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Footprints of climate change in the Arctic marine ecosystem

PAUL WASSMANN*, CARLOS M. DUARTE†, SUSANA AGUSTÍ† and MIKAEL K. SEJR‡

**Department of Arctic and Marine Biology, Faculty of Bioscience, Fishery and Economy, University of Tromsø, 9037 Tromsø, Norway, †Department of Global Change Research, IMEDEA (CSIC-UIB) Instituto Mediterráneo de Estudios Avanzados, Miquel Marqués 21, 07190 Esporles, Mallorca, Spain, ‡National Environmental Research Institute, Aarhus University. Vejlsøvej 25, DK-8600 Silkeborg, Denmark*

Abstract

In this article, we review evidence of how climate change has already resulted in clearly discernable changes in marine Arctic ecosystems. After defining the term 'footprint' and evaluating the availability of reliable baseline information we review the published literature to synthesize the footprints of climate change impacts in marine Arctic ecosystems reported as of mid-2009. We found a total of 51 reports of documented changes in Arctic marine biota in response to climate change. Among the responses evaluated were range shifts and changes in abundance, growth/condition, behaviour/phenology and community/regime shifts. Most reports concerned marine mammals, particularly polar bears, and fish. The number of well-documented changes in planktonic and benthic systems was surprisingly low. Evident losses of endemic species in the Arctic Ocean, and in ice algae production and associated community remained difficult to evaluate due to the lack of quantitative reports of its abundance and distribution. Very few footprints of climate change were reported in the literature from regions such as the wide Siberian shelf and the central Arctic Ocean due to the limited research effort made in these ecosystems. Despite the alarming nature of warming and its strong potential effects in the Arctic Ocean the research effort evaluating the impacts of climate change in this region is rather limited.

Keywords: Arctic Ocean, baseline data, climate change, ecological footprints, marine ecosystems

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Introduction

Less than 110 years have elapsed since the first scientific expedition to the ice-covered Arctic Ocean (Nansen, 1897) and yet humanity faces the likely prospect of an Arctic Ocean devoid of ice in the summer. Indeed, the Arctic is warming at two to three times the global rate (ACIA, 2004; Trenberth *et al*., 2007). The most striking evidence of abrupt climate change has occurred at sea, where the rapid reduction of Arctic sea ice in 2007 generated worldwide concern (Stroeve *et al*., 2007; Comiso *et al*., 2008). In contrast, assessment of impacts of climate change on Arctic ecosystems has typically focused on terrestrial ecosystems, with discussion of evidence from the marine ecosystems largely being limited to mammals (e.g. Fischlin *et al*., 2007; Post *et al*., 2009) in spite of the fact that the vulnerability of Arctic marine biota to climate change is well established (Vibe, 1967; Gradinger, 1995).

Correspondence: Paul Wassmann, Department of Arctic and Marine Biology, Faculty of Bioscience, Fishery and Economy, University of Tromsø, 9037 Tromsø, Norway, tel. + 4777644459, fax + 4777646020, e-mail: paul.wassmann@uit.no

Despite the steep rate of change in Arctic climate, the marine ecosystem is often neglected in evaluations of impacts of climate change because of the relative paucity of research efforts on Arctic marine ecosystems. Internationally available literature records on marine Arctic ecology were scarce far into the 1970s. Whereas the coastal nations surrounding the Arctic Ocean (USA, Canada, Norway, Denmark, Russia) contribute more than 50% of the global output of marine ecology research, relatively little effort is focused on the Arctic. A search on Web of Science™ showed a major difference in the number of publications on marine biology and ecology emanating from Arctic vs. Antarctic research (Fig. 1). The mean number of Arctic publications on the subject is 51% of Antarctic publications over the period 1991–2008. However, the records contained in the Web of Science (or any other international repository) grossly underrepresent the marine Arctic research conducted by the USSR, which carried out extensive programs from the 1920s and onwards along the Siberian shelf (summarized by Zenkevich, 1963; Vetrov & Romankevich, 2004), from drifting ice islands (e.g. Ugryumov & Koronin, 2004) and on the eastern Barents Sea shelf (e.g. Zenkevich, 1963; Kuznetsov & Schoschina, 2003).

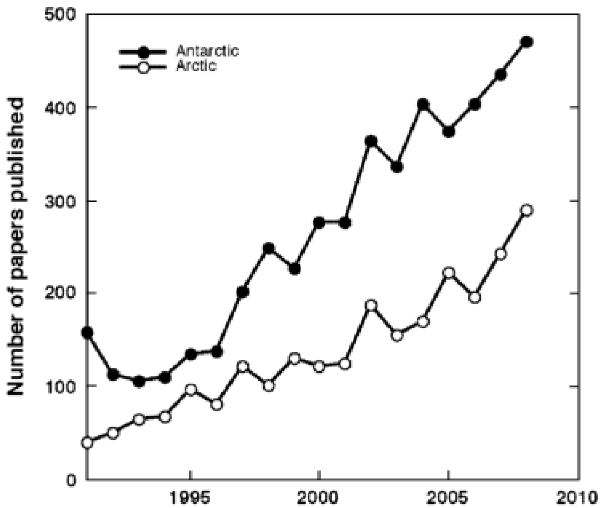

Fig. 1 Number of papers published from 1991 to 2008 on Arctic and Antarctic marine biology and ecology. The data were derived from a search on Web of Science TM (accessed on 9 September, 2009) searching the topic (title, abstract, keywords) for the string [Arctic AND (Bio* OR Eco*) AND (Marine OR Ocean*)] and [(Antarctic* OR 'Southern Ocean') AND (Bio* OR Eco*) AND (Marine OR Ocean*)], respectively.

Unfortunately, these valuable records have not percolated through to the international community and databases, nor have they been followed up by contemporary efforts to detect footprints of climate change. Indeed, most research on the Arctic has been and is still based on national efforts, in contrast to research in the Southern Ocean, where the Antarctic Treaty has provided substantial impetus to collaborative international research.

Despite these limitations, evidence of impacts of climate change on the Arctic ecosystem abounds in the literature. However, the reports have not yet been summarized. Here, we review the literature published as of mid-2009 to synthesize the footprints of climate change in marine Arctic ecosystems reported to date.

Footprint definition and applied procedures

In this paper, we use the term footprint in the sense of '*a marked effect or impact*' (Merriam-Webster Dictionary). Hence, by biological footprints of climate change, we refer to documented changes in the range, community structure, abundance, phenology, behaviour, growth or condition of marine organisms in the Arctic consistent with or apparently in response to current climate change. We adhere to the criteria established by International Panel of Climate Change (IPCC) working group II for assessing impacts of climate change on biota (Fischlin *et al*., 2007): studies *(1) ending in 1990 or later; (2) spanning a period of at least 20 years; and (3) showing a significant change in either direction, as assessed in individual studies*. Responses inferred from logical arguments, experimental evidence, models, or analogies to changes observed in individual anomalous years are not included as footprints.

We searched the peer-reviewed literature using Web of Science™, Google Scholar™, and the contents of publications devoted to polar research and climate change for footprints of climate change on Arctic marine biota. We considered as valid reports those where authors measured a change or a trend in biological or ecosystem components of the Arctic that they identified as possibly related to climate change. Attribution of the involvement of anthropogenic climate change on the responses documented is usually based on correlations, and, as often acknowledged by authors, alternative explanations may be possible. When discussed, these alternative explanations were also recorded.

Most of the observed increase in globally averaged temperatures since the mid-20th century is *very likely* due to the observed increase in anthropogenic greenhouse gas concentrations (IPCC, 2007). We focus on footprints of what we consider, based upon IPCC, to be most likely anthropogenic climate change in the region that is most strongly subjected to recent global warming: the Arctic. We thus do not include reports of changes associated to climatic fluctuations in the past (e.g. before 1960), predating the evident anthropogenic signal on the global climate, as reflected by and analysed in IPCC reports. Hence, we first summarize the changes in the Arctic that are directly or indirectly derived from anthropogenic climate change.

The changing scenarios of the Arctic Ocean

Global climate change is likely amplified in the Arctic by several positive feedbacks, including ice and snow melting that decreases surface albedo, atmospheric stability that traps temperature anomalies near the surface, and cloud dynamics that magnify change (Overpeck *et al*., 1997). Consequently, the temperature in the Arctic is increasing at a rate of two to three times that of the global average temperature estimated to be 0.4 °C over the past 150 years (IPCC, 2007). Atmospheric warming has increased Arctic Ocean temperature and resulted in decreased extent and thickness of sea ice (Comiso, 2003; Kwok & Rothrock, 2009). The sea ice extent is now decreasing at a rate of 10% per decade (Comiso *et al*., 2008) prompting concern that the Arctic Ocean could be ice-free in summer by 2050 (Arzel *et al*., 2006). Warming combined with increased precipitation has caused freshwater discharge into the Arctic Ocean from the six largest Eurasian rivers to increase at a rate of $2.0 \pm 0.7\,km^3$ per year between 1936 and 1999 (Peterson *et al*., 2002). Currently, there is an unprecedented amount of fresh water in the surface layer of the Arctic Ocean (e.g. Yamamoto-Kawai *et al*., 2009a) that results in heating of surface layers up to 3 °C above average in ice-free regions that previously were ice covered (McPhee *et al*., 2009). Input of inorganic sediments and organic carbon to the Arctic Ocean by rivers and eroding coastlines may have increased as well: although earlier analyses of available time series did not show identifiable long-term trends (Holmes *et al*., 2002), signs of change are now starting to emerge for some regions (Spencer *et al*., 2009).

Past long-term oscillations in Arctic climate can be inferred from geological records and ice cores. Since the beginning of the Quaternary period, starting 2.6 Ma ago, the Arctic has experienced repeated glacial/interglacial cycles, which have strongly influenced the hydrography and sea level of the Arctic Ocean (Darby *et al*., 2006). The ice extent was greatest approximately 24–21 ka ago during the Last Glacial Maximum. From the Last Glacial Maximum the Arctic was exposed to an abrupt warming, resulting in a transition from widespread glacial conditions to full interglacial conditions attained approximately 10 ka ago (IPCC, 2001). After that the climate remained relatively stable compared with previous glacial periods. However, also the past 1000 years have exhibited periods of warming and cooling (Berner *et al*., 2010). The Medieval Warm Period, from approximately the early 9th to mid-15th century, brought warm temperatures to areas in and around the North Atlantic. In contrast, the Little Ice Age, from approximately the mid-16th to early 20th century reduced average temperatures in these same areas (Darby *et al*., 2006).

Evidence for impacts of past climate fluctuations on Arctic marine biota is abundant. Oral as well as written records from the past few centuries and archaeological remains of Inuit hunting communities from the last 4000 to 5000 years provide evidence for large migratory fluxes of sea mammals and sea birds in response to climatic fluctuations (Vibe, 1967). During early postglacial periods the boreal species *Mytilus edulis* was established as far north as Spitsbergen, after which the species disappeared again (Berge *et al*., 2005). In the 1920s and 1930s the North Atlantic experienced a dramatic increase in atmospheric and ocean temperatures resulting in marine ecosystem changes (reviewed by Drinkwater, 2009) including a northward range expansion of boreal fish species (Jensen, 1949; Perry *et al*., 2005), phytoplankton species (e.g. Smyth *et al*., 2004) and benthic invertebrates into the Barents Sea (Blacker, 1965). The arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800 000 years provides an additional case for recent climate change (Reid *et al*., 2007). More such evidence might become available if high-resolution paleontological studies were combined with biogeographic studies of shell-bearing organisms, but such approaches require not just excellent taxonomic skills, but also decadal time resolution of sediment cores that can only be achieved in high accumulation regions, which are rare in the Arctic Ocean.

There are limitations to what can be inferred about the consequences of present climate change from analogy with past climatic fluctuations, as the present warming trend may result in unprecedented disappearance of summer sea ice and habitat loss for ice-associated biota. Additionally, climate change does not act in isolation, but interacts with other, simultaneous pressures, such as hunting and fisheries, and rising levels of pollutants. For instance, the combination of endocrine-disrupting chemicals and climate change has been claimed to pose a major threat to Arctic marine mammals and seabirds (e.g. Jenssen, 2006).

Do we have a reliable baseline?

Whereas studies that speculate or attempt to forecast impacts of current climate change in Arctic marine biota are numerous, documented impacts are much fewer. One of the stumbling blocks for efforts to document ecological impacts of Arctic climate change is the lack of reliable baseline information from which change can be identified. In the Arctic, the baseline information on ecosystem structure and functioning that pre-dates anthropogenic climate change suffers from limitations on both spatial and temporal scales. On the spatial scale, the lack of biological data – especially from the central Arctic Basin and the Russian shelves – precludes the assessment of environmental impacts in important regions of the Arctic. On the temporal scale, our knowledge of seasonal and inter-annual variation has increased during the past decades. However, the physical environment of the Arctic Seas is under the influence of multi-annual to decadal oscillatory atmospheric processes, characterized by indices such as the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO), which may confound the interpretation of changes. Although studies of ecosystem changes during different phases of human-induced climate change can increase our understanding of biological responses, the effects of climate change are superimposed on those of climatic fluctuations on a shorter time-scale. Discrimination of ecological effects of multiannual to decadal oscillations in climate from those of the more unidirectional anthropogenic climate change requires time series of climatic drivers and potential biological responses spanning several decades. Such data series are few and derive almost entirely from national climate monitoring programs (but see Loeng & Sætre, 2001). One of these few is the world's longest oceanographic time series, the Kola section, run by Norway and Russia in the southern Barents Sea. We can improve our capacity to derive appropriate Arctic baselines by building further upon existing time series in the Arctic and by increased efforts at data mining to extract historical data from surveys that have not yet been fully incorporated into the scientific literature.

There are no straightforward answers regarding the existence of reliable baselines in nonsteady-state systems like the Arctic Ocean. The applicability of a baseline depends on the time scales investigated and conclusions must always take into account the natural variability of the processes or organisms involved, which in turn must have been adequately investigated during the relevant time intervals. The present warming, reduction in ice extent and thickness, and model predictions in the last three decades suggest that today's climatic situation in the Arctic Ocean is beyond the variability range or baseline from the last 1000 years, during which short-term variability of sea surface temperature had a time scale of 80–120 years (Berner *et al.*, 2010). Time series data from periods preceding the last three decades are thus likely closer to the baseline from which footprints of climate change can be evaluated.

The Arctic Ocean is a circular system engirdled by land, i.e. a mediterranean sea (*sensu* Dietrich *et al.*, 1980; Tomczak & Godfrey, 2001), and as such has several distinctive characteristics. At present, the scientific exploration of this ocean is still inadequate for determination of circumpolar features, local/regional disparities and the complexities of the Arctic Ocean ecosystem (Wassmann, 2006). The lack of reliable baseline information is due to the relative scarcity of studies on Arctic marine ecology and biology. The reasons are multiple, including the difficulty of international cooperation and access to the Arctic during the Cold War period, when most bases in the Arctic were military and international access to the Siberian shelf was banned. The fact that the Third International Polar Year in 1958 focused on Antarctic Research, with the Antarctic Treaty of 1961 as an outcome, and the absence of an analogous treaty to foster scientific research in the Arctic contributed to the isolation of the scientific endeavours carried out by the five major Arctic nations. Investigations were limited to indisputable national territories and were primarily carried out along south-north transects rather than the basin-wide approaches that are essential to address the nature of the Arctic Ocean as a mediterranean ocean (Carmack & Wassmann, 2006). Major national projects from the mid-1980s and onwards, such as PRO MARE (Sakshaug *et al.*, 1991) and CABANERA (Wassmann *et al.*, 2008) by Norway, NOW (Deming *et al.*, 2002) and CASES (Fortier, 2008) by Canada, NWE (Hirche & Deming, 1997) by Germany/USA and SBI (Grebmeier *et al.*, 2009) by the USA, along with icebreaker crossings (e.g. Carmack *et al.*, 1997; Anderson *et al.*, 2003; Olli *et al.*, 2007) contributed to a slow, but steady increase of marine ecological knowledge of the Arctic Ocean. The Fourth International Polar Year (2007–2009) along with the mounting evidence of warming, accelerated ice loss and climatic change in the Arctic (e.g. ACIA, 2004; IPCC, 2007) has stimulated Arctic marine biology and ecology research in recent years, but its legacy will enrich the peer-reviewed literature only gradually over time.

The evidence: footprints of impacts of climate change on Arctic marine biota

We found a total of 51 reports of documented changes in Arctic marine biota in response to climate change (Tables 1–5). A detailed account of the location, species, nature and causes of the changes observed is provided in Tables S1 through S5 in the Suppoting Information. Most reports concerned marine mammals, particularly polar bears (Table 5), and fish (Table 3), and the observed responses were dominated by reports of changes in growth and condition (Fig. 2). The physical drivers for these changes attributed to anthropogenic climate change included increased penetration of warm Atlantic and Pacific water into the Arctic Ocean, increased seawater temperature, reduced cover of sea ice and increased submarine irradiance (Tables 1–5).

The responses observed involved northward range shifts for various subarctic and even temperate species and there was one report of an event when a Pacific diatom was transported across the Arctic to the Atlantic sector. The range shifts of predator organisms led to changes in the abundance of key organisms and a rearrangement of food webs and communities, affecting fisheries yields (e.g. shifts in cod and shrimp fishery in Greenland). In contrast, the abundance and reproductive output of some Arctic species declined. For example, ice-associated seals have been reported to be negatively impacted by the effect of climate change on ice conditions, reducing abundance and pup production (Table 5). The reports provide evidence for an increased phytoplankton biomass and primary production in the open Arctic Ocean, particularly the Pacific sector (Table 1). The abundance of larger zooplankton and amphipod species associated with sea ice was reported to decline, while jellyfish abundance was reported to increase (Table 1).

Table 1 Reports of changes in Arctic plankton in response to climate change showing the organism and region investigated, the period of observation, and the response observed

Subject	Region	Climatic driver	Footprint	References	Code
Primary production	Arctic Ocean	Ice changes	Increased annual primary production	Arrigo *et al.* (2008)	1
Phytoplankton biomass	Barents Sea	Ice changes	Increased phytoplankton biomass	Qu *et al.* (2006)	2
Primary production	Arctic Ocean	Ice changes	Increased primary production	Pabi *et al.* (2008)	3
Planktonic diatom	Labrador Sea	Altered circulation	Range shift of *Neodenticula seminae*	Reid *et al.* (2007)	4
Primary production	Beaufort Sea	Ice changes	Increased primary production	Mundy *et al.* (2009)	5
Amphipods	Kongsfjord, Svalbard	Altered circulation	Increasing proportion of *Themisto abyssorum* to *T. libellula*	Hop *et al.* (2006)	6
Zooplankton community	West Greenland	Warming	Changes in zooplankton abundance and composition	Pedersen & Rice (2002)	7
Copepods	Kongsfjord, Svalbard	Altered circulation	Increasing contribution of smaller copepods	Hop *et al.* (2006)	8
Jellyfish	Bering Sea	Warming	Increase in jellyfish biomass	Brodeur *et al.* (1999)	9

The code number identifies the corresponding symbol in Fig. 3

Although the large reduction of multi-year ice cover in the Arctic is allegedly the major change observed in the Arctic in response to climate change, reports of impacts on the sea ice community are limited to those on polar bears, seals and amphipods associated with sea ice. A decrease in multi-year sea ice in the marginal ice zones must reasonably have occurred, and led to a major decline in the productivity of sea-ice algae, and that of organisms depending on this resource, but this has not been quantified and remains a matter of speculation. Indeed, examination of the geographic distribution of the reports (Fig. 3) shows that most reports are derived from subarctic locations (SW Greenland, the Bering Sea, the Barents Sea) and the Svalbard archipelago. Apart from reports of increased phytoplankton proliferation derived from remote sensing, there are no data from the parts of the Arctic basin that were formerly occupied by perennial ice. In addition, we found no documentation of changes anywhere in the extensive Siberian shelf (Fig. 3). Along the outer sector of the Siberian shelves the Nansen and Amundsen Basins Observational System (NABOS) provides a quantitative, observationally based assessment of circulation, water mass transformations, and transformation mechanisms in the Eurasian and Canadian Basins of the Arctic Ocean. However, this system was not established primarily to provide evidence of footprints of impacts of climate change on Arctic biota. A sustained NABOS, piggy-backed by ecosystem and biodiversity analyses, could compensate for this lack. The number of documented footprints declines, therefore, with increasing latitude, with most reports concentrated between 65 and 75°N (Fig. 3).

The paucity of reports for the Arctic basin does not derive from lack of impacts of climate change, but from the lack of the sustained research efforts in this region required to detect change. Although a few expeditions have been conducted to the high Arctic (e.g. Carmack *et al*., 1997; Anderson *et al*., 2003), these have provided isolated data focussed largely on physical and chemical properties that cannot be used to assess climate change impacts on biota (but see e.g. Gosselin *et al*., 1997; Wheeler *et al*., 1997; Olli *et al*., 2007). It is now a matter of urgency to carry out complementary ecological investigations, as the perennial ice region of the Arctic is likely to disappear (e.g. Kwok & Rothrock, 2009), along with the ecosystem it supports, before the end of the century (Gao *et al*., 2009; Steinacher *et al*., 2009; Shakhova *et al*., 2010). Based upon the project Canada's Three Oceans (C3O; dfo-mpo.gc.ca/science/Publications/article/2008/17-06-2008-eng.htm), Li *et al*. (2009) provide a first example of such investigations. The authors discovered that the smallest algae thrive as the Arctic Ocean freshens. If the trend toward a community of

Table 2 Reports of changes in Arctic benthos in response to climate change showing the organism and region investigated, the period of observation, and the response observed

Subject	Region	Climatic driver	Footprint	References	Code
Benthic algae	Spitsbergen fjords	Altered circulation	Advance to upper littoral	Jan Marsin Weslawski, personal communication	10*
Macroalgae	Svalbard Bays	Increased river discharge	Reduced UVR damage to *Saccharina latissima*	Roleda *et al.* (2008)	11
Amphipods	Chirikov Basin, Bering Sea	Possibly climate change	Decline of *Byblis* spp.	Moore *et al.* (2003)	12
Benthic community	N Bering Sea	Warming	Decline in benthic biomass	Grebmeier *et al.* (2006)	13
Blue mussel	Svalbard	Altered circulation	Northward range shift of *Mytilus edulis*	Berge *et al.* (2005)	14
Clam	Chukchi Sea	Warming	Increase in *Macoma calcarea* biomass	Sirenko & Gagaev (2007)	15
Clam	Greenland	Ice changes	Changes in *Clinocardium ciliatum* growth	Sejr *et al.* (2009)	16
Benthic community structure	Bering Sea	Warming	Cod invasion reduces crab abundance	Orensanz *et al.* (2004)	17
Decapods	Svalbard	Warming	Change in composition	Berge *et al.* (2009)	18
Crustaceans	S Svalbard	Altered circulation	Increase in *Gammarus oceanicus* proportion	Jan Marsin Weslawski, personal communication	19*
Shrimp	SW Greenland	Possibly climate change	Increased shrimp catch	Overland *et al.* (2004)	20
Snow crab	Bering Sea	Warming and ice changes	Decrease in snow crab in their southern range	Otto & Stevens (2003)	21
Snow crab	Chukchi Sea	Altered circulation	Change in abundance	Bodil Bluhm, personal communication	22*
Greenland Cockle	NW Svalbard	Climate change	Changes in *Serripes groenlandicus* growth	Ambrose *et al.* (2006)	23

The code number identifies the corresponding symbol in Fig. 3. The code numbers with asterisk are changes that have not been documented in the published literature as yet, and therefore offer a weaker basis for the assessment.

Table 3 Reports of changes in Arctic fish in response to climate change showing the organism and region investigated, the period of observation, and the response observed

Subject	Region	Climatic driver	Footprint	References	Code
Cod	Barents Sea	Warming	Increased cod recruitment and length	Overland *et al.* (2004)	24
Cod and Shrimp	West Greenland	Warming	Replacement of cod by shrimp	Hamilton *et al.* (2003)	25
Greenland Turbot	Bering Sea	Warming and ice changes	Increased spawning biomass	Overland & Stabeno (2004)	26
Pacific Cod	Bering Sea	Warming and reduced sea ice	Reduced spawning biomass	Overland & Stabeno (2004)	27
Cod	North Atlantic	Warming	Northward spread and increased spawning stock biomass and recruitment	Drinkwater (2009)	28
Cod	Barents Sea	NAO/temperature	Positive relation between cod recruitment and temperature	Ottersen & Stenseth (2001)	29
Snake Pipefish	W Svalbard	Warming	Northward range shift	Fleischer *et al.* (2007)	30
Walleye Pollock	Chukchi and Bering Seas	Warming	Northward range shift	Mecklenburg *et al.* (2007)	31
Walleye Pollock	Bering Sea	Warming and ice changes	Increased biomass	Overland & Stabeno (2004)	32

The code number identifies the corresponding symbol in Fig. 3.

Table 4 Reports of changes in Arctic sea birds in response to climate change showing the organism and region investigated, the period of observation, and the response observed

Subject	Region	Climatic driver	Footprint	References	Code
Sea ducks	Hudson Bay	Warming and ice changes	Increased duck mortality	Gilchrist & Robertson (2000)	33
Spectacle eider	Bering Sea	Climate change	Change in abundance of preferred benthic prey	Richman & Lovvorn (2003)	34
Thick-billed and Common Murre	Panarctic	Warming	Changes in population size	Irons *et al*. (2008)	35
Thick-billed Murre	Coats Island, Canada	Ice changes	Advanced egg-laying	Gaston *et al*. (2005)	36
Thick-billed Murre	Prince Leopold Island, Canada	Ice changes	Reproduction success increased at Northern range	Gaston *et al*. (2005)	37
Thick-billed Murre	Hudson Bay	Warming	Changes in diet composition	Gaston *et al*. (2003)	38
Ivory gull	Canadian Arctic	Possibly climate change	Decline in colony size	Gilchrist & Mallory (2005)	39

The code number identifies the corresponding symbol in Fig. 3.

smaller cells is sustained, biological production of higher trophic levels will decline.

Whereas we have identified over 50 reports of documented impacts of climate change in the Arctic, some of the changes observed may have other explanations, including the effects of fisheries and hunting for exploited species, and density-dependent effects for some populations of abundant species (Tables 1–5). Moreover, there are of course also reports that sought, but were unable to find, evidence of climate-change induced impacts, such as the lack of responses in benthic community structure in the Van Mijen fjord, Spitsbergen (Renaud *et al*., 2007). There is the possibility that these reports are underrepresented in the literature, which is in general biased against the reporting of negative results. However, some of these studies were also relatively limited in their power to resolve climate change impacts, and may therefore make a type II error (i.e. concluding that there was no effect even though there may be one). Conversely, reports of climate change impacts may be confused by other factors. For example, evidence on range shifts may be confounded by poor sampling density and incomplete taxonomic inventories. Also, since the evidence for change is correlative in nature, it provides no guaranties of causation. Observed responses may also turn out to be mere fluctuations as time series grow (e.g. Pearson & Dawson, 2003).

However, the range of responses observed is consistent with *a priori* expectations derived from the Arctic Climate Impact Assessment (ACIA) exercise (ACIA, 2004), which predicted that climate change in the Arctic would accelerate, contributing to major physical, ecological, social, and economic changes that will also affect the rest of the world. Although some of the observations summarized here were available at the time the ACIA report was produced, many were published later and therefore represent an independent validation of the predicted changes with climate change in the ACIA report. The consistency between the nature of the changes observed (Table 6) and *a priori* expectations strengthens the attribution of the changes to climate change. Moreover, whereas alternative explanations are possible for some of the footprints, we know of no alternative explanation that would account for all of them. Climate change provides a single, parsimonious explanation for the range of changes summarized here (Tables 1–6). Although not a confirmation of the involvement of climate change, the parsimony of climate change as the explanation again strengthens the attribution of the documented changes to climate change.

Overall, the impacts of climate change seem to be driven by the increased penetration of warmer Atlantic and Pacific water masses into the Arctic Ocean, increased residence time of that warmer water, and changes in the seasonality and extent of ice cover, rather than by direct warming. Recent experimental evidence suggests that the metabolism of Arctic planktonic communities must be very sensitive to warming, with community respiration rates increasing steeply with warming (Vaquer-Sunyer *et al*., 2010). However, the absence of time series reporting respiration in Arctic planktonic communities *in situ* precludes validation of this prediction, particularly as the respiration rates in natural communities may already have been affected.

Further predictions of changes in the Arctic are rendered difficult because current trends, as represented by the footprints identified, cannot be simply

Table 5 Reports of changes in Arctic marine mammals in response to climate change showing the organism and region investigated, the period of observation, and the response observed

Subject	Region	Climatic driver	Footprint	References	Code
Grey Whale	Bering Sea	Warming and ice changes	Northward shift in Grey Whale feeding grounds	Moore *et al.* (2003)	40
Polar Bear	W Hudson Bay	Reduced sea ice	Decline in the Polar Bear population of western Hudson Bay	Stirling *et al.* (1999)	41
Polar Bear	W Hudson Bay	Reduced sea ice	Decline in conditions and altered behaviour	Stirling & Parkinson (2006)	42
Polar Bear	W Hudson Bay	Reduced sea ice	Decline in population size	Regehr *et al.* (2007)	43
Polar Bear	N Alaska	Reduced sea ice	Landward shift of Polar Bear denning	Fischbach *et al.* (2007)	44
Polar Bear	N Alaska	Reduced sea ice	Increasing numbers of bears on the Alaska coast during summer and autumn	Schliebe *et al.* (2006)	45
Polar Bear	S Beaufort Sea	Reduced sea ice	Decline condition and survival of cubs	Regehr *et al.* (2006)	46
Polar Bear	Beaufort Sea	Reduced sea ice	Drowned, emaciated and cannibalised bears	Monnett & Gleason (2006)	47
Polar Bear	Svalbard	Reduced sea ice	Decreased natality rate and litter production	Derocher (2005)	48
Polar Bear	W Hudson Bay	Reduced sea ice	Decline in female condition	Derocher & Stirling (1995)	49
Harp Seals	White Sea	Reduced sea ice	Reduced birth rates	Chernook & Kuznetsov (2002)	50
Ringed Seals	W Hudson Bay	Warming and ice changes	Reduced reproduction, pup survival, and recruitment	Ferguson *et al.* (2005), Stirling (2005)	51

The code number identifies the corresponding symbol in Fig. 3.

extrapolated into the future because the changes in the Arctic are exceeding those anticipated by available models (e.g. Serreze, 2009). The extent of the Arctic Ocean ice cover has shown an overall negative trend for 1979–2006 (Stroeve *et al*., 2007). After the rapid melting in 2007, the slower negative trend was re-established in 2008 and 2009, but the Arctic Ocean will be largely ice-free in late summer in two to three decades, with a cover of mostly first-year ice in winter. In addition, the average thickness of ice has decreased steadily (Kwok & Rothrock, 2009), freshwater inputs have increased (McPhee *et al*., 2009; Yamamoto-Kawai *et al*., 2009a) and transport towards the Fram Strait has increased (von Eye *et al*., 2009). The prediction of the future of the Arctic ecosystem remains challenged by the ever-accelerating nature of the changes.

Prospects of climate change in the Arctic

Essentially simultaneously with the presentation of IPCC predictions showing that the ice is unlikely to disappear from the Arctic Ocean in summer within the 21st century (IPCC, 2007), summer sea ice cover declined abruptly (Stroeve *et al*., 2007; Comiso *et al*., 2008) and remains low. Predictions have been revised to contemplate an ice-free Arctic Ocean in September by 2037 or 2040 (Holland *et al*., 2006; Wang & Overland, 2009, respectively). This implies not just rapid and major changes to the ecosystem function of the Arctic Ocean, but an almost instantaneous alteration. Climate change is not on the verge of approaching the Arctic; it has already arrived to the extent that realized changes exceed expectations year by year. In many ways the projected future of the Arctic can be seen today.

Once the entire Arctic Ocean becomes a seasonal ice zone, its ecosystem will change fundamentally as sea ice constitutes by far the key forcing factor in polar oceans. Various projects examining polynyas and marginal ice zones [e.g. International North Water Polynya Study (NOW), Canadian Arctic Shelf Exchange Study (CASES), Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change (CABANERA), the Circumpolar Flaw Lead System Study (IPY-CFL; www.ipy-api.gc.ca/pg_IPYAPI_029-eng.html), iAOOS-Norway: Closing the loop (www.iaoos.no)] can contribute with basic information on rates, processes and key ecosystem components at the edge of the seasonal ice zone. However, there are great uncertainties as to how this zone will perform when it widens from the shelf edge where it is currently situated to encompass the entire width of the Arctic Ocean and leaves. Thus, even our predictions of basic ecosystems features, such as primary production, cannot reliably be based on extrapolations of current knowledge to regions adjacent to

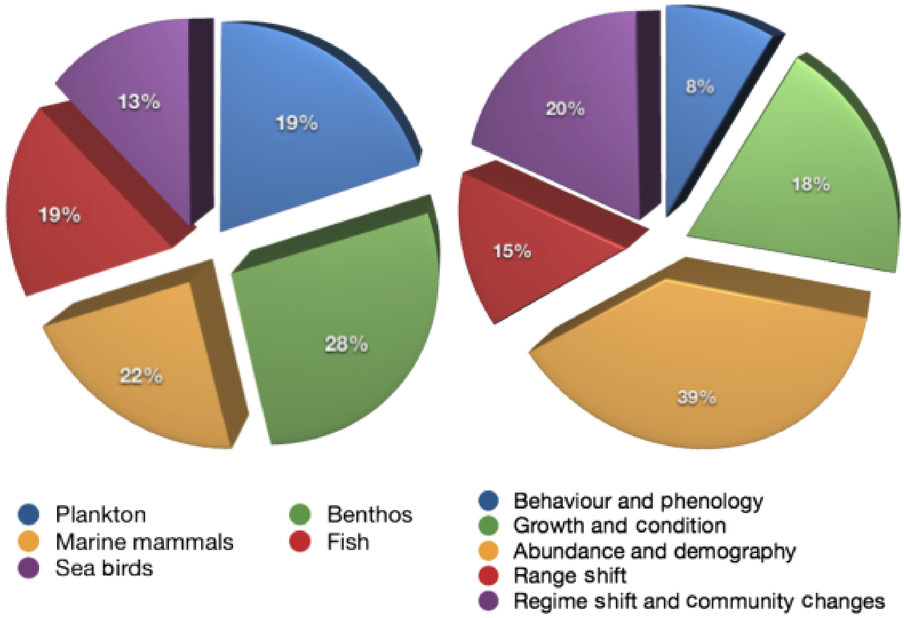

Fig. 2 Percent distribution of documented footprints of climate change (Tables 1–5) on Arctic biota onto different types of organisms and responses.

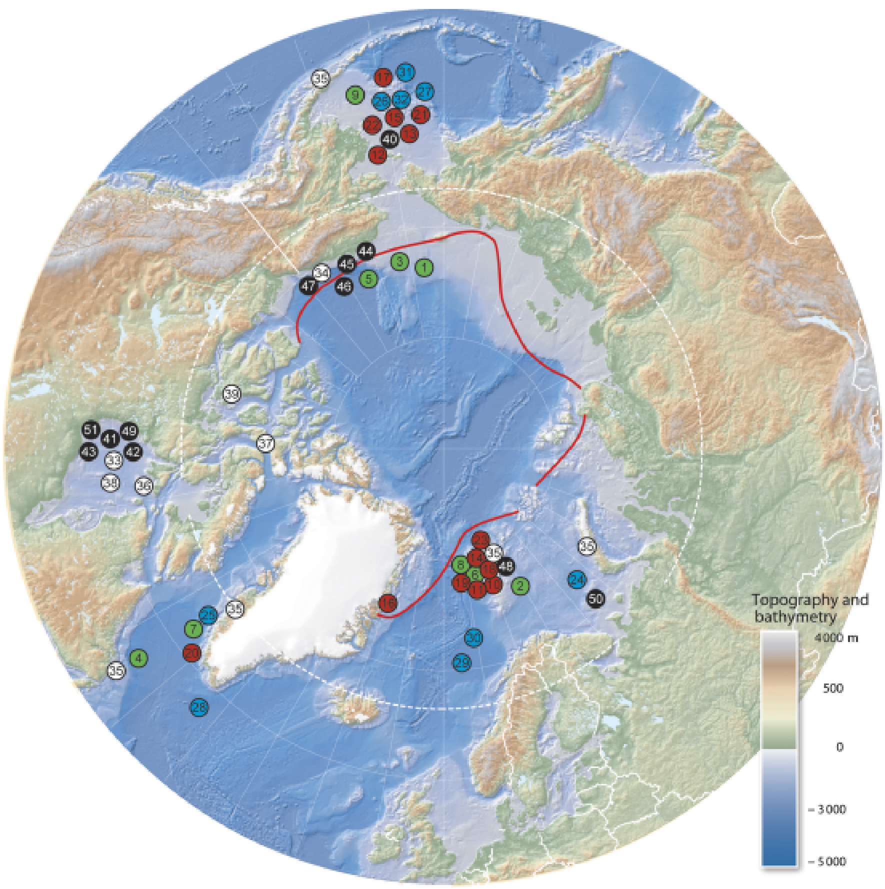

Fig. 3 Map of the Arctic showing the locations where footprints of climate change impacts on marine biota have been reported. The Arctic shelves and the mean minimum extent of ice (1979–2000) are indicated. The number of the symbols identifies the entry in Tables 1–5, and the colours identify the reported organisms: Green: plankton; Red: benthos; Blue: fish; White: birds; Black: mammals.

Table 6 Summary of types of footprints of responses of Arctic marine organisms to climate change

Responses	Nature of changes
Range shift	Northward displacement of subarctic and temperate species, cross-Arctic transport of organisms from the Pacific to the Atlantic sectors
Abundance	Increased abundance and reproductive output of subarctic species, decline and reduced reproductive success of some Arctic species associated to the ice and species now used as prey by predators whose preferred prey have declined
Growth and condition	Increased growth of some subarctic species and primary producers, and reduced growth and condition of ice-bound, ice-associated, or ice-born animals
Behaviour and phenology	Anomalous behaviour of of ice-bound, ice-associated, or ice-born animals with earlier spring phenological events and delayed fall events
Community and regime shifts	Changes in community structure due to range shifts of predators resulting in changes in the predator-prey linkages in the trophic network

well-known ones such as the Barents Sea (Wassmann *et al.*, 2010). Model simulations further predict that the Arctic will experience the greatest acidification within the global ocean, with pH decreasing by 0.45 units, a change that is amplified by more than 20% due to freshening and increased carbon uptake in response to sea ice retreat (Steinacher *et al.*, 2009). The surface waters of the Arctic Ocean will become corrosive to aragonite if atmospheric CO_2 rises to >450 ppm, which at current emission rates may occur within a decade, but the first signs of aragonite undersaturation have already been observed (e.g. Yamamoto-Kawai *et al.*, 2009b). Arctic marine biota thus face a plethora of unprecedented challenges that are beyond what science can document based on available data.

The endemic species in the Arctic Ocean are extremely exposed to climate change. However, the inventory of endemic Arctic marine species is far from complete and the ocean appears to contain many more species than hitherto believed. Some overviews of Arctic marine biodiversity have recently become available to the international public through Arctic Ocean Diversity (ArcOD; http://www.arcodiv.org) and the first of seven volumes of an illustrated key to the free-living invertebrates of the Eurasian Arctic Seas (Vassilenko & Petryashov, 2009) has lately been published. However, far more work is needed before Arctic marine biodiversity is sufficiently well known to allow reliable monitoring of ecosystem responses to climate warming. As many as 21 macroalgal species in the Arctic are considered endemic (R. Wilce, personal communication); 60 previously unknown benthic invertebrate species have been discovered off the shore of Alaska that are so far only known to exist in the Arctic Ocean (B. Bluhm, personal communication). In the relatively well explored Laptev Sea, 307 endemic species have been detected from among a total of about 1500 species (B. Sirenko, personal communiciton). Intense research in the past few years in Kongsfjorden, Svalbard, has shown that even in relatively well-studied ecosystems there are still undiscovered species in the pelagic (Schulz & Kwasniewski, 2004) as well as in the benthic realms (Kuklinski & Hayward, 2004). Fish species such as cod, haddock and capelin – previously rare in Kongsfjorden – are now common and can be caught in quantities that are of commercial interest (H. Hop and J. Berge, personal communication). The reader will note that these statements are largely based on personal communications, which exemplifies the difficulty of evaluating biodiversity and endemic species in the under-studied Arctic Ocean. It is, therefore, not surprising that a recent review on impacts of climate on the Arctic ecosystem (Post *et al.*, 2009) was largely focused on terrestrial species, with very limited attention to marine biota.

The endemic species associated with sea ice, including amphipods (*Apherusa glacialis*, *Gammarus wilkitzkii*, *Onisimus nanseni* and *Onisimus glacialis*, e.g. Werner *et al.*, 1999; Hop *et al.*, 2000), ice algae such as *Melosira arctica* growing into metre-long 'curtains' under multi-year sea ice (Usachev, 1949; Melnikov, 1997) and polar bears and narwhals are arguably the most vulnerable species (Melnikov, 2009). Narwhals, the most specialized of the Arctic cetaceans, are highly adapted to pack ice habitat, resulting in a strictly Arctic distribution (Laidre *et al.*, 2008). Change in sea ice algae will propagate along the pelagic food web (e.g. Søreide *et al.*, 2010) and to benthic habitats (McMahon *et al.*, 2006; Tamelander *et al.*, 2009).

New efforts and perspectives

Our review demonstrates that evidence of impacts of climate change in the Arctic is already available, but also shows an urgent need for heightened efforts to detect footprints of climate change in the Arctic. Documented footprints most certainly represent but a small set of the changes that have taken place. Future efforts will necessarily require international collaboration and support, particularly from the affluent nations in the

Northern Hemisphere that will be most strongly exposed to the effects of Arctic climate change. Scientific efforts in Arctic regions are not in themselves adequate to address the needs of humankind. A plethora of international statements argue for immediate actions to alleviate the accelerating pace of change (e.g. ACIA, 2004; Allison *et al.*, 2009; AMAP, 2009). An important role of the scientific efforts must be to provide the knowledge necessary to take such actions.

Recent manoeuvering on the part of the powerful coastal nations of the Arctic to extend the boundaries of their economic exclusive zones have so far not been particularly beneficial for international efforts to better understand changes in the Arctic as a whole. Whereas research funds to study the Arctic region are increasing, research priorities are often dictated by national agendas, rather than by an assessment of knowledge gaps and needs. Pan-Arctic integration and comprehension thus has to be achieved a posteriori based upon national, sector-specific endeavours, but cannot fill geographic gaps. Dedicated programs of oceanographic and marine ecological research along and across the Siberian shelf, comprising almost half of the pan-Arctic perimeter and up to >1000 km wide, are few [but see Nansen and Amundsen Basins Observational System (NABOS; http://nabos.iarc.uaf.edu) and Russian-American Long-term Census of the Arctic (RUSALCA; http://www.arctic.noaa.gov/aro/russian-american)]. National marine ecological research plans by Russia for the extensive Siberian shelf and adjacent Arctic Ocean have not been made available to the international scientific community. The prospects for a rapid increase in essential knowledge from the Arctic Ocean are thus unsatisfactory. Attaining that knowledge will require major impetus, also after the end of the Fourth International Polar Year.

Challenged with the steep climatic and environmental changes and the need of adequate data we suggest that new efforts in four categories are indispensable: (1) time series, (2) adequate seasonal coverage in key regions, (3) new technologies, (4) making older Russian data internationally accessible.

It is vital to continue the few existing time series at permanent stations in the Arctic Ocean (e.g. Canada's Three Oceans, those of Hausgarten and Kongsfjord, St. Lawrence Island, Kola section). The decisive work to resolve the functioning of the permanent-ice-covered region of the Arctic, which Dunbar called for as early as 1953, i.e. 'routine observations going every year, or at regular intervals, not only upon the fauna itself, but upon the hydrographic conditions which, more than anything else, determine the composition of the fauna' (Dunbar, 1953), is still in its early stages today, half a century later. The international community ought to start new time series in Arctic Ocean regions that are *most likely to be affected* by climate change.

Marine ecosystem studies suffer from inadequate seasonal coverage. Good winter data are only available from the Chukchi Sea (SHEBA), Franklin Bay (CASES) and Banks Island (CFL). Good as they are, these studies do not provide enough information to serve as a baseline for detecting footprints of climate change the Arctic Ocean. Footprints could be caused by changes in overwintering conditions as well as by circumstances during the productive period. More information is available on late winter/early spring, but such data are still rare (e.g. Wassmann *et al.*, 1999; Seuthe *et al.*, 2007; Søreide *et al.*, 2010). For important regions such as the Kara Sea ecological data are only available from the early autumn period (e.g. Hirche *et al.*, 2006). Current knowledge on the Arctic ecosystem can be used strategically to inform new efforts to detect footprints of climate change in the Arctic where they are critically needed. We need first of all basic knowledge from three key regions: (a) the Fram Strait area that accounts for more than 50% of all exchanges of water to and from the central Arctic Ocean (Schauer *et al.*, 2004); (b) the extensive Siberian shelf, to which none of the footprints identified here refer, but which is a key area to detect changes because of the very large increase in river discharge of water and materials (e.g. sediments, dissolved organic matter, nutrients, toxic substances) with climate warming (Peterson *et al.*, 2002; Fortier, 2008); and (c) the Central Arctic Ocean, arguably the least studied region of the ocean, for which no ecological information on biological impacts of climate change is available. These three areas are expected to experience particularly large changes, but the lack of research efforts or failure to report them gives scientists little opportunity to trace footprints. Moreover, these areas constitute 60% of the Arctic Ocean, for which our knowledge of realized impacts of climate change is nil.

New tools to detect footprints of climate change are also required. A few are becoming available, including molecular tools that make it possible to discriminate populations of different origins within species (e.g. *Calanus glacialis*, Nelson *et al.*, 2009) or phylum (e.g. *Archaea*, Galand *et al.*, 2008). Other tools, such as remote sensing with optical sensors (chlorophyll, ocean colour, temperature), will not contribute as much in the Arctic Ocean as they do elsewhere due to extensive cloud- and ice cover that limit remote sensing of the Arctic marine ecosystem. However, an increased number of satellite observations could improve the coverage of the Arctic Ocean. Speedy development of better techniques to identify climate change impacts on marine ecosystems at the pan-Arctic scale (e.g. Carmack & Wassmann, 2006; Carmack *et al.*, 2006) is indispensable and urgently needed to propel our knowledge on the Arctic Ocean ecosystem onto a significantly higher level.

A lack of biological data from the central Arctic Basin and the Russian shelves pre-dating anthropogenic climate change precludes the assessment of footprints of climate change in these key Arctic regions. Such data appear to exist in reports and field work journals, but the information is scattered, frequently neither compiled nor systematized, and basically never published, not even in Russian. Emphasis should be placed on making these data available for an international audience.

Enhanced research efforts are particularly important not only because of the ecological changes that may take place, but also because several key regions of the Arctic Ocean are strategically located near tipping elements of the Earth System (Lenton *et al*., 2008; Schellnhuber, 2010). This includes the freshwater outflow from the Arctic, potentially affecting deep water formation in the North Atlantic and the global thermohaline circulation (e.g. Notz, 2009) and the large pools of methane hydrates stored in the Siberian shelf, which are already venting to the atmosphere and may greatly increase greenhouse gas concentrations in the atmosphere if released (Shakhova *et al*., 2010). Increased efforts to monitor changes in the Arctic must engage the broader scientific community and be boosted by solid collaborative frameworks involving the Arctic coastal nations as well as the international community.

Outlook

The review conducted here provides compelling evidence of impacts of climate change on almost all components of the marine ecosystems, from planktonic communities to large mammals. These changes point to a poleward range shift of subarctic species, impacting the condition and demographics of Arctic species and displacing them from current food webs. There is little doubt that evidence shows only a subset of the changes that have already taken place, and that may have major impact on grossly under-studied ice communities. Many of the impacts that are already being felt probably remain to be documented; others cannot be documented due to insufficient baseline data. The nature of the changes compiled here is consistent with expectations derived from previous assessments (ACIA, 2004), demonstrating that the predictions were well founded. There is, therefore, concern about the fate of Arctic species, particularly those in ice-associated communities.

Confronted with the steep climatic and environmental changes and the paucity of adequate baseline data there is a pressing need for the international research community to focus on and allocate effort to Arctic research. The Fourth International Polar Year has mobilized the research community and may provide the impetus required to increase our knowledge on the impacts of climate change in the Arctic ecosystem. Change in the Arctic is likely to be abrupt in the near future. The review provided here indicates some changes that have already been documented, but also signals at changes that may occur and suggests how and where efforts should be focussed to ensure that the likely basin-wide regime shift in the Arctic Ocean ecosystem does not escape notice.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Reports of changes in Arctic plankton in response to climate change showing the organism and region investigated, the period of observation, and the response observed. The code number identifies the corresponding symbol in Fig. 3.

Table S2. Reports of changes in Arctic benthos in response to climate change showing the organism and region investigated, the period of observation, and the response observed. The code number identifies the corresponding symbol in Fig. 3. The code numbers with asterisk are changes that have not been documented in the published literature as yet, and therefore offer a weaker basis for the assessment.

Table S3. Reports of changes in Arctic fish in response to climate change showing the organism and region investigated, the period of observation, and the response observed. The code number identifies the corresponding symbol in Fig. 3.

Table S4. Reports of changes in Arctic sea birds in response to climate change showing the organism and region investigated, the period of observation, and the response observed. The code number identifies the corresponding symbol in Fig. 3.

Table S5. Reports of changes in Arctic marine mammals in response to climate change showing the organism and region investigated, the period of observation, and the response observed. The code number identifies the corresponding symbol in Fig. 3.

Table S6. Summary of types of footprints of responses of Arctic marine organisms to climate change.