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Authors

Macias-Fauria, Marc
Post, Eric

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Author for correspondence:
Marc Macias-Fauria
e-mail: marc.maciasfauria@ouce.ox.ac.uk

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Effects of sea ice on Arctic biota: an emerging crisis discipline

Marc Macias-Fauria[1] and Eric Post[2]

[1]School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK
[2]Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616-8571, USA

(iD) MM-F, 0000-0002-8438-2223; EP, 0000-0002-9471-5351

The rapid decline in Arctic sea ice (ASI) extent, area and volume during recent decades is occurring before we can understand many of the mechanisms through which ASI interacts with biological processes both at sea and on land. As a consequence, our ability to predict and manage the effects of this enormous environmental change is limited, making this a *crisis discipline*. Here, we propose a framework to study these effects, defining *direct effects* as those acting on life-history events of Arctic biota, and *indirect effects*, where ASI acts upon biological systems through chains of events, normally involving other components of the physical system and/or biotic interactions. Given the breadth and complexity of ASI's effects on Arctic biota, Arctic research requires a truly multidisciplinary approach to address this issue. In the absence of effective global efforts to tackle anthropogenic global warming, ASI will likely continue to decrease, compromising the conservation of many ASI-related taxonomic groups and ecosystems. Mitigation actions will rely heavily on the knowledge acquired on the mechanisms and components involved with the biological effects of ASI.

1. Introduction

The extent, area and volume of Arctic sea ice (ASI) have shrunk sharply in the past decades: these changes are occurring most especially, but not exclusively, in minimum late summer extent [1,2], and a seasonally ice-free Arctic Ocean is predicted by the mid-twenty-first century [3]. High temperatures (*radiative/thermal forcing*) and atmospheric circulation controlling sea ice export out of the Arctic Ocean (*dynamic/wind forcing*) have been identified as ASI drivers [4–7]. ASI is also a key driver of Arctic climate, feeding back on regional and global climate and modifying both water and energy budgets. Its high albedo and low thermal conductivity are key to (i) reflect a large part of the incoming solar radiation (*albedo feedback*); (ii) prevent heat transfers from the relatively warm ocean to the cold atmosphere in autumn and winter (*conduction feedback*) and (iii) prevent the atmospheric boundary layer from picking up moisture (*cloud-ice feedback*). Furthermore, (iv) ASI influences the formation of deep water in the North Atlantic [8]. Together with feedbacks linked to the presence of snow and ice on land, these processes constitute an important component of the large temperature oscillations recorded in the Arctic (i.e. faster rates of climate change than at lower latitudes), known as Arctic Amplification (AA; [9]), which has been operating since at least the Cretaceous [10]. Non-ASI-related processes also play important roles in the AA, such as temperature feedbacks in the vertical structure of the warming (*lapse-rate feedback*) and the relationship between radiative forcing, temperature and longwave emission (*Planck's feedback*) [9,11]. The net effect of ASI dynamics on climate (in the Arctic and beyond) is yet unquantified, constituting a highly active research area. Its proposed impacts range from positive regional warming, changes in hemispheric atmospheric circulation patterns, sea surface temperature dynamics, the marine carbon cycle,
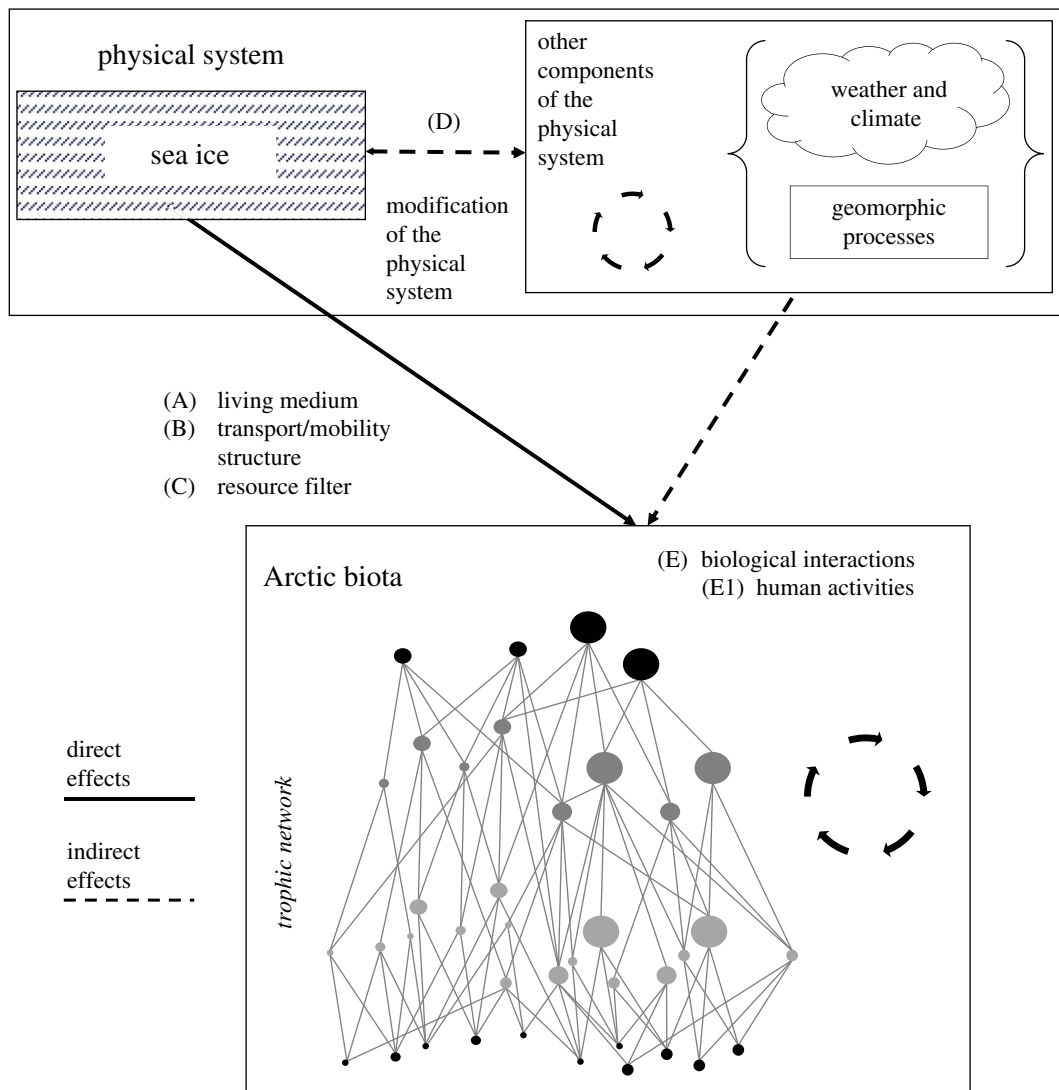
Figure 1. ASI effects on Arctic biota. *Direct* (solid line): ASI modifies Arctic biota's life-history events, acting as a (A) living medium [12], (B) transport/mobility-affecting structure [13–15] or (C) resource filter [16]. *Indirect* (dashed line): ASI affects Arctic biota through chains of events, normally involving (D) physical system modification [17–19] and/or (E) biotic interactions [20–24], which include (E1) human activities [25,26], or through combinations of *direct* and *indirect effects* (*compound effects*, see the text). *Bidirectional arrow* in D indicates feedbacks between ASI and *other components of the physical system*, which can modulate ASI's *indirect effects* on Arctic biota. *Arrow cycles* indicate possible interactions within other components of the physical system (e.g. ASI affecting climate, which in turn affects geomorphology, which indirectly affects Arctic biota) or *Arctic biota* (e.g. ASI's triggered trophic chain responses).

ocean acidification, to abrupt cooling events (electronic supplementary material, S1).

2. Ecological impacts of Arctic sea ice

ASI dynamics are known to impact Arctic biota (marine and terrestrial) adapted to—or at least affected by—its presence. ASI may affect life-history events of Arctic biota directly (*direct effects*), or through chains of events (*indirect effects*) involving the modification of components of the physical system (mostly weather/climate and geomorphological processes such as coastal erosion) and/or biotic interactions, or through a combination of both (*compound effects*) (figure 1).

(a) Direct effects

Many organisms interact with sea ice cover, which can serve as a (i) living medium, (ii) transport/mobility-affecting structure or (iii) resource filter (figure 1).

(i) Living medium

Multiple taxonomic groups inhabit the diversity of habitats provided by the ASI matrix. This include (i) nutrient-poor *melt ponds*, which can become highly productive if the underlying sea ice melts completely; (ii) inhospitable and hypersaline *interior layers* of solid ice, where microbial communities flourish within the brine draining system; (iii) highly productive *bottom- and platelet-ice*, rich in algal and microbial biomass; and (vi) suspended diatom communities attached to the bottom of sea ice (*strand communities*) [27]. ASI reduction translates into changes in abundance, distribution, composition and seasonality of these highly adapted communities. Many other animals actively or passively use ASI as a structure to hunt, mate, rest, whelp, rear offspring or avoid predators. Moore & Huntington [28] evaluated the ASI dependence of Arctic mammal species, recognizing (i) *ice-obligate species*—requiring ice as a platform for resting, breeding and/or hunting, such as polar bear (*Ursus maritimus* (Phipps, 1774)), walrus (*Odobenus rosmarus*

(Linnaeus, 1758)) or bearded (*Erignathus barbatus* (Erxleben, 1777)) and ringed (*Pusa hispida* (Schreber, 1775)) seals; (ii) *ice-associated species*—those adapted to the Arctic marine ecosystem, using ASI for whelping or feeding, such as harp (*Pagophilus groenlandicus* (Erxleben, 1777)), hooded (*Cystophora cristata* (Erxleben, 1777)), ribbon (*Histriophoca fasciata* (Zimmerman, 1783)) and spotted (*Phoca largha* (Pallas, 1811)) seals, or bowhead (*Balaena mysticetus* (Linnaeus, 1758)), beluga (*Delphinapterus leucas* (Pallas, 1776)) and narwhal (*Monodon monoceros* (Linnaeus, 1758)) whales; and (iii) *seasonally migrant species*, such as fin (*Balaenoptera physalus* (Linnaeus, 1758)), minke (*Balaenoptera acutorostrata* (Lacépède, 1804)), humpback (*Megaptera novaeangliae* (Borowski, 1781)), grey (*Eschrichtius robustus* (Lilljeborg, 1861)) and killer (*Orcinus orca* (Linnaeus, 1758)) whales. This classification can be applied to other taxa: the spectacled eider (*Somateria fischeri* (Brandt, 1847)) uses pack ice as a wintering ground [29] and is thus an ice-obligate species. The Arctic cod (*Boreogadus saida* (Lepechin, 1774)), which is a primary prey of narwhal, beluga, ringed seal and seabirds, is well adapted to ASI (finding protection from predation under rugged sea ice), but also found in ice-free areas, being thus an ice-associated species. Ice-obligate species are predicted to undergo decreased fitness with declining ASI; ice-associated species to show trade-offs between opportunities and increased competition, and seasonally migrant species to benefit from it [28].

(ii) Transport/mobility structure

ASI has been reported to directly affect the migration and/or seasonal movement patterns of multiple taxa [30] (electronic supplementary material, S1). ASI has been seen as a barrier to movement for many marine species, effectively isolating populations (e.g. walrus; [31]). At a smaller scale, Laidre *et al.* [13] found that reduced sea ice extent and seasonal duration make the fjords of large and wide tidewater glaciers in Greenland, abundant in clear freshwater, increasingly accessible to narwhals (to which, like belugas, they are attracted). ASI has also been proposed as an effective long-distance dispersal platform for many terrestrial plants, lichens, fungi and animals, including benthic intertidal species (electronic supplementary material, S1). As early as 1925, Bristowe [32] proposed sea ice bridges connecting Jan Mayen and Greenland as transport platforms for Arctic foxes (*Vulpes lagopus* L.). Indeed, genetic evidence points to ASI being very important for the connectivity between populations of Arctic foxes ([33], pan-Arctic), and wolf (*Canis lupus* L.) and caribou (*Rangifer tarandus* L.) in the Canadian Arctic Archipelago (CAA; [34], electronic supplementary material, S1). Jenkins *et al.* [14] used genetic fingerprinting and geodesic distance between populations to infer that sea ice had acted as an effective connectivity landscape feature for Peary caribou in the CAA. They estimated that landscape resistance has increased by approximately 15% since 1979 due to sea ice loss. Bristowe [32] further pointed to sea ice-encased driftwood as the means for insects and plants to reach Jan Mayen. Seeds of many circum-Arctic plants and propagules of lichens may not only drift with ASI, but also travel long distances over it pushed by wind ([35], electronic supplementary material, S1), being deposited on ice and re-entrained by wind in ways not facilitated by an open water ocean. This has long been proposed as a key mechanism in the amphi-Atlantic and West-Arctic elements of Arctic flora described by

Hultén [36,37]. Supporting it, Alsos *et al.* [15] provide evidence for first colonization dates of 102 vascular plant species in Svalbard related to abundant sea ice as inferred from palaeo-environmental data.

(iii) Resource filter

ASI can act as a very effective resource filter, such as in regulating the amount of light that reaches the upper layers of the ocean, which in turn affects ocean productivity and carbon sequestration ([27], electronic supplementary material, S1). Kahru *et al.* [16] report an approximately 47% increase in pan-Arctic monthly maximum phytoplankton primary productivity and an advance of up to 50 days in the annual timing of phytoplankton blooms in the Arctic Ocean (from 1997 to 2015) as a result of increased open water extent and duration of the open water season.

(b) Indirect effects

Indirect effects of ASI on biota are numerous and widespread, some even reaching lower latitudes (e.g. [38]). They can be broadly classified as (i) modification of the physical system and (ii) biological interactions (figure 1).

(i) Modification of the physical system

Climate/weather modification: ASI's modification of local and/or regional weather and climate may affect many ecological systems. Most indirect effects on terrestrial tundra are linked to ASI/AA feedbacks. For example, increased tundra primary productivity has been linked to such feedbacks, with higher ambient temperatures favouring increased productivity of some tundra plants, especially deciduous shrubs ([39], electronic supplementary material, S1), as have fungal community composition shifts [17]. Other proposed indirect effects include moisture limitation linked to declining ASI and thus reduced plant productivity [18]. Post *et al.* [19] report on individualistic rates of phenological change in tundra plants of Western Greenland over a 12-year period, with early-emerging species displaying stronger relationships with ASI, advancing their emergence more than late-emerging ones: here, ASI is assumed to modify a suite of local climate conditions key to local plant phenology. Recently, Arctic terrestrial vegetation has also been shown to be locally controlled by sea ice influence on weather in Svalbard [40].

Modification of geomorphological processes: ASI controls coastal erosion rates by governing fetch and wave action. ASI-induced increased erosion rates can lead to major changes in coastal environments, as well as modifying sediment supply to adjacent continental shelf waters and their ecosystems by affecting, e.g. primary productivity ([41], electronic supplementary material, S1). Chains of indirect effects involving weather/climate and geomorphological processes are possible (e.g. ASI-modified weather impacting the active layer and eventually terrestrial and freshwater ecosystems).

Biological interactions: Direct/indirect effects of ASI on biotic components may modify others (e.g. through trophic relations, such as West Greenland's *phenological community shifts* enhancing *trophic mismatch* between plants and caribou [42]). The assemblages of archaea, bacteria, microalgae, protists and metazoans (cnidarians, rotifers, nematodes, nudibranchs, larvae of molluscs, annelids, amphipods, copepods, euphausiids and small fish) living within the ASI matrix are preyed by a host of pelagic animals and, when

dead, descend through the water column providing food to benthic ecosystems [27]. Many seabirds are associated with *bottom-up* processes driven by ASI, as shown in sea ice spring retreat times driving phytoplankton and thus zooplankton abundances. These drive population numbers of walleye pollock (*Gadus chalcogrammus* (Pallas, 1814)) on which seabirds rely in the Bering Sea [20]. Mandt's black guillemot's (*Cepphus grylle mandtii* (Lichtenstein, 1822)) and ivory gull's (*Pagophila eburnean* (Phipps, 1774)) show a year-round association with the marginal sea ice zone and high sea ice concentrations for roosting (direct effect; Mandt's black guillemots) and prey availability (indirect, both) [21,22]. Increased phytoplankton productivity [16] indirectly affects organisms that feed on photosynthetic microorganisms and thus depend on its altered distribution and timing, observed in the recent northward shift in the Bering Sea ecological assemblages, or in the dependence of some Arctic marine mammals on ASI-dwelling prey (electronic supplementary material, S1). Increased availability of *in situ* produced copepods and euphausiids advected from the south through the Bering Strait boosts food delivery to baleen whales in the Pacific Arctic region, and although new seasonally ice-free areas enhance the influx of subarctic species (e.g. humpback, fin and minke whales), which may result in resource competition with Arctic bowhead and grey whales, this might be limited by both migration timing and species-specific foraging capabilities—*habitat* and/or niche *partitioning* [23].

However, the effects of subarctic seasonal migrants are not always neutral, even in the presence of ample prey abundance. O'Corry-Crowe *et al.* [24] show that despite their highly adaptive behaviour to changing ASI conditions and strong philopatry, beluga whales modified their spring migration routes in highly anomalous sea ice years in response to increased occurrence of predatory killer whales. This finding is in line with a progressive *borealization* of fish communities in the Arctic linked to ASI decline [43]. Interestingly, some of these responses differed between sexes, highlighting sex-asymmetrical adaptations to ASI. Furthermore, changes in the distribution of Arctic species and the expansion of subarctic species in response to ASI decline will cause new interactions, potentially including local competitive exclusion of adapted Arctic species and/or effects through the trophic chain. ASI's decline might show very different indirect effects on Arctic dwellers depending on their prey. For instance, walrus and bearded seals prey on benthic bivalves supported by a tight pelagic–benthic coupling transferring ice-associated production to the sea floor and might thus suffer from its decoupling if ASI recedes to deeper ocean areas. By contrast, reduced sea ice is hypothesized to favour pelagic over benthic production ([28], electronic supplementary material, S1) and thus increase food availability to piscivorous ringed seals (but note that ringed seals also require ASI as a platform to rest and breed—see §2(a)).

Biological interactions include human activities, which span from traditional subsistence activities to industrial fishing, natural resource extraction and international sea transport, the latter three adding further pressure to ASI-dependent Arctic biota (e.g. disrupted caribou migration by human-induced sea ice breaking; electronic supplementary material, S1) and being Arctic sources of greenhouse gas emissions. Mass reindeer starvation and its consequences for Nenets herders were linked to winter sea ice loss in the Barents and Kara Seas [25]. Open ocean water promoted moisture delivery and unseasonably above-freezing temperatures on the adjacent Yamal Peninsula, resulting in extensive rain-on-snow and the formation of an ice crust on the snow once normal temperatures returned that prevented reindeer from feeding. Technological advances can help practitioners of subsistence activities to adapt to the changing environment: powerful and fuel-efficient out-board engines aid subsistence hunters in Northern Alaska in adapting to ASI-modified migration times, distribution and behaviour of marine mammals [26]. However, this is jeopardized by the increased industrial activity linked to fossil fuel extraction and transportation.

(ii) Compound effects

Whereas conceptualizing the effects of ASI on Arctic biota as direct or indirect is useful for determining the nature of these interactions, compound effects (where direct and indirect effects act in combination) are expected to be the norm at the ecosystem level. These can be seen as complex indirect effects. Polar bears use ASI as a hunting platform and as a transportation platform (in turn affected by drift; [44]; direct effect). Indeed, the statistical relationship between polar bear numbers and ASI duration was the basis to forecast the species' decline [12]. However, the interactions between polar bears and ASI are more nuanced. Their main sources of prey, bearded and ringed seals, are ASI-obligate year-round for rearing pups and moulting. Ringed seals require early ASI so that enough snow accumulates on it to construct lairs, whereas bearded seals require ASI over shallow waters to prey on benthic communities [45]. ASI's direct effects on these species cascade to polar bears: some polar bear individuals have been reported to increase predation on ground-nesting seabird colonies as a response to seal scarcity, further affecting other taxa ([46]; indirect effects). Furthermore, ASI's direct effect on marine primary productivity drives all other trophic levels (including polar bears; indirect effects). Thus, ASI affects polar bear populations directly, indirectly and through the interaction of direct and indirect effects (biotic and abiotic).

3. A crisis discipline

Information on the interactions between ASI and Arctic biota is obtained from observations and proxy data. Observations consist largely of (i) extremely valuable, spatially patchy and temporally short studies, (ii) a wealth of less quantitative and often undervalued traditional ecological knowledge (TEK) and (iii) increasingly rich and available remote sensing data. Cold Arctic environments generally favour the preservation of a range of proxy biological and environmental records, such as ancient DNA and organic matter preserved in the permafrost (e.g. [47]). However, low sedimentation rates in the Arctic Ocean and the frequent glacial/periglacial disturbance in depositional environments on land (including ebbs and flows of valley glaciers and ice sheets, large oscillations in the sea level resulting in marine transgressions and regressions in the lowlands, and active layer processes) limit and bias the quality and availability of sedimentary sequences.

Such data gaps (i.e. patchy, short observations and challenging proxy material) limit our understanding of Arctic

biota's association with and response to environmental change, and exist at a time of extreme ASI decline; the study of the dependence of Arctic biota to ASI thus qualifies as a *crisis discipline*, according to the criteria proposed by Soulé [48] in the context of *conservation biology*. In crisis disciplines, decisions need to be made (i.e. urgency exists) in the face of large uncertainty. Ceballos *et al.* [49] reported on alarming rates of species extinctions and abundance and range reductions, with high latitudes showing higher-to-much-higher than average reductions (relative to their overall richness) in birds and mammals. They enumerated six main global drivers of biodiversity loss that are applicable to ASI's consequences on ecological processes, namely:

(a) *Habitat conversion* (fragmentation/land cover change): whereas ASI decline tends to enhance gene flow between some populations of marine species and hence can be seen as a landscape de-fragmentation, it also decreases the connectivity between populations of many taxonomic groups that use ASI as a means of transport (actively or passively), increasing *landscape resistance*, and directly affects those taxa living on it. Moreover, through changing the conditions in the photic zone of the ocean, ASI's decline modifies primary productivity, with generalized bottom-up consequences across all trophic levels.

(b) *Climate disruption/climate change*: current changes in ASI are a direct consequence of changes in climate, and ASI dynamics are linked to feedbacks with climate, in particular the AA, thereby accelerating climate change in the region (and potentially beyond) and adding further stress to Arctic biota.

(c) *Species invasions*: the disappearance of ASI and the warming of Arctic Ocean waters facilitate the range expansion of subarctic marine species into the Arctic [43]. However, less ASI has also been linked with reduced long-distance transport of terrestrial taxa, thus reducing the likelihood of invasions of many terrestrial species to Arctic islands, although this might be offset by (i) increased trade routes, mobility and human presence and (ii) improved conditions for the successful establishment of many terrestrial taxa in the Arctic, both in turn affected by ASI. The net effect of species invasions on Arctic biodiversity will depend on the degree to which, and pace at which, these can outcompete, displace and eventually eliminate Arctic-adapted taxa.

(d) *Toxification/pollution*: ASI decrease enhances the circulation of pollutants in the Arctic Ocean [50]. Moreover, increased marine traffic and human presence in the region increases *in situ* pollution. Further compounding this issue is evidence that (i) global surface circulation currents accumulate plastics and other debris from more polluting and densely populated regions of the Earth in the more accessible, low ASI Arctic Ocean [51] and (ii) contaminants delivered to the Arctic Ocean by rivers (originated through human activities, but also from enhanced permafrost melt) are affected by the dynamics of ASI (e.g. [52]).

(e) *Overexploitation/overharvesting*: many of ASI's effects on Arctic biota, notably on mammals, occur against a background of historical overexploitation that reduced population numbers, genetic variability and distribution ranges, likely establishing legacies on their ability to respond to present changes. For example, Alter *et al.* [53]

show much lower present bowhead whales' genetic diversity when compared with historical populations, and current grey whale numbers (approx. 22 000) are estimated to be approximately 3–5 times lower than pre-whaling [54].

(f) *Disease*: although largely unknown and unquantified, ASI decline may be linked with disease dynamics by rendering the Arctic (i) more accessible to large-scale human activities, (ii) warmer, and (iii) more amenable to species invasions. Furthermore, species affected by ASI decline might show an increased number of weakened/stressed individuals, rendering them more susceptible to disease. Indirectly, ASI decline contributes to enhanced AA and thus melting of the permafrost, which has already caused disease outbreaks, e.g. anthrax outbreak in Yamal [55].

4. Conclusion

Accelerated climate change in the Arctic has brought the region beyond the 2°C safety threshold (e.g. https://data.giss.nasa.gov/gistemp/) recently agreed in Paris under the United Nations Framework Convention on Climate Change (UNFCCC; [56]), ASI's decline rates having made even the boldest model projections fall short (e.g. [57]). With daily anomalies exceeding +16°C in many high Arctic locations during the 2016/2017 winter, and such events becoming more frequent [58], a 'new normal' cannot be safely defined, because the region's climate and the environment are in the midst of a sharp transition.

Given the breadth and complexity of the effects that ASI exerts on Arctic biota (full-year or seasonally resident) and their interactions, Arctic research requires a truly multidisciplinary approach to address the biological consequences of such pressing environmental change (across all groups, from microorganisms and invertebrates to traditionally more studied taxa such as large marine mammals). Traditional site-based ecological studies (plus marine studies performed along the routes of oceanographic expeditions) need to be complemented with information not only derived from other disciplines such as remote sensing, climate/sea ice modelling, glaciology, geomorphology, oceanography, physiology, palaeo-ecology, palaeo-climatology and molecular ecology, but also from the extensive TEK of Arctic peoples.

The present special feature covers a wide range of these disciplines and demonstrates that a large body of knowledge already exists on the relationship between ASI and Arctic biota. A systematic review (e.g. [59]) would help identify where the existing evidence on the effects of ASI on Arctic biota resides across all these disciplines, and where the most pressing gaps (geographical, taxonomical, technical and/or conceptual) lie. ASI-related ecological consequences are difficult to mitigate directly, because only a global effort to address climate warming would potentially reverse current ASI trends (e.g. [2]). In the absence of effective global action, ASI will most likely continue to decline [3]. Only by understanding the mechanisms that link ASI to Arctic biota will we be in the position to anticipate future scenarios, manage the present crisis and target processes that have the potential to interact with ASI decline, such as anthropogenic pressure in the form of increased large-scale activities or pollution.

References

1. Stroeve J, Serreze M, Holland M, Kay J, Malanik J, Barrett A. 2012 The Arctic's rapidly shrinking sea ice cover: a research synthesis. *Clim. Change* **110**, 1005–1027. (doi:10.1007/s10584-011-0101-1)

2. Serreze MC. 2011 Climate change: rethinking the sea-ice tipping point. *Nature* **471**, 47–48. (doi:10.1038/471047a)

3. Liu J, Song M, Horton RM, Hu Y. 2013 Reducing spread in climate model projections of a September ice-free Arctic. *Proc. Natl Acad. Sci. USA* **110**, 12 571–12 576. (doi:10.1073/pnas.1219716110)

4. Stroeve JC, Maslanik J, Serreze MC, Rigor I, Meier W, Fowler C. 2011 Sea ice response to an extreme negative phase of the Arctic Oscillation during winter 2009/2010. *Geophys. Res. Lett.* **38**, L02502. (doi:10.1029/2010gl045662)

5. Perovich DK, Richter-Menge JA. 2009 Loss of sea ice in the Arctic. *Ann. Rev. Mar. Sci.* **1**, 417–441. (doi:10.1146/annurev.marine.010908.163805)

6. Rigor IG, Wallace JM. 2004 Variations in the age of Arctic sea-ice and summer sea-ice extent. *Geophys. Res. Lett.* **31**, L09401. (doi:10.1029/2004gl019492)

7. Rothrock DA, Zhang J. 2005 Arctic Ocean sea ice volume: what explains its recent depletion? *J. Geophys. Res.* **110**, C01002. (doi:10.1029/2004JC002282)

8. Goosse H, Roche DM, Mairesse A, Berger M. 2013 Modelling past sea ice changes. *Quat. Sci. Rev.* **79**, 191–206. (doi:10.1016/j.quascirev.2013.03.011)

9. Serreze MC, Barry RG. 2011 Processes and impacts of Arctic amplification: a research synthesis. *Glob. Planet. Change* **77**, 85–96. (doi:10.1016/j.gloplacha.2011.03.004)

10. Miller GH, Alley RB, Brigham-Grette J, Fitzpatrick JJ, Polyak L, Serreze MC, White JWC. 2010 Arctic amplification: can the past constrain the future? *Quat. Sci. Rev.* **29**, 1779–1790. (doi:10.1016/j.quascirev.2010.02.008)

11. Pithan F, Mauritsen T. 2014 Arctic amplification dominated by temperature feedbacks in contemporary climate models. *Nat. Geosci.* **7**, 181–184. (doi:10.1038/ngeo2071)

12. Regehr EV et al. 2016 Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. *Biol. Lett.* **12**, 20160556. (doi:10.1098/rsbl.2016.0556)

13. Laidre KL, Moon T, Hauser DDW, McGovern R, Heide-Jørgensen MP, Dietz R, Hudson B. 2016 Use of glacial fronts by narwhals (*Monodon monoceros*) in West Greenland. *Biol. Lett.* **12**, 20160457. (doi:10.1098/rsbl.2016.0457)

14. Jenkins DA, Lecomte N, Schaefer JA, Olsen SM, Swingedouw D, Côté SD, Pellissier L, Yannic G. 2016 Loss of connectivity among island-dwelling Peary caribou following sea ice decline. *Biol. Lett.* **12**, 20160235. (doi:10.1098/rsbl.2016.0235)

15. Alsos IG, Ehrich D, Seidenkrantz M-S, Bennike O, Kirchhefer AJ, Geirsdottir A. 2016 The role of sea ice for vascular plant dispersal in the Arctic. *Biol. Lett.* **12**, 20160264. (doi:10.1098/rsbl.2016.0264)

16. Kahru M, Lee Z, Mitchell BG, Nevison CD. 2016 Effects of sea ice cover on satellite-detected primary production in the Arctic Ocean. *Biol. Lett.* **12**, 20160223. (doi:10.1098/rsbl.2016.0223)

17. Geml J, Semenova TA, Morgado LN, Welker JM. 2016 Changes in composition and abundance of functional groups of Arctic fungi in response to long-term summer warming. *Biol. Lett.* **12**, 20160503. (doi:10.1098/rsbl.2016.0503)

18. Forchhammer M. 2017 Sea-ice induced growth decline in Arctic shrubs. *Biol. Lett.* **13**, 20170122. (doi:10.1098/rsbl.2017.0122)

19. Post E, Kerby J, Pedersen C, Steltzer H. 2016 Highly individualistic rates of plant phenological advance associated with Arctic sea ice dynamics. *Biol. Lett.* **12**, 20160332. (doi:10.1098/rsbl.2016.0332)

20. Renner M et al. 2016 Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea. *Biol. Lett.* **12**, 20160276. (doi:10.1098/rsbl.2016.0276)

21. Divoky GJ, Douglas DC, Stenhouse IJ. 2016 Arctic sea ice a major determinant in Mandt's black guillemot movement and distribution during non-breeding season. *Biol. Lett.* **12**, 20160275. (doi:10.1098/rsbl.2016.0275)

22. Gilg O et al. 2016 Living on the edge of a shrinking habitat: the ivory gull, *Pagophila eburnea*, an endangered sea-ice specialist. *Biol. Lett.* **12**, 20160277. (doi:10.1098/rsbl.2016.0277)

23. Moore SE. 2016 Is it 'boom times' for baleen whales in the Pacific Arctic region? *Biol. Lett.* **12**, 20160251. (doi:10.1098/rsbl.2016.0251)

24. O'Corry-Crowe G, Mahoney AR, Suydam R, Quakenbush L, Whiting A, Lowry L, Harwood L. 2016 Genetic profiling links changing sea-ice to shifting beluga whale migration patterns. *Biol. Lett.* **12**, 20160404. (doi:10.1098/rsbl.2016.0404)

25. Forbes BC et al. 2016 Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. *Biol. Lett.* **12**, 20160466. (doi:10.1098/rsbl.2016.0466)

26. Huntington HP, Quakenbush LT, Nelson M. 2016 Effects of changing sea ice on marine mammals and subsistence hunters in northern Alaska from traditional knowledge interviews. *Biol. Lett.* **12**, 20160198. (doi:10.1098/rsbl.2016.0198)

27. Arrigo KR. 2014 Sea ice ecosystems. *Ann. Rev. Mar. Sci.* **6**, 439–467. (doi:10.1146/annurev-marine-010213-135103)

28. Moore SE, Huntington HP. 2008 Arctic marine mammals and climate change: impacts and resilience. *Ecol. Appl.* **18**, S157–S165. (doi:10.1890/06-0571.1)

29. Lovvorn JR, Grebmeier JM, Cooper LW, Bump JK, Richman SE. 2009 Modeling marine protected areas for threatened eiders in a climatically changing Bering Sea. *Ecol. Appl.* **19**, 1596–1613. (doi:10.1890/08-1193.1)

30. Eidesen PB, Ehrich D, Bakkestuen V, Alsos IG, Gilg O, Taberlet P, Brochmann C. 2013 Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. *New Phytol.* **200**, 898–910. (doi:10.1111/nph.12412)

31. O'Corry-Crowe G. 2008 Climate change and the molecular ecology of Arctic marine mammals. *Ecol. Appl.* **18**, S56–S76. (doi:10.1890/06-0795.1)

32. Bristowe WS. 1925 The fauna of the Arctic Island of Jan Mayen and its probable origin. *J. Nat. His. Ser. 9* **15**, 480–485. (doi:10.1080/00222932508633236)

33. Geffen ELI et al. 2007 Sea ice occurrence predicts genetic isolation in the Arctic fox. *Mol. Ecol.* **16**, 4241–4255. (doi:10.1111/j.1365-294X.2007.03507.x)

34. Carmichael LE, Krizan J, Nagy JA, Fuglei E, Dumond M, Johnson D, Veitch A, Berteaux D, Strobeck C. 2007 Historical and ecological determinants of genetic structure in Arctic canids. *Mol. Ecol.* **16**, 3466–3483. (doi:10.1111/j.1365-294X.2007.03381.x)

35. Birks HH. 2008 The Late-Quaternary history of Arctic and alpine plants. *Plant Ecol. Divers.* **1**, 135–146. (doi:10.1080/17550870802328652)

36. Hultén E. 1958 *The amphi-Atlantic plants and their phytogeographical connections*. Stockholm, Sweden: Almqvist & Wiksell.

37. Nordal I. 1987 Tabula rasa after all? Botanical evidence for ice-free refugia in Scandinavia reviewed. *J. Biogeogr.* **14**, 377–388. (doi:10.2307/2844945)

38. Girardin MP, Guo XJ, De Jong R, Kinnard C, Bernier P, Raulier F. 2014 Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. *Glob. Change Biol.* **20**, 851–866. (doi:10.1111/gcb.12400)

39. Post E et al. 2013 Ecological consequences of sea-ice decline. *Science* **341**, 519–524. (doi:10.1126/science.1235225)

40. Macias-Fauria M, Karlsen SR, Forbes BC. 2017 Disentangling the coupling between sea ice and tundra productivity in Svalbard. *Sci. Rep.* **7**, 8586. (doi:10.1038/s41598-017-06218-8)

41. Overeem I, Anderson RS, Wobus CW, Clow GD, Urban FE, Matell N. 2011 Sea ice loss enhances

wave action at the Arctic coast. *Geophys. Res. Lett.* **38**, L17503. (doi:10.1029/2011GL048681)

42. Kerby JT, Post E. 2013 Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Phil. Trans. R. Soc. B* **368**, 20120484. (doi:10.1098/rstb.2012.0484)

43. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV. 2015 Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* **5**, 673–677. (doi:10.1038/Nclimate2647)

44. Durner GM, Douglas DC, Albeke SE, Whiteman JP, Amstrup SC, Richardson E, Wilson RR, Ben-David M. 2017 Increased Arctic sea ice drift alters adult female polar bear movements and energetics. *Glob. Change Biol.* **23**, 3460–3473. (doi:10.1111/gcb.13746)

45. Kovacs KM, Lydersen C, Overland JE, Moore SE. 2010 Impacts of changing sea-ice conditions on Arctic marine mammals. *Mar. Biodiv.* **41**, 181–194. (doi:10.1007/s12526-010-0061-0)

46. Hamilton CD, Kovacs KM, Ims RA, Aars J, Lydersen C. 2017 An Arctic predator–prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. *J. Anim. Ecol.* **86**, 1054–1064. (doi:10.1111/1365-2656.12685)

47. Willerslev E *et al.* 2003 Diverse plant and animal genetic records from Holocene and Pleistocene sediments. *Science* **300**, 791–795. (doi:10.1126/science.1084114)

48. Soulé ME. 1985 What is conservation biology? A new synthetic discipline addresses the dynamics and problems of perturbed species, communities, and ecosystems. *BioScience* **35**, 727–734. (doi:10.2307/1310054)

49. Ceballos G, Ehrlich PR, Dirzo R. 2017 Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl Acad. Sci. USA* **114**, E6089–E6096. (doi:10.1073/pnas.1704949114)

50. Newton R, Pfirman S, Tremblay B, DeRepentigny P. 2017 Increasing transnational sea-ice exchange in a changing Arctic Ocean. *Earths Future* **5**, 633–647. (doi:10.1002/2016ef000500)

51. Cózar A *et al.* 2017 The Arctic Ocean as a dead end for floating plastics in the North Atlantic branch of the thermohaline circulation. *Sci. Adv* **3**, e1600582. (doi:10.1126/sciadv.1600582)

52. Fisher JA, Jacob DJ, Soerensen AL, Amos HM, Steffen A, Sunderland EM. 2012 Riverine source of Arctic Ocean mercury inferred from atmospheric observations. *Nat. Geosci.* **5**, 499–504. (doi:10.1038/ngeo1478)

53. Alter SE *et al.* 2012 Gene flow on ice: the role of sea ice and whaling in shaping Holarctic genetic diversity and population differentiation in bowhead whales (*Balaena mysticetus*). *Ecol. Evol.* **2**, 2895–2911. (doi:10.1002/ece3.397)

54. Alter SE, Rynes E, Palumbi SR. 2007 DNA evidence for historic population size and past ecosystem impacts of gray whales. *Proc. Natl Acad. Sci. USA* **104**, 15 162–15 167. (doi:10.1073 pnas.0706056104)

55. Gainer R. 2016 Yamal and anthrax. *Can. Vet. J.* **57**, 985–987.

56. James R, Washington R, Schleussner CF, Rogelj J, Conway D. 2017 Characterizing half-a-degree difference: a review of methods for identifying regional climate responses to global warming targets. *Wiley Interdiscip. Rev. Clim. Change* **8**, e457. (doi:10.1002/wcc.457)

57. Stroeve J, Holland MM, Meier W, Scambos T, Serreze M. 2007 Arctic sea ice decline: faster than forecast. *Geophys. Res. Lett.* **34**, 3498. (doi:10.1029/2007gl029703)

58. Simpkins G. 2017 Snapshot: extreme Arctic heat. *Nat. Clim. Change* **7**, 95. (doi:10.1038/nclimate3213)

59. Martin AC, Jeffers ES, Petrokofsky G, Myers-Smith I, Macias-Fauria M. 2017 Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach. *Environ. Res. Lett.* **12**, 085007. (doi:10.1088/1748-9326/aa7989)