



HAL
open science

Ecological impacts of climate change on Arctic marine megafauna

David Grémillet, Sébastien Descamps

► **To cite this version:**

David Grémillet, Sébastien Descamps. Ecological impacts of climate change on Arctic marine megafauna. *Trends in Ecology & Evolution*, 2023, 38 (8), pp.773-783. 10.1016/j.tree.2023.04.002 . hal-04254762

HAL Id: hal-04254762

<https://hal.science/hal-04254762>

Submitted on 25 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Title**

2 Ecological impacts of climate change on Arctic marine megafauna

3

4 **Authors**

5 David Grémillet,^{1,2,*} and Sébastien Descamps^{3,*}

6

7 ¹ CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

8 ² Percy FitzPatrick Institute, DST/NRF Excellence Center at the University of Cape Town, Cape Town,
9 South Africa

10 ³ Norwegian Polar Institute, Framsenteret, Tromsø, Norway

11

12 *Corresponding authors: David Grémillet (david.gremillet@cefe.cnrs.fr ; ORCID 0000-0002-7711-9398)

13 and Sébastien Descamps (sebastien.descamps@npolar.no ; ORCID 0000-0003-0590-9013)

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. *Rossia 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 km²),
114 followed by Norwegian waters (30 studies per million km²) and, to a lesser extent, Canadian,
115 Greenlandic and Icelandic waters (12, 11 and 9 studies per million km², respectively). The analysis
116 stressed the deficit of studies within Russian waters (6 studies per million km²), 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.

304

305

306
307
308
309
310
311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336
337
338
339
340
341

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

356 **Acknowledgements**

357 DG is funded by the French National Center for Scientific Research (CNRS) and the French Polar
358 Institute IPEV (through the ADACLIM program IPEV 388, led by David Grémillet and Jérôme Fort), and
359 the European Horizon 2020 Program EcoScope project under the grand agreement number
360 101000302. SD is funded by the program SEAPOP (<http://www.seapop.no/en/>), the program MOSJ
361 (<http://www.mosj.no/en/>) and the project FACE-IT (The Future of Arctic Coastal Ecosystems –
362 Identifying Transitions in Fjord Systems and Adjacent Coastal Areas) funded by the European Union’s
363 Horizon 2020 research and innovation program under grant agreement number 869154. We thank
364 Manon Amiguet, Maria Gavrilo and Joanna Sulich for bibliographic and illustrative assistance.

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.

384

	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

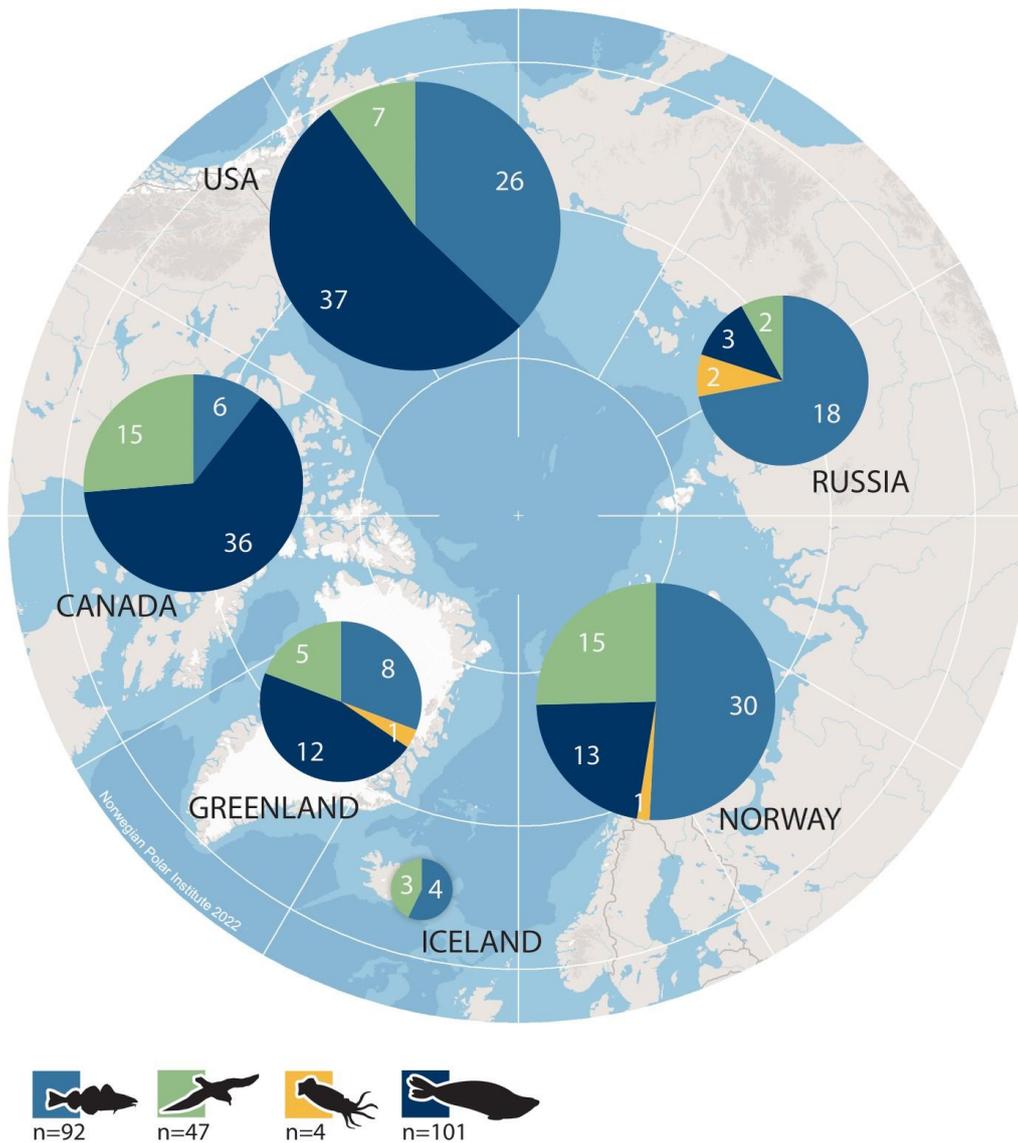
385

386



387

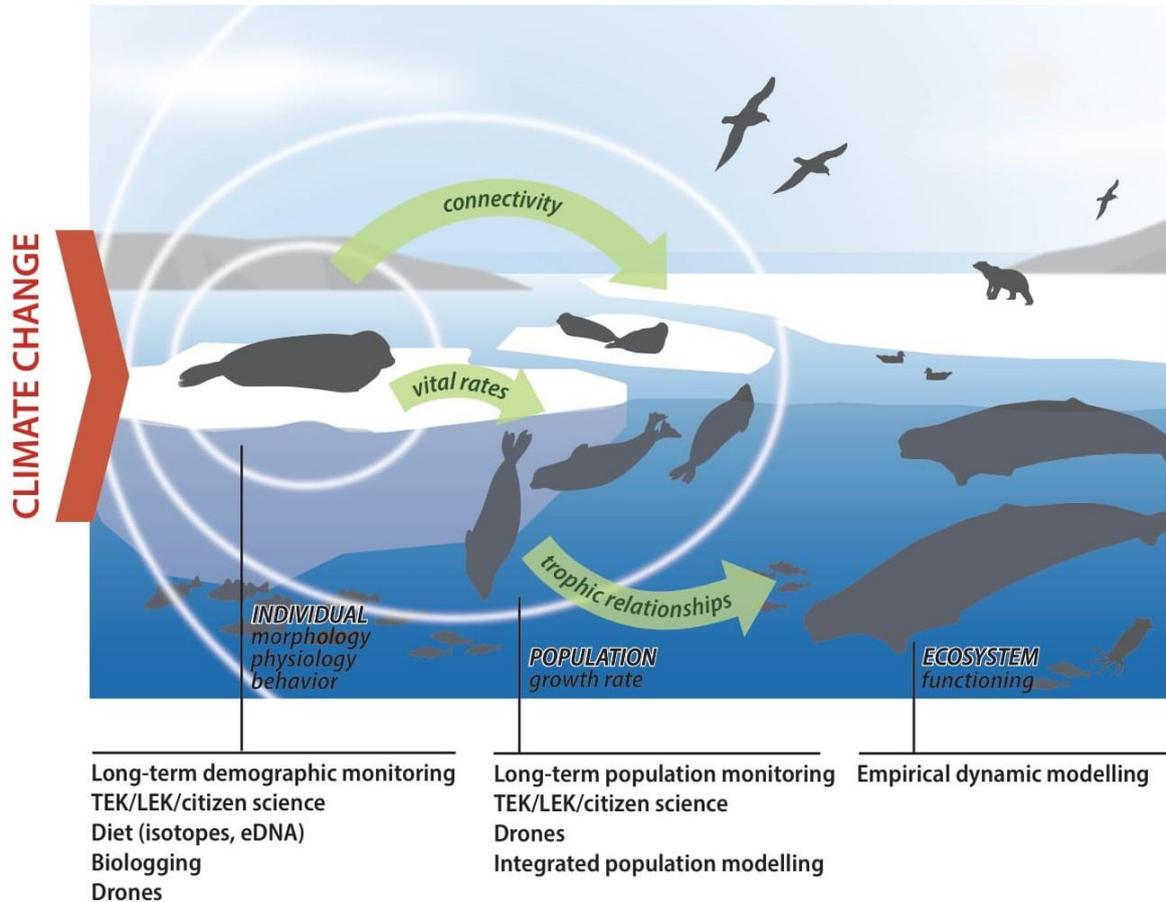
388 **Figure 1:** Examples of Arctic marine megafauna. Top: Arctic tern *Sterna paradisaea* (credit S.
 389 Descamps), Atlantic cod *Gadus morhua* (W. T. Fiege), Walrus *Odobenus rosmarus* (D. Grémillet).
 390 Centre: *Gonatus fabricii*, the Boreo-atlantic Armhook Squid (www.descna.com), Common eider
 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).



395

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).

405



406

407 **Figure 3:** The way forward – Outline of future research work, necessary to assess climate change
 408 impacts on Arctic marine megafauna. Climate change affects individual vital rates through changes in
 409 physiology, behaviour or even morphology. These effects can be mediated by changes in habitats (e.g.
 410 connectivity) or trophic relationships (e.g. dietary changes through shifts in prey availability, changes
 411 in inter-species competition). The integration of complementary methods based on new technologies,
 412 new statistical methods, as well as citizen science are needed to understand ongoing changes in
 413 megafauna populations and marine ecosystems.

414

415 **References**

- 416 1. Rantanen, M. *et al.* (2022) The Arctic has warmed nearly four times faster than the globe since
 417 1979. *Commun. Earth Environ.* 3, 168
- 418 2. Previdi, M. *et al.* (2021) Arctic amplification of climate change: a review of underlying
 419 mechanisms. *Environ. Res. Lett.* 16, 093003
- 420 3. Box, J.E. *et al.* (2019) Key indicators of Arctic climate change: 1971–2017. *Environ. Res. Lett.* 14,
 421 045010
- 422 4. Henderson, G.R. *et al.* (2021) Local and Remote Atmospheric Circulation Drivers of Arctic
 423 Change: A Review. *Front. Earth Sci.* 9, 549
- 424 5. Moon, T.A. *et al.* (2019) The expanding footprint of rapid Arctic change. *Earths Future* 7, 212–
 425 218
- 426 6. Sonne, C. *et al.* (2021) Emerging contaminants and biological effects in Arctic wildlife. *Trends*
 427 *Ecol. Evol.* 36, 421–429
- 428 7. Svavarsson, J. *et al.* (2021) Pollutants from shipping-new environmental challenges in the
 429 subarctic and the Arctic Ocean. *Mar. Pollut. Bull.* 164, 112004
- 430 8. Post, E. *et al.* (2019) The polar regions in a 2 C warmer world. *Sci. Adv.* 5, eaaw9883
- 431 9. Polyakov, I.V. *et al.* (2018) Stability of the arctic halocline: a new indicator of arctic climate
 432 change. *Environ. Res. Lett.* 13, 125008
- 433 10. Lewis, K. *et al.* (2020) Changes in phytoplankton concentration now drive increased Arctic
 434 Ocean primary production. *Science* 369, 198–202
- 435 11. Ingvaldsen, R.B. *et al.* (2021) Physical manifestations and ecological implications of Arctic
 436 Atlantification. *Nat. Rev. Earth Environ.* 2, 874–889
- 437 12. Delgado-Baquerizo, M. *et al.* (2020) The proportion of soil-borne pathogens increases with
 438 warming at the global scale. *Nat. Clim. Change* 10, 550–554
- 439 13. Chan, F.T. *et al.* (2019) Climate change opens new frontiers for marine species in the Arctic:
 440 Current trends and future invasion risks. *Glob. Change Biol.* 25, 25–38
- 441 14. Clairbaux, M. *et al.* (2019) Climate change could overturn bird migration: Transarctic flights and
 442 high-latitude residency in a sea ice free Arctic. *Sci. Rep.* 9, 1–13
- 443 15. Florko, K.R. *et al.* (2021) Predicting how climate change threatens the prey base of Arctic
 444 marine predators. *Ecol. Lett.* 24, 2563–2575
- 445 16. Anderson, D.M. *et al.* (2021) Evidence for massive and recurrent toxic blooms of *Alexandrium*
 446 *catenella* in the Alaskan Arctic. *Proc. Natl. Acad. Sci.* 118, e2107387118
- 447 17. Grose, S.O. *et al.* (2020) Climate change will re-draw the map for marine megafauna and the
 448 people who depend on them. *Front. Mar. Sci.* 7, 547
- 449 18. Moleón, M. *et al.* (2020) Rethinking megafauna. *Proc. R. Soc. B* 287, 20192643
- 450 19. Hauser, D.D. *et al.* (2021) Co-production of knowledge reveals loss of Indigenous hunting
 451 opportunities in the face of accelerating Arctic climate change. *Environ. Res. Lett.* 16, 095003
- 452 20. Nuttall, M. (2019) Indigenous peoples, self-determination and the Arctic environment. In *The*
 453 *Arctic*, pp. 377–409, Routledge
- 454 21. Townhill, B.L. *et al.* (2021) Pollution in the Arctic Ocean: An overview of multiple pressures and
 455 implications for ecosystem services. *Ambio* 51, 471–483
- 456 22. Lescroël, A. *et al.* (2016) Seeing the ocean through the eyes of seabirds: A new path for marine
 457 conservation? *Mar. Policy* 68, 212–220
- 458 23. Wassmann, P. *et al.* (2011) Footprints of climate change in the Arctic marine ecosystem. *Glob.*
 459 *Change Biol.* 17, 1235–1249
- 460 24. Hansen, E.S. *et al.* (2021) Centennial relationships between ocean temperature and Atlantic
 461 puffin production reveal shifting decennial trends. *Glob. Change Biol.* 27, 3753–3764
- 462 25. Campana, S.E. *et al.* (2020) Shifting fish distributions in warming sub-Arctic oceans. *Sci. Rep.* 10,
 463 1–14
- 464 26. Golikov, A.V. *et al.* (2020) Diet and life history reduce interspecific and intraspecific competition
 465 among three sympatric Arctic cephalopods. *Sci. Rep.* 10, 21506

- 466 27. Golikov, A.V. *et al.* (2017) First assessment of biomass and abundance of cephalopods *Rossia*
467 *palpebrosa* and *Gonatus fabricii* in the Barents Sea. *J. Mar. Biol. Assoc. U. K.* 97, 1605–1616
468 28. Scholander, P. *et al.* (1950) Body insulation of some arctic and tropical mammals and birds. *Biol.*
469 *Bull.* 99, 225–236
470 29. Ste-Marie, E. *et al.* (2020) A first look at the metabolic rate of Greenland sharks (*Somniosus*
471 *microcephalus*) in the Canadian Arctic. *Sci. Rep.* 10, 1–8
472 30. Clairbaux, M. *et al.* (2021) Meeting Paris agreement objectives will temper seabird winter
473 distribution shifts in the North Atlantic Ocean. *Glob. Change Biol.* 27, 1457–1469
474 31. Choy, E.S. *et al.* (2021) Limited heat tolerance in a cold-adapted seabird: implications of a
475 warming Arctic. *J. Exp. Biol.* 224, jeb242168
476 32. Pauly, D. (2021) The gill-oxygen limitation theory (GOLT) and its critics. *Sci. Adv.* 7, eabc6050
477 33. Terhaar, J. *et al.* (2020) Emergent constraint on Arctic Ocean acidification in the twenty-first
478 century. *Nature* 582, 379–383
479 34. Kunz, K.L. *et al.* (2018) Aerobic capacities and swimming performance of polar cod (*Boreogadus*
480 *saida*) under ocean acidification and warming conditions. *J. Exp. Biol.* 221, jeb184473
481 35. Dahlke, F.T. *et al.* (2018) Northern cod species face spawning habitat losses if global warming
482 exceeds 1.5 C. *Sci. Adv.* 4, eaas8821
483 36. Pilfold, N.W. *et al.* (2021) Long-term increases in pathogen seroprevalence in polar bears (*Ursus*
484 *maritimus*) influenced by climate change. *Glob. Change Biol.* 27, 4481–4497
485 37. Bender, M.L. *et al.* (2021) Combined effects of crude oil exposure and warming on eggs and
486 larvae of an arctic forage fish. *Sci. Rep.* 11, 1–17
487 38. Bergmann, M. *et al.* (2022) Plastic pollution in the Arctic. *Nat. Rev. Earth Environ.* 3, 323–337
488 39. Albert, C. *et al.* (2021) Seasonal variation of mercury contamination in Arctic seabirds: a pan-
489 arctic assessment. *Sci. Total Environ.* 750, 142201
490 40. Amélineau, F. *et al.* (2019) Arctic climate change and pollution impact little auk foraging and
491 fitness across a decade. *Sci. Rep.* 9, 1–15
492 41. Jansen, T. *et al.* (2021) Larval drift dynamics, thermal conditions and the shift in juvenile capelin
493 distribution and recruitment success around Iceland and East Greenland. *Fish. Res.* 236, 105845
494 42. Grémillet, D. *et al.* (2012) Little auks buffer the impact of current Arctic climate change. *Mar.*
495 *Ecol. Prog. Ser.* 454, 197–206
496 43. Hamilton, C.D. *et al.* (2019) Contrasting changes in space use induced by climate change in two
497 Arctic marine mammal species. *Biol. Lett.* 15, 20180834
498 44. Yurkowski, D.J. *et al.* (2018) A temporal shift in trophic diversity among a predator assemblage
499 in a warming Arctic. *R. Soc. Open Sci.* 5, 180259
500 45. Breed, G.A. *et al.* (2017) Sustained disruption of narwhal habitat use and behavior in the
501 presence of Arctic killer whales. *Proc. Natl. Acad. Sci.* 114, 2628–2633
502 46. Griffith, G.P. *et al.* (2019) Ecological resilience of Arctic marine food webs to climate change.
503 *Nat. Clim. Change* 9, 868–872
504 47. Kuletz, K. *et al.* (2020) Distributional shifts among seabird communities of the Northern Bering
505 and Chukchi seas in response to ocean warming during 2017–2019. *Deep Sea Res. Part II Top.*
506 *Stud. Oceanogr.* 181, 104913
507 48. Burrows, M.T. *et al.* (2019) Ocean community warming responses explained by thermal
508 affinities and temperature gradients. *Nat. Clim. Change* 9, 959–963
509 49. Bouchard, C. *et al.* (2020) West Greenland ichthyoplankton and how melting glaciers could
510 allow Arctic cod larvae to survive extreme summer temperatures. *Arct. Sci.* 7, 217–239
511 50. Stempniewicz, L. *et al.* (2017) Marine birds and mammals foraging in the rapidly deglaciating
512 Arctic fjord-numbers, distribution and habitat preferences. *Clim. Change* 140, 533–548
513 51. Bertrand, P. *et al.* (2021) Fine-scale spatial segregation in a pelagic seabird driven by differential
514 use of tidewater glacier fronts. *Sci. Rep.* 11, 1–11
515 52. Collard, F. and Ask, A. (2021) Plastic ingestion by Arctic fauna: A review. *Sci. Total Environ.* 786,
516 147462

- 517 53. Harris, S.M. *et al.* (2020) Personality predicts foraging site fidelity and trip repeatability in a
518 marine predator. *J. Anim. Ecol.* 89, 68–79
- 519 54. Davidson, S.C. *et al.* (2020) Ecological insights from three decades of animal movement tracking
520 across a changing Arctic. *Science* 370, 712–715
- 521 55. Reimer, J.R. *et al.* (2019) Modeling optimal responses and fitness consequences in a changing
522 Arctic. *Glob. Change Biol.* 25, 3450–3461
- 523 56. Pagano, A.M. *et al.* (2018) High-energy, high-fat lifestyle challenges an Arctic apex predator, the
524 polar bear. *Science* 359, 568–572
- 525 57. Bouchard, C. *et al.* (2017) Climate warming enhances polar cod recruitment, at least transiently.
526 *Prog. Oceanogr.* 156, 121–129
- 527 58. Yasumiishi, E.M. *et al.* (2020) Climate-related changes in the biomass and distribution of small
528 pelagic fishes in the eastern Bering Sea during late summer, 2002–2018. *Deep Sea Res. Part II*
529 *Top. Stud. Oceanogr.* 181, 104907
- 530 59. Gutowsky, S. *et al.* (2022) Sea ice extent and phenology influence breeding of high-Arctic
531 seabirds: 4 decades of monitoring in Nunavut, Canada. *Oecologia* 198, 393–406
- 532 60. Descamps, S. and Ramírez, F. (2021) Species and spatial variation in the effects of sea ice on
533 Arctic seabird populations. *Divers. Distrib.* 27, 2204–2217
- 534 61. Chambault, P. *et al.* (2020) The impact of rising sea temperatures on an Arctic top predator, the
535 narwhal. *Sci. Rep.* 10, 1–10
- 536 62. Strøm, H. *et al.* (2020) Population status and trend of the threatened ivory gull *Pagophila*
537 *eburnea* in Svalbard. *Endanger. Species Res.* 43, 435–445
- 538 63. Florko, K. *et al.* (2018) Decreasing sea ice conditions in western Hudson Bay and an increase in
539 abundance of harbour seals (*Phoca vitulina*) in the Churchill River. *Polar Biol.* 41, 1187–1195
- 540 64. Henri, D.A. *et al.* (2020) Inuit knowledge of Arctic Terns (*Sterna paradisaea*) and perspectives
541 on declining abundance in southeastern Hudson Bay, Canada. *PloS One* 15, e0242193
- 542 65. Razgour, O. *et al.* (2018) An integrated framework to identify wildlife populations under threat
543 from climate change. *Mol. Ecol. Resour.* 18, 18–31
- 544 66. Heath, M.R. *et al.* (2022) Ecosystem approach to harvesting in the Arctic: Walking the tightrope
545 between exploitation and conservation in the Barents Sea. *Ambio* 51, 456–470
- 546 67. Reimer, J.R. *et al.* (2019) Ringed seal demography in a changing climate. *Ecol. Appl.* 29, e01855
- 547 68. Bårdsen, B.-J. *et al.* (2018) Multiple stressors: modeling the effect of pollution, climate, and
548 predation on viability of a sub-arctic marine bird. *Ecosphere* 9, e02342
- 549 69. Rode, K.D. *et al.* (2021) Seal body condition and atmospheric circulation patterns influence
550 polar bear body condition, recruitment, and feeding ecology in the Chukchi Sea. *Glob. Change*
551 *Biol.* 27, 2684–2701
- 552 70. Laidre, K.L. *et al.* (2020) Interrelated ecological impacts of climate change on an apex predator.
553 *Ecol. Appl.* 30, e02071
- 554 71. de Kroon, H. *et al.* (1986) Elasticity: the relative contribution of demographic parameters to
555 population growth rate. *Ecology* 67, 1427–1431
- 556 72. Cleasby, I.R. *et al.* (2017) Climatic conditions produce contrasting influences on demographic
557 traits in a long-distance Arctic migrant. *J. Anim. Ecol.* 86, 285–295
- 558 73. Lack, D. (1966) *Population studies of birds*, Clarendon P.
- 559 74. Descamps, S. and Strøm, H. (2021) As the Arctic becomes boreal: ongoing shifts in a high-Arctic
560 seabird community. *Ecology* 102, e03485
- 561 75. Suggitt, A.J. *et al.* (2018) Extinction risk from climate change is reduced by microclimatic
562 buffering. *Nat. Clim. Change* 8, 713–717
- 563 76. Heinze, C. *et al.* (2021) The quiet crossing of ocean tipping points. *Proc. Natl. Acad. Sci.* 118,
564 e2008478118
- 565 77. Duarte, C.M. *et al.* (2012) Tipping elements in the Arctic marine ecosystem. *Ambio* 41, 44–55
- 566 78. May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states.
567 *Nature* 269, 471–477
- 568 79. Bintanja, R. (2018) The impact of Arctic warming on increased rainfall. *Sci. Rep.* 8, 1–6

- 569 80. Descamps, S. *et al.* (2017) Circumpolar dynamics of a marine top-predator track ocean warming
570 rates. *Glob. Change Biol.* 23, 3770–3780
- 571 81. Bellard, C. *et al.* (2012) Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15,
572 365–377
- 573 82. Cardinale, B.J. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature* 486, 59–67
- 574 83. Mérillet, L. *et al.* (2022) Fish Assemblages of a Sub-Arctic Fjord Show Early Signals of Climate
575 Change Response Contrary to the Benthic Assemblages. *Front. Mar. Sci.* 9, 257
- 576 84. Mueter, F.J. *et al.* (2021) Changes in diversity and species composition across multiple
577 assemblages in the Eastern Chukchi Sea during two contrasting years are consistent with
578 borealization. *Oceanography* 34, 38–51
- 579 85. Gall, A.E. *et al.* (2017) Ecological shift from piscivorous to planktivorous seabirds in the Chukchi
580 Sea, 1975–2012. *Polar Biol.* 40, 61–78
- 581 86. Frainer, A. *et al.* (2017) Climate-driven changes in functional biogeography of Arctic marine fish
582 communities. *Proc. Natl. Acad. Sci.* 114, 12202–12207
- 583 87. Aune, M. *et al.* (2018) Functional roles and redundancy of demersal Barents Sea fish: ecological
584 implications of environmental change. *Plos One* 13, e0207451
- 585 88. Dey, C.J. *et al.* (2017) Increasing nest predation will be insufficient to maintain polar bear body
586 condition in the face of sea ice loss. *Glob. Change Biol.* 23, 1821–1831
- 587 89. Breed, G.A. *et al.* (2017) Sustained disruption of narwhal habitat use and behavior in the
588 presence of Arctic killer whales. *Proc. Natl. Acad. Sci.* 114, 2628–2633
- 589 90. Mallory, M.L. *et al.* (2018) Financial costs of conducting science in the Arctic: examples from
590 seabird research. *Arct. Sci.* 4, 624–633
- 591 91. Gray, P.C. *et al.* (2022) Drones address an observational blind spot for biological oceanography.
592 *Front. Ecol. Environ.* 20, 413–421
- 593 92. Bohmann, K. *et al.* (2014) Environmental DNA for wildlife biology and biodiversity monitoring.
594 *Trends Ecol. Evol.* 29, 358–367
- 595 93. Grémillet, D. *et al.* (2022) Big data approaches to the spatial ecology and conservation of
596 marine megafauna. *ICES J. Mar. Sci.* 79, 975–986
- 597 94. Saleh, A. *et al.* (2022) Computer vision and deep learning for fish classification in underwater
598 habitats: A survey. *Fish Fish.* 23, 977–999
- 599 95. Hayes, M.C. *et al.* (2021) Drones and deep learning produce accurate and efficient monitoring
600 of large-scale seabird colonies. *The Condor* 123, duab022
- 601 96. Brown, E.D. and Williams, B.K. (2019) The potential for citizen science to produce reliable and
602 useful information in ecology. *Conserv. Biol.* 33, 561–569
- 603 97. Peacock, S.J. *et al.* (2020) Linking co-monitoring to co-management: bringing together local,
604 traditional, and scientific knowledge in a wildlife status assessment framework. *Arct. Sci.* 6,
605 247–266
- 606 98. Gill, M. *et al.* (2011) Arctic Marine Biodiversity Monitoring Plan (CBMP-MARINE PLAN).
- 607 99. Barry, T. *et al.* (2020) How does the Arctic Council support conservation of Arctic biodiversity?
608 *Sustainability* 12, 5042
- 609 100. Vindenes, Y. and Langangen, Ø. (2015) Individual heterogeneity in life histories and eco-
610 evolutionary dynamics. *Ecol. Lett.* 18, 417–432
- 611