Trends in
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Review

Ecological impacts of climate change on Arctic marine megafauna

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Global warming affects the Arctic more than any other region. Mass media constantly relay apocalyptic visions of climate change threatening Arctic wildlife, especially emblematic megafauna such as polar bears, whales, and seabirds. Yet, we are just beginning to understand such ecological impacts on marine megafauna at the scale of the Arctic. This knowledge is geographically and taxonomically biased, with striking deficiencies in the Russian Arctic and strong focus on exploited species such as cod. Beyond a synthesis of scientific advances in the past 5 years, we provide ten key questions to be addressed by future work and outline the requested methodology. This framework builds upon long-term Arctic monitoring inclusive of local communities whilst capitalising on high-tech and big data approaches.

Highlights

Marine megafauna (fishes, jellyfishes, cephalopods, seabirds, and marine mammals) play a pivotal role within aquatic food webs and may be used as ecological indicators of marine ecosystems.

Global warming affects the Arctic more than any other region on Earth, supposedly transforming the ecology of marine megafauna and the functioning of oceanic ecosystems.

Understanding these processes is essential, but existing knowledge is spatially and taxonomically biased, with a strong focus on commercial or emblematic species and knowledge deficiency in Russian waters.

We provide conceptual and methodological guidance to address these burning issues.

Notably, combining existing long-term monitoring programs with high-tech approaches and citizen science will help us to fully understand climate change impacts on pan-Arctic marine megafauna.

Climate change and Arctic marine megafauna

The Arctic is warming nearly four times faster than the rest of the planet, overshooting predictions [1]. These exceptional trends are due to **Arctic amplification** (see Glossary) [2], and abiotic consequences are manifold. Those include enhanced precipitation, sea surface temperatures, and storminess; a declining **cryosphere**; intensified hydrological cycles; and coastal erosion [3]. Such changes affect ocean circulation at both local and global scales, with feedback effects on atmospheric circulation, extreme weather events, and sea-level rise, also at lower latitudes [4,5]. In addition, a vanishing cryosphere leads to the release of chemicals and plastics, some of them toxic [6], and to increased anthropogenic activities also contributing to enhanced pollution [7].

The Arctic is ~67% a marine region, and climatic changes have profound abiotic effects on aquatic ecosystems [8], notably through a transformed light environment following the disappearance of sea ice, changes in ocean stratification, acidification, enhanced nutrient fluxes from land to sea and benthopelagic coupling, as well as shifting haloclines (salinity stratification) [3,9,10]. From a biotic point of view, Arctic marine food webs are rapidly transformed by the spread of northern temperate species, leading to a **borealisation** of the Arctic [11]. Warming also opens the door to new pathogens, parasites and non-Indigenous species [12,13] and enhances connectivity, such as through new species dispersal between the Pacific and Atlantic oceans, across the Arctic basin [14]. The architecture of food webs is thereby transformed through new predator–prey relationships, new competitors, and shifting phenologies [15]. In this context, one of the most prominent changes is the modified spatiotemporal occurrence of algal blooms, potentially leading to a 'marine greening of the Arctic' [10], but also to new harmful algal blooms [16]. These shifts reverberate across Arctic marine biophysical systems, and those are currently entering new, unprecedented states [3].

Within such rapidly changing landscapes, Arctic marine megafauna (AMM) (Figure 1) and First Nations relying on traditional food sources seem to share a destiny [17]. Marine megafauna are

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Figure 1. Examples of Arctic marine megafauna. Top: Arctic tern *Sterna paradisaea* (credit S.D.), Atlantic cod *Gadus morhua* (W.T. Fiege), Walrus *Odobenus rosmarus* (D.G.). Centre: *Gonatus fabricii*, the Boreo-Atlantic armhook squid (www.descna.com), common eider *Somateria mollissima* (D.G.). White-beaked dolphin *Lagenorhynchus albirostris* (foreground) and fin whale *Balaenoptera physalus* (background) (S.D.). Bottom: bearded seal *Erignathus barbatus* (S.D.), polar cod *Boreogadus saida* (P. Leopold), polar bear *Ursus maritimus* (M. Andersen).

defined as all cnidarian (e.g., jellyfish), molluscs (e.g., squid), fishes, reptiles, birds, and mammals that are larger than other marine species and/or are predators playing a key functional role in food webs [18]. With the exception of peoples of the reindeer, Arctic First Nations are coastal and tightly linked to the aquatic environment and its resources [19]. Marine megafauna are therefore economically and culturally essential for Arctic peoples as food base and key elements of founding narratives. Both these elements foster the resilience of Arctic First Nations, in the past and when facing current global change [20]. For instance, the narwhal (*Monodon monoceros*) is hunted from Alaska to Greenland, and its skin is highly valued as traditional food. The species is also subjected to a legend, told across the Arctic in slightly different versions, according to which the narwhal's tusk is made of the rolled-up hair of a drowned woman. Close relatedness between Arctic people and marine megafauna is also underlined by the pan-Arctic legend of the mother of the sea, a woman who rules over all marine animals and is married to a seabird, the northern fulmar (*Fulmarus glacialis*).

As keystone species at the apex of food chains, AMM integrate underlying processes: their food base depends upon marine productivity, and they are also exposed to contaminants bioaccumulated across trophic levels [21]. In this context, marine megafauna not only function as ecological indicators providing information about the state of marine ecosystems; they may also become flagship organisms motivating decision makers to act for nature conservation [22].

For these different reasons, it is essential to better understand the ecological impacts of climate change on AMM, and knowledge has recently been gathered in this matter. We review these insights and assess whether they are sufficient to test the impacts of Arctic climate change on ecological processes affecting marine megafauna. To guide future work, we outline ten key research questions and provide a novel, integrative research framework and methodological toolkit. This

Glossary

Arctic amplification: faster warming in the Arctic as compared with the rest of the globe (nearly four times faster during 1979–2021). This amplification can be explained by several factors, among which are changes in albedo due to decreasing sea ice and ocean heat transport.

Biologging: the study of living organisms via the use of data-recording devices. In animal ecology, biologging technologies are generally used to gather information on animal behaviour (e.g., 3D movement) or physiology (e.g., heart rate).

Borealisation: the ongoing expansion of so-called boreal (i.e., north temperate) species into arctic biomes. In the marine environment, this process may be driven by the advection of warmer and saltier waters from the Atlantic or Pacific oceans into the polar basins. These phenomena are called 'Atlantification' or 'Pacification' of the Arctic.

Cryosphere: the part of Earth's surface layer consisting of frozen water in the form of snow, permafrost, glaciers, and sea ice.

Deep learning: a branch of artificial intelligence (AI) that uses algorithms to enable computer systems to learn and improve from experience without being explicitly programmed. In ecology, deep learning is used to automatically detect specific features in large and/or complex data (e.g., to identify or count individuals, classify behaviours).

DNA metabarcoding: a molecular technique that allows identifying the species present in a sample (e.g., soil, water) by analysing all DNA sequences present in this sample and comparing them with reference databases.

Ecotoxicology: the study of the toxic chemicals present in living organisms. It aims at understanding the mechanisms of toxicity and assessing consequences on organism physiology, behaviour, or demography. For instance, persistent organic pollutants (POPs) and per- and polyfluoroalkyl substances (PFAS) are key contaminants in Arctic wildlife with known detrimental consequences.

Functional biogeography: combines knowledge on species distribution with information on species' functional traits to understand how large-scale distributional changes may affect ecosystem functioning.

Gill-oxygen limitation theory: the oxygen-carrying capacity of water is limited by its temperature, salinity, and rationale blends a wide range of techniques, including long-term monitoring, emerging technologies, and citizen science programs.

A synthesis of ecological impacts

We reviewed recent existing knowledge on the ecological impacts of climate change on AMM. We thereby focused on the 5 years following the Paris Agreement under the United Nations Framework Convention on Climate Change, which is considered a major landmark for international awareness on climate change impacts. To this end, we searched the Web of Knowledge (in English) and CyberLeninka (in Russian) in February–April 2022, focusing on climate change-related articles published since 2017 on fish, jellyfish, squid, seabirds, and marine mammals (see details in Supplementary Information 1). A focus on scientific knowledge of the past 5 years also follows the guidelines for reviews in *Trends in Ecology and Evolution*. We acknowledge the fact that this may omit some previous work, partly compensated by 25 years of polar research and knowledge by the two authors. Moreover, our conclusions are supported by former reviews focused on Arctic marine ecosystem functioning [23]. Finally, because Arctic climate change mainly accelerated in recent years [1], it seemed appropriate to focus on investigations conducted during this specific period.

Our analysis yielded 250 relevant publications (Supplement 1). Fifty percent of the studies using empirical data (n = 173) were based on >11 years of data and 17% on ≥30 years of data (maximum 131 years [24]). Overall, there was a major focus on fish (36% of all studies). The analysis also revealed a strong bias towards a limited number of species: 40% of fish studies focused on Atlantic and polar cod (*Gadus morhua* and *Boreogadus saida*, respectively), and 20% (n = 49) of all studies dealt with climate change impacts on polar bears (*Ursus maritimus*). These species were the most studied because they are either of high commercial value (Atlantic cod), play a key role in ecosystem functioning (polar cod), or are emblematic of the Arctic (polar bear). A relatively large number of fish species were considered (>80), because many studies were based on survey tows (e.g., 82 species included in [25]). Very few studies were conducted on cephalopods (four in total, including two reviews), and the two most abundant species in the Arctic, that is, *Rossia palpebrosa* (warty bobtail squid) and *Gonatus fabricii* (Boreo-Atlantic armhook squid) were the focus of only two case studies [26,27]. Nineteen species of marine mammals were studied, with the beluga (or white) whale *Delphinapterus leucas* being the second most-studied species (n = 13 studies) after the polar bear. Forty-four seabird species were studied, but many were part of general at-sea surveys and not the direct focus of the work. The Brünnich's guillemot (*Uria lomvia*) was the most-studied seabird and appeared in 52% (n = 27) of all seabird-related publications.

Most of the studies dealt with six main topics (Table 1). The relative importance of each topic varied among guilds, but spatial distribution/habitat use and individual state (body condition, growth, physiological state) were the most common topics for fish, seabirds, and marine mammals. Despite the potential importance of diet shifts for marine megafauna population dynamics, very few studies investigated fish or seabird diets. Finally, whatever the guild considered, very few studies addressed changes at the community or ecosystem level (Table 1).

We also identified a strong geographical bias (Figure 2): the most intensively studied areas were US Alaskan waters as defined by the country's exclusive economic zone (136 studies per 1 million km^2); followed by Norwegian waters (30 studies per 1 million km^2); and, to a lesser extent, Canadian, Greenlandic, and Icelandic waters (12, 11, and nine studies per 1 million km^2, respectively). The analysis stressed the deficit of studies within Russian waters (six studies per 1 million km^2), with the exception of the Barents Sea, where research by Norwegian and Russians scientists is leading to advanced ecological understanding.

pressure. Colder water therefore holds more dissolved oxygen than warmer water. As water temperature increases or salinity decreases, the oxygen-carrying capacity of the water decreases, making it more difficult for aquatic organisms to extract oxygen. In fishes, growth and maximum sizes are consequently limited by water oxygen-carrying capacity and the size of the gills.

Shannon diversity: a biodiversity measure that takes into account the number of different species present in a given ecosystem and their relative abundance.

Tipping point: critical thresholds in climate conditions above which abrupt and potentially irreversible changes in ecosystem structure and dynamics occur.

Table 1. Main topics addressed in studies linking marine megafauna and climate change[a]

	Community	Habitat use	Population dynamics	Demography	Individual state	Diet	Other
Cephalopod	25	0	25	0	0	25	25
Fish	9	21	20	9	28	5	17
Seabird	6	21	30	32	23	9	15
Marine mammal	1	36	13	22	33	19	12

[a]Each cell of the table gives the percentage of studies dealing with each topic. The sum for each guild is usually >100% because a given study may address several topics. 'Community' refers to studies dealing with ecosystem or community structure; 'habitat use' to studies dealing with spatial distribution, habitat use, or movement; 'population dynamics' to studies dealing with population trajectory, abundance, or age structure; 'demography' to studies dealing with vital rates (survival, reproduction) or phenology; and 'individual state' to studies dealing with body condition, physiology, energetics, or pollutants. The column 'Other' corresponds to a variety of themes and includes reviews or opinion articles, as well as studies based on Indigenous ecological knowledge.

Therefore, the first prominent conclusion of our review is that existing knowledge on climate change impacts on AMM is extremely biased with respect to studied species and geographical coverage. On the basis of this limited knowledge, our current understanding of ecological processes at the individual, populational, ecosystem, and landscape levels can be summarised as outlined next.

Physiological and behavioural responses

Although this was a major research focus in the past [28], morphological and physiological adaptation to Arctic climates has been critically understudied in recent years [29]. Well-insulated Arctic endotherms such as guillemots (*Uria* sp.) may save energy in warmer winter conditions [30] but easily overheat in summer [31], with consequences for their water and energy balance, and potential casualties during heat waves. In ectothermic fish, higher temperatures boost metabolic rates, but the **gill-oxygen limitation theory** predicts that warmer Arctic waters will contain less oxygen, therefore limiting growth and maximum size of water-breathing organisms [32]. Warming also goes along with acidification of Arctic waters [33]. In Atlantic cod (*G. morhua*) and polar cod (*B. saida*), such acidification impairs adult swimming capacity [34] and causes a narrowing of embryonic thermal ranges, with a potentially critical impact on juvenile fitness [35]. Further synergetic adverse effects of Arctic warming involve enhanced zoonotic pathogen exposure, such as in polar bears [36], as well as contamination by chemical pollutants [37] and plastics [38]. In this context, Arctic **ecotoxicology** is currently booming [39], but with a limited number of analyses testing fitness consequences of contaminant exposure [40].

In contrast to the paucity of physiological studies investigating the consequences of Arctic warming for marine megafauna, most recent publications focused on behavioural adjustments to rapidly changing environmental conditions, notably the disappearance of sea ice and shifting prey distributions [41]. These investigations confirmed the pivotal role of flexible foraging behaviour, enabling some marine species to buffer the consequences of Arctic climate change [42,43]. For instance, long-term stable isotopic analyses showed dietary shifts in beluga whales, ringed seals (*Pusa hispida*), Greenland halibut (*Reinhardtius hippoglossoides*), and anadromous Arctic char (*Salvelinus alpinus*) from Cumberland Sound, Nunavut [44]. Such trophic rearrangements may affect the architecture of entire food webs [45,46]. Foraging plasticity also triggers shifting foraging habitats, such as for ringed seal in Hudson Bay [15], and ultimately leads to community-wide northward shifts, as recorded for seabirds in the Northern Bering and Chukchi seas [47]. Finally, fish communities may also seek deeper habitats as the sea warms [48]. Spatial

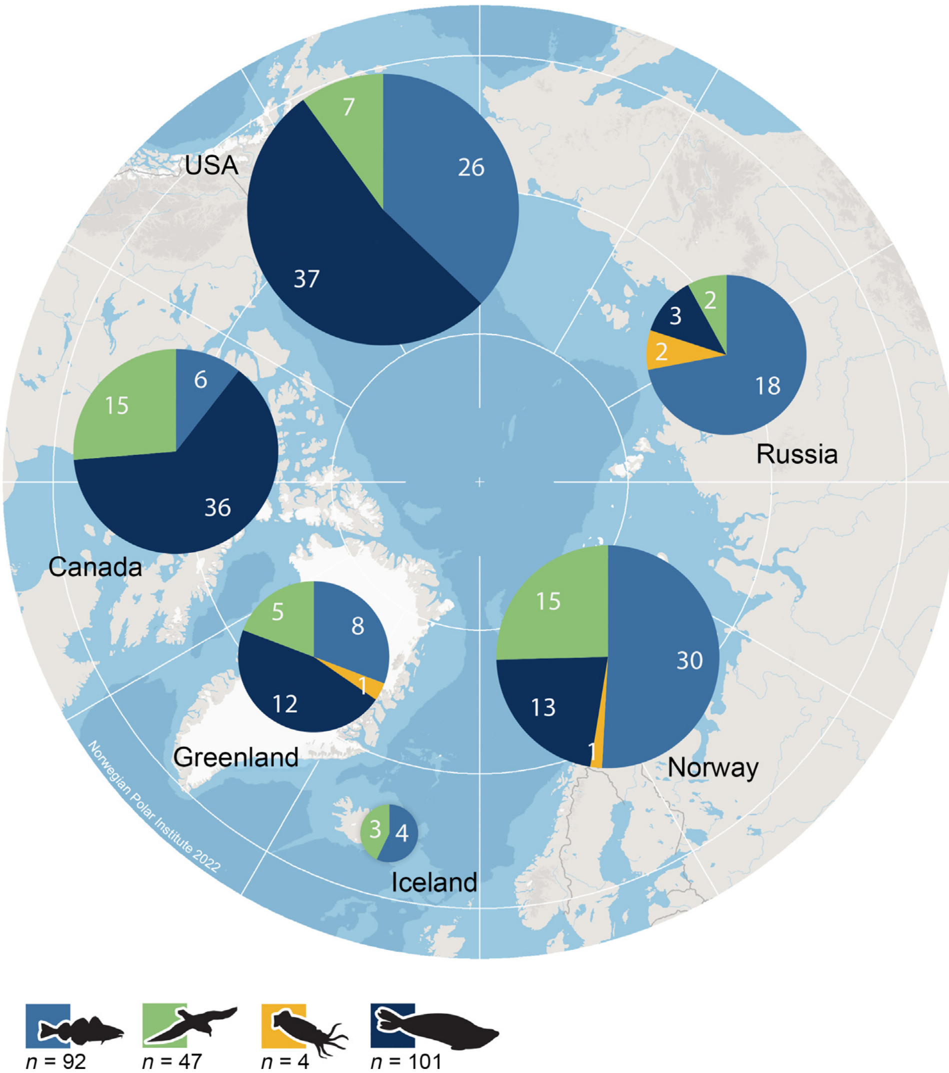

Figure 2. Distribution of recent Arctic marine megafauna studies. (See methods and Supplement 1 for definitions and time frame.) Colours correspond to the different megafauna groups as pictured below the map, and the proportion of each colour per pie is indicative of the number of studies per megafauna group and area. Pies are sized relative to the total number of megafauna studies per area (see methods). The vast majority of the Russian studies took place in the Barents Sea. The number on each pie represents the number of studies dealing with each guild. The total number of studies per guild is indicated under the guild icons (note that a given study may concern several guilds, so that the total number of studies here does not correspond to the total number of studies reported in our review).

rearrangements may occur during residency, as well as during migration, potentially leading to the colonisation of new habitats and enhancing the likelihood of speciation events [14]. As sea ice habitats vanish, recent work stressed the importance of coastal glacier fronts as refugia attracting Arctic fish [49], birds, and mammals [50]. Those new habitats have lower temperatures and localised upwelling enhancing prey availability [51], but also promote predator contamination by pollutants and plastics [52]. Yet, spatial and trophic plasticity is likely more the exception than the norm in AMM, especially in long-lived species such as marine mammals, seabirds, and some fishes. This is due to the strong repeatability and persistence of their foraging behaviour, of their marked philopatry [53], and to the lack of alternative habitats for the northernmost species, which cannot shift further poleward. Overall, recent big data approaches based on **biologging** triggered major advances in our understanding of behavioural and ecophysiological responses of marine megafauna to Arctic warming [54], but only a minority of those infer fitness consequences [55]. In this context, assessing the energy balance of animals facing environmental change by linking information on their foraging behaviour and their energetics appears as a major avenue to understand individual responses and their fitness costs [56].

Demographic and populational impacts

The effect of climate change on Arctic megafauna demography and population trajectories remains largely unknown, especially for marine mammals (Table 1). A few studies on fish [57,58], seabirds [59,60], or mammals [61] identified significant relationships between population abundance and environmental stressors associated with climate change (e.g., sea surface temperature, timing of sea ice breakup) based on empirical long-term data. Several others identified long-term trends in megafauna populations [62,63] and explained these trends in relation to climate change, but without formally testing for such associations. The small number of such studies is a direct consequence of the paucity in long-term time series on Arctic megafauna population size. However, even in the absence of empirical abundance data, approaches based on traditional ecological knowledge [64] or modelling may help in understanding how Arctic populations are, or will be, responding to climate change [14,65–68].

A common alternative consists in looking at effects on single demographic parameters to infer the potential development of a given population [24,37,69]. For example, early sea ice breakup and longer ice-free periods led to smaller litter size for polar bears in Baffin Bay (between Canada and Greenland), suggesting a negative effect of Arctic warming on the regional polar bear population [70]. However, such results should be interpreted with caution. Indeed, links between changes in a single demographic parameter and changes in population growth rate also depend on the sensitivity of population growth rate with respect to this parameter [71] and changes in other demographic parameters. Thereby, different parameters may show antagonistic responses to environmental change [72], and analyses integrating the response of multiple demographic parameters are needed to understand population dynamics. Ideally, these analyses should also consider environmental conditions throughout the life cycle, because many megafauna species are migratory and do not stay in the Arctic all year round. Environments encountered on the winter grounds may be of paramount importance in driving population dynamics, as highlighted >50 years ago by D. Lack [73], and should also be incorporated in demographic studies.

Overall, whatever the approach used, no general conclusion can be drawn yet: climate warming may have positive, negative, or no effects on the vital rates and/or population trajectories of Arctic megafauna, depending on the species and/or region considered. Endemic Arctic species may respond more negatively to climate warming [48,74], but this is not an absolute pattern either. For example, the biomass of the polar cod, a true Arctic species, in the Canadian Arctic was positively correlated to sea surface temperature [57]. Beyond interspecific variation in climate change response, it is also essential to consider spatial variation in intraspecific responses. For example, relationships between sea ice extent and the colony size of black-legged kittiwakes varied among fjords in Svalbard, potentially due to contrasting local oceanographic conditions [60]. Also, loss of sea ice had negative effects on polar bears in Baffin Bay [70], but these effects were null or positive in the Chukchi Sea [69]. Such spatial variation in the effects of climate warming may reflect local variability in other environmental parameters [75]. Alternatively, they may also be the consequence of potentially crucial but often overlooked nonlinear effects. For instance, polar bears in the Chukchi Sea maintained body condition despite vanishing sea ice [69], contrary to bears from the Bering Sea, whose condition declined [70]. These findings suggesting that Chukchi Sea bears are not currently limited by sea ice [69], maybe due to nonlinearity between sea ice conditions and polar bear life history. Notably, in the Chukchi Sea, sea ice cover may still be above the threshold below which a declining sea ice has detrimental effects [69]. The concept of threshold, or **tipping point** [76,77], thereby remains essential [78]. Even if the increase in temperature is more or less a linear process, it is associated with nonlinear changes in other climatic parameters (e.g., snowfall [79]). Equally, the behavioural, physiological, and population responses to all these numerous and complex environmental changes have no reason to be linear [24,80].

Overall, species-specific and spatial variation in climate change effects, combined with potential nonlinearity in these effects, hinders our capacity to make general predictions regarding Arctic megafauna population trajectories. One key limiting factor is the lack of long-term abundance data for most species and/or regions.

Impacts on biodiversity and ecosystem functioning

Predicting how biodiversity responds to climate change [81] and how changes in biodiversity affect ecosystem functioning [82] are active fields of research. However, very few studies on Arctic megafauna have been undertaken in these specific areas. Our literature review identified only one that has explicitly assessed the impact of climate change on Arctic megafauna biodiversity. This study [83] found a positive global warming effect on fish biodiversity in an Arctic fjord in northern Norway, whereby species richness and **Shannon diversity** of fishes increased following the arrival of warm-water species. Other studies focused on species composition [74,84,85] as a metric for species richness. These findings generally support the borealisation of the Arctic marine environment, with north temperate (or 'boreal') species becoming more abundant. Species richness represents, however, only one facet of biodiversity [82] so that reported changes in species composition, though highly valuable, do not give a complete representation of ongoing changes in Arctic megafauna biodiversity.

Investigations on climate change impacts on Arctic marine ecosystem functioning are equally scarce. Griffith *et al.* [46] modelled the arrival of Atlantic species (such as capelin *Mallotus villosus*) and showed they may increase the resilience of marine fjord systems, with maintained food web structure. Furthermore, Frainer *et al.* [86] based their work on fish **functional biogeography** to address how ecosystem functioning may be affected by climate change in the Barents Sea. Their results also support an ongoing borealisation of Arctic marine ecosystems with large boreal species replacing small Arctic ones, likely affecting biomass production. Other analyses of functional redundancy [87] or specific species interactions [45,88] have also been performed to explore changes in ecosystem functioning due to climate change. These studies confirm that ongoing climate change has the potential to affect Arctic marine ecosystem functioning, even though the exact consequences remain extremely difficult to apprehend.

The way forward

Rigorously assessing climate change impacts on marine megafauna at the scale of the Arctic is a formidable task (Figure 3). Ecologists thereby face the combined challenges of an immensely vast terrain of drastic weather conditions and staggering operational costs [89]. In addition, the current socioeconomic crisis questions the environmental footprint of research operations and reduces available funding. Finally, international tensions prevent collaboration between Russian scientists and the rest of the world. This considerably slows AMM data acquisition in least-known areas.

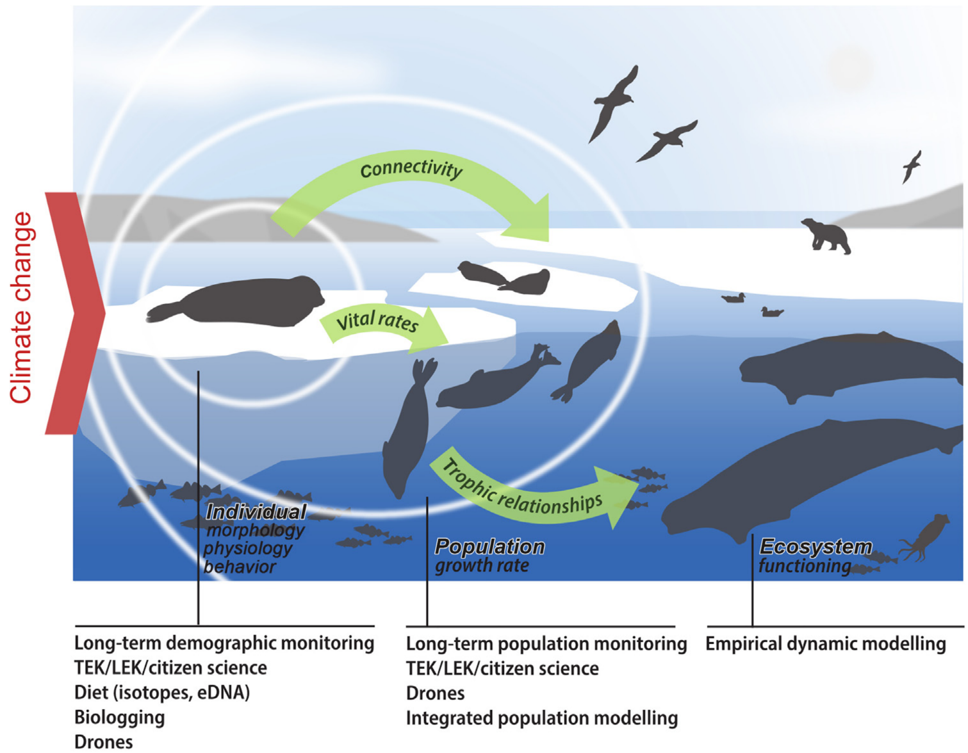

Figure 3. The way forward – outline of future research work necessary to assess climate change impacts on Arctic marine megafauna. Climate change affects individual vital rates through changes in physiology, behaviour, or even morphology. These effects can be mediated by changes in habitats (e.g., connectivity) or trophic relationships (e.g., dietary changes through shifts in prey availability, changes in interspecies competition). The integration of complementary methods based on new technologies, new statistical methods, as well as citizen science are needed to understand ongoing changes in megafauna populations and marine ecosystems. Abbreviations: LEK: local ecological knowledge; TEK: traditional ecological knowledge.

Despite these hurdles, and thanks to the dedication of passionate individuals within Arctic communities and the international scientific community, research on marine megafauna is progressing. Three powerful leverages outlined below permit such advances, now and in the near future.

1. Modern technologies allow remote, large-scale data collection on previously totally unknown aspects of AMM ecology. This starts with satellite remote sensing of multiple biotic and abiotic parameters all across the Arctic, which nonetheless only assesses conditions at the sea surface. *In situ*, aerial and underwater autonomous vehicles (e.g., drones) automatically survey areas ranging from one to millions of cubic meters of ocean [90]. They provide fine-scale information on environmental conditions, notably on the spatiotemporal abundance of potential prey for marine megafauna (e.g., zooplankton and small pelagic fish aggregations). In addition, biologging devices attached to animals opened worlds of knowledge on their spatial ecology and their energetics in a changing ocean [54], and combined analyses provide information on contaminant levels in animals and their environment [6]. Finally, further rapidly emerging techniques such as **DNA metabarcoding** are transforming the field of population ecology [91].
2. Beyond these technological revolutions in data acquisition, marine megafauna ecology has now entered the realm of big data science: information technology allows the design of

completely new frameworks for acquiring, storing, sharing, analysing, visualising, and publicising data [92]. Big data approaches are notably based on the use of artificial intelligence and **deep learning** scheme, which drastically reduce analysis duration and costs [93,94], and online platforms greatly enhance data sharing [54].

3. All above-mentioned approaches may be complemented with citizen science initiatives [95,96]. Those may allow additional data collection within scientific blind spots, notably species distribution and abundance, and assist in long-term monitoring when such activities become impossible for conventional research teams, as during the recent coronavirus disease 2019 (COVID-19) pandemic. Participatory science programs may also contribute to the empowerment of local communities, in many areas of the Arctic where the predominance of non-Indigenous scientists may be perceived as postcolonial.

These research targets, which aim at understanding global change impacts on AMM while better involving local communities, are highly coherent with the objectives of the Arctic Marine Biodiversity Monitoring Plan of the Arctic Council [97]. This initiative should use scientific evidence to improve biological conservation in the Arctic, but the political will and international collaboration necessary to transform research into action still seems in its infancy [98].

Concluding remarks: key research gaps and questions on AMM

- With a few exceptions, it is not possible to conclude on recent trends in AMM populations and the interspecies and spatial variations in these trends. Basic data about population size are still lacking for most species and regions.
- Individual variations in responses to climate change, their drivers (e.g., age, physiological status, experience) and their implications to buffer climate change impacts also remain largely unknown. Such individual variations are, however, crucial to assess populational responses to environmental changes [99].
- The shapes of the relationships (linear/nonlinear) between AMM physiological, behavioural, or demographic traits and the direct and indirect (e.g., pollutants and pathogens, shifting human activities) consequences of climate change are critically understudied. This prevents any reliable predictions about the fate of AMM in response to future climate change scenarios.

From these knowledge gaps, as well as following two decades of interactions with the Arctic research community and its many panarctic stakeholders, in particular the Arctic Council and its working groups, we identified ten research avenues (see Outstanding questions). Those are particularly far-ranging and aim at presenting a general framework beyond our review of recent knowledge. They start with interrogations about individual and populational responses of AMM to climate change, subsequently leading to wider considerations at the interface between the fate of AMM and that of Arctic peoples.

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Declaration of interests

No interests are declared.

Outstanding questions

What are the consequences of physiological and behavioural responses to Arctic environmental change for individual energy balance and fitness?

What is the spatial variation and the shape of relationships between environmental changes and individual physiological, behavioural, and demographic responses?

Do individuals and life stages vary in their responses to environmental change (including extreme events), and can such variation buffer climate change impacts on Arctic marine megafauna (AMM) populations?

What are the consequences of environmental changes on AMM functional biodiversity and ecosystem functioning?

What are the synergetic individual and populational consequences of the exposure of AMM to direct and indirect climate change impacts?

What is the evolutionary past of AMM and its consequences for the capacity of the different species/taxonomic groups to buffer the impact of current climate changes via phenotypic plasticity/microevolution?

Given the huge geographical extent of the Arctic and financial and logistic constraints, are there ways to nonetheless provide a general analysis of climate change impacts on AMM?

How can research on AMM best contribute to their international conservation and that of Arctic biota in a climate change context?

What are the modalities for a better involvement of Arctic peoples in AMM monitoring in the context of climate change?

Can research on climate change impacts on AMM be used to foster pan-Arctic diplomacy and peacekeeping?

Supplementary information

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