



UvA-DARE (Digital Academic Repository)

Migratory vertebrates shift migration timing and distributions in a warming Arctic

Lameris, T.; Hoekendijk, J.; Aarts, G.; Aarts, A.; Allen, A.M.; Bienfait, L.; Bijleveld, A.I.; Bongers, M.F.; Brasseur, S.; Chan, Y.-C.; de Ferrante, F.; de Gelder, J.; Derksen, H.; Dijkgraaf, L.; Dijkhuis, L.R.; Dijkstra, S.; Elbertsen, G.; Ernsten, R.; Foxen, T.; Gaarenstroom, J.; Gelhausen, A.; van Gils, J.A.; Grosscurt, S.; Grundlehner, A.; Hertlein, M.L.; van Heumen, A.J.P.; Heurman, M.; Huffeldt, N.P.; Hutter, W.H.; Kamstra, Y.; Keij, F.; van Kempen, S.; Keurntjes, G.; Knap, H.; Loonstra, A.H. Jelle; Nolet, B.A.; Nuijten, R.; Mattijssen, D.; Oosterhoff, H.; Paarlberg, N.; Parekh, M.; Pattyn, J.; Polak, C.; Quist, Y.; Ras, S.; Reneerkens, J.; Ruth, S.; van der Schaar, E.; Schroen, G.; Spikman, F.; van Velzen, J.; Voorn, E.; Vos, J.; Wang, D.; Westdijk, W.; Wind, M.; Zhemchuzhnikov, M.K.; van Langevelde, F.

DOI

[10.1515/ami-2020-0112](https://doi.org/10.1515/ami-2020-0112)

Publication date

2021

Document Version

Final published version

Published in

Animal Migration

License

CC BY-NC-ND

[Link to publication](#)

Citation for published version (APA):

Lameris, T., Hoekendijk, J., Aarts, G., Aarts, A., Allen, A. M., Bienfait, L., Bijleveld, A. I., Bongers, M. F., Brasseur, S., Chan, Y.-C., de Ferrante, F., de Gelder, J., Derksen, H., Dijkgraaf, L., Dijkhuis, L. R., Dijkstra, S., Elbertsen, G., Ernsten, R., Foxen, T., ... van Langevelde, F. (2021). Migratory vertebrates shift migration timing and distributions in a warming Arctic. *Animal Migration*, 8(1), 110-131. <https://doi.org/10.1515/ami-2020-0112>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

UvA-DARE is a service provided by the library of the University of Amsterdam (<https://dare.uva.nl>)

Research Article

Thomas K. Lameris*, Jeroen Hoekendijk, Geert Aarts, Aline Aarts, Andrew M. Allen, Louise Bienfait, Allert I. Bijleveld, Morten F. Bongers, Sophie Brasseur, Ying-Chi Chan, Frits de Ferrante, Jesse de Gelder, Hilmar Derksen, Lisa Dijkgraaf, Laurens R. Dijkhuis, Sanne Dijkstra, Gert Elbertsen, Roosmarijn Ernten, Tessa Foxen, Jari Gaarenstroom, Anna Gelhausen, Jan A. van Gils, Sebastiaan Grosscurt, Anne Grundlehner, Marit L. Hertlein, Anouk J.P. van Heumen, Moniek Heurman, Nicholas Per Huffeldt, Willemijn H. Hutter, Ynze J. J. Kamstra, Femke Keij, Susanne van Kempen, Gabi Keurntjes, Harmen Knap, A.H. Jelle Loonstra, Bart A. Nolet, Rascha J.M. Nuijten, Djan Mattijssen, Hanna Oosterhoff, Nienke Paarlberg, Malou Parekh, Jef Pattyn, Celeste Polak, Yordi Quist, Susan Ras, Jeroen Reneerkens, Saskia Ruth, Evelien van der Schaar, Geert Schroen, Fanny Spikman, Joyce van Velzen, Ezra Voorn, Janneke Vos, Danyang Wang, Wilson Westdijk, Marco Wind, Mikhail K. Zhemchuzhnikov, Frank van Langevelde

Migratory vertebrates shift migration timing and distributions in a warming Arctic

<https://doi.org/10.1515/ami-2020-0112>

received June 29, 2021; accepted October 10, 2021

***Corresponding author: Thomas K. Lameris**, Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands
Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands, Email: thomaslameris@gmail.com,

Jeroen Hoekendijk, Geert Aarts, Allert I. Bijleveld, Sophie Brasseur, Ying-Chi Chan, Jan A. van Gils, Jeroen Reneerkens, Mikhail K. Zhemchuzhnikov, Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands

Andrew M. Allen, Bart A. Nolet, Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands

Geert Aarts, Aline Aarts, Louise Bienfait, Morten F. Bongers, Frits de Ferrante, Jesse de Gelder, Hilmar Derksen, Lisa Dijkgraaf, Laurens R. Dijkhuis, Sanne Dijkstra, Gert Elbertsen, Roosmarijn Ernten, Tessa Foxen, Jari Gaarenstroom, Anna Gelhausen, Sebastiaan Grosscurt, Anne Grundlehner, Marit L. Hertlein, Anouk J.P. van Heumen, Moniek Heurman, Willemijn H. Hutter, Ynze J. J. Kamstra, Femke Keij, Susanne van Kempen, Gabi Keurntjes, Harmen Knap, Rascha J.M. Nuijten, Djan Mattijssen, Hanna Oosterhoff, Nienke Paarlberg, Malou Parekh, Jef Pattyn, Celeste Polak, Yordi Quist, Susan Ras, Saskia Ruth, Evelien van der Schaar, Geert Schroen, Fanny Spikman, Joyce van Velzen, Ezra Voorn, Janneke Vos, Danyang Wang, Wilson Westdijk, Marco Wind, Frank van Langevelde, Wildlife Ecology & Conservation Group, Wageningen University, Wageningen, The Netherlands

Geert Aarts, Sophie Brasseur, Wageningen Marine Research, Wageningen University and Research, Den Helder, the Netherlands
Ying-chi Chan, Jan van Gils, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, the Netherlands

Nicholas Per Huffeldt, Greenland Institute of Natural Resources, Nuuk, Greenland & Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, Roskilde, Denmark

A.H. Jelle Loonstra, Altenburg & Wymenga, Feanwâlden, the Netherlands

Bart A. Nolet, Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, the Netherlands

Rascha J.M. Nuijten, Interdisciplinary Centre for Conservation Science, Department of Zoology, University of Oxford, Oxford, UK

Abstract: Climate warming in the Arctic has led to warmer and earlier springs, and as a result, many food resources for migratory animals become available earlier in the season, as well as become distributed further northwards. To optimally profit from these resources, migratory animals are expected to arrive earlier in the Arctic, as well as shift their own spatial distributions northwards. Here, we review literature to assess whether Arctic migratory birds and mammals already show shifts in migration timing or distribution in response to the warming climate. Distribution shifts were most prominent in marine mammals, as expected from observed northward shifts of their resources. At least for many bird species, the ability to shift distributions is likely constrained by available habitat further north. Shifts in timing have been shown in many species of terrestrial birds and ungulates, as well as for polar bears. Within species, we found strong variation in shifts in timing and distributions between populations. Our review thus shows that many migratory animals display shifts in migration timing and spatial distribution in reaction to a warming Arctic. Importantly, we identify large knowledge gaps especially concerning distribution shifts and timing of autumn migration, especially for marine mammals. Our understanding of how migratory animals respond to climate change appears to be mostly limited by the lack of long-term monitoring studies.

Keywords: birds; mammals; marine mammals; phenological mismatch; range shift; migration phenology

1 Introduction

The Arctic region is characterised by strong seasonality. During winter, the Arctic forms an inhospitable environment for most animals, with low temperatures, extensive snow and ice cover and long phases of darkness. The summer season is relatively short with long light phases and temperatures above freezing, associated with strong changes in environmental conditions, including melt of snow and break-up of sea ice. In both terrestrial and marine ecosystems, the Arctic summer is also a period of peak productivity, creating a short period of high resource abundance for many species. These strong seasonal changes in environmental conditions explain why many vertebrates occurring in the Arctic have a migratory lifestyle [1, Figure 1]. This allows them to profit from high resource abundance in the Arctic summer, while escaping harsh climatic conditions during winter.

The Arctic climate is changing disproportionately fast [2], with temperature increases three times as fast as the rest of the globe [3], especially accelerating in recent decades [4]. Increases in temperature throughout the year coincide with loss of Arctic sea ice, shorter seasonal duration of snow cover [5], and overall increased ‘greening’ of tundra regions [but with strong variation between sites, 6]. Such changes are predicted to further accelerate in the near future [7]. The warming climate has strong impacts on the availability of resources for Arctic migratory animals. Earlier disappearance of ice and snow in the season can result in shifts in timing and distribution of the main food resources for migrants, including vegetation [8,9] and arthropods on land [10–12], and phytoplankton abundance at sea [13,14]. If migratory animals do not change the timing of their migration and reproduction or their summer distribution in response, phenological mismatches with their food resources may occur, potentially resulting in reduced fitness [15,16] which might affect population dynamics.

To adjust to changes in the timing of resource availability in the Arctic, migratory animals could advance their timing of arrival on the breeding grounds. Given the limited leeway to increase the speed of migration once underway [17,18] for birds which have relatively high travel speeds, this likely also necessitates advancements in migratory fuel deposition and departure from the wintering grounds [19]. Besides changes in spring migration in response to earlier resource availability, longer Arctic summer seasons associated with later freeze-up and snowfall [5] could also drive delays in the timing of autumn migration [20].

In addition to shifts in the timing of migration, animals may respond to a warming Arctic by shifting their summer

distribution northward to locations with later phenology. Animals making this northward shift may then experience the same timing of resource availability in spring without advancing migration timing (Figure 2), although it could also result in later arrival given longer migration distances. However, distributional shifts might be limited by topography or by increased travel costs for some Arctic animals. First, many terrestrial animals in the Arctic already find themselves at the most northern edge of the continent, resulting in shrinking habitat range or “polar squeeze” (Figure 2). Second, suitable habitats may not be present further north. For example, marine mammals are largely reliant on sea ice for feeding (and reproducing in case of pinnipeds), and may find themselves without any available habitat with the predicted disappearance of sea ice in summer [21]. Changes in timing of migration and reproduction [22,23], and to a limited extent shifts in breeding distribution [24,25], have already been observed in Arctic migratory animals. Those species which have been unable to shift timing of reproduction sufficiently, often suffer from reductions in reproductive success and survival [15,16]. As Arctic migratory animals are an essential part of local Arctic ecosystems [26,27], as well as provide important resources for local Indigenous Peoples [28,29], any changes in the migration timing and distribution of migratory animals will have far-reaching consequences.

Here we review literature on Arctic migratory animals for evidence of shifts in timing of migration and shifts in distribution. We focus on groups of endothermic migratory vertebrates that perform seasonal migrations to, or within, the Arctic, including terrestrial and marine birds, ungulates, cetaceans, pinnipeds and polar bears (Figure 1). These animals differ strongly in their habitats (marine, coastal and terrestrial habitats) as well as in their diet (plankton, benthic invertebrates, fish, pinnipeds, plants, arthropods, rodents). We expect to find variation in both shifts in timing and distribution across taxonomic groups of Arctic migratory animals. Concerning migration timing, we predict that long-distance migrants (most birds and cetaceans, with one-way journeys on average exceeding 2000 kilometres) will show smaller shifts in migration timing in comparison to short-distance migrants (including some cetaceans, all ungulates, pinnipeds and polar bear), as long-distance migrants cannot predict conditions in the Arctic from their distant wintering grounds [30,31]. Concerning shifts in distribution, we expect terrestrial animals (including land-breeding marine birds), to be more constrained in making large shifts [32] compared to marine animals. For terrestrial animals, suitable alternative habitat further northward may not be available due to lagging changes in suitable vegetation communities, or



Figure 1: Examples of warm-blooded vertebrates migrating to the Arctic, showing (top left), reindeer (*Rangifer tarandus*) crossing a frozen river on the way to their calving grounds, (top right), red knots (*Calidris canutus*) on a spring staging site in northern Norway, (bottom left), walrus (*Odobenus rosmarus*) resting on sea ice with their young, and (bottom right), a minke whale (*Balaenoptera acutorostrata*) in a fjord in Svalbard. Photographs by Paul Asman & Jill Lenoble (top left), GRID Arendal (top right), Alaska Region US Fish & Wildlife (bottom left), and Guillaume Baviere (bottom right).

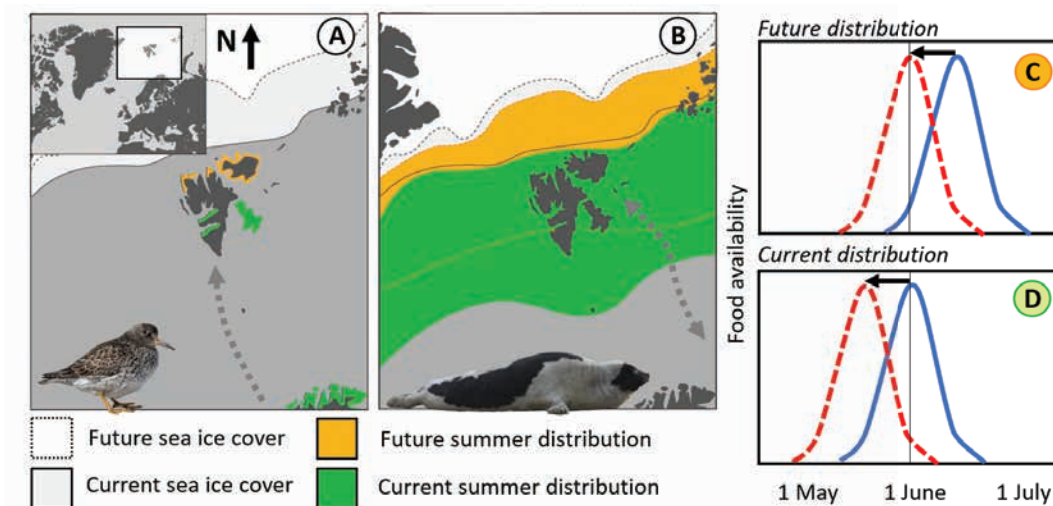


Figure 2: (A-B) Maps showing examples of current (green) and hypothetical future summer distributions (orange) of purple sandpipers *Calidris maritima* (A) and harp seals *Pagophilus groenlandicus* (B) around Svalbard. While harp seals can shift their distribution northward with retreating sea ice, purple sandpipers are constrained by available land mass of Svalbard to shift their distributions far north. Median sea ice cover (during summer months 1981 - 2010) is shown as light grey area in the north, outlined by a solid black line, and hypothetical change in future ice cover is depicted by the white area outlined by dashed black line. Grey dashed arrows show migration directions of the sandpipers and seals. Distributions and migration directions are based on [73,195,231]. (C-D) With a warming climate, timing of food availability (blue lines) is expected to advance (red dashed lines), both in current distributions (D) as well as hypothetical future distribution ranges (C). To maintain a synchrony with these peaks in food availability, animals are expected to advance their own timing of migration, but may also be able to maintain a synchrony by shifting their distribution northward (towards distribution C) where the food becomes available later in the season.

as it is limited by topographical barriers in the landscape such as the northern edge of the continent (Figure 2). In comparison, animals in marine environments that can freely navigate the oceans and enter the Arctic basin, may show stronger shifts in their distribution [32], for example by following the edge of pack ice, or the distribution shifts of their main prey [33,34].

In this review, we first introduce the focal taxonomic groups of endothermic vertebrates and their migrations. Thereafter we introduce the resources on which animals depend and discuss how the phenology and abundance of these resources are expected to change in a warming climate. Finally, following a systematic literature search, we review scientific literature on evidence for shifts in timing of migration and shifts in distribution of focal taxonomic groups, and quantify whether shifts in timing differ between taxonomic groups.

2 Migrations of Arctic, warm-blooded vertebrates

2.1 Bird migration

The most abundant birds with Arctic distributions are seabirds, shorebirds, and waterfowl, with other less represented species groups including passerines, grouse and birds of prey [1]. Most of these species are migratory [35] and spend the winter in more southern regions. The extent of these migrations varies enormously, with some seabird species wintering in Arctic waters [36,37], most waterfowl, passerines, and birds of prey wintering in temperate regions [38–40], and many shorebird and seabird species wintering in areas that range from temperate and tropical regions [41–43] down to Antarctic waters [44,45]. Differences in wintering areas, and therefore migration distance, likely relate strongly to availability of suitable wintering habitat with available resources. Fish-eating seabirds may be able to winter in Arctic waters as long as fish are available and accessible [46,47], while shorebirds, depending on benthic invertebrates, travel to temperate and tropical intertidal flats that do not freeze in winter [42]. Given long migration distances, many bird species require stopover sites to gain energy stores between leaps of migration [48]. During spring migration, at least some species of waterfowl appear to track peaks in food quality and availability [49–51] and the onset of ice break-up and snowmelt at staging sites [52,53]. This, however, does not appear to be the case for all species of waterfowl [51] nor for

shorebirds [54]. Birds of prey also track snowmelt during northward migration, possibly as areas with melting snow contain high availability of rodent prey [38]. All Arctic migratory birds reproduce during the Arctic summer, and many species (including waterfowl, shorebirds and marine birds) appear to attempt to synchronize their reproduction with prey availability for their offspring.

2.2 Ungulate migration

The Arctic is inhabited by a limited set of ungulate species, including reindeer (*Rangifer tarandus*), moose (*Alces alces*), muskox (*Ovibos moschatus*), Dall's sheep (*Ovis dalli*) and snow sheep (*Ovis nivicola*). Movements of the three latter species are limited to short-distances (up to 100 km), which can be seasonal but often follow nomadic patterns [55] in search for suitable foraging grounds. On the other hand, moose [56,57] and reindeer are considered partial migrants, and especially some populations of reindeer make large migratory movements up to 1300 km [58] from taiga wintering areas to calving grounds at coastal Arctic tundra zones. Other populations of reindeer migrate shorter distances [59] or are resident [60]. By migrating, ungulates can winter in areas with more suitable conditions for both adults and their offspring [56], travel northwards in spring along a wave of vegetation green-up [61], and match calving with local peaks in food quality [15,62]. Studies on the migrations of moose are largely limited to their southern ranges, and in this review we therefore focus on reindeer.

2.3 Cetacean migration

Cetaceans occurring in the Arctic are mostly represented by baleen whales (Mysticeti), including rorquals (Balainopteridae) and grey whales (*Eschrichtius robustus*), and fewer toothed whales (Odontoceti), including belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), sperm whales (*Physeter macrocephalus*) and northern beaked whales (*Hyperoodon ampullatus*). With the exception of the pagophilic (i.e. sea-ice loving) beluga, narwhal and bowhead whale (*Balaena mysticetus*), which make seasonal migrations within the Arctic, cetaceans are seasonal visitors to the Arctic. In contrast to birds and ungulates that migrate to the Arctic for reproduction, migratory whales use the high latitude summer grounds exclusively for feeding, while reproduction occurs in low latitude winter grounds, where food availability is generally scarce or non-existent [63]. The mechanism driving this migra-

tory pattern remains largely unknown. It has been suggested that whales migrate to reduce predation pressure on calves [64,65], or that the higher temperatures of low latitude waters bring thermoregulation benefits for calves (and/or adults) [66,67]. However, recent new evidence suggests that deferred skin moult could be the main driver of long-distance cetacean migration [67]. In colder waters, cetaceans reduce blood flow to their skin to conserve body heat. It appears that cetaceans migrate to warmer waters at lower latitudes to reduce heat loss during moult, a period during which they enlarge blood flow through the skin. Similarly, the pagophilic species that remain in the Arctic year-round, make seasonal migrations towards warmer waters in estuaries and shallows to moult [68–70].

2.4 Pinniped migration

Several pinniped species are year-round residents in the Arctic regions, like harp seal (*Pagophilus groenlandicus*), ringed seal (*Pusa hispida*), hooded seal (*Cystophora cristata*), bearded seal (*Erignathus barbatus*), spotted seal (*Phoca largha*), ribbon seal (*Histiophoca fasciata*) and walrus (*Odobenus rosmarus*). In addition, the distributions of other species like harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), Steller sea lion (*Eumetopias jubatus*) and northern fur seal (*Callorhinus ursinus*) extend into the polar regions. While pinnipeds feed at sea, they require land or ice to reproduce, moult and periodically rest, which severely constrains their at-sea distribution. To avoid land predators, most Arctic pinnipeds spend the breeding and moulting season on land-fast ice or free-floating pack ice in late winter and spring [71], after which they disperse. While some individuals move long distances away from the ice (e.g. harp seals and walrus), most pinniped species remain associated with outer edges of the pack ice, where they feed on fish and invertebrates [72], while using the pack ice as resting platforms. Resident Arctic pinnipeds feed on prey that is present and accessible in the Arctic regions year-round, which provides no strong incentive to leave the Arctic region altogether, as opposed to most birds and cetaceans. However, pinnipeds do show seasonal long-distance movements [73], but this seasonal migratory pattern mostly involves movement between foraging areas, breeding and moulting locations, largely driven by the extent of the pack ice [74].

2.5 Polar bear migration

Polar bears (*Ursus maritimus*) depend on sea ice platforms to hunt fatty, energy-dense pinniped prey [75], primarily ringed seals and bearded seals [76]. The bears consume around two-thirds of their annual food intake from February up to mid-April, when seals give birth on the sea ice [75,77]. When sea ice melts and becomes fractured in spring, the polar bears' mobility and seal hunting technique become inefficient [78], and bears either move with the receding pack ice, or migrate towards terrestrial habitats [75]. The summer is typically a period of fasting for polar bears during which they rely on endogenous energy reserves [79]. Most polar bears move back onto the pack ice after autumn, when pack ice extent increases, while pregnant female bears will enter terrestrial maternity dens along the coast where they give birth to their young [80].

3 Changing resources under climate warming

Temperatures in the Arctic are increasing year-round, with temperatures above freezing occurring earlier in spring [81], associated with earlier timing of snow melt, active layer melt and ice break-up [5]. These climatic changes can result in earlier availability of resources for migrants (although the relative importance of climatic factors may differ at regional scales, e.g. [82]). In addition, higher summer temperatures may lengthen the period of resource availability, and climatic changes may also cause a northward shift in the spatial distribution of resources, as well as of suitable habitats for migrants. We discuss these aspects in detail in the following sections.

3.1 Earlier resource availability

Lower trophic levels, including the food resources for many migratory animals (Figure 3), are known to rapidly adjust their phenology to a warming climate [83]. In terrestrial habitats, earlier snowmelt and increasing temperatures have led to an advancement in the growing season of many plants [84], and thereby an advancement in the moment of peak quality and availability of forage plants for herbivorous birds and ungulates [8,9,85]. Arthropods, which form the main prey for Arctic-breeding shorebirds and passerines [86], respond to earlier dates of snow and active layer melt and increasing temperatures by earlier emergence [10,22,87] and changes in their abundance

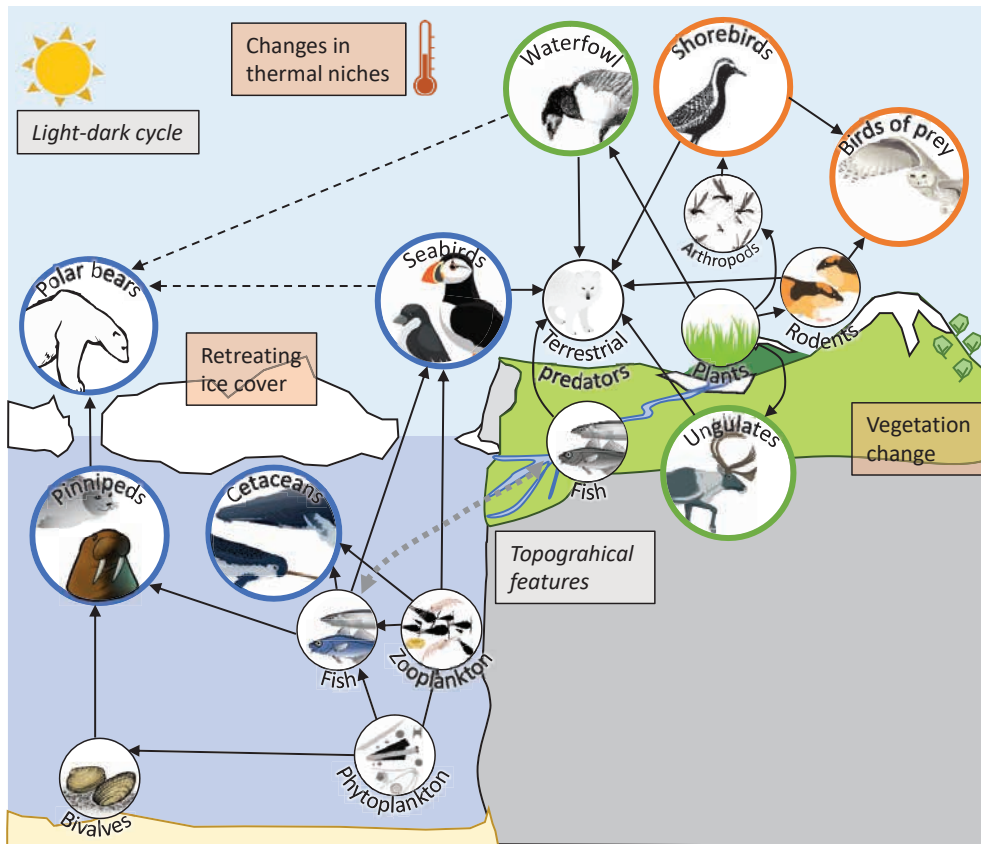


Figure 3: Simplified food webs in marine Arctic habitats (left) and terrestrial habitats (right), with the focal groups of marine migrants (blue), terrestrial herbivore migrants (green) and terrestrial carnivores (orange) displayed in circles. Resources, as well as predators which do not display typical migratory behaviour, are displayed in black, smaller circles. Several marine fish species make semelparous migrations to streams and rivers to spawn (as indicated by the grey dashed arrow), and are thus available as resource to both marine and terrestrial animals. In marine habitats, migratory seabirds, cetaceans and pinnipeds are expected to adjust timing of migration and / or distribution with availability of zooplankton, benthic organisms such as bivalves, and fish, which in turn rely on phytoplankton (including ice algae). Polar bears rely on the presence of pack ice to prey on pinnipeds during winter months, but with a warming climate spend more time in terrestrial habitats where they have started to prey on bird's eggs. In terrestrial habitats, herbivores feed on forage plants and time arrival with peaks in nutritional quality of plants. Shorebirds time migration in synchrony with availability of arthropods, and birds of prey rely on availability of rodents for successful reproduction. In turn, terrestrial predators such as Arctic foxes prey on bird's nests, especially in years when cyclic rodent populations are depressed. Besides shifts in phenology of resources, climate warming may also impact habitat suitability via changes in thermal niches, retreating pack ice and vegetation community change (shown in orange boxes). Other aspects such as light-dark cycles and topographical features (such as cliffs which seabirds require for nesting, shown in grey boxes) will not change, potentially constraining distribution shifts of animals.

[10]. The annual cycles of Arctic rodents, the main prey of Arctic raptors and skuas [88], seem to be little impacted by a warming climate [89] (but see reports on irregularity of these cycles [90]). At the same time, the accessibility of rodents as prey for birds is potentially dependent on snow cover, with high concentrations of accessible rodents around the time of snow melt [38]. Despite increasing temperatures, increasing precipitation in winter (another aspect of climate change in the Arctic, 91) may also result in abundant snow and late melt thereof, which has the potential to largely disrupt reproduction of all terrestrial animals [92].

In marine environments, ice algae and phytoplankton form the most important primary producers and are the basis of the Arctic marine food web [93]. Ice algae grow under thinning ice edges, and their phenology is regulated by light [94]. While a warming climate would result in a more permeable ice layer and earlier ice algal blooms may be expected, short day-length at high latitudes limit phenological advancements of ice algae [94,95]. The other main primary producer, phytoplankton, blooms later in the season at ice edges, regulated by light and nutrient upwelling [95]. Earlier ice disappearance has caused an advancement in timing of phytoplankton blooms [96]

and a decreasing time-lag between ice algae and phytoplankton blooms [95], which together form the main food resource for many species of bivalves and zooplankton [97]. Zooplankton may suffer from reductions in survival (measured as lower available zooplankton biomass) when they are not able to adjust their phenology in response to advanced phytoplankton blooms [97–99], as well as possibly due to the segregation of ice algae and phytoplankton blooms. Nevertheless, other studies found stable zooplankton biomass following earlier phytoplankton blooms [100]. Zooplankton is the main food resource for fish species, and both zooplankton and fish are eaten by most baleen whales, pinnipeds and seabirds [101,102]. Both timing and abundance of zooplankton may affect the abundance and availability of fish species as prey for higher trophic levels. For seabirds and whales, important prey fish species may occur earlier in the season, or decrease in abundance due to phenological mismatches with algal and plankton blooms.

3.2 Longer period of resource availability

While a warming climate will advance the timing when resources become available, it can also impact the abundance of resources [10], as well as result in a longer period of availability of resources. Although their nutritional value declines over the season, forage plants are available for herbivorous birds until covered by first snowfall in autumn, which is occurring later in the season in recent years [5]. This is also beneficial for many ungulates, which, despite their ability to find forage plants under shallow layers of snow, cannot deal with deeper layers of snow [103] or ice crust formation [104]. Terrestrial arthropods may remain active as long as temperatures are above freezing, but their availability to predators could be limited due to a restricted number of generations emerging in one season [105] but see [106], and Arctic shorebirds are thus unlikely to profit from a longer breeding season through re-nesting [107]. With increasing temperatures, warming Arctic waters may facilitate longer resource availability, by driving the emergence of a second phytoplankton bloom [100,108] and a second generation of copepods [109] during autumn.

3.3 Northward shifts in suitable habitats and resources

A change in climate is expected to change the habitat suitability for migratory animals as well as for their resources, and both may show northward shifts of their distribution in response (Figure 2). First of all, many organisms thrive within a specific ‘thermal niche’ or ‘thermal preference’, and experience fitness reductions outside this niche [110,111]. With a warming climate, the location of this thermal niche and therefore the suitability of habitats is predicted to shift northwards [34,112]. This may lead to distribution shifts for endothermic vertebrates, as well as for their food resources, often ectothermic animals or vegetation. Although at high latitudes most endothermic animals live at temperatures well below their thermal maximum and thus have leeway under increasing temperatures [113,114], habitat suitability of ectothermic organisms is more sensitive to changing temperatures [110], and these potentially make larger distribution shifts [115]. At the same time, vegetation communities and thereby distribution of specific plant species appear to change at relatively slow rates [6,116]. Such shifts in the distribution of resources will also change habitat suitability for migrants. For example, in marine environments, many fish species are showing northward distribution shifts, changing local community composition of potential prey species for marine predators [117]. At the same time, some fish species from lower latitudes may be unable to find refuge away from predators during the continuous light of polar summer, which may constrain their abundance under certain climate change scenarios [118].

Some factors of habitat suitability are closely linked to climatic conditions, including the thermal niche and resource distribution as explained above, as well as specific environmental aspects of habitats, such as cover of sea ice as resting platforms for pinnipeds and hunting platforms for polar bears. While climate warming will directly change these aspects of habitat suitability, other aspects are geographically fixed, for example topographical features (e.g. cliffs making up suitable nesting habitat for seabirds) and the duration of the light-dark cycle (which is fixed by latitude and date). Advances in the timing of resource availability and rapid-changing aspects of habitat suitability as a result of climate warming may drive northward distribution shifts of animals, but slow-changing or fixed aspects of habitat suitability may at the same time form constraints for distribution shifts [118,119]. Moreover, such differences in the rate of northward shifts could cause reductions in suitable habitat altogether.

4 Shifts in migration timing and distributions

4.1 Methods to quantify differences in responses between taxonomic groups

To review whether vertebrates display shifts in migration timing and distributions in response to a warming climate, we searched for relevant papers using the Web of Science database. We used the search term Arctic AND (range shift OR migration timing) AND (bird OR avian OR ungulate OR herbivore OR cetacean OR whale OR beluga OR narwal OR pinniped OR seal OR walrus OR polar bear). This query resulted in 486 papers, from which we only included papers that (1) dealt with Arctic migratory species, (2) reporting on changes in either timing of spring or autumn migration, timing of reproduction or changes in distribution, (3) either as trends over time (as measured over a period of at least 5 years) or (4) in relation to climatic and environmental conditions in the Arctic (as measured over a period of at least 3 years). To determine which species are considered ‘Arctic species’, we used species lists as provided by the Arctic Biodiversity Assessment [35], with the exception that we only included bird species for which the majority or complete population breeds in the Arctic. We excluded papers that did not report species-specific results. Eventually this selection resulted in 32 papers. In addition to these papers, we added 35 relevant papers (matching the criteria mentioned above) that we found within reference lists of the 32 selected papers, as well as relevant papers found within the reference lists of two review studies on marine mammals [74,120].

For every paper, we recorded (1) the study species and taxonomic group (bird, ungulate, cetacean, pinniped, polar bear), (2) the region where the study was conducted, and (3) whether evidence was reported for shifts in timing of spring migration, reproduction and autumn migration and shifts in summering distribution. For shifts in timing, we considered evidence to be significant shifts in timing over years (considering study periods of at least 5 years) or with changing climatic variables. For shifts in distribution, we considered evidence to include both increases in the number of sightings (but only when evident that this was unrelated to population increase) as well as latitudinal change in observations [121]. We noted the rate of change in timing of spring and autumn migration (in days per year) when this was reported in studies.

In order to quantify how taxonomic groups differed in responses to changing climatic conditions, we compared the relative number of species per taxonomic group for

which shifts in migration and distribution were recorded. We quantified whether shifts in migration timing differed between taxonomic groups by comparing slopes of reported shifts in spring and autumn migration. In addition, comparing the number of species and study regions for which we found relevant studies allowed us to quantify how knowledge gaps differed between groups and regions.

4.2 Shifts in migration timing

4.2.1 Terrestrial and marine birds

Most of the time series available on migration timing of terrestrial birds show no clear advancements in the timing of migration departure from wintering areas [16,22,122–124]. However, in the last decades, some species of waterfowl and one shorebird have shown profound shifts in timing of departure [123,125–128], but these shifts appear mostly linked to changes in suitable stopover sites along their migratory route. At the same time, many terrestrial bird species have advanced timing of arrival in the Arctic, with studies showing species to adjust migration timing to annual variation in climatic conditions in the Arctic [16,22,129–131] and some studies also showing clear trends of advanced arrival over time [22,132–134]. While one study shows stronger shifts in advancement of arrival in short-distance migrants compared to long-distance migrants [133], other studies find no clear differences between short- and long-distance migrants [129]. Along with advancements in migration timing, some terrestrial bird species show advancements in the timing of reproduction [22,135–139], but this is not found for all species [11,140,141], and advancements in reproduction timing can lag behind advancements in arrival [16]. Trends in autumn migration are mixed, with some species showing delayed arrival in wintering grounds, associated with higher temperatures at northern summering and staging sites [126,142]. Several other species show earlier arrivals of adult birds [142,143], possibly explained by disrupted breeding seasons.

In contrast to many terrestrial bird species, less is known about changes in timing of migration in Arctic seabirds. For species for which data are available, advancements in migration timing are relatively small, with the exception of Arctic-breeding guillemots (*Uria* spp.) which have advanced arrival in breeding colonies all over the Arctic [144]. A large meta-analysis, that included many Arctic breeding seabirds, showed that seabirds in general have not adjusted their timing of reproduction in response

to higher sea-surface temperature [145]. In the Arctic, advancements in reproduction phenology over time have been found for surface-feeding species (gulls and tubenoses) in the Pacific ocean but not in the Atlantic ocean, while pursuit-diving species (alcids) showed no trends in either ocean [146]. While this may be the general pattern, some pursuit-diving and benthic-feeding species do show advancements in reproduction timing in response to local earlier ice break-up [147–149] and increases in air temperature [150]. We did not find studies reporting trends in timing of autumn migration in sea birds.

4.2.2 Ungulates

A variety of trends on reindeer migration timing emerge from the literature. A delay in spring migration over time was found for reindeer populations on Newfoundland up to the year 2000 [59], earlier spring departures but not earlier arrivals were shown for populations in Northern Quebec between 2000 and 2011 [151] and no trends in departure dates but earlier arrival were found for populations in north-western Canada and Alaska between 2000 and 2017 [23]. It is suggested that reindeer adjust departure dates and travel speed to local as well as large-scale climatic conditions [23], allowing them to pass through areas just prior to snowmelt [62], which facilitates easier passage over partly frozen soil and ice [152]. In addition, by pacing migration speed with local timing of snowmelt, reindeer may be able to optimally time their arrival on the calving grounds to match local dates of snow melt and vegetation green-up [23,62]. As a result, calving date has advanced in several populations of reindeer in response to a warming climate [153]. However, large variation exists in the extent to which reindeer appear to be able to keep up their timing of reproduction with the local climate. Domestic reindeer in Northern Finland have been able to advance timing of calving with earlier springs [154], which has benefitted reproductive success [155]. On the other hand, reindeer populations in Svalbard and Western Greenland do not seem to advance calving dates with earlier springs [15,156], and a mismatch with phenology of local forage plants has resulted in a reduction in reproductive success in Western Greenland [15,85,157,158]. While longer summer seasons could extend the summer period during which forage plants are available, reindeer have been found to advance autumn migration timing [59,151]. It is possible that such changes are a response to resource depletion, but it is yet unclear whether this is mainly driven by climate change or population dynamics.

4.2.3 Cetaceans

An increasing asynchrony between the arrival of migratory cetacean species and local abundance of prey (due to spatial and temporal shifts) has been predicted [71], but long-term data on the timing of migration of Arctic cetacean species is rare, and the few available studies paint a mixed picture [120]. Spring migration phenology shows either no change (beluga whales) or has been delayed (bowhead and grey whale), which could suggest that these species might not keep up with advancing phenology of their prey in the Arctic. In autumn, delays in departure from northern waters have been found for beluga whales, which appears to be a response to later ice formation [159]. However, further south along the migration route, migrating baleen whales are observed on autumn migration earlier in recent years [160].

4.2.4 Pinnipeds

The seasonal distribution of pinnipeds in the Arctic is heavily influenced by the spatial extent of the sea pack ice, which shows large seasonal and inter-annual variation. Most pinnipeds associate with the ice well before the breeding season, which means that ice regions need to be accessible at the onset of the breeding season and remain stable throughout the breeding period in order to be suitable [74]. Some species (e.g. ringed seals) breed on (more stable) fast-ice, as they have a relatively long nursing period (~ 6 weeks) [161,162]. In contrast, pinnipeds that rely on floating pack ice such as hooded seals generally have a shorter nursing period. Hooded seals breed several weeks later than harp seals, during the start of the seasonal ice break-up. To combat the effect of drift, their lactation period is extremely short (~ 4 days). Due to the strong association with sea pack ice, Arctic pinnipeds will be highly influenced by climatic changes in temperature. However, currently, little information is available about changes in phenology of pinnipeds in response to increasing temperatures and changes in ice cover [163]. We found only one study reporting on shifts in timing in pinnipeds, showing a long-term advancement in the arrival of walrus in their summering range, as observed by local Inuit hunters in the Canadian Arctic [29].

4.2.5 Polar bears

Although pinnipeds, the main prey of polar bears, have not been reported to display major shifts in phenology,

climate warming is strongly reducing the seasonal availability of pack ice [164,165], used by pinnipeds and polar bears as haul-out sites and foraging habitat, respectively. Polar bears time their migration towards terrestrial habitats with the break-up of pack ice in spring [166]. As a result, bears have advanced their arrival in terrestrial habitats with earlier ice break-up [78,165], as well as delayed the time when they travel back to the pack ice in winter, which also impacts their condition when entering maternity dens [167]. By shifting their migration timing, bears have increased the fasting period in terrestrial habitats during which they have no access to their pinniped prey [78]. In addition, due to reduced availability of pack ice, bears often have to travel longer distances on terrestrial habitats and swim larger distances in order to migrate back to the pack ice [75]. Longer fasting periods and higher travelling costs have been shown to cause reductions in population vital rates [75,79,168].

4.3 Changes in winter and summer distributions

4.3.1 Terrestrial and marine birds

Northward shifts in wintering distribution of Arctic migratory birds, also named ‘short-stopping’, have in the past decades been shown for multiple species of Arctic-breeding waterfowl and shorebirds [126,169–171]. For birds wintering in Europe, this mostly translates to shifts in a north-easterly direction up to 13 km/year (as reported for Bewick’s swans, 126). Changing energetic requirements and prey availability under different scenarios of future climate are also expected to affect the winter distributions of the five most numerous species of seabirds in the North Atlantic, many of which breed in the Arctic [172], but shifts in winter distributions have not yet been shown for these species.

The investigation of shifts in breeding distributions of Arctic species is in its infancy, but theoretical exercises predicting shifts in winter and summer ranges are contributing a basis for forecasting potential changes. Shifts in breeding distribution have been predicted for Arctic-breeding shorebirds [173] as well as for Arctic seabirds [174] given the northward shifts of their prey [175]. In this way, climate change may result in shifts in migration destinations and even flyways, for example the predicted establishment of wintering populations of little auks (*Alle alle*) in the Pacific, which would facilitate trans-Arctic migrations [174]. Likewise, Arctic seabirds may also cease migration completely and become year-round residents of

the Arctic. Nevertheless, so far there is little evidence that shifts in breeding distribution are already taking place. In part, this is because range shifts are typically picked up in long-term monitoring studies with high spatial coverage [176], which are rare in the Arctic. In Finland, an average northward shift of 0.8 km/year has been observed in a suite of Arctic bird species [24]. A long-term local study in Arctic Russia has revealed a strong decline in densities of typical high-Arctic breeding shorebird species, while species typical for southern tundra habitats have increased [177].

4.3.2 Ungulates

Reindeer have often been considered to display strong site fidelity, especially during the calving season in summer [178,179]. This idea of site fidelity is under discussion, as reindeer can shift their wintering ranges following overgrazing of pastures [180], and recently, two reindeer herds have started to adjust their calving grounds to annual variation in forage quality, moving further westwards into Alaska in earlier springs [25,181]. Similarly, moose in Alaska have shifted their summering ranges northwards following shrub encroachment in tundra habitats [182].

4.3.3 Cetaceans

For cetacean species, it is predicted that the ranges of 88% of all cetaceans may be affected due to global warming [183]. In accordance, northward shifts in distribution have been revealed for several migratory baleen whales, including typical southern Arctic species [184,185]. Also short-distance migrants, bowhead whales and beluga whales, are shifting their distributions within the Arctic, likely in response to changes in sea ice cover [186,187]. Killer whales (*Orcinus orca*) typically avoid heavy ice concentrations, and are increasingly occurring in the Arctic following reductions in sea ice cover which has opened up movement corridors [188,189]. The increase of this top predator might in turn influence the distribution of cetaceans and pinnipeds restricted to the Arctic. Sea ice reduction might also provide opportunities for cetacean species to move between the North Pacific and North Atlantic, as is supported by recent reports of grey whales in the Mediterranean Sea [190].

4.3.4 Pinnipeds

Most species of pinnipeds restricted to the Arctic are heavily reliant on sea ice for reproduction, moult and resting. During the winter months the sea ice connects to all landmasses surrounding the Arctic Ocean (i.e. Russia, Alaska, Canada, Greenland). However, as a result of climate change, the Arctic sea ice extent, as well as its thickness and age, have decreased [191], with the largest changes during the summer months. Currently, the summer sea ice only connects to the shallow waters of Greenland and Northern Canada [192], and, somewhere between 2030 and 2050, it is expected that the Arctic will be completely ice-free during summer [21,193]. Since most arctic pinnipeds are reliant on sea ice and generally feed in shallower (and coastal) waters, the distribution of sea ice relative to the coastal waters will likely have a main impact on the distribution of Arctic pinnipeds. Probably in a result to changing sea ice conditions, range shifts in pupping grounds have been shown for harp seals [194,195], as well as in summering distributions of harp seal, bearded seal and ringed seal around Svalbard, which show a northward latitudinal trend [121]. In addition, some species (e.g. walrus) are forced to haul-out on land more often in the absence of sea ice, and this may impose additional safety and energy expenditure costs [196], also considering density-dependent effects as fewer haul-out sites are available [197]. The disappearance of sea ice may also provide opportunities for the more temperate seal species that rely on land to rest, moult and reproduce, and these species, like harbour seals, which show an increase in numbers in the Arctic [121,198].

4.3.5 Polar bears

Following reductions in pack ice and earlier ice break-up, polar bears have been observed to have shifted their winter ranges northward [199–201]. Also, polar bears have shifted their maternity dens more often to terrestrial coastal areas rather than on pack ice, in response to absence of stable old ice [202]. In summer, available habitat on pack ice has contracted for several populations of polar bears [199,201], and the number of polar bears spending the summer in terrestrial habitats is increasing [203]. In some regions polar bears are able to cope with sea ice loss by making use of coastal seasonal ice [200]. However, the increasing distance between wintering habitats on pack ice and ter-

restrial summering habitats makes polar bears vulnerable to climate change [75,202].

4.4 Comparisons between species groups

4.4.1 Available data

Most of the studies that we found were on shifts in the timing of migration, while much fewer studies were available on changes in distribution (Figure 4A). Shifts in timing were more often studied for spring migrations and less often for autumn migrations. While terrestrial and marine birds, with data available for 46 out of 126 species, as well as ungulates and polar bear appeared to be well studied, much less studies were available for cetaceans and pinnipeds. Most studies originated from the American and Canadian Arctic, as well as from the Atlantic Arctic (Greenland and Svalbard) (Figure 4B). Much fewer studies were available for the European and West-Russian Arctic, and we found no studies reporting shifts in migration timing and distribution from the East-Russian Arctic.

4.4.2 Shifts in timing

Advancements in spring migration timing were reported for many terrestrial and marine birds, as well as for polar bear and some populations of reindeer, but less often for cetaceans and pinnipeds (Figure 4A). Although few studies were available, polar bears showed stronger advancements in spring migration timing compared to birds (Figure 4C). Unexpectedly, some cetacean species and populations of reindeer showed a delay in spring migration timing. Shifts in autumn migration timing also showed mixed results, with both delayed and advanced timing in birds and cetaceans, advancements in ungulates and a delay for one sub-population of polar bears (reported in one study, Figure 4C).

4.4.3 Shifts in distribution

Despite the low number of studies, it appears that a northward shift in distribution was found for relatively more species of both marine (cetaceans, pinnipeds and polar bear) and terrestrial mammals (ungulates) compared to bird species (Figure 4A).

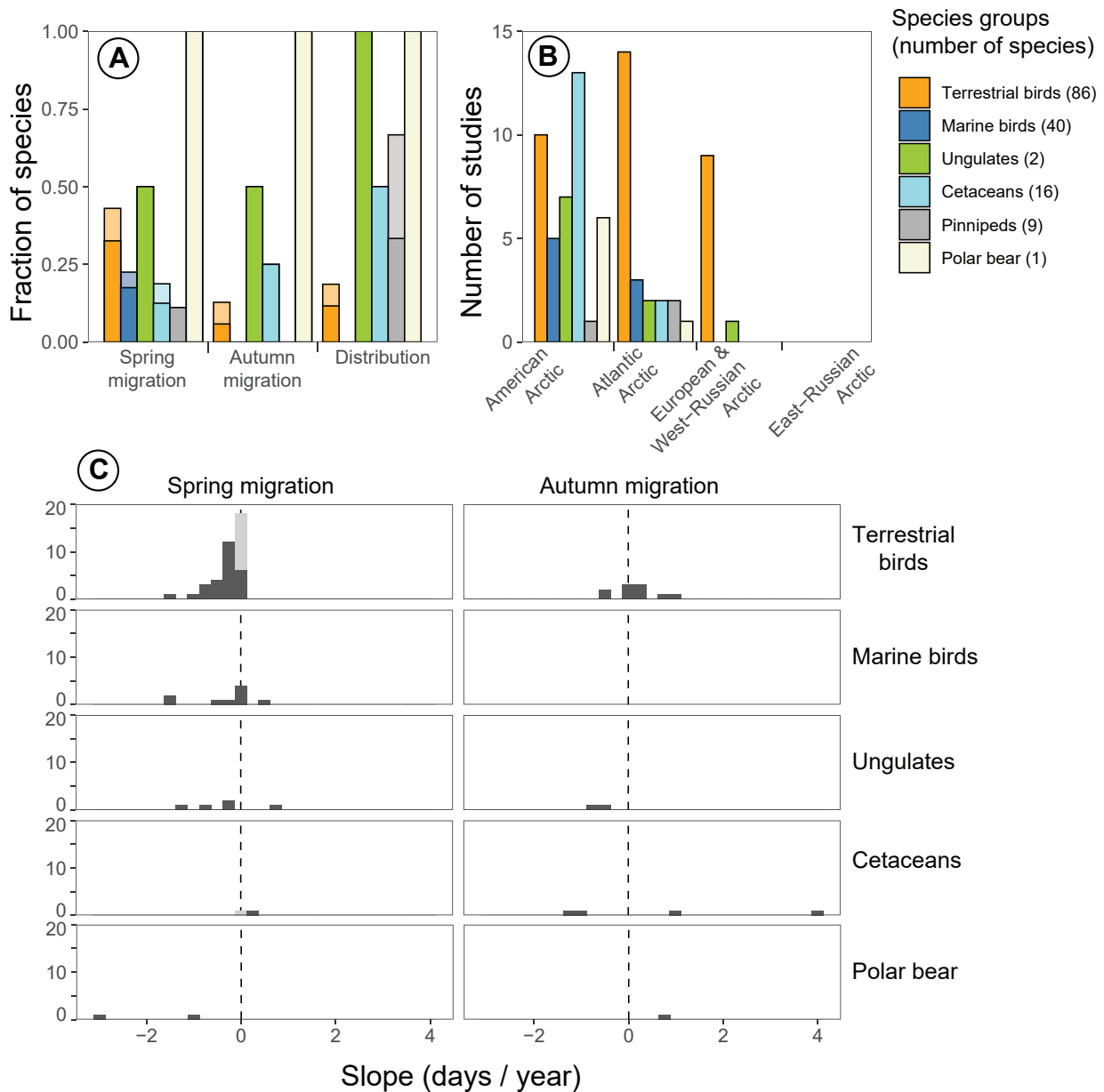


Figure 4: (A) The fraction of species per taxonomic group for which shifts in spring migration timing, autumn migration timing and distribution have been studied (light-coloured bars) and have been observed (dark-coloured bars). The total number of species for each group is noted in brackets in the legend. (B) The number of studies conducted within the four different geographic regions of the Arctic, shown per species group. (C) Histograms of reported trends in migration timing (as the slope in days of change over years), shown in bins of 0.25 as black bars. Grey bars show the number of studies reporting no change in migration timing over years without quantifying the slope. Histograms are shown for spring (left) and autumn migrations (right) and for terrestrial birds, sea birds, ungulates, cetaceans and polar bear. For pinnipeds no trends were reported.

5 Discussion

5.1 Shifts in timing

While many studies highlight the potential for trophic mismatches for Arctic migrants due to their inadequate

advancement of timing of arrival on their summering grounds in a warming climate [15,16,204], our review shows that there are many examples of advancement of migration timing of especially terrestrial Arctic-breeding birds, as well as for polar bears and some populations of ungulates. Advancements are observed both over long time spans (several decades) and in association with

changing environmental conditions, such as increasing temperatures and earlier snowmelt and ice break-up. This suggests that animals adjust their migration timing to locally changing conditions, either as they aim to match reproduction timing with local food abundance, or simply because warmer conditions allow [52,53], or even force, earlier migrations [78]. In comparison to most bird species, polar bears show especially rapid trends in migration timing, matching arrival and departure from pack ice with timing of ice freeze-up and break-up [78]. However, not all species show such flexible changes in timing, as shown by observations of multiple species at a single study site, showing advancements in reproduction timing in some species but not for others [139]. Differential responses in migration timing may also occur within species, which is notable in the differential migration timing for different reindeer populations. Whereas we had expected to find stronger shifts in migration timing for short-distance migrants (ungulates, pinnipeds, polar bear and some cetaceans) compared to long-distance migrants (birds and most cetaceans), we find large variation in both short- and long-distance migrants. Whether or not species and populations advance migration timing therefore likely depends on other factors as well, for example (1) variation in the environmental change that species experience, (2) strategies which animals use for reproduction, as well as (3) potential physiological constraints for making changes in the timing of migration. All these factors may differ between species. First, Arctic regions differ in the rate of climate warming and local response in for example advancement of resource abundance [205], date of snowmelt [135] or sea ice dynamics [159], which can drive differentiation in responses in migration timing. Second, flexibility in migration timing may depend on reproduction strategies, depending on whether animals reproduce in the Arctic or southern wintering grounds [159,160], or whether animals rely more on internal energy reserves or on local resources for successful reproduction [206–208]. Third, Arctic migrants may also be constrained to make advancements in timing by, for example, the time needed for fuel deposition [19,209], little potential to increase travel speed [17], a lack of relevant cues to time their migration [30], or physical barriers during migration, such as earlier ice break-up in rivers [152,210] or available light [119].

Our review suggests that few species of cetaceans and pinnipeds display shifts in migration timing. Admittedly, very few data appear to be available to test for shifts in timing [74,163], and it is therefore a possibility that the low number of observed shifts is caused by the difficulty in observing migration timing in these animals.

Moreover, a publication bias might exist where studies finding no shifts are less often published. In theory, shifts in timing for marine mammals could be constrained by their relatively low travel speed [18], but given the short migration distances of Arctic pinnipeds, this should not form a major constraint for many species. While climate warming changes the trophic interactions between marine mammals and their prey resources, changes in abundance and distribution of resources may have a larger effect on populations than changes in timing. Therefore, as a primary response to a warming climate, marine mammals may be more likely to display shifts in distribution. The same may hold for marine Arctic-breeding birds, for which we find less evidence for shifts in migration timing as compared to terrestrial birds.

5.2 Shifts in distribution

Shifts in distribution over the past decades appear to occur more often in marine mammals, which is in confirmation of our hypothesis. For cetaceans, pinnipeds and polar bears, relatively many species display northward distribution shifts, and it is likely that such shifts are a response to changes in sea ice cover [74] and associated shifts in suitable areas for feeding and reproduction. Most Arctic cetaceans and pinnipeds depend on high food abundance close to the edge of the pack ice, and as a result are expected to shift their ranges with retreating ice cover [186]. Moreover, pinnipeds also rely on sea ice as haul-out platforms for reproduction and moult, and their life-histories are strongly tied to sea ice [195]. The close association with pack ice is also evident for polar bears, for which a large extent of available data shows a combination of northward shifts in winter, matching changes in pack ice, and shifts to terrestrial habitats during summer. With longer stays in terrestrial habitats, an increasing number of bears is preying on eggs of waterfowl and seabirds [203,211], even though this prey is unlikely to compensate for the increasing periods of fasting under declining sea ice [212].

Our review suggests distribution shifts to be less evident for marine and terrestrial bird species. Although this could be explained by the rarity of long-term monitoring programmes with extensive cover, there are also ecological explanations. Marine birds, given observed distribution shifts of their prey [117], would be expected to show shifts in distribution, similar to marine mammals. Instead, observed shifts in diet show that some species of marine birds may cope with shifts in prey species distribution by preying on different resources [213–215]. While

such diet shifts may be a possibility for generalist species, like certain cetacean and pinniped species [216], species with a more specialized diet (e.g. planktivorous marine birds) may not be able to switch prey, and face potentially severe fitness impacts following shifts in prey species distribution, should they not be able to respond adequately by shifting their own distribution [217–219]. In addition, distribution shifts in marine birds are also potentially constrained by available habitat for their breeding colonies at higher latitudes.

For terrestrial bird species, our review suggests relatively few distribution shifts, which is possibly explained by adequate responses in migration timing, as well as no clear evidence for shifts in distribution ranges of prey resources. In addition, several terrestrial bird species have been shown to be rather flexible in choice of habitat within their current range [220] and their choice for prey species [221], which could also reduce the need for distribution shifts. For ungulates, several studies show shifts in calving grounds, presumably to locations with higher food abundance and more suitable habitats. Possibly, terrestrial ungulates possess such adaptive responses to changing conditions, as they continuously need to shift ranges in response to overgrazing events [210].

Remarkably, in the cases where shifts in distributions are observed, these often show sub-Arctic species extending their range into the Arctic, such as common seals, southern cetacean species, and shorebird species of southern tundra regions [74,177,198]. At the same time, shifts in distribution for species within the Arctic are less often observed.

5.3 Implications of inadequate shifts in timing and distribution

Many populations of Arctic migratory endothermic vertebrates appear able to shift their timing of migration and their distributions, yet not all species are making such shifts, nor do we know whether such shifts are in fact adequate responses to changes in distribution and abundance of food. As a result from inadequate responses in either the timing of migration and reproduction, or inadequate shifts in distribution, phenological mismatches between the period of offspring growth and timing of peak food abundance may arise. Such mismatches have been shown for several species of Arctic terrestrial birds [16,204], marine birds [149] and terrestrial ungulates [15], resulting in reductions in reproductive success. In temperate-breeding migratory songbirds, slow adjustments in migration timing have even been linked to population declines [222]

but see [223]. At the same time, not all species which show little change in timing of breeding and reproduction, experience mismatches with reductions in reproductive success (e.g. [11]). While generally, timing of food availability may advance in a warming Arctic, and more rapidly when compared with temperate regions [4,224], the rate of warming and the responses of prey species can strongly differ between regions [205]. Such regional differences could be an important explanation for the absence of shifts in timing and distribution of migratory species, rather than it reflecting suboptimal behaviour. Fitness consequences for Arctic migratory species may also arise from increased competition with sub-Arctic species, extending their ranges into the Arctic. However, northward shifts in distribution by some species originating from outside the Arctic circle may be constrained by the unique light environment at high latitudes [118,119], complicating forecasts of future ranges of birds and mammals in the Arctic. As such, it is difficult to predict whether or not migratory populations will suffer from reproductive consequences in a warming climate, based on whether populations are showing shifts in their migratory behaviour and distributions.

5.4 Future outlook

This review suggests the potential for many Arctic migratory animals to make shifts in the timing of migration and in their distribution in the Arctic, potentially allowing them to adequately respond to changed resource distribution in a warming Arctic. Yet, our review also highlights potential constraints for animals to make such shifts, which could eventually result in inadequate or no shifts, with possible negative effects on fitness. The potential for animal populations to make shifts in distribution and timing likely relies on the potential for making shifts in migration schedules and strategies, either by individual flexibility [127], or by changes in subsequent generations [225]. In the latter case, the ability of populations to shift in response to a warming climate is linked to its reproductive success under current conditions.

Our review also suggests a severe lack of data, limiting our ability to identify shifts in timing and distribution. Data are especially lacking for migration timing in cetaceans and pinnipeds, but also in other taxonomic groups potential shifts in timing and distribution have not been studied. It is striking that shifts in spring migration timing have received much more attention than shifts in autumn migration timing [226], and also there are relatively few studies on shifts in distribution. Our review also suggests strong regional differences in available data, with most

data available for Arctic vertebrates in Alaska, Northern Canada, Greenland, Svalbard and Scandinavia, and fewer data for the European and Russian Arctic. The need for long-term data collection over the entire Arctic region is well recognised [227], as advised in recent reports on population monitoring for marine as well as terrestrial monitoring [228,229]. Given the rate of climatic changes in the Arctic, it is likely that shifts in timing of migration and distribution of migratory animals will become more prominent. Better monitoring of migratory animals will allow an increased understanding of the responses of these animals to global warming, which may help to identify the possible limitations that restrict adaptations of animals to the globally changing conditions, and the potential impacts on their populations. Such data will be essential for the conservation of migratory species in a warming climate, as well as for the persistence of Indigenous and local human communities in the Arctic, which are often culturally and nutritionally dependent on the presence of migratory vertebrates [230].

Acknowledgements

This review is compiled from essays written by participants of the Movement and Migration Ecology course, which was organised at the Wageningen University in 2020. We would like to thank Jacintha van Dijk, Patrick Jansen, Janne Ouwehand and Judy Shamoun-Baranes who also provided guest lectures for this course, as well as all the students that participated in the course.

References

- [1] Fox TAD. Ecology of Arctic Birds. In: Thomas DN, editor. Arctic Ecology. New York, USA: Wiley-Blackwell; 2021. p. 385–408.
- [2] Serreze MC, Barrett AP, Stroeve JC, Kindig DN, Holland MM. The emergence of surface-based Arctic amplification. *Cryosph*. 2009;3:11–9.
- [3] AMAP, 2021. Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers. Arctic Monitoring and Assessment Programme (AMAP), Tromsø, Norway. 16 pp
- [4] Post E, Steinman BA, Mann ME. Acceleration of phenological advance and warming with latitude over the past century. *Sci Rep*. 2018;8:1–8.
- [5] Box JE, Res E, Box JE, Colgan WT, Christensen TR, Schmidt NM, et al. Key indicators of Arctic climate change: 1971–2017. 2019;14:045010
- [6] Myers-Smith IH, Kerby JT, Phoenix GK, Bjerke JW, Epstein HE, Assmann JJ, et al. Complexity revealed in the greening of the Arctic. *Nat Clim Change*. 2020;10:106–17.
- [7] IPCC. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, et al., editors. 2019.
- [8] Doiron M, Gauthier G, Lévesque E. Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *J Ecol*. 2014;102:508–17.
- [9] Lameris TK, Jochems F, van der Graaf AJ, Andersson M, Limpens J, Nolet BA. Forage plants of an Arctic-nesting herbivore show larger warming response in breeding than wintering grounds, potentially disrupting migration phenology. *Ecol Evol*. 2017;7:2652–60.
- [10] Høye TT, Loboda S, Koltz AM, Gillespie MAK, Bowden JJ, Schmidt NM. Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. *Proc Natl Acad Sci U S A*. 2021;118:1-8
- [11] Reneerkens J, Schmidt NM, Gilg O, Hansen J, Hansen LH, Moreau J, et al. Effects of food abundance and early clutch predation on reproductive timing in a high Arctic shorebird exposed to advancements in arthropod abundance. *Ecol Evol*. 2016;6:7375–7386.
- [12] Tulp I, Schekkerman H. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic*. 2008;61:48–60.
- [13] Asch RG, Stock CA, Sarmiento JL. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. *Glob Change Biol*. 2019;25:2544–59.
- [14] Henson SA, Cole HS, Hopkins J, Martin AP, Yool A. Detection of climate change-driven trends in phytoplankton phenology. *Glob Change Biol*. 2018;24:e101–11.
- [15] Post E, Forchhammer MC. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philos Trans R Soc B*. 2008;363:2369–75.
- [16] Lameris TK, van der Jeugd HP, Eichhorn G, Dokter AM, Bouten W, Boom MP, et al. Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Curr Biol*. 2018;28:2467–73.
- [17] Schmaljohann H, Both C. The limits of modifying migration speed to adjust to climate change. *Nat Clim Change*. 2017;7:573–576.
- [18] Alerstam T, Bäckman J. Ecology of animal migration. *Curr Biol*. 2018;28:R968–72.
- [19] Lindström Å, Alerstam T, Hedenström A. Faster fuelling is the key to faster migration. *Nat Clim Change*. 2019;9:288–9.
- [20] Xu F, Si Y. The frost wave hypothesis: How the environment drives autumn departure of migratory waterfowl. *Ecol Indic*. 2019;101:1018–25.
- [21] Wang M, Overland JE. A sea ice free summer Arctic within 30 years? *Geophys Res Lett*. 2009;36:2–6.
- [22] Rakhimberdiev E, Duijns S, Camphuysen CJ, Castricum V, Dekinga A, Dekker R, et al. Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nat Commun*. 2018;9:4263.
- [23] Gurarie E, Hebblewhite M, Joly K, Kelly AP, Adamczewski J, Davidson SC, et al. Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations. *Ecosphere*. 2019;10:1-32

- [24] Brommer JE, Lehikoinen A, Valkama J. The breeding ranges of central European and Arctic bird species move poleward. *PLoS One*. 2012;7:1–7.
- [25] Severson JP, Johnson HE, Arthur SM, Leacock WB, Saitor MJ. Spring phenology drives range shifts in a migratory Arctic ungulate with key implications for the future. *Glob Change Biol*. 2021;27:4546–4563.
- [26] Bauer S, Hoyer BJ. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*. 2014;344(6179).
- [27] Choi RT, Beard KH, Leffler AJ, Kelsey KC, Schmutz JA, Welker JM. Phenological mismatch between season advancement and migration timing alters Arctic plant traits. *J Ecol*. 2019;107:2503–18.
- [28] Wenzel GW. Canadian Inuit subsistence and ecological instability - If the climate changes, must the Inuit? *Polar Res*. 2009;28:89–99.
- [29] Martinez-Levasseur LM, Furgal CM, Hammill MO, Henri DA, Burness G. New migration and distribution patterns of Atlantic walrus (*Odobenus rosmarus rosmarus*) around Nunavik (Québec, Canada) identified using Inuit Knowledge. *Polar Biol*. 2021;44:1833–45.
- [30] Kölzsch A, Bauer S, de Boer R, Griffin L, Cabot D, Exo K-M, et al. Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. *J Anim Ecol*. 2015:272–83.
- [31] Lameris TK, Scholten I, Bauer S, Cobben MMP, Ens BJ, Nolet BA. Potential for an Arctic-breeding migratory bird to adjust spring migration phenology to Arctic amplification. *Glob Change Biol*. 2017;23:4058–4067.
- [32] Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, et al. Species better track climate warming in the oceans than on land. *Nat Ecol Evol*. 2020;4:1044–59.
- [33] Oziel L, Baudena A, Ardyna M, Massicotte P, Randelhoff A, Sallée JB, et al. Faster Atlantic currents drive poleward expansion of temperate phytoplankton in the Arctic Ocean. *Nat Commun*. 2020;11:1–8.
- [34] Sunday JM, Bates AE, Dulvy NK. Thermal tolerance and the global redistribution of animals. *Nat Clim Change*. 2012;2:686–90.
- [35] CAFF 2013. Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Akureyri
- [36] Fort J, Moe B, Strøm H, Grémillet D, Welcker J, Schultner J, et al. Multicolony tracking reveals potential threats to little auks wintering in the North Atlantic from marine pollution and shrinking sea ice cover. *Divers Distrib*. 2013;19:1322–32.
- [37] Linnebjerg JF, Frederiksen M, Kolbeinsson Y, Snaethórsson AÖ, Thórisson B, Thórarinnsson TL. Non-breeding areas of three sympatric auk species breeding in three Icelandic colonies. *Polar Biol*. 2018;41:1951–61.
- [38] Curk T, Pokrovsky I, Lecomte N, Aarvak T, Burnham K, Dietz A, et al. Arctic avian predators synchronise their spring migration with the northern progression of snowmelt. *Sci Rep*. 2020;10:1–11.
- [39] Fox, A.D. & Leafloor, J.O. (eds.) 2018. A global audit of the status and trends of Arctic and Northern Hemisphere goose populations. Conservation of Arctic Flora and Fauna International Secretariat: Akureyri, Iceland. ISBN 978-9935-431-66-0
- [40] Macdonald CA, Mckinnon EA, Gilchrist HG, Love OP. Cold tolerance, and not earlier arrival on breeding grounds, explains why males winter further north in an Arctic-breeding songbird. *J Avian Biol*. 2016;47:7–15.
- [41] Bemmelen R Van, Moe B, Hanssen SA, Schmidt NM, Hansen J, Lang J, et al. Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua. *Mar Ecol Prog Ser*. 2017;578:197–211.
- [42] Meltofte H. Are African wintering waders really forced south by competition from northerly wintering conspecifics? Benefits and constraints of northern versus southern wintering and breeding in waders. *Ardea*. 1996;84:31–44.
- [43] Reneerkens J, Versluijs TSL, Piersma T, Alves JA, Boorman M, Corse C, et al. Low fitness at low latitudes: wintering in the tropics increases migratory delays and mortality rates in an Arctic-breeding shorebird. *J Anim Ecol*. 2019;89:691–703.
- [44] Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *PNAS*. 2010;107:2078–81.
- [45] Fijn RC, Hiemstra D, Phillips RA, Van Der Winden J. Arctic Terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, East Antarctica. *Ardea*. 2013;101:3–12.
- [46] Fort J, Porter WP, Grémillet D. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *J Exp Biol*. 2009;212:2483–90.
- [47] Hunt Jr. GL. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Res*. 1990;8:43–54.
- [48] Alerstam T. Optimal bird migration revisited. *J Ornithol*. 2011;152:S5–23.
- [49] van der Graaf AJ, Stahl J, Klimkowska A, Bakker JP, Drent RH. Surfing on a green wave-how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea*. 2006;94:567–77.
- [50] Shariatnajaabadi M, Wang T, Skidmore AK, Toxopeus AG, Kölzsch A, Nolet BA, et al. Migratory herbivorous waterfowl track satellite-derived green wave index. *PLoS One*. 2014;9:e108331.
- [51] Wang X, Cao L, Fox AD, Fuller R, Mitchell C, Zhao Y, et al. Stochastic simulations reveal few green wave surfing populations among spring migrating herbivorous waterfowl. *Nat Commun*. 2019;10:2187.
- [52] Nuijten RJM, Kölzsch A, van Gils JA, Hoyer BJ, Oosterbeek K, de Vries PP, et al. The exception to the rule: retreating ice front makes Bewick's swans *Cygnus columbianus bewickii* migrate slower in spring than in autumn. *J Avian Biol*. 2014;45:113–22.
- [53] Li H, Fang L, Wang X, Yi K, Cao L, Fox AD. Does snowmelt constrain spring migration progression in sympatric wintering Arctic-nesting geese? Results from a Far East Asia telemetry study. *Ibis*. 2020;162:548–55.
- [54] Tucker AM, McGowan CP, Catalano MJ, DeRose-Wilson A, Robinson RA, Zimmerman J. Foraging ecology mediates response to ecological mismatch during migratory stopover. *Ecosphere*. 2019;10:1–17.
- [55] Schmidt NM, Van Beest FM, Mosbacher JB, Stelvig M, Hansen LH, Nabe-Nielsen J, et al. Ungulate movement in an extreme seasonal environment: Year-round movement patterns of high-arctic muskoxen. *Wildlife Biol*. 2016;22:253–67.

- [56] Ball JP, Nordengren C, Wallin K. Partial migration by large ungulates: Characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biol.* 2001;7:39–47.
- [57] Allen AM, Mansson J, Sand H, Malmsten J, Ericsson G, Singh NJ. Scaling up movements: From individual space use to population patterns. *Ecosphere.* 2016;7:1–16.
- [58] Joly K, Gurarie E, Sorum MS, Kaczynsky P, Cameron MD, Jakes AF, et al. Longest terrestrial migrations and movements around the world. *Sci Rep.* 2019;9:1–10.
- [59] Mahoney SP, Schaefer JA. Long-term changes in demography and migration of Newfoundland caribou. *J Mammal.* 2002;83:957–63.
- [60] Tyler ANJC, Øritsland NA. Why don't svalbard reindeer migrate? *Holarct Ecol.* 1989;12:369–76.
- [61] Merkle JA, Monteith KL, Aikens EO, Hayes MM, Hersey KR, Middleton AD, et al. Large herbivores surf waves of green-up during spring. *Proc R Soc B Biol Sci.* 2016;283:1–8.
- [62] Laforge MP, Bonar M, Vander Wal E. Tracking snowmelt to jump the green wave: phenological drivers of migration in a northern ungulate. *Ecology.* 2021;102:1–11.
- [63] Fokkema W, Jeugd HP Van Der, Lameris TK, Dokter AM. Ontogenetic niche shifts as a driver of seasonal migration. *Oecologia.* 2020;193:285–97.
- [64] Connor RC, Corkeron PJ. Predation past and present: Killer whales and baleen whale migration. *Mar Mammal Sci.* 2001;17:436–9.
- [65] Corkeron PJ, Connor RC. Why do baleen whales migrate? *Mar Mammal Sci.* 1999;15:1228–45.
- [66] Lockyer C, Brown S. The migration of whales. In: Aidley DJ, editor. *Animal Migration.* 1981. p. 105–37.
- [67] Pitman RL, Durban JW, Joyce T, Fearnbach H, Panigada S, Lauriano G. Skin in the game: Epidermal molt as a driver of long-distance migration in whales. *Mar Mammal Sci.* 2020;36:565–94.
- [68] Smith TG, Aubin DJ St., Hammill MO. Rubbing behaviour of belugas, *Delphinapterus leucas*, in a high Arctic estuary. *Can J Zool.* 1992;70:2405–2409.
- [69] Chernova OF, Shpak O V., Kiladze AB, Azarova VS, Rozhnov V V. Summer molting of bowhead whales *Balaena mysticetus* Linnaeus, 1758, of the Okhotsk Sea population. *Dokl Biol Sci.* 2016;471:261–5.
- [70] Fortune SME, Koski WR, Higdon JW, Trites AW, Baumgartner MF, Ferguson SH. Evidence of molting and the function of “rock-nosing” behavior in bowhead whales in the eastern Canadian Arctic. *PLoS One.* 2017;12:1–15.
- [71] Kovacs KM, Lydersen C. Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. *Science Progress.* 2008;91:117–150.
- [72] Crawford JA, Quakenbush LT, Citta JJ. A comparison of ringed and bearded seal diet, condition and productivity between historical (1975–1984) and recent (2003–2012) periods in the Alaskan Bering and Chukchi seas. *Prog Oceanogr.* 2015;136:133–50.
- [73] Svetochev VN, Kavtsevich NN, Svetocheva ON. Satellite tagging and seasonal distribution of harp seal (juveniles) of the White sea-Barents sea stock. *Czech Polar Reports.* 2016;6:31–42.
- [74] Kovacs KM, Lydersen C, Overland JE, Moore SE. Impacts of changing sea-ice conditions on Arctic marine mammals. *Mar Biodivers.* 2011;41:181–94.
- [75] Pilfold NW, McCall A, Derocher AE, Lunn NJ, Richardson E. Migratory response of polar bears to sea ice loss: to swim or not to swim. *Ecography.* 2017;40:189–99.
- [76] Parks EK, Derocher AE, Lunn NJ. Seasonal and annual movement patterns of polar bears on the sea ice of Hudson Bay. *Can J Zool.* 2006;84:1281–94.
- [77] Stirling I, Øritsland NA. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Can J Fish Aquat Sci.* 1995;52:2594–612.
- [78] Cherry SG, Derocher AE, Thiemann GW, Lunn NJ. Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *J Anim Ecol.* 2013;82:912–21.
- [79] Molnár PK, Bitz CM, Holland MM, Kay JE, Penk SR, Amstrup SC. Fasting season length sets temporal limits for global polar bear persistence. *Nat Clim Change.* 2020;10:732–8.
- [80] Ramsay MA, Stirling I. Fidelity of female polar bears to winter-den sites. *J Mammal.* 1990;71:233–6.
- [81] Assmann JJ, Myers-Smith IH, Phillimore AB, Bjorkman AD, Ennos RE, Prevéy JS, et al. Local snow melt and temperature - but not regional sea ice - explain variation in spring phenology in coastal Arctic tundra. *Glob Change Biol.* 2019;25:2258–74.
- [82] John C, Miller D, Post E. Regional variation in green-up timing along a caribou migratory corridor: Spatial associations with snowmelt and temperature. *Arctic, Antarct Alp Res.* 2020;52:416–23.
- [83] Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, et al. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob Change Biol.* 2010;16:3304–13.
- [84] Kelsey K, Pedersen S, Leffler A, Sexton J, Feng M, Welker J. Winter snow and spring temperature have differential effects on vegetation phenology and productivity across Arctic plant communities. *Glob Change Biol.* 2021;27:1572–1586.
- [85] Post E, Pedersen C, Wilmers CC, Forchhammer MC. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proc R Soc B Biol Sci.* 2008;275:2005–13.
- [86] Wirta HK, Vesterinen EJ, Hambäck PA, Weingartner E, Rasmussen C, Reneerkens J, et al. Exposing the structure of an Arctic food web. *Ecol Evol.* 2015;5:3842–56.
- [87] Koltz AM, Schmidt NM, Høye TT. Differential arthropod responses to warming are altering the structure of arctic communities. *R Soc Open Sci.* 2018;5:171503.
- [88] Wiklund CG, Angerbjörn A, Isakson E, Kjellén N, Tannerfeldt M. Lemming predators on the Siberian tundra. *Ambio.* 1999;28:281–6.
- [89] Ehrich D, Schmidt NM, Gauthier G, Alisauskas R, Angerbjörn A, Clark K, et al. Documenting lemming population change in the Arctic: Can we detect trends? *Ambio.* 2019;49:786–800.
- [90] Nolet BA, Bauer S, Feige N, Kokorev YI, Popov IY, Ebbinge BS. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. *J Anim Ecol.* 2013;82:804–13.
- [91] Vincent LA, Zhang X, Brown RD, Feng Y, Mekis E, Milewska EJ, et al. Observed trends in Canada's climate and influence of low-frequency variability modes. *J Clim.* 2015;28:4545–60.

- [92] Schmidt NM, Reneerkens J, Christensen JH, Olesen M, Roslin T. An ecosystem-wide reproductive failure with more snow in the Arctic. *PLoS Biol.* 2019;17: e3000392.
- [93] Post E. Implications of earlier sea ice melt for phenological cascades in arctic marine food webs. *Food Webs.* 2017;13:60–6
- [94] Tedesco L, Vichi M, Scoccimarro E. Sea-ice algal phenology in a warmer Arctic. *Sci Adv.* 2019;5:1-12.
- [95] Ji R, Jin M, Varpe Ø. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. *Glob Change Biol.* 2013;19:734–41.
- [96] Kahru M, Brotas V, Manzano-Sarabia M, Mitchell BG. Are phytoplankton blooms occurring earlier in the Arctic? *Glob Change Biol.* 2011;17:1733–9.
- [97] Søreide JE, Leu EVA, Berge Jør, Graeve M, Falk-Petersen S. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob Change Biol.* 2010;16:3154–63.
- [98] Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Prog Oceanogr.* 2011;90:18–32.
- [99] Janout MA, Hölemann J, Waite AM, Krumpfen T, von Appen WJ, Martynov F. Sea-ice retreat controls timing of summer plankton blooms in the Eastern Arctic Ocean. *Geophys Res Lett.* 2016;43:12,493-12,501.
- [100] Dalpadado P, Arrigo KR, van Dijken GL, Skjoldal HR, Bagøien E, Dolgov A V., et al. Climate effects on temporal and spatial dynamics of phytoplankton and zooplankton in the Barents Sea. *Prog Oceanogr.* 2020;185:102320.
- [101] Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM. Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biol.* 2007;30:167–81.
- [102] Wold A, Jæger I, Hop H, Gabrielsen GW, Falk-Petersen S. Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. *Polar Biol.* 2011;34:1147–55.
- [103] Heggberget TM, Gaare E, Ball JP. Reindeer (*Rangifer tarandus*) and climate change: Importance of winter forage. *Rangifer.* 2002;22:13.
- [104] Tyler NJC. Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rangifer tarandus* L.). *Ecol Monogr.* 2010;80:197–219.
- [105] Koltz AM, Culler LE. Biting insects in a rapidly changing Arctic. *Curr Opin Insect Sci.* 2021;47:75–81.
- [106] Høye TT, Kresse JC, Koltz AM, Bowden JJ. Earlier springs enable high-Arctic wolf spiders to produce a second clutch. *Proc R Soc B Biol Sci.* 2020;287:20200982.
- [107] Saalfeld ST, Hill BL, Hunter CM, Frost CJ, Lanctot RB. Warming Arctic summers unlikely to increase productivity of shorebirds through re-nesting. *Sci Rep.* 2021;11:15277.
- [108] Ardyna M, Babin M, Gosselin M, Devred E, Rainville L, Tremblay J-E. Fall phytoplankton blooms. *Geophys Res Lett.* 2014;41:6207–12.
- [109] Weydmann A, Walczowski W, Carstensen J, Kwaśniewski S. Warming of subarctic waters accelerates development of a key marine zooplankton *Calanus finmarchicus*. *Glob Change Biol.* 2018;24:172–83.
- [110] Buckley LB, Kingsolver JG. Functional and phylogenetic approaches to forecasting species' responses to climate change. *Annu Rev Ecol Evol Syst.* 2012;43:205–26.
- [111] Lesica P, McCune B. Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *J Veg Sci.* 2004;15:679–90.
- [112] Pearson RG, Phillips SJ, Lorant MM, Beck PSA, Damoulas T, Knight SJ, et al. Shifts in Arctic vegetation and associated feedbacks under climate change. *Nat Clim Change.* 2013;3:673–7.
- [113] Khaliq I, Hof C, Prinzing R, Böhning-Gaese K, Pfenninger M. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc R Soc B Biol Sci.* 2014;281:20141097.
- [114] Sunday JM, Bates AE, Dulvy NK. Global analysis of thermal tolerance and latitude in ectotherms. *Proc R Soc B Biol Sci.* 2011;278:1823–30.
- [115] Sheldon KS, Yang S, Tewksbury JJ. Climate change and community disassembly: Impacts of warming on tropical and temperate montane community structure. *Ecol Lett.* 2011;14:1191–200.
- [116] Bjorkman AD, García Criado M, Myers-Smith IH, Ravolainen V, Jónsdóttir IS, Westergaard KB, et al. Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. *Ambio.* 2020;49:678–92.
- [117] Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov A V. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat Clim Change.* 2015;5:673–7.
- [118] Ljungström G, Langbehn TJ, Jørgensen C. Light and energetics at seasonal extremes limit poleward range shifts. *Nat Clim Change.* 2021;11:530–6.
- [119] Huffeldt NP. Photoc barriers to poleward range-shifts. *Trends Ecol Evol.* 2020;35:652–5.
- [120] van Weelden C, Towers JR, Bosker T. Impacts of climate change on cetacean distribution, habitat and migration. *Clim Chang Ecol.* 2021;1:100009.
- [121] Bengtsson O, Hamilton CD, Lydersen C, Andersen M, Kovacs KM. Distribution and habitat characteristics of pinnipeds and polar bears in the svalbard archipelago, 2005-2018. *Polar Res.* 2021;40:2005–18.
- [122] Tombre IM, Høgda KA, Madsen J, Griffin LR, Kuijken E, Shimmings P, et al. The onset of spring and timing of migration in two arctic nesting goose populations: the pink-footed goose *Anser bachelianus* and the barnacle goose *Branta leucopsis*. *J Avian Biol.* 2008;39:691–703.
- [123] Eichhorn G, Drent RH, Stahl J, Leito A, Alerstam T. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *J Anim Ecol.* 2009;78:63–72.
- [124] Clausen KK, Clausen P. Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia.* 2013;173:1101–12.
- [125] Fox AD, Weegman MD, Bearhop S, Hilton GM, Griffin L, Stroud D a, et al. Climate change and contrasting plasticity in timing of a two-step migration episode of an Arctic-nesting avian herbivore. *Curr Zool.* 2014;60:233–42.
- [126] Nuijten RJM, Wood KA, Haitjema T, Rees EC, Nolet BA. Concurrent shifts in wintering distribution and phenology in

- migratory swans : Individual and generational effects. *Glob Change Biol.* 2020;26: 4263-4275.
- [127] Conklin JR, Lisovski S, Battley PF. Advancement in long-distance bird migration through individual plasticity in departure. *Nat Commun.* 2021;12:1–9.
- [128] Bauer S, Van Dintner M, Høgda K-A, Klaassen M, Madsen J. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *J Anim Ecol.* 2008;77:654–60.
- [129] Ely CR, Mccaffery BJ, Jr REG. Shorebirds adjust spring arrival schedules with variable environmental conditions: Four decades of assessment on the Yukon–Kuskokwim Delta, Alaska. In: Trends and traditions: Avifaunal change in western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.). *Western Field Ornithologists*, Camarillo. 2018. p. 296–311.
- [130] Boelman NT, Krause JS, Sweet SK, Chmura HE, Perez JH, Gough L, et al. Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds. *Oecologia.* 2017;185:69–80.
- [131] Oliver RY, Ellis DPW, Chmura HE, Krause JS, Pérez JH, Sweet SK, et al. Eavesdropping on the Arctic: Automated bioacoustics reveal dynamics in songbird breeding phenology. *Sci Adv.* 2018;4:1–10.
- [132] Boyd H, Petersen Æ. Spring arrivals of migrant waders in Iceland in the 20th century. *Spring arrivals of migrant waders in Iceland in the 20th century.* *Ringing Migr.* 2006;23:107–15.
- [133] Ward DH, Helmericks J, Hupp JW, Mcmanus L, Budde M, Douglas DC, et al. Multi-decadal trends in spring arrival of avian migrants to the central Arctic coast of Alaska: Effects of environmental and ecological factors. *J Avian Biol.* 2016;47:197–207.
- [134] Gunnarsson TG, Tómasson G. Flexibility in spring arrival of migratory birds at northern latitudes under rapid temperature changes. *Bird Study.* 2011;58:1–12.
- [135] Lameris TK, Jong ME De, Boom MP, Jeugd HP Van Der, Litvin KE. Climate warming may affect the optimal timing of reproduction for migratory geese differently in the low and high Arctic. *Oecologia.* 2019;191:1003–14.
- [136] Liebezeit JR, Gurney KEB, Budde M, Zack S, Ward D. Phenological advancement in arctic bird species: Relative importance of snow melt and ecological factors. *Polar Biol.* 2014;37:1309–20.
- [137] Saalfeld ST, Lanctot RB. Multispecies comparisons of adaptability to climate change: A role for life-history characteristics? *Ecol Evol.* 2017;7:10492–10502.
- [138] Smith PA, Gilchrist HG, Forbes MR, Martin JL, Allard K. Inter-annual variation in the breeding chronology of arctic shorebirds: Effects of weather, snow melt and predators. *J Avian Biol.* 2010;41:292–304.
- [139] Grabowski MM, Doyle FI, Reid DG, Mossop D, Talarico D. Do Arctic-nesting birds respond to earlier snowmelt? A multi-species study in north Yukon, Canada. *Polar Biol.* 2013;36:1097–105.
- [140] Kwon E, English WB, Weiser EL, Franks SE, Hodkinson DJ, Lank DB, et al. Delayed egg-laying and shortened incubation duration of Arctic-breeding shorebirds coincide with climate cooling. *Ecol Evol.* 2018;8:1339–51.
- [141] Ross M V., Alisauskas RT, Douglas DC, Kellett DK. Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic. *Ecology.* 2017;98:1869–83.
- [142] Lehtikoinen A, Jaatinen K. Delayed autumn migration in northern European waterfowl. *J Ornithol.* 2012;153:563–70.
- [143] Barshep Y, Meissner W, Underhill LG. Timing of migration of the Curlew Sandpiper (*Calidris ferruginea*) through Poland in relation to Arctic breeding conditions. *Ornis Fenn.* 2012;89:120–9.
- [144] Merkel B, Descamps S, Yoccoz NG, Danielsen J, Daunt F, Erikstad KE, et al. Earlier colony arrival but no trend in hatching timing in two congeneric seabirds (*Uria* spp.) across the North Atlantic. *Biol Lett.* 2019;15:1–6.
- [145] Keogan K, Daunt F, Wanless S, Phillips RA, Walling CA, Agnew P, et al. Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nat Clim Change.* 2018;8:313–7.
- [146] Descamps S, Ramírez F, Benjaminsen S, Anker-Nilssen T, Barrett RT, Burr Z, et al. Diverging phenological responses of Arctic seabirds to an earlier spring. *Glob Change Biol.* 2019;25:4081–91.
- [147] Love OP, Gilchrist HG, Descamps S, Semeniuk CAD, Bêty J. Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia.* 2010;164:277–86.
- [148] Gaston AJ, Gilchrist HG, Hipfner JM. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich’s guillemot (*Uria lomvia* L.). *J Anim Ecol.* 2005;74:832–41.
- [149] Gaston AJ, Gilchrist HG, Mallory ML, Smith PA. Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: a case of progressive mismatching. *Condor.* 2009;111:111–9.
- [150] Moe B, Stempniewicz L, Jakubas D, Angelier F, Chastel O, Dinessen F, et al. Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Mar Ecol Prog Ser.* 2009;393:235–46.
- [151] Le Corre M, Dussault C, Côté SD. Weather conditions and variation in timing of spring and fall migrations of migratory caribou. *J Mammal.* 2017;98:260–71.
- [152] Leblond M, St-Laurent MH, Côté SD. Caribou, water, and ice - fine-scale movements of a migratory arctic ungulate in the context of climate change. *Mov Ecol.* 2015;4:1–12.
- [153] Davidson SC, Bohrer G, Gurarie E, LaPoint S, Mahoney PJ, Boelman NT, et al. Ecological insights from three decades of animal movement tracking across a changing Arctic. *Science.* 2020;370:712–5.
- [154] Paoli A, Weladji RB, Holand Ø, Kumpula J. Winter and spring climatic conditions influence timing and synchrony of calving in reindeer. *PLoS One.* 2018;13:1–21.
- [155] Paoli A, Weladji RB, Holand Ø, Kumpula J. The onset in spring and the end in autumn of the thermal and vegetative growing season affect calving time and reproductive success in reindeer. *Curr Zool.* 2020;66:123–34.
- [156] Danielsen P. Climate trends, weather fluctuations and calving phenology in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). MSc thesis. Trondheim. Norwegian University of Science and Technology; 2016.
- [157] Eikelenboom M, Higgins RC, John C, Kerby J, Forchhammer MC, Post E. Contrasting dynamical responses of sympatric

- caribou and muskoxen to winter weather and earlier spring green-up in the Arctic. *Food Webs*. 2021;27:e00196.
- [158] Kerby JT, Post E. Advancing plant phenology and reduced herbivore production in a terrestrial system associated with sea ice decline. *Nat Commun*. 2013;4:1–6.
- [159] Hauser DDW, Laidre KL, Stafford KM, Stern HL, Suydam RS, Richard PR. Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. *Glob Change Biol*. 2017;23:2206–17.
- [160] Ramp C, Delarue J, Palsbøll PJ, Sears R, Hammond PS. Adapting to a warmer ocean - Seasonal shift of baleen whale movements over three decades. *PLoS One*. 2015;10:1–15.
- [161] Smith TG, Lydersen C. Availability of suitable land-fast ice and predation as factors limiting ringed seal populations, *Phoca hispida*, in Svalbard. *Polar Res*. 1991;10:585–94.
- [162] Smith TG, Hammill MO. Ecology of the ringed seal, *Phoca hispida*, in its fast ice breeding habitat. *Can J Zool*. 1981;59:966–81.
- [163] Laidre KL, Stern H, Kovacs KM, Lowry L, Moore SE, Regehr E V., et al. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv Biol*. 2015;29:724–37.
- [164] Castro de la Guardia L, Derocher AE, Myers PG, Terwisscha van Scheltinga AD, Lunn NJ. Future sea ice conditions in Western Hudson Bay and consequences for polar bears in the 21st century. *Glob Change Biol*. 2013;19:2675–87.
- [165] Guardia LC de la, Myers PG, Derocher AE, Lunn NJ, Terwisscha van Scheltinga AD. Sea ice cycle in western Hudson Bay, Canada, from a polar bear perspective. *Mar Ecol Prog Ser*. 2017;564:225–33.
- [166] Cherry SG, Derocher AE, Lunn NJ. Habitat-mediated timing of migration in polar bears: an individual perspective. *Ecol Evol*. 2016;6:5032–42.
- [167] Derocher AE, Andersen M, Wiig, Aars J, Hansen E, Biuw M. Sea ice and polar bear den ecology at Hopen Island, Svalbard. *Mar Ecol Prog Ser*. 2011;441:273–9.
- [168] Pagano AM, Durner GM, Rode KD, Atwood TC, Atkinson SN, Peacock E, et al. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science*. 2018;359:568–72.
- [169] Maclean IMD, Austin GE, Rehfish MM, Blew J, Crowe O, Delany S, et al. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Glob Change Biol*. 2008;14:2489–500.
- [170] Elmberg J, Hessel R, Fox AD, Dalby L. Interpreting seasonal range shifts in migratory birds: A critical assessment of “short-stopping” and a suggested terminology. *J Ornithol*. 2014;155:571–9.
- [171] Clausen KK, Madsen J, Cottaar F, Kuijken E, Verscheure C. Highly dynamic wintering strategies in migratory geese: Coping with environmental change. *Glob Change Biol*. 2018;24:3214–25.
- [172] Clairiaux M, Cheung WWL, Mathewson P, Porter W, Courbin N, Fort J, et al. Meeting Paris agreement objectives will temper seabird winter distribution shifts in the North Atlantic Ocean. *Glob Change Biol*. 2021;27:1457–69.
- [173] Wauchope HS, Shaw JD, Varpe Ø, Lappo EG, Boertmann D, Lancot RB, et al. Rapid climate-driven loss of breeding habitat for Arctic migratory birds. *Glob Change Biol*. 2017;23:1085–1094.
- [174] Clairiaux M, Fort J, Mathewson P, Porter W, Strøm H, Grémillet D. Climate change could overturn bird migration: Transarctic flights and high-latitude residency in a sea ice free Arctic. *Sci Rep*. 2019;9:1–13.
- [175] Frederiksen M, Anker-Nilssen T, Beaugrand G, Wanless S. Climate, copepods and seabirds in the boreal Northeast Atlantic – current state and future outlook. *Glob Change Biol*. 2013;19:364–72.
- [176] Devictor V, Van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliölä J, et al. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat Clim Change*. 2012;2:121–4.
- [177] Soloviev MY, Syroechkovskiy EE, Dmitriev AE, Golovnyuk V V, Morozov VE, Lappo EG, et al. Implementing AMBI AFEU 2.1 in the Russian Arctic: status and trend report of AMBI priority shorebird species in Western Russian Arctic breeding grounds in connection with climate change and predator-prey dynamics. Akureyri, Iceland; In press.
- [178] Ferguson SH, Elkie PC. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *J Zool*. 2004;262:125–34.
- [179] Schaefer JA, Bergman CM, Luttich SN. Site fidelity of female caribou at multiple spatial scales. *Landsc Ecol*. 2000;15:731–9.
- [180] Ferguson MAD, Messier F. Mass emigration of Arctic tundra caribou from a traditional winter range: population dynamics and physical condition. *J Wildl Manage*. 2000;64:168–78.
- [181] Gunn A, Poole KG, Wierzchowski J. A geostatistical analysis for the patterns of caribou occupancy on the Bathurst calving grounds 1966–2007. 2008. Unpublished report submitted to Indian & Northern Affairs Canada. Yellowknife.
- [182] Tape KD, Gustine DD, Ruess RW, Adams LG, Clark JA. Range expansion of moose in arctic Alaska linked to warming and increased shrub habitat. *PLoS One*. 2016;11:1–12.
- [183] MacLeod CD. Global climate change, range changes and potential implications for the conservation of marine cetaceans: A review and synthesis. *Endanger Species Res*. 2009;7:125–36.
- [184] Brower AA, Clarke JT, Ferguson MC. Increased sightings of subArctic cetaceans in the eastern Chukchi Sea, 2008–2016: population recovery, response to climate change, or increased survey effort? *Polar Biol*. 2018;41:1033–9.
- [185] Storrie L, Lydersen C, Andersen M, Wynn RB, Kovacs KM. Determining the species assemblage and habitat use of cetaceans in the Svalbard Archipelago, based on observations from 2002 to 2014. *Polar Res*. 2018;37:1–22.
- [186] Druckenmiller ML, Citta JJ, Ferguson MC, Clarke JT, George JC, Quakenbush L. Trends in sea-ice cover within bowhead whale habitats in the Pacific Arctic. *Deep Res Part II Top Stud Oceanogr*. 2018;152:95–107.
- [187] Heide-Jørgensen MP, Laidre KL, Borchers D, Marques TA, Stern H, Simon M. The effect of sea-ice loss on beluga whales (*Delphinapterus leucas*) in West Greenland. *Polar Res*. 2010;29:198–208.
- [188] Higdon JW, Ferguson SH. Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. *Ecol Appl*. 2009;19:1365–75.
- [189] Ferguson SH, Loseto LL, Mallory ML. The rise of killer whales as a major Arctic predator. A little less Arctic: top predators

- in the world's largest northern inland sea, Hudson Bay. 2010;117-136.
- [190] Drake N. Wayward whale not a fluke. *Nature*. 2011;473:16.
- [191] Meier WN, Hovelsrud GK, van Oort BEH, Rey JR, Kovacs KM, Michel C, et al. Arctic sea ice in transformation: A review of recent observed changes and impacts on biology and human activity. *Rev Geophys*. 2014;51:185–217.
- [192] Perovich D, Meier W, Tschudi M, Hendricks S, Petty AA, Divine D, et al., 2020: Sea Ice. Arctic Report Card 2020.
- [193] IPCC. Summary for Policymakers. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, et al., editors. *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University press; 2013.
- [194] Rosing-Asvid A. A new harp seal whelping ground near South Greenland. *Mar Mammal Sci*. 2008;24:730–6.
- [195] Stenson GB, Haug T, Hammill MO. Harp Seals: Monitors of Change in Differing Ecosystems. *Front Mar Sci*. 2020;7:569258.
- [196] Jay C V., Taylor RL, Fischbach AS, Udevitz MS, Beatty WS. Walrus haul-out and in water activity levels relative to sea ice availability in the Chukchi Sea. *J Mammal*. 2017;98:386–96.
- [197] MacCracken JG. Pacific Walrus and climate change: Observations and predictions. *Ecol Evol*. 2012;2:2072–90.
- [198] Blanchet MA, Lydersen C, Ims RA, Lowther AD, Kovacs KM. Harbour seal *Phoca vitulina* movement patterns in the high-arctic archipelago of Svalbard, Norway. *Aquat Biol*. 2014;21:167–81.
- [199] Laidre KL, Born EW, Atkinson SN, Wiig Ø, Andersen LW, Lunn NJ, et al. Range contraction and increasing isolation of a polar bear subpopulation in an era of sea-ice loss. *Ecol Evol*. 2018;8:2062–75.
- [200] Laidre KL, Atkinson SN, Regehr E V., Stern HL, Born EW, Wiig Ø, et al. Transient benefits of climate change for a high-Arctic polar bear (*Ursus maritimus*) subpopulation. *Glob Change Biol*. 2020;26:6251–65.
- [201] Wilson RR, Regehr E V., Rode KD, St Martin M. Invariant polar bear habitat selection during a period of sea ice loss. *Proc R Soc B Biol Sci*. 2016;283:20160380.
- [202] Fischbach AS, Amstrup SC, Douglas DC. Landward and eastward shift of Alaskan polar bear denning associated with recent sea ice changes. *Polar Biol*. 2007;30:1395–405.
- [203] Prop J, Aars J, Bårdsen B-J, Hanssen SA, Bech C, Bourgeon S, et al. Climate change and the increasing impact of polar bears on bird populations. *Front Ecol Evol*. 2015;3:1–12.
- [204] Saalfeld ST, Mcewen DC, Kesler DC, Butler MG, Cunningham JA, Doll AC, et al. Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. *Ecol Evol*. 2019;9:6693–707.
- [205] Kwon E, Weiser EL, Lanctot RB, Brown SC, Gates HR, Gilchrist G, et al. Geographic variation in the intensity of warming and phenological mismatch between Arctic shorebirds and invertebrates. *Ecol Monogr*. 2019;89:1–20.
- [206] Kerby J, Post E. Capital and income breeding traits differentiate trophic match-mismatch dynamics in large herbivores. *Philos Trans R Soc B Biol Sci*. 2013;368:20120484.
- [207] Hupp JW, Ward DH, Soto DX, Hobson KA. Spring temperature, migration chronology, and nutrient allocation to eggs in three species of arctic-nesting geese: Implications for resilience to climate warming. *Glob Change Biol*. 2018;24:5056–71.
- [208] Ejsmond A, Forchhammer M, Varpe Ø, Jónsson JE, Jørgensen C. Nesting synchrony and clutch size in migratory birds: Capital versus income breeding determines responses to variable spring onset. *Am Nat*. 2021;198:E000.
- [209] Lameris TK, Dokter AM, van der Jeugd HP, Bouten W, Koster J, Sand SHH, et al. Nocturnal foraging lifts time constraints in winter for migratory geese but hardly speeds up fueling. *Behav Ecol*. 2021;32:539–52.
- [210] Kauffman MJ, Cagnacci F, Chamaillé-Jammes S, Hebblewhite M, Hopcraft JGC, Merkle JA, et al. Mapping out a future for ungulate migrations. *Science*. 2021;372:566–9.
- [211] Hamilton CD, Kovacs KM, Ims RA, Aars J, Lydersen C. An Arctic predator–prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. *J Anim Ecol*. 2017;86:1054–64.
- [212] Dey CJ, Richardson E, McGeachy D, Iverson SA, Gilchrist HG, Semeniuk CAD. Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea ice loss. *Glob Change Biol*. 2017;23:1821–31.
- [213] Provencher JF, Gaston AJ, O'Hara PD, Gilchrist HG. Seabird diet indicates changing Arctic marine communities in eastern Canada. *Mar Ecol Prog Ser*. 2012;454:171–82.
- [214] Vihtakari M, Welcker J, Moe B, Chastel O, Tartu S, Bech C, et al. Black-legged kittiwakes as messengers of Atlantification in the Arctic. *Sci Rep*. 2017;8:1–11.
- [215] J. Divoky G, Lukacs PM, Druckenmiller ML. Effects of recent decreases in arctic sea ice on an ice-associated marine bird. *Prog Oceanogr*. 2015;136:151–61.
- [216] Yurkowski DJ, Hussey NE, Ferguson SH, Fisk AT. A temporal shift in trophic diversity among a predator assemblage in a warming Arctic. *R Soc Open Sci*. 2018;5:180259.
- [217] Dorresteijn I, Kitaysky AS, Barger C, Benowitz-Fredericks ZM, Byrd G V., Shultz M, et al. Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. *Mar Ecol Prog Ser*. 2012;454:207–20.
- [218] Kitaysky AS, Golubova EG. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *J Anim Ecol*. 2000;69:248–62.
- [219] Kitaysky AS, Kitaiskaia E V., Piatt JF, Wingfield JC. A mechanistic link between chick diet and decline in seabirds? *Proc R Soc B Biol Sci*. 2006;273:445–50.
- [220] Kondratyev A, Zaynagutdinova E, Kruckenberg H. Barnacle Goose *Branta leucopsis* abundance on Kolguev Island - Current status and history of population growth. *Wildfowl*. 2013;63:56–71.
- [221] Fufachev IA, Ehrich D, Sokolova NA, Sokolov VA, Sokolov AA. Flexibility in a changing arctic food web: Can rough-legged buzzards cope with changing small rodent communities? *Glob Change Biol*. 2019;25:3669–79.
- [222] Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K, et al. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc R Soc B*. 2011;278:835–42.

- [223] Reed TE, Grøtan V, Jenouvrier S, Sæther B-E, Visser ME. Population growth in a wild bird is buffered against phenological mismatch. *Science*. 2013;340:488–91.
- [224] Zhemchuzhnikov MK, Versluijs TSL, Lameris TK, Reneerkens J, Both C, van Gils JA. Exploring the drivers of variation in trophic mismatches: A systematic review of long-term avian studies. *Ecol Evol*. 2021;11:3710–25.
- [225] Gill JA, Alves JA, Sutherland WJ, Appleton GF, Potts PM, Gunnarsson G. Why is timing of bird migration advancing when individuals are not? *Proc R Soc B*. 2014;281:20132161.
- [226] Gallinat AS, Primack RB, Wagner DL. Autumn, the neglected season in climate change research. *Trends Ecol Evol*. 2015;30:169–76.
- [227] Gauthier G, Bêty J, Cadieux M-C, Legagneux P, Doiron M, Chevallier C, et al. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. *Philos Trans R Soc Lond B Biol Sci*. 2013;368:20120482.
- [228] CAFF. State of the Arctic Marine Biodiversity Report. Akureyri, Iceland: Conservation of Arctic Flora and Fauna International Secretariat; 2017. 197 p.
- [229] Aronsson M, Heiðmarsson S, Jóhannesdóttir H, Barry, Braa J, Burns CT, et al. State of the Arctic Terrestrial Biodiversity Report. Akureyri, Iceland: Conservation of Arctic Flora and Fauna International Secretariat; 2021. 123 p.
- [230] Meakin, S., Kurvits, T., Fillion, M., 2014, The State of Food (In)security in the Arctic, Arctic Change 2014 International Conference, December 8-12, Ottawa, Canada., 1, Published
- [231] Birdlife International. Species factsheet: *Calidris maritima*. IUCN Red List for birds. 2021.