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A review of climate change impacts on migration patterns of marine vertebrates in Arctic and Subarctic ecosystems

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Climate change is impacting marine ecosystems throughout the circumpolar Arctic, altering seasonal habitats and the food bases for fishes, seabirds, and marine mammals. Arctic and Subarctic regions provide resources for resident species and for species that migrate to the north from more southerly regions. Changes in northerly latitudes thus impact endemic as well as non-endemic animals. Herein, we review what is known about climate-driven changes in the migration patterns of Arctic and Subarctic marine vertebrates, including: 1) Arctic residents with seasonal movements – those fishes, seabirds, and marine mammals that complete their entire life cycle within the Arctic but exhibit seasonal movements; 2) Breeding migrants – many seabirds enter the Arctic to breed and subsequently migrate south in the fall; and 3) Summer visitors for feeding – certain species of boreal fishes, seabirds and marine mammals arrive during the northern summer to feed on abundant prey though they breed elsewhere. Migratory movements are often driven by the timing and extent of sea ice, which defines suitable habitat for some animals and limits access to open water and prey for others. Longer open-water seasons, warmer ocean temperatures, and stronger winds have resulted in earlier production blooms in spring and often, extended open-ocean plankton blooms into late summer, resulting in altered prey types and distributions. A common thread among taxa is that shifts in distribution and timing of migrating animals indicate they are traveling farther north, or shifting longitudinally, and migrations are occurring over longer seasonal time frames. Species performing multiple lifetime migrations or long-distance migrants may need to adjust migration timing or routing iteratively to match changes in marine productivity. Altered animal distributions or phenology, and reduced sea ice, affects access to animals that are critical nutritional, economical, and cultural components of Indigenous

people's lives in the Arctic. Ongoing changes challenge the resilience and adaptability of Arctic people and ecosystems, and will require adaptive research and management approaches.

KEYWORDS

Arctic, distributional shift, fish migrations, marine mammal migrations, phenology, sea-ice loss, seabird migrations, subsistence harvest

1 Introduction

Animal migrations have evolved in response to spatial and temporal changes in resource availability (Newton, 2008; Milner-Gulland et al., 2011; Evans and Bearhop, 2022). In the Arctic, much of the marine-based prey that support upper trophic level taxa are only available during the brief Arctic summer and fall. Animals that remain in the Arctic year-round often conduct seasonal movements within Arctic areas (Alerstam et al., 2007; Pettitt-Wade et al., 2021), while Subarctic and temperate animals that depend on the Arctic's summer production period migrate north as sea ice retreats and return south as winter advances and darkness and low temperatures prevail (Berge et al., 2015a). Migration strategies depend on reasonable levels of ecosystem predictability to ensure timely access to prey for replenishment of energy stores and for breeding success. Among migratory species, the ability to adjust to spatial and temporal variability in resources varies along a continuum from narrow to flexible (Corkeron and Conner, 1999; Evans and Bearhop, 2022). However, climate change is altering marine systems such that resources and other environmental conditions are becoming more unpredictable in space and time (UNEP/CMS, 2006; Robinson et al., 2009; Gilg et al., 2012). This unpredictability is a current and future challenge for marine vertebrates that rely on migration to or within the Arctic to maximize their survival and reproductive success. Indigenous communities that rely on animal harvests are also impacted (Huntington et al., 2016; Hauser et al., 2021).

As climate change alters the timing and spatial distribution of resources, animals may need to alter their phenologies and migratory routes or staging areas. Changes in their traditional patterns and altered resource bases are likely to result in expending more energy searching for food and issues with finding adequate prey densities to support large-bodied animals (Bauer et al., 2008; Howard et al., 2018). Concurrently, other species may gain access to more direct routes, and more or higher-quality food over a longer season, reducing individual energetic expenditures of migration. Climate change induced impacts to migration can therefore affect reproductive success and overwintering survival, with repercussions to entire populations (Harrison et al., 2011). Ultimately, ecosystems will be impacted, as some fish species that are being negatively affected by climate change constitute key species in Arctic marine food webs, upon which many of the top trophic feeders depend (Welch et al., 1992; Hop and Gjosæter, 2013). As upper trophic level consumers, predatory fishes, seabirds, and marine mammals serve as sentinels of ecosystem health (Moore et al., 2014; Sydeman et al., 2015; Moore and Kuletz, 2019). These three animal groups also constitute important food resources to people who rely on Arctic marine ecosystems for subsistence and many species serve as

cultural cornerstones (Guyot et al., 2006; Huntington et al., 2013; 2016).

Migratory animals have significant impacts upon the marine ecosystems to which they migrate, serving as prey, predators, contributors to, and cyclers of, nutrients (Bauer and Hoye, 2014). Because animal migrations cross national boundaries, the United Nations established a global treaty on the Conservation of Migratory Species of Wild Animals (UNEP-WCMC, 2024), which defines a migratory species as: "The entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries." While this definition overlooks migratory movements that only occur within national boundaries, it does recognize the impact of climate change on animal migrations, and the need to address how current and future environmental changes will impact animals that rely on migration strategies to maintain their populations.

The timing and extent of sea-ice retreat is a primary driver of Arctic marine systems, and in spring it affects water-column characteristics, phenology and spatial extent of primary production, and consequently, abundance of lower trophic organisms, species composition, and nutritional quality (Gaston et al., 2009; Daase et al., 2013; Leu et al., 2015; Stige et al., 2019). The decline in area, thickness, and seasonal duration of sea ice within the last 20 years has greatly altered Arctic ecosystems, and these declining trends in sea ice will continue as northern latitude air and water temperatures increase (Barber et al., 2015; Hunt et al., 2016; Meredith et al., 2019; IPCC et al., 2023). With warmer conditions, early sea-ice melt in spring has resulted in earlier spring blooms, increased chlorophyll, and higher zooplankton biomass that experiences higher turnover, albeit of smaller, low-nutrient prey species, from zooplankton to fishes (Österblom et al., 2008; Hop and Gjosæter, 2013; Renaud et al., 2018; Møller and Nielsen, 2020; Copeman et al., 2022). Such changes also affect competition among species at different trophic levels (Bogstad et al., 2015; Stige et al., 2018). Subsequently, the distribution of zooplankton, pelagic and benthic invertebrates, and forage fishes affect the upper trophic level vertebrates that migrate to or within the Arctic, including annual (e.g., seabirds and marine mammals) and life-cycle stages (e.g., anadromous fishes).

Most migration to the Arctic occurs latitudinally, in the extreme, from the Antarctic to the Arctic (Egevang et al., 2010), but migration also occurs longitudinally across the circumpolar realm (Alerstam and Gudmundsson, 1999; Alerstam et al., 2007). Migratory patterns can be influenced by the presence or absence of ice and impacts vary across taxa (McKeon et al., 2016; Briscoe et al., 2017; Clairbaux et al., 2019). Migration patterns of nearshore foragers and anadromous fishes could also be affected by changes in riverine and coastal systems, as freshwater runoff, thawing terrestrial permafrost,

retreating glaciers, increased sedimentation, and lack of shore-fast ice alter the coastal domains (Carmack et al., 2015). Likewise, populations that rely on transport by surface currents for successful migration may be affected by changes in ocean circulation patterns (Frederiksen et al., 2016; Eriksen et al., 2020).

The forms of migration vary widely within and among taxa. Resident species may spend most or all of their life cycle within Subarctic or Arctic areas but exhibit regular movements within those areas. Such patterns are exhibited by some species of anadromous and marine fishes (Pettitt-Wade et al., 2021), certain marine mammals (Von Duyke et al., 2020; Shuert et al., 2023; Storrie et al., 2023) and at least three species of seabirds (Divoky et al., 2016; Gilg et al., 2016a; b; Frederiksen et al., 2021). Breeding migrants include some seabird species that migrate from the Subarctic and elsewhere to breed in the Arctic. Non-breeding migrants arrive during summer and fall only to feed in the Arctic. Among these species, some arrive as post-breeders from the Subarctic or nearby temperate realms, including species of seabirds (Kuletz et al., 2015; Gaston et al., 2017; Piatt et al., 2021) and migrant baleen whales (Storrie et al., 2018; Moore et al., 2022). This pattern also includes some marine fishes that migrate seasonally to the Arctic, e.g., capelin (*Mallotus villosus*) and several gadid species (Haug et al., 2017; Mueter et al., 2021). A few avian species are long-distance migrants from the Southern Hemisphere and travel to the Subarctic and Arctic only to feed and increase body reserves (Kuletz et al., 2015; Yamamoto et al., 2015; Nishizawa et al., 2017). Regardless of origin or strategy, animals need to match the phenology of their movements to the availability of food resources, which can be particularly critical for species that move to the Arctic to breed (Klaassen, 2003). For example, most seabirds are highly philopatric to colony breeding sites (Hamer et al., 2001), and for certain anadromous fishes, migration to freshwater breeding sites may be site-specific and rather inflexible (Hendry and Sterns, 2004).

Migratory strategies of animals can range from extreme “income migrants” (also known as a “fly-and-forage” strategy) to “capital migrants” (Evans and Bearhop, 2022). Income migrants forage as they move towards their migration endpoint, with little or no physiological alteration to prepare for migration and rely on multiple ecosystems for replenishment while *en route*. At the opposite extreme are capital migrants, individuals that must store adequate reserves for the entire journey, often undergoing physiological alterations to conserve energy until they reach their endpoint (Evans and Bearhop, 2022). For capital migrants, the timing of movements is critical and depends on the availability of food and suitable environmental conditions immediately upon arrival. As our knowledge regarding foraging patterns of migrants increases, it appears that most animals fall somewhere along this continuum, and some may even alter their strategies at different stages of their migratory journey (e.g., Lydersen et al., 2020). Our goal was to review available scientific literature to provide a synthesis of information on the impact of climate change on migratory Arctic marine vertebrates (fishes, seabirds, and marine mammals), and thereby inform decision-makers about these conservation challenges.

2 Methods

2.1 Spatial and temporal scope

For our review we primarily considered the marine and associated freshwater inflows across the circumpolar Arctic as defined by the Arctic Council’s Conservation of Arctic Flora and Fauna (CAFF) boundaries, which includes Arctic and Subarctic waters (Figure 1; <https://caff.is/work/projects/arctic-biodiversity-data-service/>). The Arctic Ocean incorporates an area of approximately 14,060,000 km², with most of its waters north of 66° N latitude, but including some Subarctic regions generally north of 60° N. The Arctic coastline within this region is ~45,390 km, although the CAFF boundary incorporates regions farther south. In the Pacific Arctic, the Subarctic includes the entire Bering Sea and portions of the northwestern Gulf of Alaska shelf. In the Atlantic Arctic, the boundary includes Hudson Bay, the Labrador Sea, and waters off southern Iceland and northern Norway (Figure 1). Because many of the migratory animals we review herein spend portions of their life cycle south of these boundaries, we also refer to areas outside our primary study area as appropriate. Our temporal scope emphasizes changes that have occurred in animal migration reported in publications over the last two decades.

In the High Arctic, the deep (mean of ~3,000 m) Central Arctic Ocean (~3.3 million km²) borders five of seven Arctic Marine Areas (AMAs) as defined by the Circumpolar Marine Biodiversity Monitoring Program (CAFF, 2017). The Arctic Ocean is bordered by six countries, with the largest basins adjacent to Russia (Eurasian Basin) and Canada (Amerasian Basin). Warm, saline water flows from lower latitudes into the Arctic via two major “gateways.” In the Pacific, the narrow (~82 km wide) and shallow (90 m) Bering Strait has inflow from the Bering Sea, with the nutrient-rich Anadyr Current on the west and the warmer, fresher Alaska Coastal Current on the east, merging with Bering Shelf Water through Bering Strait and diverging across the shallow (~80 m) Chukchi Shelf (Weingartner et al., 1999). The Chukchi shelf slope is also influenced by the eastward-flowing deep Atlantic water of the Arctic Basin and the westward-flowing Beaufort Gyre. The Atlantic gateway is the wide (~450 km) and deep (5,500 m) Fram Strait, with the relatively warm West Spitsbergen Current as the primary inflow. It continues eastwards along the shelf north of Svalbard as the Atlantic Water Boundary Current (Renner et al., 2018) into the Nansen Basin of the Arctic Ocean. The Fram Strait is also a primary outflow on the west side of the Atlantic with the colder and fresher East Greenland Current (Karpouzoglou et al., 2024). Large river systems drain into the Arctic Ocean from multiple points, especially the large Russian rivers, resulting in fresher, cooler waters near coastal areas, which influence coastal currents (Feng et al., 2021).

Throughout the circumpolar Arctic and Subarctic, seasonal and long-term sea ice have been important structural components of marine ecosystems, which have been changing dramatically in recent decades (Taylor et al., 2022; IPCC et al., 2023). Historically, seasonal sea-ice formation expanded from November to March. On the Pacific side, sea ice could extend south across the central Bering Sea shelf and retract in late spring, and the Bering Strait would not be ice-free until June (Stabeno and Bell, 2019). As seasonal sea ice retreated, a layer of cool, fresh water influenced

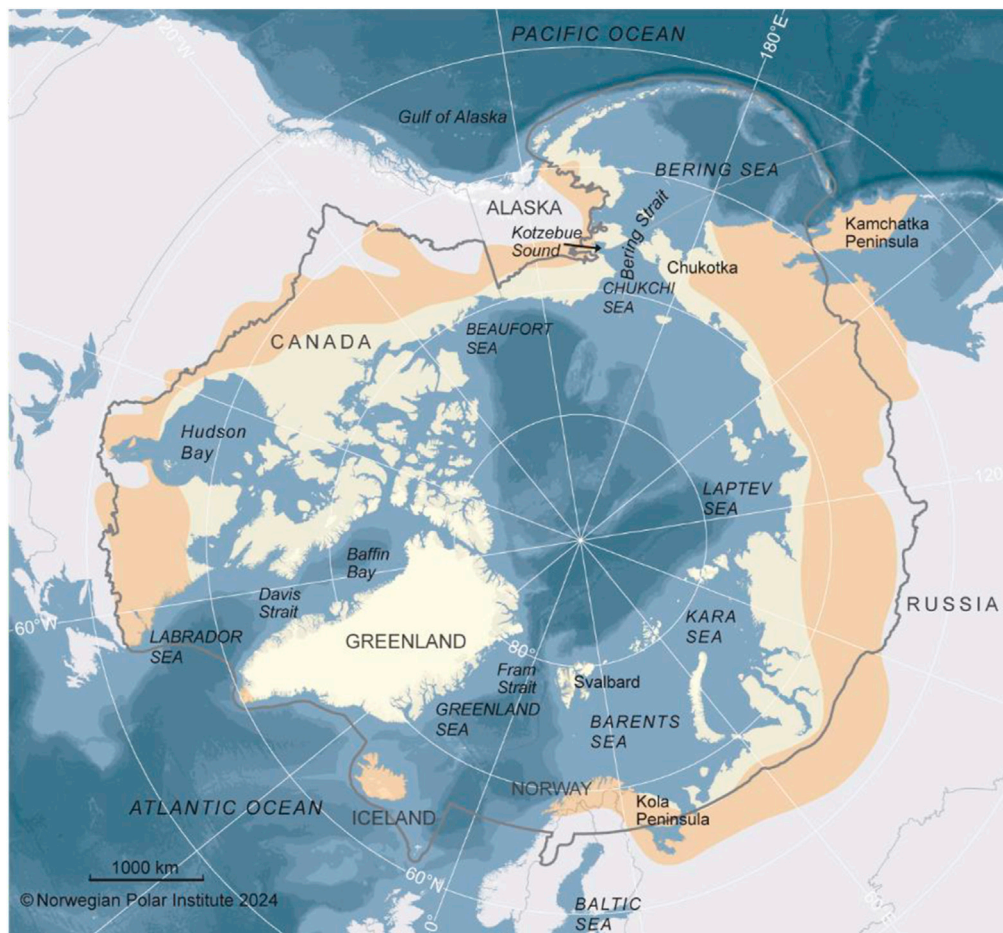


FIGURE 1
The Circumpolar study region, showing the CAFF boundaries, which include Arctic (pale yellow shading) and Subarctic (light brown shading) regions.

water masses, currents, and productivity (Lin et al., 2019; Danielson et al., 2020). The Atlantic Arctic is changing more rapidly than any other Arctic area. The region is heavily influenced by mixed Atlantic Water entering the Barents Sea from the south in two currents—one that goes eastward into the southern Barents Sea and one that flows north along the west coast of Svalbard (Ingvaldsen et al., 2021). The volume and temperature of these currents have changed over recent decades, altering sea-ice conditions at high latitudes dramatically (Efstathiou et al., 2022; Isaksen et al., 2022; Polyakov et al., 2023). In recent decades, sea-ice loss has drastically altered the physical and biological properties of Arctic marine systems (Fossheim et al., 2015; Descamps et al., 2017; Baker et al., 2020; Danielson et al., 2020). The open water season in the gateway areas currently extends from May to December (Stabeno and Bell, 2019; Efstathiou et al., 2022; Isaksen et al., 2022; Urbanski and Litwicka, 2022).

2.2 Review process

Our review of Arctic marine ecology as related to migration includes fishes, seabirds, and marine mammals, with expert representation from both the Pacific and Atlantic Arctic sectors. We included sources published in scientific journals, books, and

publicly accessible agency reports. We relied on the expertise of the team and used internet search engines, including Google Scholar and Web of Science to survey the literature. Key words searched included taxa-specific names, plus combinations of: climate change, Arctic, migration, global warming impacts, timing of migrations, distributional shift, phenology, and movement patterns.

3 Results

3.1 Anadromous and marine fishes

3.1.1 Life histories and migrations

The migration of fishes is typically a “migration triangle,” as they move seasonally or in life stages among nursery, feeding, and spawning grounds (Harden-Jones, 1968). In Arctic and Subarctic regions, migratory fishes consist of two general types: anadromous and strictly marine. Anadromous fishes hatch in fresh water, migrate to the ocean, and return to reproduce in freshwater; individuals of some species perform multiple seasonal migrations during their lives (Hendry et al., 2004). In contrast, strictly marine fishes complete their entire life cycle in the ocean. Marine migrations, the focus of this review (i.e., freshwater stages of anadromous fishes are not

considered), are influenced by a myriad of factors, including water temperature, ice phenology, ice extent, wind direction, and primary and secondary production. Changes in these factors can cause changes in timing and spatial extent of fish migrations. Because of their different life histories and migratory patterns, and their relative importance to subsistence (predominantly anadromous) versus commercial fisheries (predominantly marine) in the north, we address anadromous and marine fishes separately.

The most abundant anadromous fishes in the Arctic are from the sub-family Salmoninae (Pacific salmon species *Oncorhynchus* spp., Atlantic salmon and sea trout *Salmo* spp., and various char *Salvelinus* spp.) and members of the Coregoninae (whitefishes and ciscoes *Coregonus* spp.) (Reist et al., 2006). They contribute to a variety of fisheries, including subsistence, commercial, and recreational in North America and Eurasia (e.g., Falardeau et al., 2022). Collectively, salmonids exhibit a great diversity in life-history characteristics including semelparous (single) or iteroparous (multiple) reproductive cycles in a lifetime, facultative or obligatory migration, partial migration, and phenotypic plasticity (Hendry and Sterns, 2004). Species that have received relatively more attention on how climate change may affect migration are Atlantic salmon (*Salmo salar*), Arctic char (*Salvelinus alpinus*), and brown trout (*Salmo trutta*), while coregonines and endemic populations of Pacific salmon north of the Bering Strait have received less research attention.

Marine fish in the Arctic consist of two main categories with respect to migratory behavior: Arctic resident species and boreal species. Arctic residents comprise a diverse fish community living in environments characterized by low temperatures and strong seasonality in photoperiod and sea-ice cover. They typically have limited migrations within Arctic waters, as they move between spawning, feeding, and overwintering areas. Most Arctic marine species are small (<35 cm) benthic forms, dominated by sculpins (Cottoidea), eelpouts (Zoarcidae), and snailfishes (Liparidae), that typically have large demersal eggs and benthic larvae or short pelagic larval phases. Thus, they generally have poor dispersal potentials and their seasonal migrations are local, often between shallow and deeper waters (Brand and Fischer, 2016). However, there are exceptions, such as the Greenland shark (*Somniosus microcephalus*), which can reach a length of 5.5 m (Lynghammar et al., 2024). Boreal species' main centers of distributions occur farther south and they undertake seasonal migrations to the Arctic to feed, typically arriving in early summer and leaving before freeze-up (Lynghammar et al., 2024). Such migrants include both pelagic and demersal species. The migration timing of Arctic marine fish is closely linked to seasonal changes in the environment, particularly temperature and sea-ice conditions, and varies among species based on their specific life history traits and ecological requirements. However, for marine fish there is no information on temporal changes in migration. Most data are based on trawling, typically performed annually rather than seasonally, which reveals information on changes in distribution over time rather than migration timing (e.g., Fossheim et al., 2015; Frainer et al., 2017; Levine et al., 2023). Distributions are generally shifting farther north with warming conditions, and this is more apparent for pelagic species than for demersal species; the latter tend to tolerate a wider range of thermal conditions (Baker, 2021).

3.1.2 Phenology of migration for anadromous fishes

Among iteroparous anadromous fishes, several factors affect the timing of seasonal migration, including ocean temperatures and in some cases, ice cover. Marine habitats in Arctic North America and eastern Eurasia are ice covered during winter, unlike areas affected by the North Atlantic Current that keep the northern coasts of Iceland and Norway ice-free year-round. Sea ice forms when seawater (35 ppt) freezes at -1.8°C , and while doing so, ejects colder briny water from the ice. Anadromous fishes are not known to contain antifreeze compounds (e.g., glycoproteins), and are thus generally limited to occupying water temperatures $>-0.7^{\circ}\text{C}$ (Cheng, 2009). Therefore, sea ice and cold water act as barriers to the movements of anadromous fishes. Increased air temperatures in the Arctic have induced earlier spring ice melt, which can determine when fish undertake their marine feeding migration to take advantage of seasonal ocean productivity (Cooley et al., 2020; Falardeau et al., 2022). Similarly, ice formation in the fall is now occurring later, resulting in a longer ice-free season and increased sea surface temperatures (SST). As many anadromous fish species' movements are governed by ice cover and water temperature (Bond and Quinn, 2013), some have responded by shifting their migration timing earlier in the spring (Kovach et al., 2013; Dempson et al., 2017) and later in the fall. Migration of char species is associated with ice presence, and some species can move below the ice in the ocean during winter and spring (Hammer et al., 2022; Smith et al., 2022), but spring coastal movements are limited by ice and are also influenced by marine temperatures (Hollins et al., 2022). Dolly Varden (*Salvelinus malma*) enter the ocean after land-fast ice has broken up and its marine dispersal is limited by sea-ice extent in summer (Gallagher et al., 2021).

3.1.3 Distributional shifts in anadromous fishes

Marine water temperatures influence the spatial distribution of anadromous salmonids during summer months (Mulder et al., 2020; Gallagher et al., 2021; Rikardsen et al., 2021; Nordli et al., 2023). In Arctic North America, the cold-adapted species Arctic char and Dolly Varden are surface oriented, typically occupying depths <5 m, and prefer temperatures between approximately 2°C and 8°C (Courtney et al., 2016; Harris et al., 2020; Mulder et al., 2020). Both species track their preferred isopleths in the ocean, which can shift spatially interannually, altering their marine distribution from year to year (Jensen et al., 2014; Harris et al., 2020; Gallagher et al., 2021). For example, Dolly Varden often occupy nearshore habitats in years with cooler SSTs but use more offshore areas in years with warmer SSTs (Gallagher et al., 2021). Additionally, SSTs impact estuarine use by Arctic char, as these habitats are typically occupied when the ocean is relatively cold, thus warming temperatures could decrease movement into estuaries (Harris et al., 2020). Increased water temperatures and higher productivity are thought to be related to the increasingly northward extent of migration in Subarctic and temperate species, such as observed for Pacific salmon species (Dunmall et al., 2013).

Other factors influencing the spatial extent of anadromous fish migrations include oceanographic fronts that typically have relatively high primary and secondary productivity. For example, an oceanographic front with high productivity, where the warm North Atlantic Current intersects with cold polar waters of the

Northeast Atlantic Arctic, is an important feeding area for Atlantic salmon (Rikardsen et al., 2021). Similarly, Dolly Varden feed at a front in the Chukchi Sea where euphausiid abundance is high (Courtney et al., 2016). As conditions in the Arctic change, frontal boundaries may move (Lu et al., 2015), which will impact location, duration, and energetic costs of migration (Rikardsen et al., 2021). Finally, prevailing wind direction may affect juvenile fish migration. For example, the intensified strength of easterly winds in the western parts of the North American Arctic (Falardeau et al., 2023), may improve juvenile Arctic cisco (*Coregonus autumnalis*) dispersal towards nursery and feeding areas favorable for recruitment (Fechhelm et al., 2007; Zimmerman et al., 2013).

3.1.4 Ontogenetic and seasonal migrations of Arctic marine fishes

The few relatively large demersal species in the Arctic that extend to the Subarctic include flatfishes, such as Greenland halibut (*Reinhardtius hippoglossoides*), Arctic skate (*Amblyraja hyperborea*) and the Greenland shark. Most flounders undertake ontogenetic migrations, moving to deeper water as they grow (Bassi et al., 2024). Older fish also move seasonally into fjords and shallow waters during the ice-free season, and into deeper water during winter (Barkley et al., 2018). In the North Atlantic, the population structure of Greenland halibut is complex, with three main components that have different migratory patterns (Vihtakari et al., 2022). In the Northeast Atlantic, the spawning area extends from Vesterålen (68° 41'N, 15° 24'E), Norway, north to Bear Island (74° 30'N, 19° 00'E). The pelagic eggs and larvae drift northward with the West Spitsbergen Current and pelagic juveniles occur north of Svalbard and in the Arctic Ocean (Ingvaldsen et al., 2023).

Arctic skates occur from moderate depths (300 m) to the lower continental slopes (2,500 m). Tagging studies indicate that their migration routes are relatively limited, generally within 30–40 km of capture sites at Baffin Island (Peklova et al., 2014). The Atlantic is the most important dispersal route for skates into the Arctic Ocean, whereas on the Pacific side, the cold bottom water in the Bering Strait restricts their dispersal into the Arctic (Lynghammar et al., 2012). Climate warming and reduction of the Bering Sea “Cold Pool” thermal barrier (bottom water ~ -1.5°C), could facilitate increased migration of skates and other fishes from the Bering Sea through the Bering Strait into the Arctic Ocean (Mueter et al., 2021).

In contrast to skates and other benthic fishes in the Arctic, the demersal Greenland shark is the most migratory elasmobranch in the Arctic, undertaking movements that are similar in extent to the Arctic whales. The Greenland shark is capable of long-distance migrations exceeding 1,000 km, and often conducts excursions between inshore and offshore waters (Campana et al., 2015; Edwards et al., 2022). Greenland sharks typically occur in coastal fjords during ice-free periods to feed (McMeans et al., 2013) and they move offshore during the period of ice reformation (November to July). On the other side of the Arctic Ocean, the Pacific sleeper shark (*Somniosus pacificus*) ranges from the Bering Sea throughout the deep waters in the Pacific and into the Southern Ocean (Yano et al., 2004), and this fish also undertakes seasonal migrations from onshore to offshore waters. Little is known about how climate warming will affect these sharks, except when they occur in

shallower coastal waters to feed and can then be caught and outfitted with biotelemetry instruments (Lydersen et al., 2016).

Arctic pelagic fishes include the Arctic cod (*Boreogadus saida*) and the polar cod (*Arctogadus glacialis*), both of which are important forage fishes for Arctic and Subarctic predators (e.g., Welch et al., 1992, 1993; Pettitt-Wade et al., 2021). On the Pacific side, the saffron cod (*Eleginus gracilis*) is abundant in the western Arctic, where it plays a significant role in food webs (e.g., Crawford et al., 2015). It is more demersal than Arctic and polar cod and it has a more southerly and nearshore distribution (De Robertis et al., 2017). Seasonal movements by Arctic cod are typically inshore/shallow during summer and are associated with juvenile development, adult feeding, and pre-spawning schooling, whereas movements to deeper areas are linked to spawning and overwintering below sea ice (Hop et al., 1997; Geoffroy et al., 2011; Benoit et al., 2014; Bouchard et al., 2016). Adult polar cod may perform long seasonal movements (<200 km) within the Arctic (Kessel et al., 2017). In the eastern Barents Sea, polar cod migrate northward in May-June, following the ice edge, with the largest fish moving first (Aune et al., 2021). In the Chukchi Sea, seasonal differences in Arctic cod abundance suggest that their migration between nursery grounds as juveniles, feeding grounds as subadults, and spawning grounds as adults, is linked to ice cover and seasonal production patterns (Forster et al., 2020). Polar cod also move between inshore and offshore areas in relation to spawning, feeding, and juvenile development, respectively (Bouchard et al., 2016; Pettitt-Wade et al., 2021). Saffron cod have different seasonal movements since they migrate inshore to spawn during winter and offshore to feed during summer (Logerwell et al., 2015). This seasonal offshore movement allows them to access abundant food resources in deeper waters. The impacts of reduced sea ice on these life stage migratory movements are largely unknown.

3.1.5 Seasonal movements of boreal fish species into the Arctic

Several boreal fish species migrate seasonally to the Arctic to feed on abundant and lipid-rich prey. In the Atlantic, the main species are capelin, Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*). Capelin juveniles and sub-adults undertake feeding migrations along the east coast of Greenland and in the eastern Fram Strait and in the Barents Sea over to the slopes of the Arctic Ocean (Carscadden et al., 2013). Their northern distributions overlap with Arctic cod and they compete for some of the same zooplankton food sources (Hop and Gjosæter, 2013; McNicholl et al., 2018).

Atlantic cod perform feeding migrations to Svalbard and the northern Barents Sea to the slopes of the Arctic Ocean, where they feed on capelin, Arctic cod, and other species (Haug et al., 2017). Such migrations are part of their life history, after pelagic eggs are released at spawning sites in northern Norway and larvae drift into the Barents Sea via the Norwegian Coastal Current (Ottersen et al., 2014). Juveniles and sub-adults disperse in the feeding areas, which include the Barents Sea as well as the shelf west and north of Svalbard to the slope of the Arctic Ocean. Adults perform annual spawning migrations to the Norwegian coast in March and subsequently migrate northwards after spawning. An increasing cod stock represents more prey for marine mammals, but also competes for some of the same food sources (Bogstad et al.,

2015). The more demersal haddock migrate northwards to areas also used by Atlantic cod, particularly on the western and northern coasts of Svalbard and adjacent slopes, where they predominately feed on benthos rather than fish (Landa et al., 2014).

In the Pacific, the reduced Bering Sea “Cold Pool” has facilitated the dispersal of juvenile walleye pollock (*Gadus chalcogrammus*) from the Bering Sea into the Chukchi Sea (Eisner et al., 2020; Grüss et al., 2021; Levine et al., 2023). This has created a migratory pattern for walleye pollock, from a source population in the northern Bering Sea, with larvae and juveniles advected into the Chukchi Sea with presumed return migration (Levine et al., 2023). However, some individuals migrate across the Arctic Ocean to the North Atlantic (Orlov et al., 2021). The same process has brought Pacific cod (*Gadus macrocephalus*) into the northern Bering Sea, and although juveniles have passed through the Bering Strait they are unlikely to survive beyond age-1 because of poor growth conditions for this species in the Chukchi Sea (Cooper et al., 2023).

Mackerel (*Scomber scombrus*) and Atlantic bluefin tuna (*Thunnus thynnus*) can occasionally undertake migrations to the Arctic from their more typical southern ranges, with respective spawning areas in the eastern North Atlantic and in the Mediterranean Sea (Mackenzie et al., 2014; Berge et al., 2015b). These expansions involve longer seasonal migrations to feeding areas, since their southern spawning areas have not changed. If ocean warming facilitates more efficient predatory fishes to move into the Arctic, this could cause cascading top-down effects on marine food webs.

3.2 Seabirds

3.2.1 Seabird life history patterns in circumpolar regions

For this review, we use the term “seabirds” to encompass species that spend most of their lives at sea and return to land to nest and raise young (families Procellariidae, Phalacrocoracidae, Laridae, Alcidae), as well as other marine-feeding birds that spend more time in terrestrial or freshwater habitats, and do not typically nest in colonies (families Anatidae, Gaviidae, Stercorariidae, and phalaropes [Scolopacidae]). In general, seabirds are highly mobile and have evolved to find food in a dynamic environment, with a wide range of life history traits among species. Approximately 64 seabird species use the Arctic, ~30 of which breed only within the CAFF boundaries of the Arctic (Irons et al., 2015). Seabirds are highly philopatric to their nesting sites, becoming central place foragers while raising chicks, and are free-ranging the rest of the year. Some seabird species and most sea ducks and phalaropes stage in marine areas prior to post-breeding migration, and then typically use a “fly and forage” strategy (e.g., red phalaropes (*Phalaropus fulicarius*) (Saalfeld et al., 2024) and track areas with high prey densities (e.g., little auks (*Alle alle*) (Amélineau et al., 2018)). Other species nest far south of our study area (e.g., *Ardenna* shearwaters) or in Subarctic regions (e.g., *Aethia* auklets), but migrate seasonally to the Arctic where they can forage opportunistically during their post-breeding periods.

Seabirds that breed in the Arctic display an array of migratory patterns, ranging from movements within an ocean basin to species that migrate between the Arctic and Antarctic (Arctic terns, *Sterna paradisaea*). Foraging behavior and diets include surface foragers

and divers, zooplanktivores, piscivores, benthivores, and omnivores. It is thus difficult to generalize regarding climate change impacts on seabirds, and indeed, the variability in foraging and migratory patterns guarantees that different responses are exhibited across families and species (Cairns, 1987; Piatt et al., 2007; Woehler and Hobday, 2024).

Most seabirds cannot store large amounts of body fat and thus require close synchronization of seasonal life phases with environmental cues. In general, photoperiod is the most important cue for avian species to initiate migratory movements, breeding, and molting (Coppack and Pulido, 2004, and citations therein). Given the Arctic’s brief summer season and seasonal extremes in daylight, temperature, open water access, and subsequent prey availability, the spatio-temporal match between a seabird and its prey is critical. Although they are highly mobile, seabirds often depend on concentrated, high densities of prey for efficient foraging (Russell et al., 1999; Jahncke et al., 2005), particularly when feeding chicks (Møller et al., 2018), and prey must be near the surface or at least within species-specific diving depth range (Benoit-Bird et al., 2013).

A few seabird species rely directly on ice-associated fauna. The Mandt’s black guillemot (*Cephus grylle mandtii*) in the Pacific Arctic (Divoky et al., 2016) and the ivory gull (*Pagophila eburnea*) (Spencer et al., 2014) and Ross’s gull (*Rhodostethia rosea*) in the Atlantic Arctic (Gilg et al., 2016b) are closely tied to sea ice year-round, often following the marginal ice zone. Ivory gulls also forage on sea ice, scavenging on the remains from polar bear (*Ursus maritimus*) or polar fox (*Vulpes lagopus*) kills (Karnovsky et al., 2009). The red-legged kittiwake (*Rissa brevirostris*), which nests on islands in the central Bering Sea, shows a strong association with sea ice-influenced waters during the winter (Orben et al., 2015a). As their current primary habitat disappears, such pagophilic species will be forced to adapt their migratory patterns in the future, if they are to survive (Spencer et al., 2014; see Case Study No.1).

3.2.2 Evidence of changes in migration routes

Few seabird surveys have been conducted in the High Arctic and little is known about the extent to which seabirds rely on cross-Arctic routes for migration between breeding and overwintering areas. However, satellite tracking of individual birds and studies utilizing tracking radar have found that such routes do exist. Alerstam et al. (2007) documented Arctic Ocean migrations that were estimated to include over 2 million birds—comprised primarily of shorebird species, but also including terns (sub-family Sternidae) and skuas (*Stercorarius*). Reduced sea ice could facilitate increases in cross-Arctic migration (Clairbaux et al., 2019). For income migrants (that depend on feeding *en route*, i.e., most seabirds), more open water increases potential access to prey, making such transits possible (McKeon et al., 2016; Briscoe et al., 2017). At least a portion of one population of black-legged kittiwake (*Rissa tridactyla*) has been documented to travel over the Arctic from a colony in the Barents Region to overwintering sites in the Chukchi and Bering seas, and more cross-Arctic migrations of kittiwakes could occur as sea ice declines (Ezhov et al., 2021).

We lack long-term studies that can detect changes to migratory movements of most Arctic seabird species, but tagging studies indicate extensive cross-Arctic and ice-associated migrations that could be impacted by changes to this habitat. Ivory gulls that nest in

the Atlantic Arctic migrate to the Bering Sea during their non-breeding season (Gilg et al., 2010), and Ross's gulls conduct cross-Arctic migrations in and among the Russian, Alaskan, and Canadian Arctic regions (Maftei et al., 2015; Gilg et al., 2016b), with most of the estimated world population moving westward past northern Alaska during October–November (Maftei et al., 2014). One four-decade study that combined distribution modeling and tracking data for thick-billed murres (*Uria lomvia*) in the Hudson Bay region, found that the greatest shift in distribution (westward and to recently ice-free waters) occurred during the fall migration period (Patterson et al., 2021).

Long-term monitoring via at-sea surveys can be used to examine seabird response to anomalously warm or ice-free conditions, perhaps a prelude to a warmer Arctic. One long-term pattern in the Pacific Arctic suggests that with longer open water seasons and increased zooplankton productivity, planktivorous seabirds have shifted post-breeding movements northward. In the eastern Chukchi Sea, zooplankton feeders such as *Aethia* auklets and short-tailed shearwaters (*Ardenna tenuirostris*) were more abundant in offshore waters during the 2000s than the local-nesting, fish-eating seabirds (alcids and larids), which had predominated in offshore waters during 1974–1995 (Gall et al., 2017). In fact, short-tailed shearwaters have gradually shifted their migratory route northward since ca. 2014 (Kuletz et al., 2020). Because the auklets and shearwaters do not nest in the region, their influx reflects a shift in their post-breeding migration, to forage on newly abundant late summer resources. However, this shift has not been a linear response to the warming Arctic; during a recent, anomalously warm period (2017–2019), substantially fewer auklets migrated into the Chukchi Sea in late summer and fall, and shearwaters altered their distribution across the Chukchi Shelf (Kuletz et al., 2024; Case Study No. 2).

Based on both satellite-tagged birds and at-sea surveys, some seabird species that nest in temperate and Subarctic regions migrate to Arctic waters for brief periods (weeks) after their breeding periods. In the North Pacific, ancient murrelets (*Synthliboramphus antiquus*) that breed on islands in British Columbia and the Aleutian Archipelago migrate to the northern Bering and Chukchi seas (Day et al., 2013; Gaston et al., 2017). Kittlitz's murrelets (*Brachyramphus brevirostris*) nest in Subarctic coastal areas of the northern Gulf of Alaska and migrate to the Arctic post-breeding (Day et al., 2013; Piatt et al., 2021). While abundance in the Arctic for both of these (primarily piscivorous) small alcid species have varied interannually, the long-term trend shows increasing numbers during late summer and fall in the northern Bering and Chukchi seas (Day et al., 2013; Kuletz et al., 2020). These species return south in the late fall when the hours of darkness increase and formation of sea ice begins (currently, October–November).

The philopatry shown by most seabird species to their traditional breeding sites limits shifts in colony formation as a rapid response to environmental change. However, northward expansions of seabird species are occurring and shifts in migrations northward to new feeding areas during the non-breeding portion of their life cycles have occurred with climate warming. For example, models based on at-sea surveys revealed that the three albatross species (*Phoebastria*) that spend portions of their non-breeding season in the Gulf of Alaska and Bering Sea have

increased in numbers and two of those species have shifted their center of distribution northward in the Bering Sea (Kuletz et al., 2014). These changes indicate new migratory and overwintering patterns because the albatrosses breed on islands in the tropical North Pacific. The locally-breeding northern fulmar (*Fulmarus glacialis*) has also shown a northward shift in its center of distribution in the Bering Sea (Renner et al., 2013), but there is so far no evidence of a shift in breeding distribution. However, in the Atlantic Arctic, a northward shift in breeding has been documented with the establishment of northern gannets (*Morus bassanus*) on the northernmost coasts of Norway and Russia, and as far north as the Bear Island (in 2011), a major northward extension of their breeding distribution. These new colonies in the Arctic are associated with the northward movement of the gannet's prey species, such as herring (*Clupea harengus*) and mackerel, as the Barents Sea is warming (Barrett et al., 2017).

3.2.3 Evidence of changes in stop-over and wintering areas

Migration strategies include the locations of stop-over, staging, and over-wintering areas (Baurer et al., 2008; Newton, 2008), and observations indicate that these portions of the migratory cycle are also undergoing climate-related changes. For example, Steller's eiders (*Polysticta stelleri*) have shifted their main wintering areas from the Baltic Sea to the White Sea, as the latter has become increasingly ice-free in winter (Aarvak et al., 2013).

Documented shifts in the distribution of molting spectacled eiders (*Somateria fischeri*) in the Bering Sea between the 1990's and ca. 2010 could not be correlated with shifts in the distribution of benthic prey or other environmental variables (Sexson et al., 2016). Although the eiders did not change their wintering areas in response to changes in ice conditions, eider survival rates were lowest at either extreme in ice conditions (i.e., having no ice for resting, or lack of open water for foraging) (Christie et al., 2018). In the northern Gulf of Alaska, benthic feeding sea ducks seem to be more resilient to changes in environmental conditions than pelagic-feeding seabirds, highlighting the importance of considering trophic interactions when modeling responses to climate change (Cushing et al., 2018; Robinson et al., 2024).

Some species exhibit long stopovers, sometimes for molting, prior to movements to overwintering sites (Mosbech et al., 2006; Frederiksen et al., 2012; Fort et al., 2013). For example, red-legged kittiwakes leave their central Bering Sea island colonies and move to the western Bering Sea in the fall, before relocating to the southwestern Bering Sea near Kamchatka and Japan in late winter (Drummond et al., 2021). Migration patterns can differ between closely related species (e.g., kittiwakes, Orben et al., 2015a; murres, Takahashi et al., 2021; and puffins, Shoji et al., 2023), and between sexes (e.g., murres, Mosbech et al., 2006; Frederiksen et al., 2016; Huffeldt et al., 2024; Ross's gulls, Gilg et al., 2016b). Both tagging studies and at-sea surveys indicate that interannual variability in spatial distribution during migration is common (e.g., short-tailed shearwaters, Yamamoto et al., 2015; black-legged kittiwakes, Orben et al., 2015b; red phalaropes, Saalfeld et al., 2024). Thick-billed murres in Hudson Bay, Canada, have adjusted timing of departure in fall and arrival in spring as the open-water season has become extended by nearly 3 weeks, and modeling indicates that overwintering sites have shifted

211 km west and 50 km north per decade (Patterson et al., 2021). Behavioral flexibility during the non-breeding season suggests that while changes in sea ice may be a key feature in the High Arctic and can influence actively migrating seabirds, birds may not alter use of overwintering areas in Subarctic regions based solely on ice conditions (e.g., red-legged kittiwakes in the Bering Sea; Orben et al., 2018).

3.2.4 Energetic aspects of climate related changes in migration

Pre-breeding and post-breeding migrations by seabirds often include the need to replenish fat reserves lost during winter or breeding, respectively, or to fuel molting (Markones et al., 2010; Fort et al., 2013). These energetic needs require most seabirds to be “income migrants,” taking advantage of concentrations of prey along their migratory paths. However, short-tailed shearwaters make few foraging stops when migrating from the Arctic back to their Australian breeding grounds (Woehler and Hobday, 2024), and the energetic costs of extending the Arctic portion of their non-breeding route (Kuletz et al., 2020; 2024) could have implications for their survival and reproductive success (Glencross et al., 2021).

3.3 Marine mammals

The Arctic marine mammal community consists of 11 resident Arctic endemic species and ca. 25 seasonally-resident species that migrate into Arctic waters to take advantage of seasonally productive foraging opportunities during the open-water period. Climate change is impacting endemic Arctic marine mammals via both direct alterations to their habitats and indirectly via ecosystem change, as well as changing patterns of human activity (e.g., Kovacs and Lydersen, 2008; Kovacs et al., 2011; 2012; 2021; Gilg et al., 2012; George et al., 2015; Laidre et al., 2015; Descamps et al., 2017; Halliday et al., 2022). Many seasonal migrants are benefitting from longer open-water seasons and are tracking northward shifts of their prey species. Northward shifts in range to track optimal environmental conditions are a predicted response to climate change for Arctic marine mammals, which are highly mobile, large animals (Gilg et al., 2012). The ongoing climate changes are influencing movement patterns on both large and small scales.

3.3.1 Shifts in phenology of Arctic endemic species

Variability in the timing of migration, induced by global warming, has been recorded for many marine mammal species, including Arctic endemics. Most populations of bowhead whales (*Balaena mysticetus*) migrate from key foraging areas, where they have access to seasonally abundant zooplankton prey during the polar summer and fall, to habitats used for mating in winter and calving in spring. Migration timing is linked to the northward sea-ice retreat in spring and the southward sea-ice expansion in the fall for most populations of bowhead whales (but see Lydersen et al., 2012). In recent years, variability in timing of migration has been linked to variability in the timing of the open water season (Druckenmiller et al., 2018). Phenological changes with both earlier migration in the spring (Noongwook et al., 2007; Huntington et al., 2021; Szesciorka and Stafford, 2023) and later migrations in fall (Stafford et al., 2021; Szesciorka et al., 2024) have

been documented in recent decades in the Pacific Arctic, where acoustical time-series data extend over decades and multi-generational Indigenous Knowledge has been documented. Sea surface temperatures have been suggested as one potential cue triggering (or delaying) migration (Tsjui et al., 2021), along with changes in sea-ice concentrations (Ferguson et al., 2010). Some individual bowheads have ceased migration entirely, remaining in their summering grounds in the Amundsen Gulf and in the eastern Beaufort Sea (Insley et al., 2021; Diogou et al., 2023) and in Cumberland Sound (Fortune et al., 2020), although this pattern may have existed undetected prior to telemetry studies.

Many populations of beluga whales (*Delphinapterus leucas*) undertake cyclical annual migrations, moving between summering grounds and offshore wintering areas, which are often within drift-ice areas or near ice edges. Large beluga whale populations that occupy High Arctic areas tend to migrate greater distances relative to small populations, which have relatively localized regional movements (Luque and Ferguson, 2009; McGuire et al., 2020; Lydersen and Kovacs, 2021). Tagging data from 1998 to 2002 and 2007–2012 indicated that during the latter period (which had less sea ice and a later freeze-up), Chukchi Sea beluga whales delayed fall migration by 2 to >4 weeks (Hauser et al., 2017).

Most narwhal (*Monodon monoceros*) populations aggregate in predictable coastal areas during summer and then migrate to ice-covered areas offshore before the onset of heavy ice formation. Kenyon et al. (2018) and Shuert et al. (2022) documented significant delays in the timing of fall migrations using tracking data that extend over two decades in the Canadian Arctic; these time frames match climate-driven rates of sea-ice loss for the region.

Few long-term tracking studies exist for Arctic endemic seals, although some species undertake extensive migrations. The Atlantic drift-ice seals, harp seals (*Pagophilus groenlandicus*) and hooded seals (*Cystophora cristata*), breed in spring in southern parts of their ranges, but migrate northward to molt and to forage throughout the summer in Arctic waters, before returning south again in fall (see Vacquié-García et al., 2024). Hooded seals have undergone significant changes in phenology of their movements, with earlier departures north and delayed departures southward (see Case Study No. 3), resulting in an extended period of Arctic residency. Summer foraging migrations of ringed seals (*Pusa hispida*) to preferred sea-ice concentrations start at similar times compared to the past, but now require longer travel distances compared to decades ago (Freitas et al., 2008; Lone et al., 2019; Ogloff et al., 2021).

Most Pacific walrus (*Odobenus rosmarus divergens*) follow seasonal migration patterns between southern wintering areas and northern summering areas. Sea-ice changes in the Pacific Arctic have resulted in changes in the phenology of migration, with walrus arriving earlier and staying later in their Chukchi Sea summering areas during 2008–2011, compared to past decades, until they return south to the Bering Sea following the expansion of winter sea ice (Jay et al., 2012).

Female polar bears generally migrate between foraging areas on offshore sea ice during summer and denning areas on land for the winter, and landfast sea ice is an important spring foraging area for mothers with young-of-the-year cubs (Rode et al., 2015). However, there are exceptions to these patterns, e.g., denning occurs on the sea ice in the Beaufort Sea, and a proportion of the Barents Sea polar

bear population remains ashore year-round (Aars et al., 2017; Rode et al., 2022). It is likely that some immature or adult male bears remain in offshore habitats year-round, but tracking data is lacking for these groups of bears. Reductions in sea ice are resulting in phenological changes to the movement patterns of bears, with some moving onto land earlier in the fall and departing later in the spring (Rode et al., 2015; Escajeda et al., 2018; Laidre et al., 2018; Atwood et al., 2021).

3.3.2 Shifts in phenology of seasonal migrants

Based on passive acoustic monitoring (2012–2019), gray whales (*Eschrichtius robustus*) have shown little change in spring arrival timing in the Pacific Arctic, but they have been departing the northern Bering Sea and southern Chukchi Sea earlier each year since 2016; it is uncertain whether this is a major phenological change or whether it is simply an east-west range shift away from the recorder sites (Moore et al., 2022). Other seasonal migrant cetaceans, including blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), minke (*B. acutorostrata*), sperm (*Physeter macrocephalus*), and killer whales (*Orcina orca*) arrive earlier to high latitudes, and depart later in the northeast Atlantic Arctic (Storrie et al., 2018; Bengtsson et al., 2022; Stafford et al., 2022; 2024). Some species (e.g., fin whales) that were summer residents in the past are currently detected acoustically at high latitudes year-round (Ahonen et al., 2021). Killer whales have extended their season of residence both in the Canadian High Arctic and in the Pacific Arctic (Higdon et al., 2014; Stafford, 2019), indicative of expanded migratory routes and timing, with evidence that some killer whales traveled to the Arctic from tropical waters (Matthews et al., 2020; 2024).

3.3.3 Shifts in distribution of Arctic endemic species

Bowhead whales in the Bering-Chukchi-Beaufort region have wintered farther north into the Chukchi Sea during 2018 and 2019, away from their typical winter home range in the western Bering Sea, which was devoid of sea ice those years (Citta et al., 2023). Aerial survey data indicate a westward shift (closer to Point Barrow) during fall migration of bowheads during 1997–2014, compared to 1982–1996, which corresponds to a shift closer to shore with more open water in recent years (Druckenmiller et al., 2018). In West Greenland, bowhead whale movements away from traditional summering areas in Disko Bay have occurred with the animals shifting southward, tracking SST patterns, with the whales specifically targeting a narrow range of temperatures, between -0.5°C and 2°C (Chambault et al., 2018).

Shifting of migratory pathways to reach new areas has been documented for narwhals that formerly resided in Eclipse Sound in the eastern Canadian Arctic, but now travel to Admiralty Inlet and Prince Regent Inlet (Kenyon et al., 2018). High levels of human disturbance associated with heavy vessel traffic servicing an industrial mine (Witting, 2023), as well as killer whale predation, have been suggested as the principle causes of this change (Lefort et al., 2020). Influx of warm Atlantic water (with associated boreal prey) has changed the coastal distribution of belugas on the west side of Svalbard. Previously, belugas in this area foraged on Arctic cod almost exclusively at tidewater glacier

fronts and migrated between such areas along the coastlines (Lydersen et al., 2001; 2014; Vacquié-Garcia et al., 2018). However, they now spend much more time away from shore in the fjords, occupying different water masses, presumably to feed on small boreal fish species (Hamilton et al., 2019). In contrast, belugas in the Pacific Arctic have not significantly shifted their habitats despite loss of sea-ice cover during 1990–2014 (Hauser et al., 2018a).

Changes in sea-ice distribution (mainly, summer sea-ice edges occurring farther north) have resulted in much longer migrations for ringed seals in the Barents Region, as well as changes in their foraging behavior (Hamilton et al., 2015). Young animals must travel farther north to reach sea ice and adult ringed seals that stay in coastal areas around Svalbard now have very restricted movement patterns compared to a few decades ago, with small home ranges, where they show increased foraging effort (Hamilton et al., 2016; 2019).

Previously, when sea ice remained throughout the year over the shallow shelf of the Pacific Arctic, female walrus and young animals remained year-round near the sea ice, which serves as a haul-out platform. With the retreat of the sea ice northward over the deep Arctic Ocean, females and young now move to land-based haul-out sites along the coasts of Alaska and Russia between feeding trips, where male walrus also gather (Jay et al., 2012). Disturbances at these mixed-sex, high-density haul-outs have resulted in increased calf mortality from stampedes, at levels that can negatively impact population demographics (Udevitz et al., 2012).

Polar bear migrations have tracked sea-ice reduction in some parts of the species' range. In Svalbard, bears no longer migrate south to islands (e.g., Hopen Island) that were previously key sites for denning, because sea ice no longer forms this far south in the late fall-early winter (Andersen et al., 2012). Female bears leave the coastal sea ice in early summer and travel on shore, feeding at ground nesting bird colonies along the west coast (Hamilton et al., 2017; Bengtsson et al., 2021). Olson et al. (2017) have documented a trend toward less denning on sea ice and more denning on land for the polar bear population in the southern Beaufort Sea. In this region, declines in sea ice have resulted in divergent movement patterns, with most of the subpopulation remaining on sea ice during summer, though some animals remain on land. The bears on ice have increased their home range sizes and migrate longer distances, while bears on land exhibit vastly smaller (88% less) annual utilization distributions (Pagano et al., 2021). Similarly, the Chukchi Sea polar bears are moving onto land for longer time periods due to reduced sea-ice cover (Rode et al., 2015; 2022). In Baffin Bay in the 1990s, summer offshore sea ice allowed polar bears to move widely, but its disappearance in the 2000s led to reduced movement rates (Laidre et al., 2018). During this time, adult females favored lower sea-ice concentrations when it provided access to the continental shelf and delayed den entry accounting for shorter denning durations (Escajeda et al., 2018). In Hudson Bay, polar bears are spending more time on sea ice that is distributed farther north than in the past (Miller et al., 2022), with their migrations to and from coastal areas being tightly coupled to sea-ice concentrations and fragmentation (Biddlecombe et al., 2021). Migrations involve significantly more swimming time for polar bears in areas where sea ice has declined, which has energetic implications for individuals (Piffold et al., 2017).

3.3.4 Shifts in distribution of seasonal migrants

Northward shifts in migration endpoints (seasonal distributions) for many migratory cetaceans including blue, fin, humpback, minke, killer, and sperm whales have been documented over recent decades (Brower et al., 2018; Storrer et al., 2018; Stafford, 2019; Stafford et al., 2022; Lydersen et al., 2020; Ahonen et al., 2021; Bengtsson et al., 2022; Heide-Jørgensen et al., 2022; Pöyhönen et al., 2024). The Nunavummiut, Inuit residents of Nunavut, have observed an increase in killer whales in Nunavut waters associated with reductions in sea ice and changing movement patterns of other marine mammals that killer whales prey upon (Higdon et al., 2014). Increasing presence of sperm whales and northern bottlenose whales (*Hyperoodon ampullatus*) has been observed in Baffin Bay, coincident with the longer open-water season and expanded northward migratory routes (Posdaljian et al., 2022; Davidson et al., 2023). Harbor porpoises (*Phocoena phocoena*) have been detected in mid-winter in Kotzebue Sound in the Chukchi Sea, which likely reflects a recent northward extension of their migration patterns (Whiting et al., 2020).

4 Discussion

The decline in area, thickness, and seasonal duration of sea ice within the last 20 years has greatly altered the Arctic ecosystem, and this trajectory is predicted to continue as northern-latitude temperatures increase (Barber et al., 2015; Hunt et al., 2016; Ballinger and Overland, 2022; IPCC et al., 2023), due to anthropogenic carbon emissions (Kumar et al., 2020; Carvalho et al., 2021). The biological importance of the marginal ice zone (MIZ), or ice edge, to Arctic vertebrates has long been recognized (Divoky, 1977; Bradstreet and Cross, 1982; Hunt et al., 1996; Stirling, 1997). For many Arctic upper trophic level animals, their migratory timing and distribution track the MIZ because the mix of open water and ice-associated primary productivity support prey from invertebrates to forage fishes, and from benthic to pelagic food webs (Bradstreet and Cross, 1982; Keđra et al., 2015; Axler et al., 2023). As the MIZ has retreated earlier in spring and moved farther north (Perrette et al., 2011), it has potential to impact migratory movements at multiple trophic levels. Although we lack historic data on the migration patterns of many Arctic species, there is mounting evidence that the rapid changes occurring in the Arctic, particularly during spring through fall, have already resulted in changes in marine vertebrate migrations.

Climate change continues to alter open water patterns, sea-ice habitat and associated prey, timing of prey availability, and accessibility of foraging and travel routes. Changes in the temporal and spatial characteristics of habitat and prey in these circumpolar regions will alter species composition, biodiversity, and food web characteristics. The reduction in sea ice will also influence human activities, with increases in vessel traffic, oil, gas, and mining exploration and extraction, and coastal construction being likely in many areas, introducing artificial light sources, ocean noise, and risks of collisions that can impact migratory behaviors of some species (Reeves et al., 2014; Ivanova et al., 2020; Gjerdrum et al., 2021; Burt et al., 2023; Witting, 2023).

Sea-ice cover influences basic marine productivity (Arrigo et al., 2008) and access to prey (Benoit et al., 2010), and therefore affects both temporal and spatial aspects of migration. However, because of the extreme seasonal patterns of daylight in the Arctic, the temporal boundaries on primary and secondary production likely restrain the effectiveness of phenological responses of marine vertebrates to environmental change, especially for species that breed in the Arctic. Adaptation will thus often require alterations in spatial patterns of migration. The extent to which upper trophic level taxa can adjust their phenologies, habitat use, prey type, and spatial distribution will determine their resilience to ecosystem changes brought about by climate change. Where data are available, the emerging pattern among Arctic vertebrates is to change both spatial routing and temporal duration of migrations.

4.1 Influence of ecological barriers and bridges on migratory routes and ecosystems

Sea-ice losses remove an “ecological barrier” for some marine animals, as more open water creates “ecological bridges” across the Arctic, with more access to prey and travel corridors (Heide-Jørgensen et al., 2011; McKeon et al., 2016; Briscoe et al., 2017). Less ice in the Central Arctic Ocean will also open up new and energetically favorable migration routes for birds (Clairbaux et al., 2019). Shifting ranges northward to track optimal environmental conditions is a predicted response to climate change for Arctic animals, particularly for highly mobile, large-bodied marine mammals (Gilg et al., 2012). Consequently, changes in migratory patterns functionally result in shifts in ranges for these animals. Northward shifts by invertebrates and fish are also likely to play a role in changes in other marine animal distributions, although predation, competition, anthropogenic noise, and other human activities might limit geographic adjustments for some species (Gilg et al., 2012; Reeves et al., 2014; Blackwell et al., 2015; Matthews et al., 2020a; ; 2020b; Halliday et al., 2022).

Northward expansions of Subarctic and temperate marine vertebrates in response to global changes (referred to as borealization, or Atlantification and Pacification), are difficult to separate from changes in migration, and in some cases may just be a matter of semantics. Clearly, migratory pathways have shifted northward or otherwise changed to track favorable habitats (e.g., glacial fjords, or shoals that entrap ice during summer), which effectively becomes a range expansion or contraction. Ectothermic fishes are particularly responsive to temperature, and warmer water temperatures have led to northward expansions of both anadromous and marine species (Dunmall et al., 2024; Haug et al., 2017; Baker, 2021). Warm phases and marine heatwaves can facilitate northward excursions by species such as juvenile Chinook salmon (*Oncorhynchus tshawytscha*) that have moved north in the Bering Sea (Murphy et al., 2017) or sub-adult Chinook salmon from the Pacific Northwest occurring in the Bering Sea (Guthrie et al., 2021). The massive and unprecedented influx of juvenile walleye pollock and Pacific cod into the Chukchi Sea during the 2017–2019 warm phase precipitated ecosystem-wide impacts (Ballinger and Overland, 2022; Cooper et al., 2023; Levine et al., 2023; Kuletz et al., 2024; Case Study No. 2). Conceivably, such shifts

in seasonal migratory patterns and accompanying ecosystem impacts, could become permanent.

The retraction of sea ice also removes essential habitat for some animals and intensifies spatial overlap of species. For example, declines in landfast ice in fjords and along Arctic coasts have increased seasonal mixes of Arctic and Subarctic fish species (Watt et al., 2016; Vihtakari et al., 2018), as well as avian and mammalian species (Higdon et al., 2014; Madsen et al., 2019; Stafford et al., 2022). Ice concentration, wind speed, and wind direction can interact to affect migratory movements; for example, polar bears in Hudson Bay move onto land when wind conditions and temperatures result in early seasonal ice breakup (Bohart et al., 2021). In the western Beaufort Sea, bowhead whales and beluga aggregate where and when favorable wind and current conditions tend to concentrate euphausiids and fish (Ashjian et al., 2010; Okkonen et al., 2011; Stafford et al., 2013). Under similar conditions, aggregations are seen for bowhead whales at Arctic hotspots in Russia, Canada, and Greenland (Citta et al., 2015; Banas et al., 2021). In the Chukchi Sea, such episodic conditions can create hotspots of foraging for seabirds and marine mammals during the late summer and fall migration period (Kuletz et al., 2015), which may influence timing and spatial patterns of migration.

Recently documented overlaps due to new migratory movements indicate disruptions in food webs and altered predator-prey relationships, such as the competition for prey between Atlantic cod and marine mammals in the Barents Sea (Bogstad et al., 2015). Increased numbers of Subarctic species can result in greater competition (e.g., diet overlap), potentially causing declines in endemic populations and affecting ecosystem structure, as postulated for Arctic cod in the Atlantic Arctic, where Subarctic fish species have encroached (Renaud et al., 2012; Christiansen, 2017). While new prey species may be available to predators, the nutrient quality vs capture effort may not be comparable. For example, Subarctic fishes often contain less lipids than Arctic species, or can be an unpredictable food source due to variable abundance, reducing their energetic value to – or predictability for – seabirds and marine mammals (Österblom et al., 2008; Gaston et al., 2009; Hop and Gjørseter, 2013; Descamps and Strøm, 2021).

While Subarctic species are expanding their distributions by altering migratory routes, the distributional ranges of some Arctic species are contracting northward to areas more influenced by sea ice, or to cold deep waters along slopes or basins of fjords (Huserbråten et al., 2019; Bonnet-Lebrun et al., 2021). As Subarctic fish species expand into the Arctic, mainly driven by increasing water temperatures and declining sea-ice distribution (Mueter et al., 2021), there is evidence of ecosystem impacts (Falk-Petersen et al., 2007; Eriksen et al., 2017). Arctic endemic fish species may reach limits in spatial adaptability when moving between breeding and non-breeding areas. The distance to summer Arctic feeding areas may limit the effectiveness of migratory adaptations, due to longer transits and new predators. For example, models for Barents Sea capelin indicate that their populations will shift east and north in summer as ocean temperatures increase, and their spawning areas could potentially also change from the Norwegian coast to include Arctic islands (Huse and Ellingsen, 2008). Increasing distances to northern ice edges are likely to become energetically limiting for some marine mammals (e.g., Freitas et al., 2008;

Lydersen et al., 2014). Likewise, for seabirds that migrate to the Arctic for post-breeding replenishment, the additional distance to prey fields that have moved farther north (Kuletz et al., 2024) may no longer be energetically beneficial for those birds. When summer ice edges occur north of the shelf seas, over deep Arctic Basin waters, low productivity because of limited nutrients affects the abundance of prey species and, thus, will likely limit the northward range expansion of predators.

4.2 Timing of migratory movements and energetic implications

The cues that trigger migratory movements may vary in importance among taxa, and will affect different aspects of their life histories. Ectothermic fishes are more directly impacted by changes in water temperatures, and larval and juvenile stages are subject to passive “migratory” movements, and thus show a rapid, and sometimes dramatic response to altered environmental conditions (Langangen et al., 2016). Fish species that perform multiple lifetime migrations may be particularly vulnerable, given the multiple times they must contend with various stressors to time their migration to match pulses of marine production during spring-summer. Some endothermic long-distance migrants, such as shearwaters, may face similar issues matching movements with prey availability as they navigate between hemispheres. Shearwaters may act more as capital migrants while in the Arctic and Subarctic, by storing fat reserves for long southerly transits with minimal foraging (Woehler and Hobday, 2024). However, large die offs of shearwaters have been observed in Alaska during marine heatwave events (Baduini et al., 2001; Jones et al., 2023), suggesting that this migratory strategy may not be adequate with continued warming of northern oceans. Alternatively, animals that are restricted to a specific type of habitat during migration, or that can only move within a small area, may face even greater impacts from alterations of that habitat due to climate change.

Seabirds are highly mobile, but their breeding season restrictions mean that the greatest shift in timing and habitat use for them are the migratory periods immediately before and after breeding. Tracking data suggest that for some species, overwintering areas can generally be consistent among years (Orben et al., 2015b), although other studies indicate that individuals show flexibility and variability (Guilford et al., 2011). Photoperiod appears to be the critical element for timing of migratory movements for seabirds, even if migratory routes vary, and this may be how mated pairs that migrate and winter apart are able to synchronize their returns to the nest site (e.g., thick-billed murre, Huffeldt et al., 2024). These evolutionary-scale relationships will be strained by the rapid changes in the Arctic environment.

Many marine mammals, which can rely on body fat reserves due to their large body size, have adjusted to changing conditions by arriving earlier and remaining longer in their summer Arctic foraging areas (Hauser et al., 2017; Szesciorka et al., 2024). Some species have individuals that currently remain in High Arctic areas year-round (Insley et al., 2021), thereby increasing opportunities for exchange among populations (Heide-Jørgenson et al., 2011; Ahonen

et al., 2021; Diogou et al., 2023). Changes in Arctic marine mammal migratory routes indicate a primarily northward shift to track suitable oceanographic conditions, ice-edge upwelling areas, or preferred prey (Storrie et al., 2018; Bengtsson et al., 2021; 2022; Citta et al., 2023). Reduced sea-ice conditions have apparently created a “boom time” for large whales in the Pacific Arctic in newly exposed areas (Moore, 2016). However, several Unusual Mortality Events among ice-dependent species of marine mammals in the Pacific Arctic have been linked to reductions in sea ice (Barratclough et al., 2023), highlighting variable results for different species in response to changes in a single driver.

4.3 Social and ecological impacts

Increases in ship traffic and other human activities have already been observed in the Arctic, with anticipated effects on movements of some fishes (e.g., Arctic cod, Ivanova et al., 2020), seabirds (Merkel and Johansen, 2011; Gjerdrum et al., 2021) and marine mammals (Reeves et al., 2014; Hauser et al., 2018b; Silber and Adams, 2019; Halliday et al., 2021). Another risk for endemic Arctic species is the possibility of novel pathogens arriving via Subarctic species spending more time in the Arctic (Greer et al., 2008; Barratclough et al., 2023).

For most Arctic, and many Subarctic species, limited historic and current data make forecasts regarding changes in migratory phenology and routes challenging. Changes that have occurred also impact the quality of species’ monitoring; for example, new wintering areas may be more remote than traditional sites already monitored (e.g., Fox et al., 2019), or new migration routes and stopovers are not yet discovered. Establishing monitoring programs that are adaptable to such changes will require planning for such contingencies and working with people that live in the Arctic (Kochanowicz et al., 2021; Hauser et al., 2023; Clairbaux et al., 2024).

Ongoing climate changes challenge the resilience and adaptability of Arctic people and ecosystems and will require a close coupling of adaptive monitoring and research, with ecosystem-based management of human activities at all levels, including those involved with Indigenous harvest practices (see Case Study No. 4), as recommended by the Arctic Council (Siron et al., 2008; <https://pame.is/projects/ecosystem-approach>). In nearshore Arctic areas, earlier ice break-up and warming air and SST impact food security and traditional cultural practices that rely on availability and access to migratory marine vertebrates (ICC-Alaska, 2015; Regehr et al., 2017; Falardeau and Bennett, 2020; Ford et al., 2021; Hauser et al., 2021; Falardeau et al., 2022; Ovitz et al., 2024). Indigenous Peoples have been adapting to changing conditions since time immemorial, yet rapid climate-driven changes require adoption of new strategies. Indigenous Knowledge and perspectives in decision-making contribute to interpretation of observed changes in animal migration and equitable solutions to Arctic change (Wong et al., 2020; Hauser et al., 2021; Yua et al., 2022). Additionally, Indigenous Knowledge provides information on long-term changes, including changes in migration phenology or evidence of population fluctuations (Mallory et al., 2003; Moore and Hauser, 2019; Clairbaux et al., 2024).

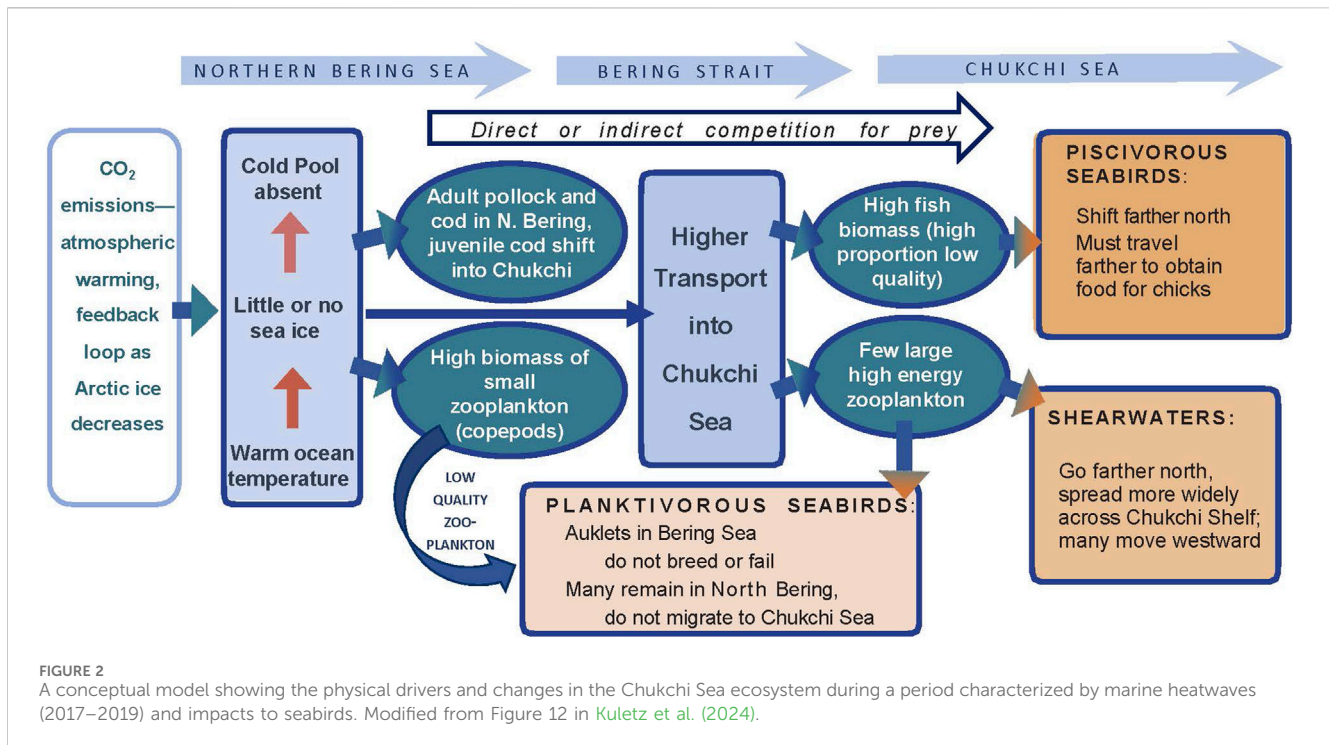
4.4 Conclusion

Unpredictability in Arctic physical and biological conditions is a key current and future challenge for marine vertebrates that rely on migration for survival and reproductive success. Fish species may respond more directly and quickly to physical changes, but many fish species are more limited in mobility than seabirds and marine mammals. Seabirds are highly mobile, but may be more restrained by photoperiod, and less able to use a capital migratory strategy because of their relatively small body sizes, thus temporal and spatial changes to prey could impede their adaptability. Marine mammals have altered their timing and spatial migratory patterns, but prey availability and new predation regimes (i.e., new and longer presence of top predators) may limit the effectiveness of altering migratory patterns. Increased human activity levels in previously ice-covered areas will also influence Arctic ecosystems, while altered animal migration routes and loss of sea ice that facilitated hunting impact Indigenous communities. Monitoring Arctic populations of fishes, seabirds, and marine mammals will require adaptive practices to track shifts in timing and distribution of these important ecosystem components. Habitat declines for ice-dependent Arctic species is a serious threat to global biodiversity, and collaboration among stakeholders is imperative to address these challenges effectively.

5 Case Studies

5.1 Case Study No.1. Ivory gull: an ice-dependent seabird

The ivory gull is probably the most Arctic of all marine birds. It is tightly linked to sea ice habitats throughout the year, where it feeds on a variety of prey ranging from marine invertebrates to seal carcasses (Gilg et al., 2016b; Spencer et al., 2016; Dumas et al., 2022). Ivory gull breeding colonies are located in the High Arctic in Canada, Greenland, and in the High Arctic archipelagos of Svalbard (Norway) and Franz Josef Land (Russia). Tracking studies and observations have shown that the main wintering areas are along ice edges in the Davis Strait and the Bering Sea (Gilg et al., 2010; Spencer et al., 2014; Frederiksen et al., 2021). Notably, ivory gulls consistently migrate along ice edges to areas south of the Arctic Circle, and overwinter where daylight remains available in mid-winter. This pattern is consistent with visual foragers that depend on sufficient light to feed. Winter sea ice is projected to retract northwards, and little ice is expected to occur south of the Arctic Circle in mid-winter by the late 21st century, particularly in the Bering Sea (DeRepenigny et al., 2020; Dörr et al., 2021). The available tracking data are insufficient to demonstrate changes in the timing or pathways of ivory gull migrations, but given the species’ close link to ice-edge habitats and the observed and expected changes in this habitat, changes are likely occurring. The retreat of the marginal ice zone favoured by the ivory gull will impact its migratory pathways, and most of the non-breeding habitat of the ivory gull is projected to disappear. Unless the ivory gull can alter its migratory patterns, such changes in the ice habitat it uses for migration and overwintering, combined with the impact of receding summer sea ice near breeding colonies, puts this iconic species at high risk of decline and possible extinction before the end of the century.



5.2 Case Study No. 2. Seabirds respond to changes in the Chukchi Sea

In the eastern Chukchi Sea of the Pacific Arctic, reduced sea ice and warmer ocean temperatures have led to longer open-water seasons, higher zooplankton abundance and increases in boreal fish species (Mueter et al., 2021). These changes have led to changes in the offshore avian community during the post-breeding period, when seabirds must replenish body reserves and prepare for winter and migrations south. Piscivorous seabirds that nest along the southern Chukchi Sea coast used to be the most abundant seabirds in offshore waters during summers (1970s–1980s), but ship-based surveys during 2007–2012 found that planktivorous seabirds had become more abundant offshore (Gall et al., 2017). The offshore increase in planktivores was primarily due to abundance increases for two species of *Aethia* auklets, which feed on copepods and small euphausiids, and short-tailed shearwaters, which feed on larger euphausiids and small fish; both groups migrate through the Bering Strait into the Chukchi Sea to forage on abundant prey in late summer (Kuletz et al., 2015; Gall et al., 2017). Auklets and other alcids conduct such post-breeding northward migrations from breeding sites in the Bering Sea or even the Gulf of Alaska (Kuletz et al., 2024 and references therein). For the shearwaters, the Chukchi Sea is the northernmost extent of their seasonal migration from Australian breeding grounds (Yamamoto et al., 2015).

Continued warming of the Pacific Arctic may further alter seabird migratory patterns. During a recent period (2017–2019) with multiple marine heatwave events, the Chukchi Sea had high biomass of small zooplankton, but low abundance of large nutrient-rich copepods and euphausiids (Spear et al., 2019; Kim et al., 2020). Concurrently, fish abundance was elevated, including an unprecedented movement of age-0 walleye pollock into the

region (Levine et al., 2023). The lack of a thermal barrier deep in the Subarctic Bering Sea known as the “Cold Pool” allowed adult pollock to shift northward and spawn near the Bering Strait, where warmer conditions led to increased advection through the strait and facilitated juvenile pollock movement into the Chukchi Sea (Baker et al., 2020; Levine et al., 2023; Figure 2). The pollock may have provided new prey to piscivorous birds but could also have competed for zooplankton with planktivorous seabirds and other forage fishes. Concurrently, abundance of the more omnivorous short-tailed shearwater increased greatly, but they were distributed across the shallow Chukchi Shelf (Kuletz et al., 2024) rather than in previously identified hotspots (Kuletz et al., 2015). In contrast, only low numbers of auklets, which experienced breeding failures in the northern Bering Sea (Will et al., 2020), traveled to the Chukchi Sea in 2019 (Kuletz et al., 2024). For highly mobile animals like seabirds, rapid changes in migratory patterns may be possible, but there are likely energetic costs incurred in traveling farther or for longer periods.

5.3 Case Study No. 3. Climate change impacts on hooded seal migration patterns

Hooded seals are Arctic endemic, drift-ice breeding, true seals that migrate between traditional pupping areas in southern parts of their range and traditional molting sites farther north, before dispersing over vast areas where they forage during summer and fall, mostly in High Arctic waters of the North Atlantic (Andersen et al., 2009; Vacquie-Garcia et al., 2017). Climate warming has resulted in increased ocean temperatures and marked reductions in sea-ice thickness, extent, and seasonal duration across the hooded seals’ North Atlantic/Arctic range over the past three decades, with Atlantification of both physical and biological conditions (Kovacs et al., 2021). Few long-term data series are

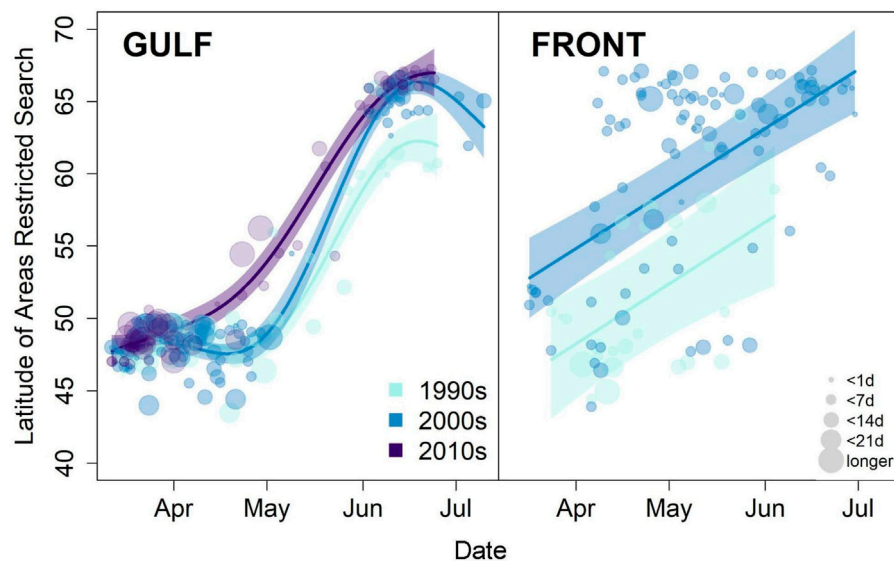


FIGURE 3
Foraging areas (identified along tracks by Areas Restricted Search [ARS] in hierarchical switching state-space models) for hooded seals, with respect to latitude and date, from the Gulf of St. Lawrence (GULF) and the FRONT north of Newfoundland, over three decades (in colors). The size of the circles represents durations of ARSs. Solid lines and shaded areas represent the fitted estimates and their respective confidence intervals (From Vacqu  -Garcia et al., 2024). Results showed earlier and more northerly locations over time (decades).

available for marine mammals that allow for exploration of how such changes influence animals' migration patterns, but a unique 30 years-long tracking data set for hooded seals from the Northwest Atlantic allowed Vacqu  -Garcia et al. (2024) to explore movement patterns in the context of climate change. They found that hooded seals from two breeding areas off the east coast of Canada targeted different environmental conditions. However, each breeding group has remained faithful in their selection of the same oceanographic conditions for their foraging activities over the whole of the study period. Despite different temperature, sea-ice concentration, depth, and salinity preferences, both populations had shifted the phenology of their migration—leaving breeding areas earlier—and also shifted their migratory endpoints to places farther north (Figure 3), to access similar oceanographic characteristics across the decades covered in the study. This northward shift is likely to continue into the future, but the limits to adaptive capacity of hooded seals with respect to the loss of traditional breeding and molting sites are unknown. Hooded seals are already experiencing markedly increased rates of polar bear predation off the east coast of Greenland, where the drift ice now occurs very close to shore compared to decades ago (McKinney et al., 2013), which has become a driver to negative population trends for Greenland Sea hooded seals (Oig  rd et al., 2014).

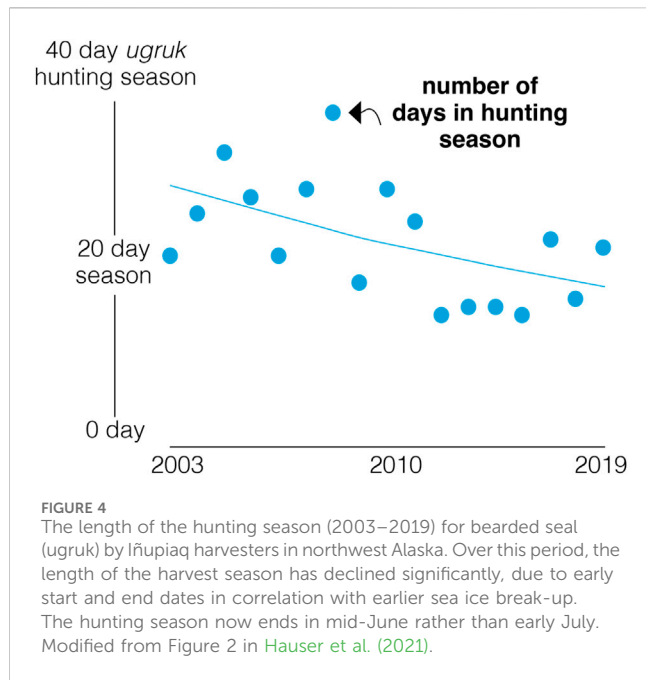
5.4 Case Study No. 4. Arctic changes impact subsistence harvests by Indigenous Peoples

Lifestyles of Indigenous coastal communities in Arctic North America, Greenland, and eastern Eurasia are closely associated with seasonal sea ice. The ability of these communities to engage in the traditional harvests on which they rely are being heavily impacted by a warming environment, largely because of changes to the

spatiotemporal patterns of migratory marine mammals, seabirds, and anadromous fishes (Badjeck et al., 2010; Brewster et al., 2016; ICC-Alaska, 2015; Savo et al., 2017; Huntington et al., 2020). In western Arctic North America, Inuit harvests of seals and anadromous fishes have been impacted by climate change (Hauser et al., 2021; Falardeau et al., 2022).

Many migratory marine mammal species are fundamental to the nutritional, spiritual, and cultural aspects of Indigenous life in coastal Arctic Alaska communities (Huntington et al., 2017). These animals are dependent on sea ice and ocean conditions, and wind and weather conditions can impact the ability of hunters to safely harvest bowhead whales and walrus during the seasonal periods in which they are available (Hansen et al., 2013; Huntington et al., 2013). In Northwest Alaska, an interdisciplinary team of researchers worked with an Inupiaq Elder Advisory Council to understand how bearded seal harvest phenology was changing relative to changing environmental conditions (Hauser et al., 2021). Bearded seals (“ugruk” in Inupiaq), migrate into the region during spring sea ice break-up, relying on ice floes for resting between foraging bouts. This study found that the duration of harvests declined significantly as break-up shifted earlier (Figure 4); this was determined by integrating harvest records, Indigenous Knowledge on conditions impacting bearded seal spring habitat and accessibility of seals to hunters, and remotely-sensed sea-ice data. Indigenous hunters have so far been able to compensate for decreased harvesting periods by changing how they searched for and hunted seals.

Climate change effects on fisheries for Arctic char and Dolly Varden during the open water season, and their quality as a food source for Inuit people, raise concerns pertaining to altered marine habitat use, diet changes affecting flesh quality, exposure to contaminants, and interactions with non-endemic species (Tran



et al., 2019; Chila et al., 2022; Harris et al., 2022; Bolduc et al., 2024; Pearce et al., 2024). Arctic char might become harder to harvest in shore-based gill net fisheries during summer, as the char follows preferred cooler temperatures to deeper areas farther from shore (Harris et al., 2022). Nearshore habitat-use and marine spatial distribution of Dolly Varden are influenced by SST and ice conditions (Gallagher et al., 2021). The increasing loss of coastal ice during summer has impacted Dolly Varden harvests as the presence of drifting ice improves catches of fish (Brewster et al., 2016; WMAC and Aklavik HTC, 2018). Additionally, increased frequency and strength of wind and wave activity impedes the travel to coastal fishing camps and also the ability to deploy gill nets, which is further exacerbated by coastal erosion (Brewster et al., 2016; Kokelj et al., 2021; Pearce et al., 2024). The challenges posed by changes in fish habitat use, accessibility to fishing locations, and long-term changes in the fish community composition in the western Arctic (Brewster et al., 2016; Priest et al., 2022; von Biela et al., 2023) require harvesters to adjust fishing practices, which will have social and economic consequences for Indigenous communities.

Author contributions

KJK: Conceptualization, Investigation, Methodology, Project administration, Supervision, Writing–original draft, Writing–review and editing, Visualization. SF: Conceptualization, Investigation, Methodology, Writing–original draft, Writing–review and editing. MF: Conceptualization, Investigation, Methodology, Writing–original draft, Writing–review and editing. CG: Conceptualization,

Investigation, Methodology, Writing–original draft, Writing–review and editing. DH: Conceptualization, Investigation, Methodology, Writing–original draft, Writing–review and editing, Visualization. HH: Conceptualization, Investigation, Methodology, Validation, Writing–original draft, Writing–review and editing. KMK: Conceptualization, Investigation, Methodology, Visualization, Writing–original draft, Writing–review and editing, Resources. CL: Conceptualization, Investigation, Methodology, Writing–original draft, Writing–review and editing. AM: Conceptualization, Investigation, Methodology, Writing–original draft, Writing–review and editing. AS: Conceptualization, Investigation, Methodology, Writing–original draft, Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer LQ declared a past co-authorship with the authors KMK and CL to the handling editor.

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