, seasonally ice-free Arctic.

3. Status on current knowledge of Arctic benthic biodiversity

The pan-Arctic species inventory has increased over the past five decades (Fig. 1), primarily related to persistent efforts of taxonomists in Russia, Poland and Germany, international collaborations such as the Russian–German Laptev Sea project (Petryashov et al., 1999), and recent biodiversity programs such as the Census of Marine Life (e.g. Sirenko, 2004, 2009; Sirenko and Denisenko, 2010). Over 90% of all Arctic fauna are benthic (Sirenko, 2001), and the current number of Arctic benthic eukaryotic species is around 4600 (Bluhm et al., 2011a; Josefson and Mokievsky, 2013) with several thousand species estimated to still be discovered (Bluhm et al., 2011b; Piepenburg et al., 2011). The main contributing metazoan taxa include Arthropoda, Annelida, Molluska and Nematoda, with Granuloreticulosa as the largest single-celled taxon (Sirenko, 2001). As part of the increasing inventory, at least 77 species new to science were discovered over the past decade, of which about half have formally been described to date (updated from Gradinger et al., 2010). About half of these new species are crustaceans, reflecting the dominance of this taxon in the overall inventory, and most species are benthic. Another part of the growing inventory is due to recent records that increased known northern distribution ranges. The majority of these records is in the Arctic deep sea, and most likely due to poor previous knowledge of the fauna rather than actual recent range extensions (Bluhm et al., 2005; MacDonald et al., 2010). A few range extensions recorded on Arctic shelves, however, are likely related to recent climate warming (see previous section). The rate of endemism is generally low for the Arctic shelves compared to the Antarctic and as high as in the global deep sea for the Arctic basins (e.g. Mironov et al., 2013).

Meiofauna studies in the last decade or two have concentrated on the Svalbard area (e.g. Urban-Malinga et al., 2005) and the deep-sea (e.g. Soltwedel et al., 2009), while macrobenthic studies have been part of all larger recent research programs across the Arctic. Of the single-celled benthos, foraminiferans appear to be the prominent taxon of interest, and moreso by paleontologists than biologists (e.g. Wollenburg and Kuhnt, 2000). Studies on microbial diversity have only begun to emerge in the last decade as tools become increasingly available (Ravenschlag et al., 2001). Taxonomic gaps, therefore, remain in the small size ranges up to certain meiofauna taxa, but also in larger groups such as Platyhelminthes.

Targeted efforts in the last decade helped fill part of the prominent regional gaps in our knowledge of the Arctic fauna, for example in the Arctic deep-sea (e.g., MacDonald et al., 2010; Bergmann et al., 2011; Boetius et al., 2013) and the East Siberian Sea (Sirenko and Denisenko, 2010), although those regions remain poorly studied largely due to their sheer size and inaccessibility. Large programs such as BIOICE around Iceland (e.g. Parapar et al., 2011), and benthic studies in Greenland (Sejr et al., 2010), are in the process of filling other prominent regional gaps. Ironically, near-shore waters remain poorly studied across most of the Arctic, with most of our knowledge derived from a handful of well-established marine stations such as those in Hornsund and Kongsfjorden in Svalbard. Sampling programs with benthic components during the International Polar Year have covered parts of most Arctic seas and their results are still being published. Post-IPY programs are concentrated in areas with commercial activity (i.e. the Barents Sea), or with planned or ongoing oil and gas exploration and exploitation (e.g. Chukchi and Beaufort Seas, Barents Sea).

Published time-series results relevant to biodiversity are sparse for Arctic benthos as yet, but have provided interesting insights into both pattern, and potential mechanisms whereby climate impacts the benthos (Table 1). Efforts to build time series with benthic components are underway, for example, as part of the Distributed Biological Observatory in the Chukchi Sea (Grebmeier and Barry, 1991), the deep-sea observatory HAUSGARTEN station in Fram Strait (e.g. Bergmann et al., 2011), and a photographic hard bottom time series in Svalbard (Kortsch et al., 2012). We discuss some of those results in this paper.

4. Examples of evidence for Arctic climate change

Observed and predicted changes in atmospheric temperature, cloud cover, wind and circulation patterns and CO_2 content have substantial implications for the environmental conditions in the Arctic Ocean and its marginal seas. The extent and thickness of Arctic sea ice is diminishing rapidly with another record low sea ice extent observed in September 2012 (Perovich et al., 2012). Continued warming is expected to result in an ice-free Arctic summer as early as 2050 (Arzel et al., 2006). The loss of sea ice combined with a warmer atmosphere has resulted in increased sea surface temperatures in summer. The warming has occurred in most of the Arctic, but has been most pronounced in the Beaufort, Laptev, and Kara Seas, with increases of up to 3 °C compared to the 1982–2006 average (Timmermans et al., 2012). An example of long-term trends in ocean surface-water is the time series from the Fylla Bank off West Greenland at 64°N (Fig. 2). The water temperature on this shallow Bank is strongly influenced by atmospheric temperature and occasionally influenced by input of cold Polar Water originating from the southward flowing East Greenland Current (Ribergaard, 2012). A general warming trend since the 1980s is evident.

Ocean surface heating only influences the shallow seabed habitats. Benthic animals living at greater depths will be more influenced by temperature changes driven by altered distribution of water masses and potential property changes within them. For example, the amount and temperature of Atlantic water flowing northward along the coast of Norway and into the Arctic is an important factor influencing the observed temperature at the Kola section in the Barents Sea along the 30°30′E meridian (Ottersen et al., 2000), and bottom temperature has increased here since the 1990s (Fig. 2). Similar observations have been made on

Fig. 1. Estimates of faunal species richness over time for various Arctic Seas. Expanded from Sirenko (2001), Gradinger et al. (2010), and Piepenburg et al. (2011). Estimates for 2011 are for Arthropoda, Echinodermata, Mollusca and Polychaeta combined, and only for continental-shelf stations.

Table 1
Summary of benthic time-series studies conducted in the Arctic. Observation period, region, response, and proposed explanation for response are provided.

Source	Taxa	Time span	Area	Response	Proposed explanation
Blacker (1965)	All	1878–1959	Barents Sea	Northward expansion of boreal species	Increased inflow of Atlantic water during 1920–1930
Grebmeier et al. (2006)	All	1988–2003	Northern Bering Sea	Decrease in biomass and benthic respiration	Increased fish and invertebrate predation
Beuchel et al. (2006) and Beuchel and Gulliksen (2008)	All	1980–2003	Kongsfjorden, Svalbard	Change in species composition and diversity	Climatic change related to North Atlantic Oscillation index
Coyle et al. (2007b)	Ampeliscid amphipods	1986–2003	Chirikov Basin	Decrease in biomass, particularly of larger size classes	Gray whale predation and/or climate warming
Renaud et al. (2007)	All	1980–2001	vanMijen fjord, Svalbard	No major changes observed	
Berge et al. (2009)	Decapods	1908–2007	Isfjorden, Svalbard	Change in species composition	
Kędra et al. (2010)	All	1997–2006	Kongsfjord, Svalbard	Homogenisation of outer and middle fjord communities	Increased influx of Atlantic Water
Węsławski et al. (2010)	Macroalgae	1988–2008	Southern Spitzbergen	Increase in biomass and vertical distribution	Reduced ice cover/ scour, increased temperature
Bergmann et al. (2011)	Megafauna	2002–2007	Fram Strait	Decrease in standing stock, relative composition of feeding guilds	
Kozlovskiy et al. (2011)	All	1927–2007	SW Kara Sea	No major changes observed	
Solyanko et al. (2011)	All	1920–2004	Gorlo Strait, White Sea	No major changes observed	
Grebmeier (2012)	Bivalves	1987–2008	St. Lawrence Island, Bering Sea	Decrease of *Nuculana radiata*	Climate warming, fining of sediments
Kortsch et al. (2012)	All	1980–2010	Svalbard fjords	Increase in macroalgae	Increased temperature and reduced sea ice cover
Krause-Jensen et al. (2012)	Macroalgae	1999–2011	Young Sound NE Greenland	Effect of ice cover on macroagal growth	Light limitation
Time series proxies					
Ambrose et al. (2006), and Carroll et al. (2011)	Bivalve growth series	1974–2009	Svalbard and vicinity	Growth corresponded positively with climatic indices	
Sejr et al. (2009)	Bivalve growth series	1979–2003	W Greenland	Growth related to open water period	Increased light leads to greater food supply
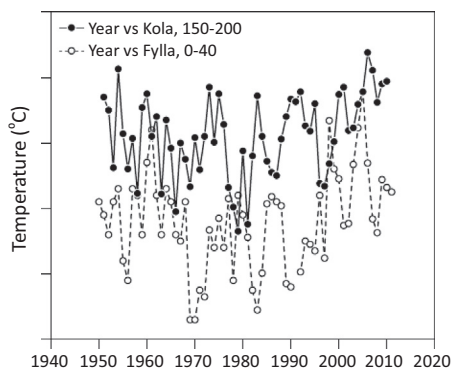
Fig. 2. Temperature records from 1950 to 2012 for Fylla Bank (0–40 m, open circles) and the Kola Transect (150–200 m, filled circles).

the west coast of Svalbard (Walczowski and Piechura, 2006), and increased inflow of relatively warm Atlantic water is suggested to be responsible for the steady increase in temperature at a rate of <0.001 °C per year observed in the deep part of the Fram Strait at 2500 m from 2002 to 2007 (Bergmann et al., 2011). Similarly,

volume transport and heat flux of Pacific water into the Arctic through Bering Strait has increased over the past decade (Woodgate et al., 2012).

In the Canada Basin, regional processes combined with large-scale atmospheric forcing has increased ocean temperature, decreased salinity and sea ice cover, and generally caused changes in ocean circulation patterns, distribution of water masses and strength of stratification (McLaughlin et al., 2011). The changes in observed temperature and salinity across the Arctic document that the inflow of Atlantic and Pacific water masses into the Arctic is changing, and with it the circulation within the central Arctic Ocean (Carmack and McLaughlin, 2011). So clearly, a combination of *in situ* surface heating, and the advection of boreal water masses, can result in warming of the Arctic seafloor at depths from the shallow subtidal to the deep sea (e.g. Fig. 4), although warming trends at abyssal depths are significantly slower (Bergmann et al., 2011).

Increased anthropogenic inputs of CO_2 to the atmosphere leads to higher CO_2 content of ocean surface water, thereby decreasing pH with implications for marine biogeochemistry (Mathis et al., 2012). Low pH may cause seawater to be corrosive to biogenic calcium carbonate minerals constituting the shells of bivalves, echinoderms and gastropods, and several recent reviews suggest some organisms may already be exhibiting negative consequences of
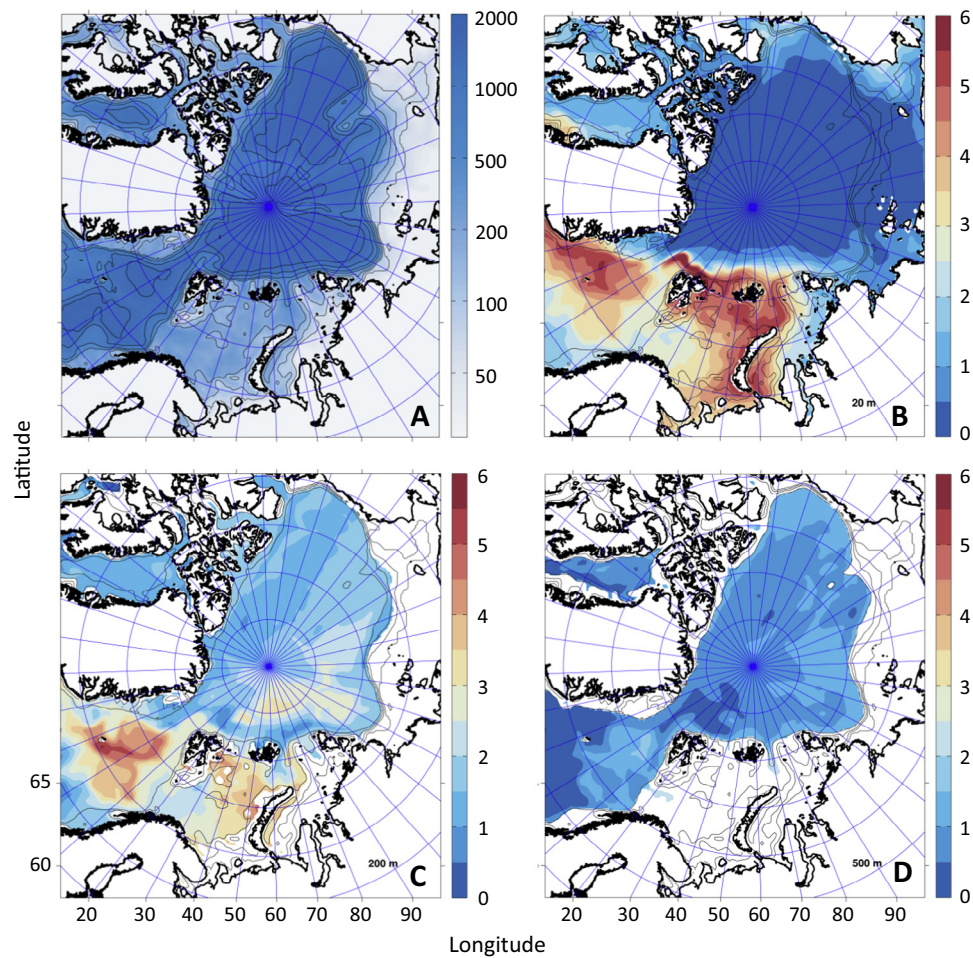
Fig. 3. Bathymetry (A) of the Arctic region covered in the domain of the coupled hydrodynamic-ecological model SINMOD (Slagstad et al., 2011, this issue). Panels B, C, and D show the difference in average August water temperature (color scale in °C at right) at three depths (20, 200, and 500 m, respectively) between the last and first decades of the 21st century. The IPCC A1B climate scenario was used to for the model.
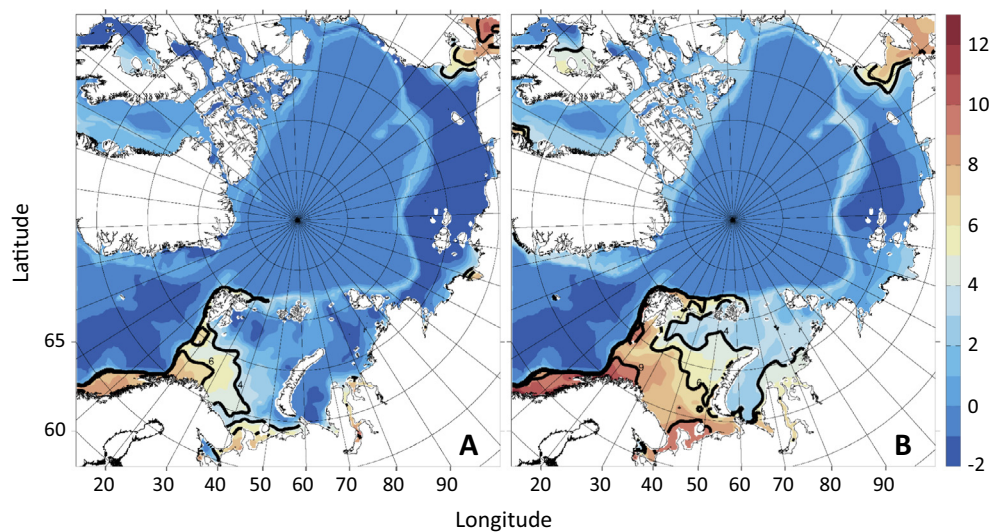
Fig. 4. Isotherms (4, 6, and 9 °C) and color scale for average August bottom temperatures for 2000–2009 (A) and 2091–2099 (B) extracted from SINMOD model runs using the IPCC A1B climate scenario (Nakicenovic et al., 2000).

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acidification including reduced survival, calcification, growth, development and abundance (Hendriks et al., 2010; Kroecker et al., 2013). Conditions characteristic of the Arctic, such as low temperatures and input of melt water, suggest resident shell-bearing inhabitants may be especially vulnerable to the impacts of acidification. The potentially negative effects of acidification for shell producing taxa could have wide ecosystem consequences as they often constitute a dominant fraction of benthic biomass, are important for the carbon flow, and serve as prey for higher trophic levels (Born et al., 2003; Bluhm et al., 2009; Sejr et al., 2009).

5. Limitations to biological expansion and invasion: consequences of climate forcing

Environmental parameters, including thermal gradients, undersea topography, and oceanographic features, are among the primary factors that determine biogeographical boundaries (e.g. Mironov and Dilman, 2010). Depending upon which factors are most important in defining the boundaries, climate change may alter the features differently. Boundaries defined by ocean current systems influencing dispersal are less likely to be altered by a general warming, but the position of the fronts and associated thermal gradients may shift (Carmack and McLaughlin, 2011). Habitat distribution, and the physiological and ecological characteristics of the taxa within each habitat, act on more local scales to determine distributional ranges. The complex interactions among these drivers make predictions of how climate change will affect these boundaries difficult (Fields et al., 1993). Two examples illustrate the importance of considering life-history, habitat characteristics, physiological and ecological constraints to forecast effects of a changing climate. First, continued warming of surface waters in the Pacific sector may promote further northward expansion of (primarily) pelagic fish species (Mueter and Litzow, 2008), but winter ice formation will continue to produce a deep cold pool that will limit the likelihood of demersal fish reaching the Chukchi in large numbers (Sigler et al., 2011). Second, two species of the marine gastropod Nucella with similar long-range dispersal ability were shown to have different abilities to spread into the sub-arctic following the last glacial maximum, depending on their different ecologies (Marko, 2004).

It seems logical that benthic organisms with pelagic life stages will be less limited in their expansion abilities than those with benthic dispersal stages. In fact, multiple studies note the importance of a planktonic stage in promoting both colonization itself and gene flow among populations following establishment (e.g. Wares et al., 2001; Harper et al., 2007; Hardy et al., 2011). Vermeij (1991), however, observed that most of the 295 mollusc species known to have transited the Arctic since the Pleiocene have benthic dispersal stages, suggesting boundaries to expansion may be less obvious than expected. Physical constraints may include currents that transport larvae/spores of coastal taxa offshore, retain them in gyres, or deposit them on ice-covered shores or where temperatures are unsuitable for survival, and these will not enhance range extensions. Larval dispersal will enhance the rate of expansion when oceanographic conditions reliably transport propagules to suitable habitats, and these ocean-current effects and habitat distribution interact with dispersal strategies to determine the patterns of expansion over evolutionary time. For example, despite the general northward current flow in the NE Pacific and the Alaska Coastal Current (Woodgate et al., 2012), poor genetic mixing has been observed between Canadian Pacific and Bering/Chukchi populations of a polychaete with long-lived pelagic larvae (Carr et al., 2011; Hardy et al., 2011). Furthermore, nearly half of the 44 species of meroplankton (larvae

of benthic organisms) found in the Kara Sea are not represented in the adult communities of the region (Fetzer and Arntz, 2008), indicating that arrival of propagules alone is not sufficient for successful colonization. Thus, pelagic dispersal is only able to bridge some of the barriers maintaining biogeographical isolation, and a mechanistic understanding of specific constraints to establishment of immigrant taxa is needed to predict impacts of climate change on future expansion.

Physiological constraints associated with cold temperatures present one of the more obvious barriers for boreal organisms colonizing or traversing the Arctic. Perennial temperatures near freezing in most areas, and air temperatures far below freezing for intertidal organisms, threaten many physiological processes, including ion balance, energetics, and maintenance of oxygen balance (e.g. Frederich et al., 2001; Aronson et al., 2007). At the same time, a warming Arctic can present novel problems for resident Arctic fauna adapted to low temperatures. High-latitude taxa have temperature ranges one-half to one-sixth that of their temperate counterparts (Peck and Conway, 2000), which limits their ability to optimize metabolic performance as temperatures rise. For both residents and immigrants, then, temperature-regulated physiological performance is likely to impact ecological interactions (competition, predation) (Pörtner and Farrell, 2008; Pörtner, 2010). Even small levels of ocean warming, however, could reduce physiological barriers for boreal immigrants. Aronson et al. (2007) predicted a rise in bottom temperatures of only 1 °C would be sufficient for invasion of decapod predators with a feeding strategy unknown to shelf regions around Antarctica. Recently, such a powerful crushing predator, a red king crab, has appeared near the Antarctic Peninsula (Smith et al., 2011), exposing resident communities to a significant and novel ecological competition. The absence of such predators in high Arctic Greenland is likely an important factor for the development of high standing stock of old and slow growing bivalves exploited by eiders and walruses in summer (Sejr et al., 2002). The (spatial and depth) distribution and intensity of warming in the future Arctic will, therefore, have significant implications for immigrant and resident Arctic benthos both directly and indirectly through species interactions.

Predictions based on physiological constraints may, therefore, be useful when considering mechanisms behind possible impacts of current warming trends. Whether it is by means of duration of sub-freezing days or minimum annual temperature, temperature thresholds for temperate and boreal species inhibit their northward spread (in the northern hemisphere). For some species, however, only a small change in average or minimum temperature may be enough to permit establishment in a new habitat (e.g. Stachowitz et al., 2002; Aronson et al., 2007). Projected temperature increases in shallow (<200 m) waters of many Arctic's marginal seas exceed 2–3 °C by 2100 (Fig. 3B and C), suggesting thermal conditions may soon become suitable for a suite of boreal taxa. Invaders might have competitive advantages over resident fauna if the latter have physiological constraints in adjusting to warmer temperatures (Peck and Conway, 2000). Southern limits of Arctic taxa have been observed to retreat as ranges of boreal taxa expand into the Arctic (Blacker, 1965), most likely as a result of both thermal-adaptation abilities and competition. Retreat of Arctic continental shelf benthos, however, can only continue until they reach the shelf break, with local extirpation of stenobathic species as a likely consequence (Renaud et al., 2008).

Ice cover is one of the most important elements structuring Arctic food webs (Carmack and Wassmann, 2006), and by all accounts, sea ice will continue to be a seasonal feature of the central Arctic. The minimum seasonal sea ice extent in September is currently decreasing by 91,600 km^2 per year, or −13% per decade, relative to the 1979–2000 average (Perovich et al., 2012). Thinner ice, earlier melting, and later freeze-up will strongly affect the light

regime in surface waters and shallow benthic habitats of the Arctic. Increased light availability is expected to enhance pelagic primary productivity (Arrigo et al., 2008), but not where nutrient supplies are limiting as in the Canada Basin (Codispoti et al., 2013). Ecological processes influencing the fate of this primary production, however, are not well understood. Timing of reproduction is tightly linked with ice seasonality for Arctic zooplankton (Søreide et al., 2010), and phenology will be an important factor determining which taxa are able to expand into the Arctic from boreal regions. Unfortunately, little is known about distribution and seasonality of larvae of benthic taxa in the Arctic (see relevant discussions in Clough et al., 1997; Fetzer et al., 2002; Fetzer and Arntz, 2008), and this could clearly be important in predicting which taxa are likely to spread. A recent study describes dramatic pulses in vertical flux of ice algal blooms to the deep Arctic basin (Boetius et al., 2013) showing that high(er) biomass production at the sea surface can be tightly linked to the benthos, even in the deep Arctic Ocean. Complex and variable relationships between primary productivity and diversity of benthic fauna have been documented for different boreal and Arctic habitats (Witman et al., 2008), however, suggesting responses of benthic diversity to changes in vertical carbon flux are unpredictable. Enhanced food supplies for larvae and new recruits of benthic taxa could lead to improved conditions for survival and growth of new benthic taxa. Threats from predation, which are related to body size in the sediments and duration of time in the plankton (reviewed in Pechenik, 1999), may, therefore, decline as a consequence of reduced ice cover. It is unclear, however, whether higher primary production will result in higher flux to the seafloor under reduced ice conditions, or if this material will be shunted to a pelagic food-web (Wassmann, 2011).

Reduced ice and increased light levels are also predicted – and have already been observed – to substantially increase annual growth and depth distribution of benthic macroalgae (kelp) (Węsławski et al., 2011; Krause-Jensen et al., 2012), with cascading effects to benthic secondary producers (Blicher et al., 2009; Sejr et al., 2009). This may result in increased competition for the relatively few endemic kelps of the Arctic, but also could provide secondary habitat facilitating expansion of a wide variety of kelp-associated fauna of boreal and temperate affinities. Macroalgae are already benefiting from increased availability of intertidal and subtidal hard-substrate (Węsławski et al., 2011), a habitat type that is most likely to increase considerably in many regions of the Arctic, including the Aleutians, Greenland, the Canadian Archipelago, and the European Arctic.

Not all predicted outcomes of climate change will increase primary productivity or obviously facilitate colonization by new taxa. Whereas scour by sea ice will be reduced in many areas, iceberg impacts on nearshore communities near glaciated areas may actually increase if more glacial calving results from a warmer climate. Winter minimum temperatures and ice scouring can be important sources of faunal mortality even in the sub-Arctic (Carroll and Highsmith, 1996; Blicher et al., 2013). Furthermore, increased sedimentation and turbidity from higher river run-off and permafrost thawing can have adverse effects on the growth of encrusting and macroalgal recruitment (Aumack et al., 2007; Konar, 2007). Many environmental changes linked with climatic shifts and acting in concert have the potential to substantially alter biodiversity patterns and biogeographical boundaries. Changes in distributions of ecologically important and habitat-forming species have the potential to reorganize community structure on a large scale, and this has important implications for rates, magnitudes, and nature of species expansions (Harley et al., 2006). Recent evidence suggests the transition between biological community types may be abrupt, and community regime shifts can occur in response to gradual changes in ice cover and temperature (Kortsch et al., 2012). The possibility of wholesale changes in community structure and new ecological relationships in a warmer, ice-free Arctic complicate predictions that, until recently, have been solely based on autecological properties of relatively few taxa.

6. New analyses predicting spatial and taxonomic patterns of faunal expansion

6.1. Analytical methodology

Identifying patterns of changes in water temperature is a prerequisite for identifying regions most likely to experience faunal expansion. We, therefore, ran the coupled 3-D oceanographic-ecological model SINMOD (Slagstad et al., 2011, updated in this volume) to estimate temperature changes throughout most of the Arctic between the first and last decades of this century. The model has a 20 km grid size, and is forced by moderately conservative IPCC A1B climate predictions (see Slagstad et al., this issue for more details). The model was also used to estimate the average (2000–2009) August bottom temperature at georeferenced distributional records of 65 benthic taxa identified by the authors or in the literature as either of boreal or Arctic biogeographical affinity. Occurrence records were extracted from the Ocean Biogeographic Information System database (www.iobis.com; extracted January 2013), as well as from the data sets underlying Stoker (1973), Carey (1977), Frost and Lowry (1983), Coyle et al. (2007a), Logerwell et al. (2011), Bluhm et al. (2009, 2011a and unpublished), Blanchard et al. (2013) and Ravelo et al. (2013). From the combined geographical observations and model-estimated temperatures, we tried to determine thermal thresholds for the different species and relate those to the predicted changes in bottom temperatures through the end of the century.

6.2. Spatial patterns of temperature change and faunal expansion in the future

Modeled temperature changes between the first and last decades of the 21st century (Ellingsen et al., 2008) show the increase in average annual temperature to be largest (up to 6 °C) near the ocean surface, and in particular in areas where ice cover has been decreasing (Fig. 3B). According to the model, large areas of Arctic shallow coastal and shelf sea floor will experience significant increases in temperature by the end of the century. The 20 km grid size in the model prohibits us from differentiating between intertidal and shallow shelf habitats. Further, spatial patterns in this temperature increase indicate that the greatest changes will be felt in inflow-shelf regions (3–5 °C: Fig. 3), i.e. the Barents and Chukchi Seas (per Carmack and Wassmann, 2006). Substantial temperature increase (2–3.5 °C) is also predicted for the northern Greenland–Iceland–Norwegian (GIN) Seas, the Kara Sea, the west Greenland coast, and the Beaufort Sea. In vertical extent, significant increases in temperature of up to 4 °C are predicted as deep as 200 m (Fig. 3C), and 1–2 °C even down to 500 m depth throughout the central Arctic Ocean (Fig. 3D). Deeper bottom temperatures are not expected to change much (Fig. 4B). Obviously, uncertainties are tied to such model predictions, but SINMOD has been continuously updated based on ground-truthing during the last 20+ years (Slagstad et al., this issue). In addition, the A1B climate scenario forcing the model is known to be relatively conservative (Füssel, 2009) since it does not account for any increase in greenhouse-gas emissions. For these reasons we are confident that the temperature change predicted here are reasonable in magnitude and spatial pattern.

Regions expected to experience the most pronounced warming are most likely to experience changes in species composition because the distributional limits of marine species are usually closely related to their thermal tolerance limits (Sunday et al., 2012). In addition to temperature change, cumulative consequences of other climate-change-related factors such as acidification and changes in sea ice coverage can be expected to exert most influence on shallow water benthos (see above). It is not clear, however, that intertidal and shallow-water benthos will change the most, despite the large temperatures changes projected, since these communities already experience large seasonal variability in environmental conditions and organisms living there may be adapted to such changes (Węsławski et al., 2011).

Suitable conditions for expansion of boreal taxa will be determined by where these new thermal regimes overlap with available and continuous habitat distribution. Expansion along inflow shelves can be expected to be faster within continuous habitats, such as shelf or deep soft bottom habitats, than in areas where disjunct habitats, such as kelp beds or available hard substrate, present potential dispersal barriers. For example, the intertidal macroalga *Ascophyllum nodosum* is not found on Svalbard, and the blue mussel *Mytilus edulis* exists only in low abundances (Berge et al., 2005), although both are very abundant along the West Greenland coast under what appear to be comparable climatic conditions (M. Sejr, pers. obs.). Thus, the greater physical isolation of Svalbard habitats from potential source populations probably limits the northern range extent of some boreal species to a greater degree than physiological thresholds.

The benthic community can be expected to react fastest to temperature changes in areas where supply of new potential boreal invaders is also high. This is determined by both distance from the source population and the speed and direction of prevailing ocean currents transporting propagules of boreal taxa. Therefore, the Barents Sea and the Chukchi/Bering Sea in particular are expected to be the major corridors of range expansions into the interior Arctic shelf seas (see also Josefson and Mokievsky, 2013). The deep parts of the GIN seas are expected to be the prime corridor into the central Arctic Basin. The average bottom water temperature is ∼2 °C in the North Atlantic (Dietrich et al., 1975) and ≤0 °C in the Arctic Basin (Carmack et al., 1997), a difference that is much less dramatic than between surface waters of those regions. Range extensions from the Norwegian and Greenland Seas through Fram Strait into the central basin are, therefore, not unlikely, and many examples exist over different time scales (Krylova et al., 2013). Still, the increase in temperature observed in the deep part of the Fram Strait at 2500 m from 2002 to 2007 was minimal (<0.001 °C per year; Bergmann et al., 2011), so it is unclear how dramatic faunal expansions will be in the deep sea in the near future. Expansions of shelf fauna into the deep-sea are also conceivable (Golikov and Scarlato, 1989).

### 6.3. Taxa most likely involved in expansion

The warming during the 1920s and 1930s in the eastern North Atlantic led to northward expansion of a large diversity of fish and benthic invertebrates into Arctic habitats (Blacker, 1965; Drinkwater, 2006; Renaud et al., 2008). These new residents persisted for years to decades until cooler climatic conditions resumed. Although current warming trends are expected to be more intense and longer-lived than this earlier period, the species identities and mechanisms considered responsible at that time can provide insight into future patterns to be expected.

We were able to retrieve at least 20 bottom temperature records for 19 Arctic and 21 boreal species. These species were primarily polychaetes, but also included bivalve and gastropod molluscs; ophiuroid and asteroid echinoderms; and cumacean, decapod and amphipod crustaceans (Appendix A). We were also constrained to records corresponding to positions within the SINMOD model domain (Fig. 3A), so for most taxa we have far fewer temperature records than species records retrieved from OBIS. The most extreme example is for the snow crab, *C. opilio*, where we retrieved over 14,000 records but only had temperature data for 151 locations (Appendix A) since all records from the Bering Sea are outside the model domain. Nearly all taxa explored have subtidal continental-shelf affinities, and there are few records for deep-sea taxa in the Arctic, too few for adequate analysis of temperature thresholds. Therefore, we cannot claim to have effectively assessed the potential for expansion of fauna from all depth strata.

The most common approach to determining climate-related changes in species distributions has been bioclimatic envelope modeling based on relationships between species distributions and environmental factors (e.g. Cheung et al., 2009; Moritz et al., 2013). Recently, these models have been improved by including life-history, population dynamics, and species-interactions components of relevant taxa (Araújo et al., 2011). These analyses are beyond the scope of this review, and arguably challenging given the lack of basic knowledge about most of the taxa. Of the species analyzed, only 7 of the Arctic species had clear upper temperature thresholds, and these ranged between 2 and 6 °C (Fig. 5 and Appendix A). These species include the polychaete *Aglaophamus malmgreni*, the bivalves *Bathyarca glacialis* and *Yoldiella frigida*, and the sea star *Ctenodiscus crispatus*. Projected northward progression of the 4, 6 and even 9 °C August isotherms (Fig. 4) suggest shrinking distribution ranges of these taxa in the future in the Barents Sea region. Seven other species had widespread thermal ranges, spanning sites with August bottom temperatures between −1 and over 10 °C (Appendix A). One of these, the snow crab (*Chionoecetes opilio*), has recently established in the Barents Sea (Alvsvåg et al., 2009; Agnalt et al., 2008) and is becoming more abundant in the Chukchi Sea (Bluhm et al., 2009). In fact, the distribution of snow crab has contracted northward in the Eastern Bering Sea in the last three decades (Orensanz et al., 2004). Six other species showed disjunct temperature ranges, with some found between −1 and 3 or 4 °C and others over 6.5 °C (Appendix A). This last group is puzzling as the respective taxa were presumed to be Arctic taxa. This finding suggests some combination of under-sampling, taxonomic misidentification, strong capacities for acclimation, and perhaps a mismatch between conditions when the animals were collected and the current (2000–2009) temperature regime. Finally, it is also possible that the model does not reproduce the actual temperatures at every location correctly.

Fourteen boreal species showed clear lower temperature thresholds, two around 4 °C, four around 6 °C, and eight between 8 and 10 °C (Fig. 6 and Appendix A). Only one of the boreal taxa examined exhibited a disjunct temperature range distribution (Appendix A). Species with the lowest thresholds, for example the polychaetes *Asychis biceps*, *Clymenura borealis*, *Eunice pennata*, *Exogone verugera*, and *Paramphinome jeffreysii*, are expected to be those species expanding first and farthest into the Arctic. Temperature-related range extensions in the Atlantic sector of the Arctic will be primarily in the Barents Sea, eastern Kara Sea, and in West Greenland. Even those species with lower thresholds around 8 or 9 °C will show significant expansion along the coast of northern Norway (Fig. 4B), continuing a trend of northward species expansions already documented for this area (Narayanaswamy et al., 2010).
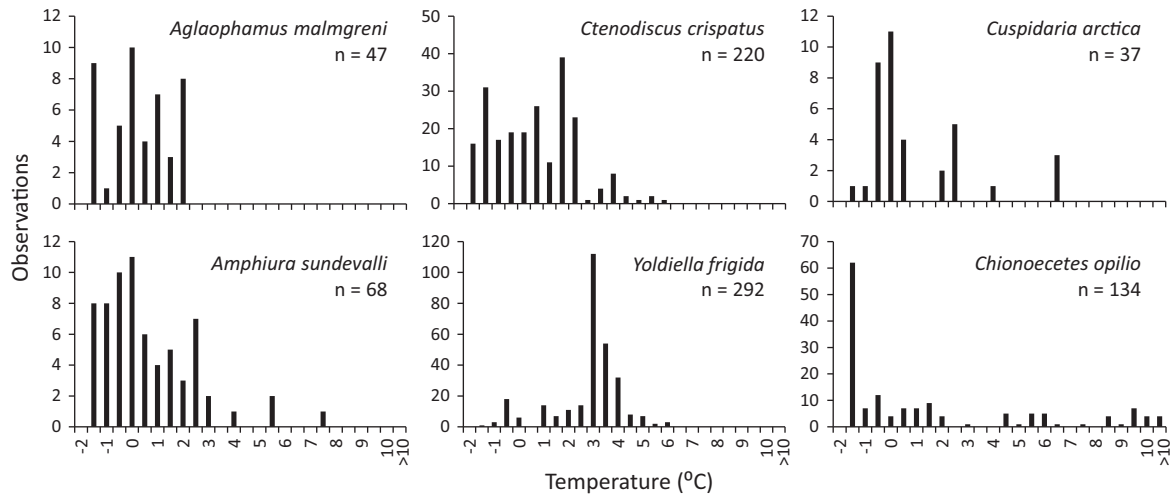
Fig. 5. Frequency histograms from temperature records for selected Arctic taxa. Geo-referenced observation records were extracted from the OBIS database (www.iobis.org, January 2013 as well as sources listed in the text), and temperature data for positions were extracted from output runs of the SINMOD coupled hydrodynamic-ecological model (Slagstad et al., 2011). The number of records for which bottom temperature (average August value for 2000–2009) was available within the model domain (see Fig. 3 for model domain) is presented for each plot.
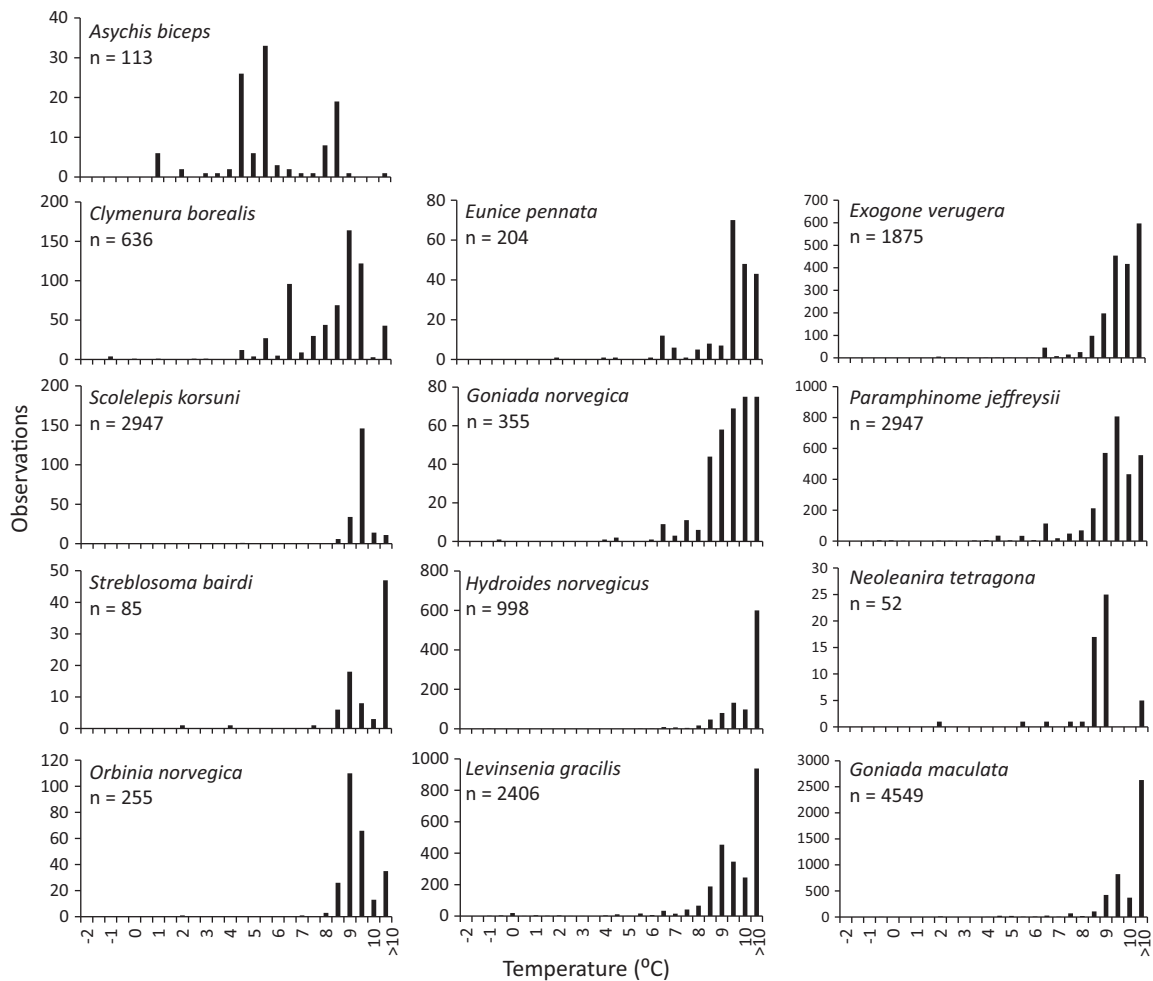
Fig. 6. Frequency histograms from temperature records for selected boreal taxa. Geo-referenced observation records were extracted from the OBIS database (www.iobis.org, January 2013 as well as sources listed in the text), and temperature data for positions were extracted from output runs of the SINMOD coupled hydrodynamic-ecological model (Slagstad et al., 2011). The number of records for which bottom temperature (average August value for 2000–2009) was available within the model domain (see Fig. 3 for model domain) is presented for each plot.

The taxa selected for this exercise were not randomly chosen, nor are they always dominants in the community. Based solely upon assumed temperature thresholds and projected temperature regimes, however, it is clear that many species common in both the Arctic and boreal faunas, taken from the most representative benthic groups, are likely to show significant, but spatially-discrete range shifts in the near future. Adequate autecological information for many taxa is lacking, and this should be included in a more systematic study to improve predictions.

7. Range extensions versus species introductions

Reductions in Arctic sea-ice and consequent increases in shipping, petroleum exploration, and tourism will dramatically increase vectors of anthropogenic species introduction (Ruiz and Hewitt, 2009). This problem will be most strongly felt along shipping lanes and developing Arctic ports in both Canada and Russia. These areas are predominantly over continental shelves and may significantly increase dispersal potential of species, even where prevailing currents suggest natural dispersal to be unfavorable, e.g. from the Chukchi to the Barents Sea. Both fouling organisms on ship hulls and propagules traveling in ballast water will be transported over long distances and eventually deposited in coastal regions. This mechanism has already been implicated in the introductions of an Atlantic ascidian to Alaska (Lambert et al., 2010) and the enigmatic snow crab in the Barents Sea (Alvsvåg et al., 2009), and is expected to result in increased numbers of non-native invasive species on Svalbard (Ware et al., 2013).

First and foremost, this process will likely serve to further homogenize the Arctic shelf fauna, a fauna already low in endemism. Physiological thresholds will likely constrain many boreal taxa from establishing in Arctic habitats, although boreal exchange between the Atlantic and Pacific may be more successful. Predicted warming of Arctic bottom waters, primarily in shelf and nearshore regions, may facilitate successful establishment after introduction by human vectors (see de Rivera et al., 2011 and discussion in previous section). As with most species introductions, it is difficult to speculate on ecosystem impacts of a successful colonization. From the example of the intentionally introduced red king crab to the Barents Sea, however, we learned that this invasive predator reduces benthic biodiversity and biomass in invaded areas (Falk-Petersen et al., 2011).

8. Research needs

Predicting patterns of expansion and invasion in a warmer Arctic is clearly a complex matter. There are large uncertainties regarding specific environmental changes and their spatial distribution across the pan-Arctic region. Further, the autecology of resident and prospective future benthic fauna is mostly poorly known. Since two of the key factors determining delivery and establishment of new taxa are physiological capacities and life-history traits, this information is vital. Ecological interactions, from food and light requirements to competitive strengths under different environmental conditions to vulnerability to predation further complicate matters. We have only recently begun a systematic census of Arctic benthic fauna, and relatively few time-series exist with which to evaluate the nature of biodiversity changes already occurring. Ultimately, benthic systems will adjust, but insights into how different the communities will look, and how differently they will function, depend on improvements in our understanding. Thus, the most pressing research needs in this area include:

1. *Immediate improvement of biodiversity monitoring.* Especially in areas likely to be most sensitive to change. Building upon existing time-series and initiatives, a network of fixed stations, transects, and sampling grids will improve surveillance in target areas suggested by current models. These efforts should be internationally driven and funded. While some effort toward this has begun (Gill et al., 2011), funding is thus far unavailable on a pan-Arctic scale.

2. *Improved understanding of the autecology of residents and potential invaders.* Integration of climate-change predictions of alterations in temperature, CO_2, ice-cover, light regimes, etc. with physiological ecology and life-history strategies will help predict which organisms persist, which become established, and where these changes will take place. Recent efforts to address organismal responses to these stressors need to be expanded to investigate multi-stressor impacts.

3. *Improved understanding of ecological interactions.* Studies of relationships between environmental characteristics and community structure (e.g. primary production and biodiversity) are needed to help predict the capacity for communities to accommodate changing distributional boundaries. In addition, current species associations/complexes and biotic interactions need to be investigated in more detail to help identify both direct and indirect effects of range extensions/contractions.

4. *Modeling based on archived data.* Our efforts presented here are crude, but improvements require more complete databases, predictions of future environmental parameters over an even broader domain, and autecological information described above that can be used in new-generation models. Increased pressure on researchers to deliver data to databases, and perhaps dedicated funds to do so, would help bring databases up to date, but until a better understanding of organismal biology is achieved, the models used will have limited utility.

5. *Improved understanding of future human contribution of invasions.* Biologists need to work with socio-economists to obtain information on likely shipping routes, key ports, and the number and nature of vessels serving as potential vectors. This, combined with surveillance of hull and ballast water residents, will help identify most sensitive locations and most likely invaders. This will hopefully lead to technologies and legislation minimizing impacts.

6. *Explore ecosystem consequences of biodiversity change.* Likely scenarios should be evaluated through integrated models using archived data and conceptual studies, and consequences studied through experimentation and modeling. These models should also consider biotic interactions that will at least in part determine the consequences of changing community composition. In this way, researchers and policy makers will be more prepared for studying and managing future Arctic ecosystems.

Appendix A

List of taxa, in alphabetical order using WoRMS-accepted names, for which distribution data were extracted in effort to determine possible thermal boundaries to distribution. Presumed affinity (Arctic or Boreal) and higher taxonomic group are presented for each taxon, as is the number of geo-referenced records (*N* records) extracted from the OBIS database (www.iobis.org, extracted January 2013). Temperature data for positions were extracted from output runs of the SINMOD coupled hydrodynamic-ecological model (see Slagstad et al., this issue), where positions were within the domain of the model (see Fig 3 for model domain). The number of records for which bottom temperature (average August value for 2000–2009) was available is provided under '*N* records.' Conclusions regarding upper or lower thermal boundaries are provided in the column on the far right. ** = Histogram provided in Figs. 5 and 6.

Taxon	Presumed affinity	Group	N records	N temp data	Thermal boundary?
Asychis biceps	Boreal	Polychaeta	220	113	**Lower limit around 4 °C
Campylaspis globosa	Boreal	Cumacea	54	16	Not enough records
Chionoecetes opilio	Boreal	Decapoda	14,509	151	**Widespread:found −1.5 to >10 °C
Clymenura borealis	Boreal	Polychaeta	702	636	**Lower limit around 4 °C
Diastylis echinata	Boreal	Cumacea	24	23	Found −1 to 9 °C
Eunice dubitata	Boreal	Polychaeta	211	204	All above 10 °C
Eunice norvegica	Boreal	Polychaeta	70	5	Not enough records
Eunice pennata	Boreal	Polychaeta	546	204	**Lower limit around 6 °C
Exogone verugera	Boreal	Polychaeta	3457	1875	**Lower limit around 6 °C
Filograna implexa	Boreal	Polychaeta	993	495	Almost all above 9 °C
Goniada maculata	Boreal	Polychaeta	6962	4549	**Lower limit around 9 °C
Goniada norvegica	Boreal	Polychaeta	551	355	** Lower limit around 6 °C
Haploops tubicola	Boreal	Amphipoda	625	421	Widespread: found −1.5 to >10 °C
Hydroides norvegicus	Boreal	Polychaeta	1265	998	**Lower limit around 8 °C
Leptostylis macrura	Boreal	Cumacea	61	13	Not enough records
Leucon spinulosus	Boreal	Cumacea	95	18	Not enough records
Levinsenia gracilis	Boreal	Polychaeta	5341	2406	**Lower limit around 8 °C
Neoleanira tetragona	Boreal	Polychaeta	75	52	**Lower limit around 8 °C
Notoproctus oculatus	Boreal	Polychaeta	120	68	Disjunct −1 to 2 °C and 8 to 10 °C
Ophiura sarsii	Boreal	Ophiuroidea	3521	664	Widespread: found −1.5 to >10 °C
Orbinia norvegica	Boreal	Polychaeta	271	255	**Lower limit around 8°C
Paramphinome jeffreysii	Boreal	Polychaeta	3506	2947	**Lower limit around 6 °C
Scolelepis korsuni	Boreal	Polychaeta	220	212	**Lower limit around 8 °C
Spiochaeopterus typicus	Boreal	Polychaeta	559	519	Widespread: found −1.5 to >10 °C
Streblosoma bairdi	Boreal	Polychaeta	146	85	**Lower limit around 8 °C
Aglaophamus malmgreni	Arctic	Polychaeta	49	47	**Upper limit around 2 °C
Amphiura borealis	Arctic	Ophiuroidea	31	31	Found 3–9 °C
Amphiura sundevalli	Arctic	Ophiuroidea	116	68	**Upper limit 3–4 °C
Axiothella catenata	Arctic	Polychaeta	44	27	Widespread: found −1.5 to >10 °C
Bathyarca glacialis	Arctic	Bivalvia	85	57	Upper limit 6 °C
Clymenura polaris	Arctic	Polychaeta	373	67	Disjunct: −1.5 to 4 °C then 7 to 9 °C
Ctenodiscus crispatus	Arctic	Asteroiodea	1059	220	**Upper limit around 4 °C
Cuspidaria arctica	Arctic	Bivalvia	41	37	**Upper limit 4–6 °C
Diplocirrus hirsutus	Arctic	Polychaeta	153	53	Found −1 to >10 °C
Diplocirrus longisetosus	Arctic	Polychaeta	14	14	Not enough records
Euchone analis	Arctic	Polychaeta	233	132	Disjunct: −1.5 to 3 °C then 6.5 to >10 °C
Frigidoalvania janmayeni	Arctic	Gastropoda	22	12	Not enough records
Glyphanostomum pallescens	Arctic	Polychaeta	73	52	Widespread: found −1.5 to >10 °C
Hemilamprops uniplicatus	Arctic	Cumacea	34	18	Not enough records
Lanassa nordenskioeldi	Arctic	Polychaeta	38	23	Widespread: found −1.5 to >10 °C
Leaena abranchiata	Arctic	Polychaeta	36	9	Not enough records
Lysippe labiata	Arctic	Polychaeta	287	116	Disjunct: −1.5 to 4 °C then 7.5 to >10 °C
Maldane arctica	Arctic	Polychaeta	8	8	Not enough records
Marenzelleria wireni	Arctic	Polychaeta	14	3	Not enough records
Melinna elisabethae	Arctic	Polychaeta	132	19	Not enough records
Nephtys paradoxa	Arctic	Polychaeta	239	169	Widespread: found −1.5 to >10 °C
Ophelina cylindricaudata	Arctic	Polychaeta	1289	706	Disjunct: −1 to 2 °C then 6.5 to >10 °C
Poraniomorpha tumida	Arctic	Asteroidea	11	10	Not enough records
Praxillura longissima	Arctic	Polychaeta	360	217	Disjunct: −1.5 to 2 °C then 8.5 to >10 °C
Pseudoscalibregma parvum	Arctic	Polychaeta	29	15	Not enough records
Sabellides borealis	Arctic	Polychaeta	86	76	Disjunct: −1 to 2 °C then 8.5 to 10 °C
Stegophiura nodosa	Arctic	Asteroidea	477	232	Widespread: found −1.5 to >10 °C
Typosyllis fasciata	Arctic	Polychaeta	14	11	Not enough records
Yoldiella frigida	Arctic	Bivalvia	351	292	**Upper limit around 4 °C

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