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1 **Title**

2 Ecological impacts of climate change on Arctic marine megafauna

3

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14

15 **Abstract**

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

24

25 **Keywords**

26 Biogeography, Citizen science, Global change, Long-term monitoring, Oceanography, Polar

27

## 28 **Climate change and Arctic marine megafauna**

29 The Arctic is warming nearly four times faster than the rest of the planet, overshooting predictions [1].  
30 These exceptional trends are due to **Arctic amplification** (see glossary) [2], and abiotic consequences  
31 are manifold. Those include enhanced precipitation, sea surface temperatures and storminess, a  
32 declining **cryosphere** (land and sea ice, permafrost), intensified hydrological cycles, and coastal erosion  
33 [3]. Such changes affect ocean circulation, both at local and global scales, with feedback effects on  
34 atmospheric circulation, extreme weather events and sea level rise, also at lower latitudes [4,5]. In  
35 addition, a vanishing cryosphere leads to the release of chemicals and plastics, some of them toxic [6],  
36 and to increased anthropogenic activities also contributing to enhanced pollution [7].

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

50 Within such rapidly changing landscapes, Arctic marine megafauna (Figure 1) and First Nations relying  
51 on traditional food sources, seem to share a destiny [17]. Marine megafauna are defined as all  
52 cnidarian (e.g. jellyfish), mollusks (e.g. squid), fishes, reptiles, birds and mammals which are larger than  
53 other marine species and/or are predators playing a key functional role in food webs [18]. With the  
54 exception of peoples of the reindeer, Arctic First Nations are coastal, and tightly linked to the aquatic  
55 environment and its resources [19]. Marine megafauna are therefore economically and culturally  
56 essential for Arctic peoples, as food base and key elements of founding narratives. Both these elements  
57 foster the resilience of Arctic First Nations, in the past and when facing current global change [20]. For  
58 instance, the narwhal (*Monodon monoceros*) is hunted from Alaska to Greenland, and its skin highly  
59 valued as traditional food. The species is also subjected to a legend, told across the Arctic in slightly  
60 different versions, according to which the narwhal's tusk is made of the rolled-up hair of a drowned  
61 woman. Close relatedness between Arctic people and marine megafauna is also underlined by the

62 panarctic legend of the mother of the sea, a woman who rules over all marine animals and is married  
63 to a seabird, the northern fulmar (*Fulmarus glacialis*).

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

69 For these different reasons, it is essential to better understand the ecological impacts of climate  
70 change on Arctic marine megafauna, and knowledge has been recently gathered in this matter. We  
71 review these insights and assess whether they are sufficient to test the impacts of Arctic climate  
72 change on ecological processes affecting marine megafauna. To guide future work, we outline ten key  
73 research questions, and provide a novel, integrative research framework and methodological toolkit.  
74 This rationale blends a wide range of techniques, including long-term monitoring, emerging  
75 technologies and citizen science programs.

76

#### 77 **A synthesis of ecological impacts**

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

90 Our analysis yielded 250 relevant publications (Suppl. 1). Fifty percent of the studies using empirical  
91 data (n=173) were based on > 11 years of data and 17% on ≥30 years of data (maximum 131 years,  
92 [24]). Overall, there was a major focus on fish (36% of all studies). The analysis also revealed a strong  
93 bias towards a limited number of species: 40% of fish studies focused on Atlantic and polar cod (*Gadus*  
94 *morhua* and *Boreogadus saida*, respectively), and 20% (n=49) of all studies dealt with climate change  
95 impacts on polar bears (*Ursus maritimus*). These species were the most studied because they are either  
96 of high commercial value (Atlantic cod), play a key role in ecosystem functioning (polar cod), or because

97 they are emblematic of the Arctic (polar bear). A relatively large number of fish species were  
98 considered (>80), because many studies were based on survey tows (e.g. 82 species included in [25]).  
99 Very few studies were conducted on cephalopods (4 in total, including 2 reviews), and the two most  
100 abundant species in the Arctic, i.e. *Rossa palpebrosa* and *Gonatus fabricii* were the focus of only two  
101 case studies [26,27]. Nineteen species of marine mammals were studied, with the beluga (or white)  
102 whale *Delphinapterus leucas* being the second most-studied species (n=13 studies) after the polar  
103 bear. Forty-four seabird species were studied, but many were part of general at-sea surveys and not  
104 the direct focus of the work. The thick-billed murre (*Uria lomvia*) was the most-studied seabird and  
105 appeared in 52% (n=27) of all seabird-related publications.

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

112 We also identified a strong geographical bias (Figure 2): the most intensively studied areas were US  
113 Alaskan waters as defined by the country's exclusive economic zone (136 studies per million km<sup>2</sup>),  
114 followed by Norwegian waters (30 studies per million km<sup>2</sup>) and, to a lesser extent, Canadian,  
115 Greenlandic and Icelandic waters (12, 11 and 9 studies per million km<sup>2</sup>, respectively). The analysis  
116 stressed the deficit of studies within Russian waters (6 studies per million km<sup>2</sup>), with the exception of  
117 the Barents Sea where research by Norwegian and Russians scientists is leading to advanced ecological  
118 understanding.

119 Therefore, the first prominent conclusion of our review is that existing knowledge on climate change  
120 impacts on Arctic marine megafauna is extremely biased with respect to studied species and  
121 geographical coverage. On the basis of this limited knowledge, our current understanding of ecological  
122 processes at the individual-, populational-, ecosystem- and landscape-level can be summarized as  
123 follows:

124

### 125 **Physiological and behavioral responses**

126 While this was a major research focus in the past [28], morphological and physiological adaptation to  
127 Arctic climates has been critically understudied in recent years [29]. Well-insulated Arctic endotherms  
128 such as murre (*Uria sp.*) may save energy in warmer winter conditions [30], but easily overheat in  
129 summer [31], with consequences for their water and energy balance, and potential casualties during  
130 heat waves. In ectothermic fish, higher temperatures boost metabolic rates, but the **gill-oxygen**  
131 **limitation theory** predicts that warmer Arctic waters will contain less oxygen, therefore limiting growth

132 and maximum size of water-breathing organisms [32]. Warming also goes along with acidification of  
133 Arctic waters [33]: In Atlantic cod (*Gadus morhua*) and polar cod (*Boreogadus saida*), such acidification  
134 impairs adult swimming capacity [34], and causes a narrowing of embryonic thermal ranges, with a  
135 potentially critical impact on juvenile fitness [35]. Further synergetic adverse effects of Arctic warming  
136 involve enhanced zoonotic pathogen exposure, for instance in polar bears [36], as well as  
137 contamination by chemical pollutants [37] and plastics [38]. In this context, Arctic **ecotoxicology** is  
138 currently booming [39], yet with a limited number of analyses testing fitness consequences of  
139 contaminant exposure [40].

140 In contrast to the paucity of physiological studies investigating the consequences of Arctic warming for  
141 marine megafauna, most recent publications focused on behavioral adjustments to rapidly changing  
142 environmental conditions, notably the disappearance of sea-ice and shifting prey distributions [41].  
143 These investigations confirmed the pivotal role of flexible foraging behavior, enabling some marine  
144 species to buffer the consequences of Arctic climate change [42,43]. For instance, long-term stable  
145 isotopic analyses showed dietary shifts in beluga whales (*Delphinapterus leucas*), ringed seals (*Pusa*  
146 *hispidus*), Greenland halibut (*Reinhardtius hippoglossoides*) and anadromous Arctic char (*Salvelinus*  
147 *alpinus*) from Cumberland Sound, Nunavut [44]. Such trophic re-arrangements may affect the  
148 architecture of entire food webs [45,46]. Foraging plasticity also triggers shifting foraging habitats, such  
149 as for ringed seal (*Pusa hispidus*) in Hudson Bay [15], and ultimately lead to community-wide northward  
150 shifts, as recorded for seabirds in the Northern Bering and Chukchi seas [47]. Finally, fish communities  
151 may also seek deeper habitats as the sea warms [48]. Spatial re-arrangements may occur during  
152 residency, as well as during migration, potentially leading to the colonization of new habitats and  
153 enhancing the likelihood of speciation events [14]. As sea-ice habitats vanish, recent work stressed the  
154 importance of coastal glacier fronts as refugia attracting Arctic fish [49], birds and mammals [50]. Those  
155 lead to lower temperatures and localized upwelling enhancing prey availability [51], but also promote  
156 predator contamination by pollutants and plastics [52]. Yet, spatial and trophic plasticity is likely more  
157 the exception than the norm in Arctic marine megafauna, especially in long-lived species such as  
158 marine mammals, seabirds and some fishes. This is due to the strong repeatability and persistence of  
159 their foraging behavior, of their marked philopatry [53], and to the lack of alternative habitats for the  
160 northernmost species, which cannot shift further poleward. Overall, recent big data approaches based  
161 on **biologging** triggered major advances in our understanding of behavioral and ecophysiological  
162 responses of marine megafauna to Arctic warming [54], but only a minority of those infer fitness  
163 consequences [55]. In this context, assessing the energy balance of animals facing environmental  
164 change by linking information on their foraging behavior and their energetics, appears as a major  
165 avenue to understand individual responses and their fitness costs [56].

166

167 **Demographic and populational impacts**

168 The effect of climate change on Arctic megafauna demography and population trajectories remains  
169 largely unknown, especially for marine mammals (Table 1). A few studies on fish [57,58], seabirds  
170 [59,60] or mammals [61] identified significant relationships between population abundance and  
171 environmental stressors associated to climate change (e.g. sea surface temperature, timing of sea-ice  
172 break-up) based on empirical long-term data. Several others identified long-term trends in megafauna  
173 populations [62,63] and explained these trends in relation to climate change, but without formally  
174 testing for such associations. The small number of such studies is a direct consequence of the paucity  
175 in long-term time-series on Arctic megafauna population size. However, even in the absence of  
176 empirical abundance data, approaches based on traditional ecological knowledge [64] or modelling  
177 may help understanding how Arctic populations are, or will be, responding to climate change [14,65–  
178 68].

179 A common alternative consists in looking at effects on single demographic parameters, to infer the  
180 potential development of a given population [24,37,69]. For example, early sea-ice break-up and  
181 longer ice-free periods led to smaller litter size for polar bears in Baffin Bay (between Canada and  
182 Greenland), suggesting a negative effect of Arctic warming on the Baffin Bay polar bear population  
183 [70]. However, such results should be interpreted with caution. Indeed, links between changes in a  
184 single demographic parameter and changes in population growth rate also depend on the sensitivity  
185 of population growth rate with respect to this parameter [71] and changes in other demographic  
186 parameters. Thereby, different parameters may show antagonistic responses to environmental change  
187 [72], and analyses integrating the response of multiple demographic parameters are needed to  
188 understand population dynamics. Ideally, these analyses should also consider environmental  
189 conditions throughout the life-cycle, as many megafauna species are migratory and do not stay in the  
190 Arctic all year round. Environments encountered on the winter grounds may be of paramount  
191 importance in driving population dynamics, as highlighted >50 years ago by D. Lack [73], and should  
192 also be incorporated in demographic studies.

193 Overall, whatever the approach used, no general conclusion can be drawn yet: climate warming may  
194 have positive, negative or no effects on the vital rates and/or population trajectories of Arctic  
195 megafauna depending on the species and/or region considered. Endemic Arctic species may respond  
196 more negatively to climate warming [48,74] but this is not an absolute pattern either. For example,  
197 the biomass of the polar cod, a true Arctic species, in the Canadian Arctic was positively correlated to  
198 sea-surface temperature [57]. Beyond interspecific variation in climate change response, it is also  
199 essential to consider spatial variation in intraspecific responses. For example, relationships between  
200 sea-ice extent and the colony size of black-legged kittiwakes varied among fjords in Svalbard,  
201 potentially due to contrasting local oceanographic conditions [60]. Also, loss of sea-ice had negative

202 effects on polar bears in Baffin Bay [70], but these effects were null or positive in the Chukchi Sea [69].  
203 Such spatial variation in the effects of climate warming may reflect local variability in other  
204 environmental parameters [75]. Alternatively, they may also be the consequence of potentially crucial,  
205 but often overlooked non-linear effects. For instance, polar bears in the Chukchi Sea maintained body  
206 condition despite vanishing sea-ice [69], contrary to bears from the Bering Sea whose condition  
207 declined [70]. These findings suggesting that Chukchi Sea bears are not currently limited by sea ice [69]  
208 may be due to non-linearity between sea-ice conditions and polar bear life history. Notably, in the  
209 Chukchi Sea, sea-ice cover may still be above the threshold below which a declining sea ice has  
210 detrimental effects [69]. The concept of threshold, or **tipping point** [76,77], thereby remains essential  
211 [78]. Even if the increase in temperature is more or less a linear process, it is associated with non-linear  
212 changes in other climatic parameters (e.g. snowfall, [79]). Equally, the behavioural, physiological and  
213 population responses to all these numerous and complex environmental changes have no reason to  
214 be linear [24,80].

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

219

## 220 **Impacts on biodiversity and ecosystem functioning**

221 Predicting how biodiversity responds to climate change [81] and how changes in biodiversity affect  
222 ecosystem functioning [82] are active fields of research. However, very few studies on Arctic  
223 megafauna have been undertaken in these specific areas. Our literature review identified only one that  
224 has explicitly assessed the impact of climate change on Arctic megafauna biodiversity. This study [83]  
225 found positive global warming effect on fish biodiversity in an Arctic fjord in Northern Norway,  
226 whereby species richness and **Shannon diversity** of fishes increased following the arrival of warm-  
227 water species. Other studies focused on species composition [74,84,85], as a metric for species  
228 richness. These findings generally support the borealisation of the Arctic marine environment, with  
229 north temperate (or “boreal) species becoming more abundant. Species richness represents, however,  
230 only one facet of biodiversity [82] so that reported changes in species composition, though highly  
231 valuable, do not give a complete representation of ongoing changes in Arctic megafauna biodiversity.  
232 Investigations on climate change impacts on Arctic marine ecosystem functioning are equally scarce.  
233 Griffith et al. [46] modelled the arrival of Atlantic species (such as capelin *Mallotus villosus*) and  
234 showed they may increase the resilience of marine fjord systems, with maintained food web structure.  
235 Further, Frainer et al [86] based their work on fish **functional biogeography** to address how ecosystem  
236 functioning may be affected by climate change in the Barents Sea. Their results also support an ongoing



237 borealisation of Arctic marine ecosystems with large boreal species replacing small Arctic ones, likely  
238 affecting biomass production. Other analyses of functional redundancy [87] or specific species  
239 interactions [88,89] have also been performed, to explore changes in ecosystem functioning due to  
240 climate change. These studies confirm that ongoing climate change has the potential to affect Arctic  
241 marine ecosystem functioning, even though the exact consequences remain extremely difficult to  
242 apprehend.

243

#### 244 **The way forward**

245 Rigorously assessing climate change impacts on marine megafauna at the scale of the Arctic is a  
246 formidable task (Figure 3). Ecologists thereby face the combined challenges of an immensely vast  
247 terrain, of drastic weather conditions and staggering operational costs [90]. In addition, the current  
248 socio-economic crisis questions the environmental footprint of research operations and reduces  
249 available funding. Finally, international tensions prevent collaboration between Russian scientists and  
250 the rest of the world. This considerably slows AMM data acquisition in least-known areas.

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

254 (1) Modern technologies allow remote, large-scale data collection on previously totally unknown  
255 aspects of AMM ecology. This starts with satellite remote-sensing of multiple biotic and abiotic  
256 parameters all across the Arctic, which nonetheless only assesses conditions at the sea surface. *In situ*,  
257 aerial and underwater autonomous vehicles (e.g. drones) automatically survey areas ranging from one,  
258 to millions of cubic meters of ocean [91]. They provide fine-scale information on environmental  
259 conditions, notably on the spatio-temporal abundance of potential prey for marine megafauna (e.g.  
260 zooplankton and small pelagic fish aggregations). In addition, biologging devices attached to animals  
261 opened worlds of knowledge on their spatial ecology and their energetics in a changing ocean [54],  
262 and combined analyses provide information on contaminant levels in animals and their environment  
263 [6]. Finally, further rapidly emerging techniques such as **DNA metabarcoding** are transforming the field  
264 of population ecology [92].

265 (2) Beyond these technological revolutions in data acquisition, marine megafauna ecology has now  
266 entered the realm of big data science: Information technology allows the design of completely new  
267 frameworks for acquiring, storing, sharing, analyzing, visualizing, and publicizing data [93]. Big data  
268 approaches are notably based upon the use of artificial intelligence and **deep learning** scheme which  
269 drastically reduce analysis duration and costs [94,95], and online platforms greatly enhance data  
270 sharing [54].

271 (3) All above-mentioned approaches may be complemented with citizen-science initiatives [96,97].  
272 Those may allow additional data collection within scientific blind spots, notably species distribution  
273 and abundance, and assist in long-term monitoring when such activities become impossible for  
274 conventional research teams, as during the recent COVID19 pandemic. Participatory science programs  
275 may also contribute to the empowerment of local communities, in many areas of the Arctic where the  
276 predominance of non-Indigenous scientists may be perceived as post-colonial.  
277 These research targets, which aim at understanding global change impacts on Arctic marine  
278 megafauna while better involving local communities, are highly coherent with the objectives of the  
279 Arctic Marine Biodiversity Monitoring Plan of the Arctic Council [98]. This initiative should use scientific  
280 evidence to improve biological conservation in the Arctic, but the political will and international  
281 collaboration necessary to transform research into action still seems in its infancy [99].

282

283 Concluding Remarks: Key research gaps and questions on Arctic marine megafauna

284

- 285 • With a few exceptions, it is not possible to conclude on recent trends in AMM populations  
286 and the inter-species and spatial variations in these trends. Basic data about population size  
287 are still lacking for most species and regions.
- 288 • Individual variations in responses to climate change, their drivers (e.g. age, physiological  
289 status, experience) and their implications to buffer climate change impacts also remain  
290 largely unknown. Such individual variations are, however, crucial to assess populational  
291 responses to environmental changes [100].
- 292 • The shape of the relationships (linear/non-linear) between AMM physiological, behavioural  
293 or demographic traits and the direct and indirect (e.g. pollutants and pathogens, shifting  
294 human activities) consequences of climate change are critically understudied. This prevents  
295 any reliable predictions about the fate of AMM in response to future climate change  
296 scenarios.

297

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

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## Glossary

- **Arctic amplification**

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

- **Borealisation**

The borealisation of the Arctic refers to 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.

- **Gill-oxygen limitation theory**

According to the Gill-Oxygen Limitation Theory, the oxygen carrying-capacity of water is limited by its temperature, salinity, and 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.

- **Cryosphere**

The cryosphere is defined as the part of Earth’s surface layer consisting of frozen water in the form of snow, permafrost, glaciers and sea-ice.

- **Tipping point**

In the context of climate change, tipping points refer to critical thresholds in climate conditions, above which abrupt and potentially irreversible changes in ecosystem structure and dynamics occur.

- **Shannon diversity**

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

- **Functional biogeography**

The field of functional biogeography combines knowledge on species distribution with information on species’ functional traits, to understand how large-scale distributional changes may affect ecosystem functioning.

- **Biologging**

Biologging refers to 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 behavior (e.g. 3D movement) or physiology (e.g. heart rate).

- **DNA metabarcoding**

342 DNA metabarcoding is a molecular technique that allows identifying the species present in a sample,  
343 (e.g. soil, water) by analyzing all DNA sequences present in this sample and comparing them to  
344 reference databases.

345                   • **Deep learning**

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

350                   • **Ecotoxicology**

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

355

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365

366 **Author contributions**

367 DG and SD conceived the study, performed the bibliographic analysis and wrote the paper.

368

369 **Declaration of interests**

370 No interests are declared

371

372 **Supplementary information**

373 Supplementary information associated with this article can be found, in the online version, at ##

374

375 **Table 1. Main topics addressed in studies linking marine megafauna and climate change.** Each cell  
 376 of the table gives the % of studies dealing with each topic. The sum for each guild is usually >100% as  
 377 a given study may address several topics. “Community” refers to studies dealing with ecosystem or  
 378 community structure, “Habitat use” to studies dealing with spatial distribution, habitat use or  
 379 movement, “Population dynamics” to studies dealing with population trajectory, abundance or age  
 380 structure, “Demography” to studies dealing with vital rates (survival, reproduction) or phenology,  
 381 and “Individual state” to studies dealing with body condition, physiology, energetics or pollutants.  
 382 The column “Other” corresponds to a variety of themes and includes reviews or opinion articles, as  
 383 well as studies based on Indigenous ecological knowledge.

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

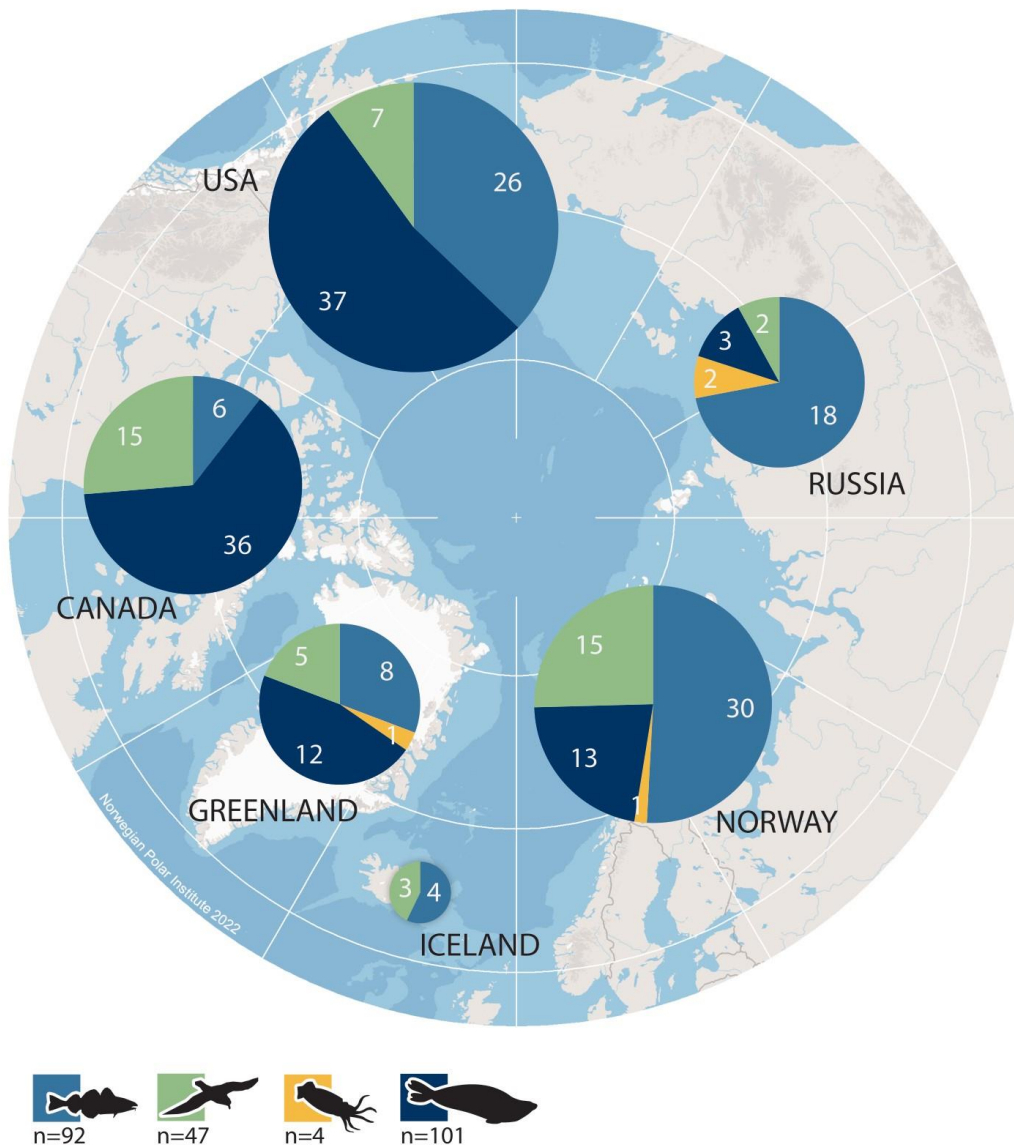
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388 **Figure 1:** Examples of Arctic marine megafauna. Top: Arctic tern *Sterna paradisaea* (credit S.  
 389 Descamps), Atlantic cod *Gadus morhua* (W. T. Fiege), Walrus *Odobenus rosmarus* (D. Grémillet).  
 390 Centre: *Gonatus fabricii*, the Boreo-atlantic Armhook Squid ([www.descna.com](http://www.descna.com)), Common eider  
 391 *Somateria mollissima* (D. Grémillet). White-beaked dolphin *Lagenorhynchus albirostris* (foreground)  
 392 and fin whale *Balaenoptera physalus* (background) (S. Descamps). Bottom: Bearded seal *Erignathus*  
 393 *barbatus* (S. Descamps), Polar cod *Boreogadus saida* (P. Leopold), Polar bear *Ursus maritimus* (M.  
 394 Andersen).

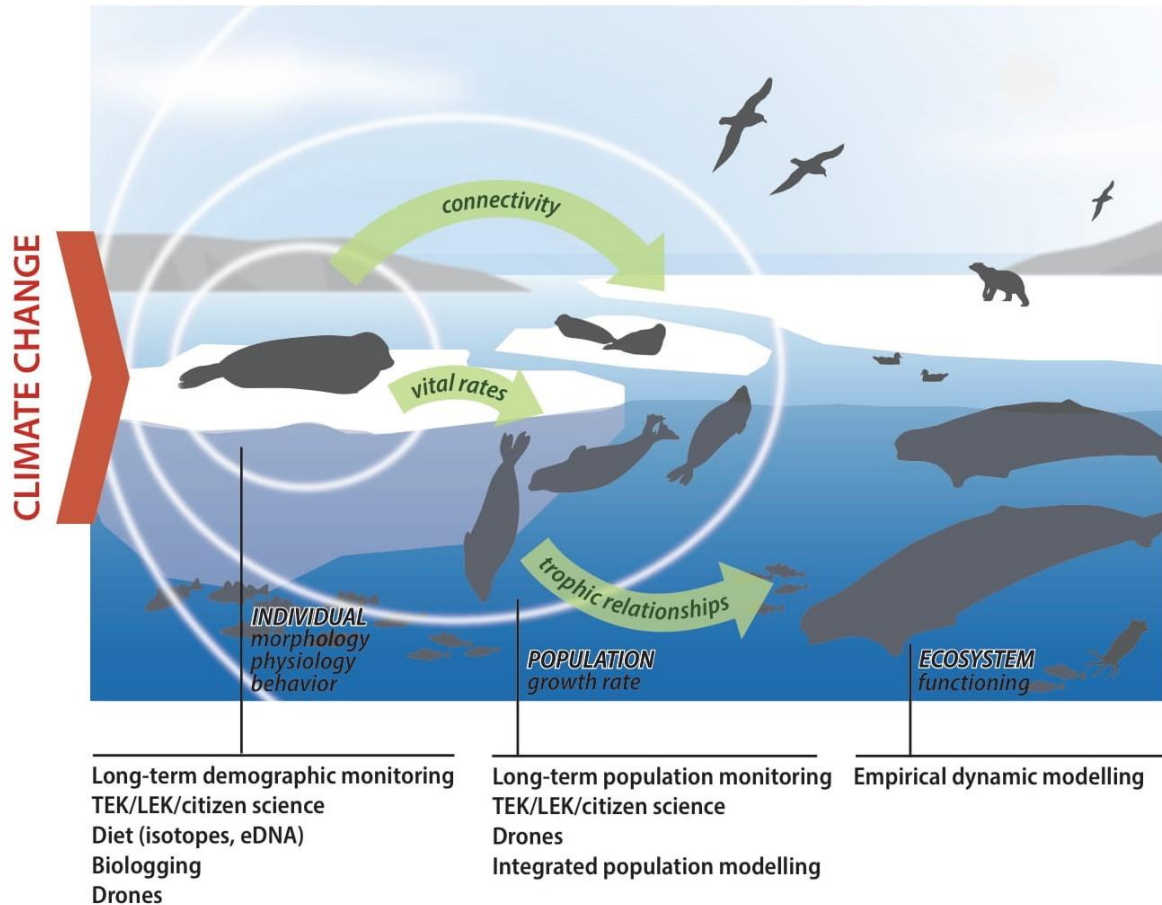


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396 **Figure 2:** Distribution of recent Arctic marine megafauna studies (see methods and Suppl. 1 for  
 397 definitions and time frame). Colours correspond to the different megafauna groups as pictured  
 398 below the map, and the proportion of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

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**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 inter-species 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.

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