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Climate change and mercury in the Arctic: Biotic interactions



Melissa A. McKinney^{a,*,1}, John Chételat^{b,1}, Samantha M. Burke^c, Kyle H. Elliott^a, Kim J. Fernie^d, Magali Houde^e, Kimmo K. Kahilainen ^f, Robert J. Letcher ^b, Adam D. Morris ^g, Derek C.G. Muir ^h, Heli Routti ⁱ, David J. Yurkowski ^j

body condition may increase biotic mercury

- a Department of Natural Resource Sciences, McGill University, Sainte-Anne-de-Bellevue, QC H9X 3 V9, Canada
- ^b Ecotoxicology & Wildlife Health, Environment and Climate Change Canada, National Wildlife Research Centre, Carleton University, Ottawa, ON K1A 0H3, Canada

GRAPHICAL ABSTRACT

How does climate change alte mercury exposure in Arctic b

- ^c Minnow Aquatic Environmental Services, Guelph, ON N1H 1E9, Canada
- d Ecotoxicology & Wildlife Health, Environment and Climate Change Canada, Burlington, ON L7S 1A1, Canada
- Aquatic Contaminants Research Division, Environment and Climate Change Canada, Montréal, QC H2Y 5E7, Canada
- f Lammi Biological Station, University of Helsinki, FI-16900 Lammi, Finland
- 8 Northern Contaminants Program, Crown-Indigenous Relations and Northern Affairs Canada, Gatineau, QC J8X 2V6, Canada
- h Aquatic Contaminants Research Division, Environment and Climate Change Canada, Burlington, ON L7S 1A1, Canada
- ⁱ Norwegian Polar Institute, Fram Centre, NO-9296 Tromsø, Norway
- ^j Arctic Aquatic Research Division, Fisheries and Oceans Canada, Winnipeg, MB R3T 2N6, Canada

HIGHLIGHTS

· Climate change effects on Hg in Arctic biota are reviewed.

- · Increased foraging on land versus sea ice may lower Hg in some predators.
- Climate change influences Hg in Arctic freshwater fishes in a lake-specific manner.
- · Hg in marine biota is associated with wind, ice, diet or body condition changes.
- · Climate processes impacting biotic Hg are complex, with uncertain net effects.

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ABSTRACT

Global climate change has led to profound alterations of the Arctic environment and ecosystems, with potential secondary effects on mercury (Hg) within Arctic biota. This review presents the current scientific evidence for impacts of direct physical climate change and indirect ecosystem change on Hg exposure and accumulation in Arctic terrestrial, freshwater, and marine organisms. As the marine environment is elevated in Hg compared to the terrestrial environment, terrestrial herbivores that now exploit coastal/marine foods when terrestrial plants are iced over may be exposed to higher Hg concentrations. Conversely, certain populations of predators, including Arctic foxes and polar bears, have shown lower Hg concentrations related to reduced sea ice-based foraging and increased land-based foraging. How climate change influences Hg in Arctic freshwater fishes is not clear, but for lacustrine populations it may depend on lake-specific conditions, including interrelated alterations in lake ice duration, turbidity, food web length and energy sources (benthic to pelagic), and growth dilution. In several marine mammal and seabird species, tissue Hg concentrations have shown correlations with climate and weather variables, including climate oscillation indices and sea ice trends; these findings suggest that wind, precipitation, and cryosphere changes that alter Hg transport and deposition are impacting Hg concentrations in Arctic marine organisms. Ecological changes, including northward range shifts of sub-Arctic species and altered body condition, have also been shown to affect Hg levels in some

E-mail address: melissa.mckinney@mcgill.ca (M.A. McKinney).

These authors contributed equally to the work.











Corresponding author.

populations of Arctic marine species. Given the limited number of populations and species studied to date, especially within Arctic terrestrial and freshwater systems, further research is needed on climate-driven processes influencing Hg concentrations in Arctic ecosystems and their net effects. Long-term pan-Arctic monitoring programs should consider ancillary datasets on climate, weather, organism ecology and physiology to improve interpretation of spatial variation and time trends of Hg in Arctic biota.

1. Introduction

Consistent with the Arctic's particular sensitivity to global climate change (Meredith et al., 2019), profound changes have been documented across Arctic terrestrial, freshwater, and marine ecosystems. In lockstep with physical changes to the cryosphere (AMAP, 2017; Box et al., 2019), documented ecological shifts include: increased marine primary production, reduced population sizes of some ice-dependent species, northward shifts in the ranges of sub-Arctic and temperate marine and terrestrial species, and altered trophic structuring (Post et al., 2009, 2013; Fossheim et al., 2015; Pecl et al., 2017). The strong seasonality of the Arctic is critical for Arctic ecosystem structure and function; thus, climate change-driven dampening of seasonal variation and the associated reduced ability of species to shift resource use through time are predicted to destabilize the Arctic's seasonally structured food webs (McMeans et al., 2015). Climate change-driven physical and ecological shifts are both likely to impact the accumulation of mercury (Hg) within Arctic biota (Stern et al., 2012).

Global climate change may impact Hg deposition and abiotic cycling, including Hg speciation, in the Arctic (Chételat et al., 2022; this issue), as well as the uptake (Poste et al., 2019; Hudelson et al., 2019) and transfer of methylmercury (MeHg) in food webs (Braune et al., 2014a; McKinney et al., 2017a; Kozak et al., 2021), all of which can modulate Hg concentrations in Arctic biota. Indeed, trends of Hg, as measured in aquatic biota, do not always track recent declining atmospheric trends well, and climate change has been suggested to be the leading cause of this discrepancy globally, including in the Arctic (Wang et al., 2019). Both direct physical change (Chételat et al., 2022) and indirect ecosystem change (see Section 2) may impact the exposure to, and accumulation of, Hg in Arctic biota. When it comes to physical changes, altered Hg transport and deposition and biogeochemical processes may impact Hg levels and forms within and among Arctic environments (Chételat et al., 2022), and thus Hg exposure and uptake at the base of terrestrial, freshwater, and marine food webs of the Arctic ecosystem. In addition, extensive climate-driven ecological and physiological changes, from altered ingestion and elimination rates to the introduction of northward-range-shifting sub-Arctic species, may alter biotic Hg exposure.

Nonetheless, climatic changes vary among Arctic ecosystems, and thus climate change influences on Hg in Arctic biota may as well. For example, the extent of air and ocean warming, sea-ice loss, and snow cover reductions varies within the Arctic (AMAP, 2017). Similarly, climate change is affecting ecological processes on multiple temporal scales and may be environment-specific, from lengthening of the Arctic growing season and increased rain-on-snow events in terrestrial ecosystems (Ernakovich et al., 2014; Peeters et al., 2019), to input of glacier melt and increases in suspended solids in freshwater ecosystems, to continued multi-decadal declines of sea-ice in marine ecosystems (AMAP, 2017). For example, the loss of multi-year sea ice in the marine environment is having ecological effects, e.g., on productivity and species interactions (Post et al., 2013), and many of those effects are not relevant to Arctic freshwater lakes. Thus, it is appropriate to evaluate spatial variation in climate change-Hg interactions in biota across terrestrial, freshwater, and marine ecosystems, as well as temporal variation across seasons, years, and decades.

The objective of this review is to summarize the scientific evidence as to how global climate change affects Hg exposures and bioaccumulation in Arctic biota, and it is based on the recent AMAP Assessment 2021: Mercury in the Arctic (AMAP, 2021). A separate article in this special issue synthesizes the available literature on how climate change affects abiotic Hg cycling in the Arctic (Chételat et al., 2022). Since the previous 2011 AMAP

Hg assessment (AMAP, 2011) a decade ago, several studies have been published documenting empirical, experimental and/or modeling evidence connecting climate change processes to influences on biotic (as well as abiotic) Hg concentrations. The current review begins by providing a brief overview of what is known about the effects of climate change on ecosystems in the Arctic. It then outlines the available studies examining connections between global climate change and Hg accumulation in Arctic biota, sequentially covering terrestrial, freshwater, and marine ecosystems (Fig. 1). This article is connected to additional articles in this special issue, including how climate change is influencing the temporal trends of Hg in Arctic biota (Morris et al., this issue), as well as the synthesis of processes affecting Arctic environmental Hg (Dastoor et al., 2022; Jonsson et al., 2022), concentrations and effects of Hg in Arctic biota (Barst et al., 2022; Dietz et al., this issue; Chastel et al., 2022) and on human health (Basu et al., 2022). The review closes by providing conclusions and recommendations for future research directions on the influence of climate change on Hg in Arctic biota.

2. How has climate change affected Arctic ecosystems?

2.1. Terrestrial ecosystems

The Arctic tundra biome makes up approximately 5% of the land surface of the Earth, and this biome is largely located in coastal areas that are less than 100 km from seasonally ice-covered seas (Ims et al., 2013). The longevity of sea ice therefore likely has a large influence on temperature and climate and consequently on the productivity of Arctic tundra ecosystems (Bhatt et al., 2010). These Arctic terrestrial ecosystems are characterized by low primary productivity, which restricts the length and complexity of food webs and decomposer webs (Ims et al., 2013).

Ecological responses of Arctic terrestrial ecosystems to climate change show generally large variation among regions, which is related to a high spatial variation in physical change itself (e.g., in temperature and snow cover) (Ims et al., 2013). Most research to date has focused on the effects of climate change on one trophic level in isolation, and mainly on either plants or herbivorous mammals. Within the Arctic tundra, vegetation is "greening" in association with increasing land surface temperatures (Jenkins et al., 2020). Monitoring and experimental studies across the circumpolar Arctic suggest that the abundances of grasses and grass-like plants and shrubs have responded positively to warming and that this pattern is expected to continue over time (Bjorkman et al., 2020; Elmendorf et al., 2012). Although some studies show earlier leaf emergence and flowering with rising temperatures, there have not been consistent responses observed in plant flowering or leaf emergence or senescence (Bjorkman et al., 2020). Within the soil, microbial decomposition of soil organic matter is accelerating due to a warming climate in the Arctic, and these decomposition processes are enhanced by the increasing presence of plant roots (Keuper et al., 2020; Schuur et al., 2015).

Among herbivorous mammals, lemmings represent an important herbivore of Arctic tundra ecosystems as they provide a key link in the transfer of energy from plants to mammalian and avian predators (Gilg et al., 2003). Although climate warming has been documented to negatively affect lemming populations in the Low Arctic, which co-occur with boreal voles, no consistent global declining trend for lemmings in the Arctic has been found (Ehrich et al., 2020). Reindeer and caribou (*Rangifer tarandus* and its subspecies) are the most abundant among the large herbivores of Arctic terrestrial ecosystems. Their large range from woodlands to the High Arctic indicates they can cope with differing environmental conditions (Yannic

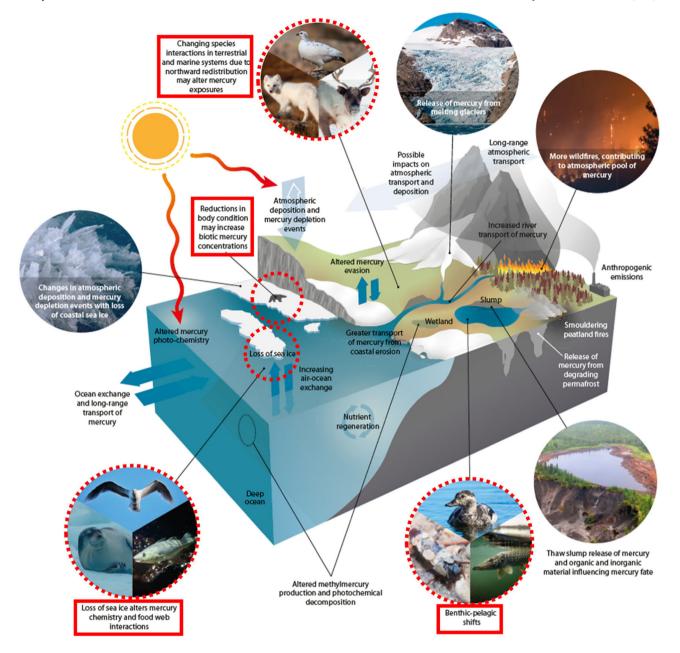


Fig. 1. Conceptual diagram highlighting key physical and ecological changes occurring in the Arctic's marine, terrestrial, and freshwater ecosystems (circled in red) within which the bioaccumulation of mercury may be affected. Abiotic interactions of climate change and mercury are discussed in Chételat et al. (2022) (this issue).

et al., 2017), which suggests possible resilience to climate change. Overall, studies focusing on the effects of climate change on reindeer and caribou suggest that the responses vary across their circumpolar distribution (Mallory and Boyce, 2017), as explained below. Warm weather and rainon-snow events that entirely cover short-growing vegetation across large areas of tundra are occurring more frequently in the High Arctic (Bintanja and Andry, 2017; Peeters et al., 2019). These events have been shown to negatively impact mortality and fecundity of High Arctic tundra herbivores at high population densities (Hansen et al., 2013). However, warmer autumns promote population growth and may counteract the effects of harsh winters (Loe et al., 2021). Contrasting responses of Svalbard reindeer (Rangifer tarandus platyrhynchus) were reported at local scales resulting in diverging population trends (Hansen et al., 2019a). The net effects of climate change were shown to be negative for a coastal Svalbard reindeer population, but positive for a continental reindeer population (Hansen et al., 2019a). Also, behavioral changes and use of alternative landscapes and food resources may provide a buffer for the effects of environmental

changes (Loe et al., 2016; Hansen et al., 2019b). For example, the proportion of Svalbard reindeer feeding along the shoreline, partly on kelp, has increased along with icier winters (Hansen et al., 2019c).

Relatively large changes have been observed in tundra bird populations, although evidence linking these changes to climate change is limited (Smith et al., 2020). In terms of shoreline and nearshore species, opposing trends have been observed for waders and waterfowl across the circumpolar Arctic: more specifically, over half of wader taxa are declining, while almost half of all waterfowl are increasing (Smith et al., 2020). Of the birds of prey, peregrine falcon (*Falco peregrinus*) and gyrfalcon (*Falco rusticolus*) populations are generally considered to be stable (Franke et al., 2020). However, the population trends for ptarmigan (*Lagopus* spp.) vary among regions (Fuglei et al., 2020).

Several studies have shown that boreal species are increasingly present in the Arctic tundra. Range expansion of moose (*Alces alces*) and several boreal and sub-Arctic birds into the tundra has been related to longer growing seasons and increasing shrub habitat (Sokolov et al., 2012; Tape et al., 2016),

whereas climate-related changes in tundra stream habitats, as well as population recovery after overhunting, may have led to beavers (*Castor canadensis*) colonizing the Arctic tundra (Tape et al., 2018). Increased abundance of red foxes (*Vulpes vulpes*) and hooded crows (*Corvus cornix*) has been reported and was suggested to be related to high mortality of domestic reindeer following icing of the snow layer in Yamal, Russia (Sokolov et al., 2016), but red fox expansion into the Canadian Arctic has been explained by increased human activity (Gallant et al., 2020).

2.2. Freshwater ecosystems

Some of the major ecological impacts of climate change in Arctic regions are related to strong increases in temperature and productivity of both terrestrial catchments and aquatic ecosystems (De Wit et al., 2016; AMAP, 2017). These increases have ubiquitous effects across ecosystems, communities, populations and individuals (e.g., Post et al., 2009; Scheffers et al., 2016; Rolls et al., 2017). Glacier melting increases concentrations and seasonal exposure of suspended solids in freshwater ecosystems, with pronounced effects: reduced light penetration, lowered temperature, and increased conductivity (Lento et al., 2019). In general, permafrost thaw and increasing rain bring more nutrients, carbon, and catchment-stored Hg into lakes and rivers (De Wit et al., 2016; AMAP, 2017; Schuster et al., 2018; Lento et al., 2019). Within lakes and streams, an increased amount of terrestrial vegetation in catchments elevates the dissolved organic carbon (DOC) concentrations in water, which leads to shading effects that limit productivity of benthic algal communities (Forsström et al., 2013). Nonetheless, these changes are occurring in a lake-specific fashion. Small and shallow lakes are reacting to such changes much faster than are large and deep lakes, which are more resilient with thermal refuges and volumetric buffering against abrupt changes to alternative states (Scheffer and Carpenter, 2003; Hayden et al., 2019).

There remain large information gaps in understanding effects of climate change on freshwater species, including fishes in different Arctic regions (Laske et al., 2022; Goedkoop et al., 2022). As is happening in terrestrial and marine ecosystems, climate warming is enhancing the range expansion of new freshwater species adapted to warmer temperatures (Post et al., 2009; Rolls et al., 2017). Such effects can be very fast in taxa with high dispersal abilities via wind (plankton, benthic invertebrates, macrophytes) and waterbirds, but dispersal of fish is limited by the requirement for connectivity of watercourses or salt tolerance when colonizing Arctic islands (Laske et al., 2022; Lau et al., 2022). Warm-adapted fish species, such as percids (Percidae), sticklebacks (Gasterosteidae) and cyprinids (Cyprinidae) are anticipated to expand their northward range, particularly between boreal and subarctic regions (Rolls et al., 2017; Laske et al., 2022). New colonizers often initially increase the number of links in food webs but may also have strong competitive and predatory interactions with native fauna with potential alterations of energy and Hg flows in food webs (Thomas et al., 2016; Rolls et al., 2017; Barst et al., 2020). In a series of sub-Arctic lakes along climatic and productivity gradients of northern Finland, lakes with higher numbers of warmer-adapted fish species had longer food chain lengths and higher Hg content in a top predator fish, northern pike, while the Hg trophic magnification slope decreased (Kozak et al., 2021). In this study, mercury trophic magnification slope was explained jointly by environmental (climate-productivity, lake morphometry, catchment characteristics) and biological factors (food chain length, top predator lipid content), illustrating the overall complexity when assessing the climate change induced changes in lake food webs.

2.3. Marine ecosystems

The Arctic Ocean and related water bodies make up about 4% of the Earth's surface. Arctic marine ecosystems are characterized by strong seasonal changes with a pulse in primary productivity in surface waters associated with melting of the sea-ice. Many taxa in Arctic marine ecosystems are pagophilic (ice-loving) and require ice for at least part of the year (Post et al., 2013). A variety of physical changes impacting oceans worldwide,

including increasing temperature, changing acidity and altered freshwater inputs, are also occurring in the Arctic (Chételat et al., 2022); but, because of the importance of pagophilic species, responses to ice, unique to polar seas, often overwhelm other ecosystem changes (Post et al., 2013; Harwood et al., 2015). Altered Arctic marine ecosystems due to a changing climate will ultimately be due to changes in physical processes (Chételat et al., 2022). However, responses can be compounded by the emergent processes occurring in complex food webs (i.e., trophic cascades and food web topologies; Zarnetske et al., 2012). Thus, responses to climate change include both direct responses (thermal or acidity tolerance) and indirect responses (top-down, bottom-up and horizontal processes).

Perhaps the greatest direct impact of climate change on marine species is loss of ice. Reduced ice is increasing solar radiation and nutrient replenishment, leading to increases in primary production in the Arctic Ocean, with impacts on biogeochemical cycling as well as on higher trophic position marine consumers (Tremblay et al., 2012). Pagophilic species themselves require ice to survive, and ice loss can have an impact on their population growth rates. For example, polar bears (Ursus maritimus) require ice to efficiently capture their preferred prey, ringed seal (Pusa hispida) pups. Similarly, under-ice algae, at the base of many Arctic marine food webs, require ice as a substrate to grow (Kohlbach et al., 2017). Ocean acidification can also directly impact species, especially calciferous benthic fauna (Walther et al., 2011). Finally, many cold-adapted Arctic animals may be unable to tolerate warmer waters. For example, Arctic cod (Boreogadus saida) do not reproduce effectively in waters above about 4 °C (Drost et al., 2014; Steiner et al., 2019). Similarly, thick-billed murres (Uria lomvia) experience stress at temperatures that are mundane for their more southerly congeners, with many dying from overheating in warm summers (Gaston and Elliott, 2013). Thus, a warmer, more acidic, and ice-free ocean may shift the range of many Arctic species northwards.

Changes in prey populations, or seasonal timing in their availability or accessibility, can lead to complex bottom-up trophic surges or temporal mismatches. For example, lack of under-ice algae, a preferred food of copepods, can lead to reduced populations of Arctic cod and consequently top predators that prefer cod (Gaston et al., 2005; Yurkowski et al., 2017, 2018). Indeed, reductions in accessible, sympagic Arctic cod are a common theme across the Arctic with reductions in Arctic cod in the diet of many marine predators; the cod may still be there but may be difficult to detect if they are not associated with readily visible ice (Gaston et al., 2005; Gaston and Elliott, 2014; Divoky et al., 2015, 2016). The match-mismatch hypothesis is a classic mechanism for bottom-up regulation associated with climate change (Thomas et al., 2001). Marine ectotherms can respond rapidly to changes in temperature and phytoplankton. Marine endotherms, such as seabirds and marine mammals, often respond in a more complex fashion to a hormonal pathway closely tied to photoperiod availability (Grémillet et al., 2015; Amélineau et al., 2019). Thus, although the timing of ice-off has advanced by over a month in Hudson Bay, Canada, the timing of the breeding of seabirds has only advanced by a few days. Consequently, seabirds are nourishing their offspring after Arctic cod, their preferred prey, is no longer accessible, leading to smaller chicks (Gaston et al., 2005; Gaston and Elliott, 2014; Divoky et al., 2015, 2016; Fig. 2). Presumably these changes are also happening in other taxa that are more difficult to directly monitor.

In contrast to bottom-up regulation, top-down regulation occurs when predators or parasites cause changes in prey populations. Examples of top-down regulation include: (1) the punctuated arrival of killer whales (*Orcinus orca*) in the Arctic during longer ice-free summers, with potential impacts on beluga (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), and bowhead whale (*Balaena mysticetus*) populations (Higdon and Ferguson, 2009; Matthews et al., 2020) and (2) increased polar bear predation on land-based foods during the ice-free period. In the latter case, because the ice-free period now overlaps to a greater degree with seabird breeding, hungry polar bears in some regions are switching to feeding on bird eggs (e.g., those of thick-billed murre and black guillemot; *Cepphus grylle mandtii*) and occasionally even eating adults (Gaston and Elliott, 2013; Divoky et al., 2015; Harwood et al., 2015). In some cases, polar

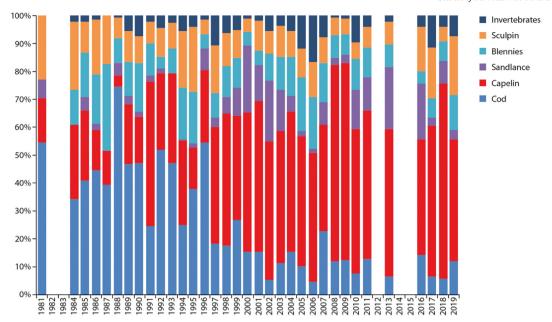


Fig. 2. Change in the diet of thick-billed murre chicks in northern Hudson Bay since 1981 showing a switch from cold-water prey (Arctic cod) in the 1980s and 1990s to warm-water prey (capelin; *Mallotus villosus*) in the 2000s and 2010s. Data based on Gaston and Elliott (2014) and updated to include additional more recent years.

bears eat tens of thousands of eggs, causing colony declines and dispersion into smaller colonies (Gaston and Elliott, 2013; Iverson et al., 2014; Prop et al., 2015). Polar bears using onshore habitat for an extended time period during the summer-fall in the southern Beaufort Sea are feeding on leftover tissues from subsistence-harvested bowhead whales (Atwood et al., 2016; McKinney et al., 2017b). Polar bears in other regions have shown long-term shifts towards greater consumption of sub-Arctic seals (McKinney et al., 2013). Parasites can also cause top-down regulation, and warm summers in recent years have increased black flies and mosquitoes in some regions, leading to reproductive failure by birds (Gaston and Elliott, 2013; Franke et al., 2016). Thus, top-down effects from both predators and parasites are having strong impacts on Arctic marine ecosystems.

One of the most widely documented consequences of climate change on ecosystems is changes in species distributions, (Post et al., 2009; Wassmann et al., 2011; Pecl et al., 2017). Reduced sea ice, increased water temperature and faster ocean current velocities are resulting in shifts in the northern boundary of many marine species, from phytoplankton (Oziel et al., 2020) to the oceans' top predator, the killer whale (Higdon and Ferguson, 2009; Bourque et al., 2018). Arctic species are moving northward with the retreating marginal ice zone and/or with their range-shifting prey, while boreal species are now present in the Arctic and for longer periods each year. Increasingly, ecosystems are changing from benthic towards pelagic species, with energy flows becoming more pelagic (Grebmeier et al., 2006; Fossheim et al., 2015) as a longer ice-free period opens pelagic ecosystems. Ultimately, the result will be community compositions that have not previously existed (i.e., 'no-analog' communities; Williams et al., 2007; Zarnetske et al., 2012), with repercussions for biodiversity across levels of organization. Such alterations in food-web links and lengths will impact the movement of energy as well as contaminants but will likely vary among regions (Bartley et al., 2019).

3. How has climate change altered mercury exposure in Arctic biota?

In the previous AMAP Hg assessment (AMAP, 2011), the chapter presenting how climate change influences Arctic Hg (Chapter 4) largely highlighted abiotic and biotic mechanisms by which climate change could *potentially* impact Hg levels in the Arctic and in Arctic species, although few empirical studies were covered (e.g., Gaden et al., 2009; Carrie et al., 2010). Since that 2011 assessment, multiple studies have evaluated associations between physical climate variables, or climate-driven ecological

variation/changes, and Hg levels in Arctic biota. Most studies have been carried out on marine organisms, with fewer studies carried out on terrestrial and freshwater biota. In this section, we focus on these new studies evaluating Hg-climate change interactions for biota in terrestrial, freshwater, and marine ecosystems. Studies on the biological effects of Hg on Arctic species are discussed in separate articles in this special issue (Dietz et al., this issue; Chastel et al., 2022; Barst et al., 2022), and, Hg along with effects of persistent organic pollutants (POPs) are addressed in a separate recent AMAP assessment (AMAP, 2018) and the subsequent paper by Dietz et al. (2019).

3.1. Terrestrial biota

There is little information available on how the exposure of terrestrial biota to Hg is affected by climate change. Concentrations of Hg in Arctic terrestrial herbivores are generally low (Aastrup et al., 2000; Dietz et al., 2000; Gamberg et al., 2020; Pacyna et al., 2018), but their exposure may vary according to space use and diet, which may be influenced by climate change. In the Canadian Arctic, Hg concentrations in lichen were enriched at coastal sites adjacent to polynyas compared to sites locked in by sea ice for the majority of the year (St Pierre et al., 2015). It could thus be hypothesized that sea ice declines may lead to increased Hg exposures in terrestrial herbivores using coastal areas. For example, Svalbard reindeer have been documented to increase feeding along the shoreline during icier winters (Hansen et al., 2019c). High intake of washed-ashore kelp among reindeer feeding along the shoreline may lead to higher Hg exposure compared to animals feeding on terrestrial plants, as kelp shows higher Hg concentrations compared to terrestrial plants (Chan et al., 1995; Wojtuń et al., 2013; Olson et al., 2019). Although changing vegetation due to climate change has been documented (Section 2.1), the effects of changing vegetation on Hg uptake and cycling in Arctic tundra ecosystems are currently unknown.

Arctic terrestrial predators may feed on both marine and terrestrial food webs (Eide et al., 2005; Dalerum et al., 2012; Ehrich et al., 2015; McGrew et al., 2014). Terrestrial prey, such as ungulates, geese, and ptarmigans, have lower levels of Hg than marine prey species, such as seals and seabirds (Aastrup et al., 2000; Dietz et al., 2000; Fant et al., 2001; Braune and Malone, 2006; Pedersen et al., 2006; Jæger et al., 2009; Pacyna et al., 2018). Consequently, coastal Arctic foxes, which feed on marine prey items based on faecal analysis and hunter observations have shown three

times higher levels of Hg than inland foxes, which mostly feed on terrestrial food items (Bocharova et al., 2013). Coastal gray wolves (Canis lupus), which similarly feed on marine prey items based on stable isotopes analysis, have shown 23 to 60 times higher levels of Hg than inland wolves (McGrew et al., 2014). Supporting this, studies using dietary tracers have indicated that Hg concentrations increase with a higher intake of high trophic level marine food items (McGrew et al., 2014; Hallanger et al., 2019). Climaterelated changes in the physical environment may affect prey availability for terrestrial predators, which has been linked to their Hg exposure. Concentrations of Hg in Arctic fox livers from Svalbard increased with sea-ice availability and decreased with increasing reindeer mortality (Hallanger et al., 2019). Arctic foxes need sea ice to scavenge seal remains from polar bear kills and to hunt newborn ringed seal pups (Gjertz and Lydersen, 1986), whereas rain-on-snow events that cause ice encapsulation of tundra vegetation (Peeters et al., 2019) are connected to reindeer mortality, and thus to the number of available reindeer carcasses for Arctic foxes (Hansen et al., 2013). Furthermore, the long-term temporal trend of Hg in Arctic foxes (1997–2014; n = 109) showed that the temporal increase in liver Hg levels was slightly faster, 7.2% (95% CI: 2.3 to 9.6%) per year, after adjustment for variation in diet proxies (stable isotopes, δ^{13} C and δ^{15} N) and food availability (availability of sea ice and reindeer mortality), whereas the actual yearly change in Hg concentrations was 3.5% (95% CI: -0.11 to 7.2%) (Hallanger et al., 2019); thus, change in diet and food availability slowed the rate of temporal increase in Hg concentrations.

3.2. Freshwater biota

Methylmercury is taken up by primary producers at the base of food webs (Morel et al., 1998). In lakes, regime shifts towards pelagicdominated energy pathways may increase Hg accumulation in food webs, as phytoplankton are more prone to absorb MeHg from the water column compared to benthic algae (Watras et al., 1998; Pickhardt and Fisher, 2007; Kozak et al., 2021). However, subsequent bioaccumulation of Hg to consumers via pelagic and benthic food-web compartments is highly variable among lakes in different Arctic regions and no clear-cut patterns can be synthesized (e.g., Power et al., 2002; Thomas et al., 2016; Chételat et al., 2018; Burke et al., 2020; Rohonczy et al., 2020). Pelagic food webs tend to accumulate Hg more efficiently than benthic ones, potentially via longer and more chain-type food webs (Power et al., 2002; Thomas et al., 2016). Melting snow and subsequently formed melting ponds could be very important sources of MeHg draining into lakes, where this substance is quickly taken up via phytoplankton. Overall, increasing precipitation is correlated with DOC leaching from catchment into fresh waters, which transport Hg and promote bacterial activity in lakes (Forsström et al., 2013; De Wit et al., 2016; Poste et al., 2019). In lakes, increasing temperature and productivity may also lead to anoxia in deep profundal habitats and sediments, promoting within-lake methylation processes by bacteria (e.g., Morel et al., 1998). Yet, development of anoxic conditions is highly dependent on lake productivity, morphometry, regional temperature and wind exposure, where change in stratification is prone to alter Hg uptake in lake food webs (Rask et al., 2010).

Shifts in community composition and species distributions in Arctic freshwater ecosystems may have implications for Hg bioaccumulation and biomagnification. The role of filter feeding *Daphnia* in MeHg uptake and transfer from phytoplankton to fishes has been recognized and may become more pervasive in the future as the range of *Daphnia* is currently limited by lake productivity and may expand as growth conditions improve with climate change (e.g., Chételat and Amyot, 2009; Kahilainen et al., 2016). However, such shifts in zooplankton fauna are less evident in Arctic ponds where zooplankton often lack fish predators and because pond food webs are governed by their ephemeral nature (e.g., potential desiccation in summer and complete freezing in winter; Rautio et al., 2011). Freshwater fishes in the Arctic are often generalists (i.e., consume a wide variety of prey) and cold-water adapted salmonid species (e.g., Arctic char; *Salvelinus alpinus*, whitefish; *Coregonus* spp.), which use both pelagic and benthic resources based on their seasonal abundance, influencing Hg concentrations

in muscle and liver tissues (e.g., Kahilainen et al., 2016; Keva et al., 2017). Arctic char, whitefish, and sticklebacks are all prone to diverge into sympatric morphs (or subspecies) using different prey items ranging from zooplankton, benthic macroinvertebrates or fish, differential feeding upon which leads to clear differences in Hg content that often peaks in planktivorous or piscivorous morphs (Willacker et al., 2013; Thomas et al., 2016; Kahilainen et al., 2017). Many Arctic regions contain anadromous fish species, including Arctic char, lake trout (Salvelinus namaycush) and Dolly Varden trout (Salvelinus malma), which are likely to retreat from warm southern regions or to switch to non-migratory freshwater populations with increasing temperatures and productivity (Finstad and Hein, 2012).

In some Fennoscandian lakes, a shift from benthic invertebrate to pelagic zooplankton prey often led to elevated Hg content in fish (Kahilainen et al., 2016, 2017; Keva et al., 2017), but there was considerable variation of patterns in different Arctic regions and different types of lakes. Another important dietary shift is related to piscivory (i.e., fishfeeding) behavior that elevates trophic level and thus the Hg content (Cabana and Rasmussen, 1994). Increasing trophic level is positively correlated with Hg concentrations within species and in food webs (Kidd et al., 2012; Clayden et al., 2013; Lescord et al., 2015; Thomas et al., 2016; Ahonen et al., 2018; Kozak et al., 2021). The new immigrating species are prone to increase the food-chain length and may lead to elevated Hg content in top predators (Thomas et al., 2016; Braaten et al., 2019; Barst et al., 2020; Kozak et al., 2021). However, many top predators feed on both pelagic and benthic prey fish, influencing their Hg content (e.g., Rohonczy et al., 2020). Hg concentrations in river-resident fish and river food webs can be spatially and temporally variable (e.g., Tran et al., 2015, 2019; Pelletier et al., 2017), but usually plankton-based food chains are absent, which often results in lower Hg content in rivers than in lakes.

Arctic lakes are often known for their relatively large adult fish populations composed of few year classes and potentially growing to very old ages (>20 years old). In such highly seasonal systems, most fish are in the adult stage and use a significant part of their energy towards gonad growth (Hayden et al., 2014; McMeans et al., 2015). In slow-growing European whitefish (Coregonus lavaretus), a year-round study indicated a continuum of summer growth dilution and winter condensation of Hg due to spawning and starvation during the long ice-covered period (Keva et al., 2017). In these mature, adult fish, very little somatic growth is observed, and yearround Hg variation exceeds annual bioaccumulation of Hg. However, anadromous Arctic char showed the opposite patterns in a Canadian lake, where summer Hg content was significantly higher than in winter (Martyniuk et al., 2020), although the underlying process was unclear, highlighting the complexity of seasonal drivers and potential outcomes in different species and regions. This difference potentially reflects the differences in the muscle composition of protein and lipids, the latter which do not bind mercury. Here, lipid content of Arctic char fluctuated seasonally, compared to more stable lipid content observed in lipid poor whitefish muscle (Kahilainen et al., 2016; Keva et al., 2017). Mercury content of Arctic char muscle is negatively correlated with lipid content and thus directly follow seasonal changes lipids (Kahilainen et al., 2016; Martyniuk et al., 2020).

In a more detailed example (Chételat et al., 2021), the Arctic char is a slow-growing, long-lived salmonid species that is widely distributed in cold, unproductive lakes across the circumpolar Arctic (Power et al., 2008). Climate-change effects, such as warmer temperatures and increased aquatic productivity, are expected to improve growth conditions for Arctic freshwater fishes, and it has been suggested that more rapid growth rates may lower Hg concentrations through somatic biodilution (Stern et al., 2012). However, recent research on Arctic char in northern Canada has demonstrated that age and dietary Hg exposure are the dominant factors controlling their Hg concentrations (van der Velden et al., 2012, 2013a,b; Chételat et al., 2021). Anadromous char typically have lower Hg concentrations in their muscle than lake-dwelling char, and they are also often larger in size for a given age (Swanson et al., 2011; van der Velden et al., 2013a; Tran et al., 2015; Barst et al., 2019). A comparison of paired marine and

lacustrine food webs in the eastern Canadian Arctic indicated that basal MeHg concentrations explained differences in muscle concentrations between anadromous and lake-dwelling char, rather than growth rate or trophic level (van der Velden et al., 2013a,b). Among lake-dwelling char, age better explained muscle-Hg concentrations than growth rate (determined by length-at-age), and fish that few faster did not show reduced muscle-Hg concentrations (van der Velden et al., 2012; Chételat et al., 2021). This lack of a growth dilution effect can be explained by elevated trophic levels of the faster-growing lacustrine Arctic char (Chételat et al., 2021). Thus, while feeding at a higher trophic level may enhance growth through greater caloric intake, it can also result in a greater intake of Hg. These findings, along with Chételat et al. (2022), combine to suggest that climatedriven environmental change that affects dietary exposure to MeHg (e.g., atmospheric deposition, production of MeHg, entry into the food web, and food web structure) may have a greater influence on Hg bioaccumulation in Arctic char than improved growth in these lake ecosystems of the eastern Canadian Arctic.

Multi-decadal time series of Hg concentrations in Arctic fishes were examined to assess the effects of climate change on bioaccumulation. Based on several publications, it is clear that the effects of climate change on fish Hg concentrations are complex and difficult to predict. For example, in the western Canadian Arctic, Hg concentrations in lake trout and burbot (Lota lota) of Great Slave Lake increased from the 1990s to 2018, but no change was observed for another resident species, northern pike (Esox lucius; see Morris et al., this issue; Evans et al., 2013). The mean annual air temperature increased in the region during the study period and was negatively correlated with length-adjusted Hg concentrations (i.e., fish had lower mean Hg concentrations in warmer years) of lake trout and burbot (Evans et al., 2013); however, the temperature effect explained little of the fish Hg variation in statistical models. Other climate variables, specifically the Pacific/North American oscillation, wind speed and precipitation had little or no explanatory effect in the Hg trend models. In addition, air temperature and sediment organic matter were found not to influence Hg fluxes to sediments, based on three sediment cores from different basins of the lake. Evans et al. (2013) concluded that temperature and lake productivity were not important drivers of increasing Hg concentrations in fishes of Great Slave Lake. Interestingly, over a similar timeframe, decreasing Hg concentrations were shown in burbot in a series of Russian rivers from 1980 to 2001 (Pelletier et al., 2017) and in Fennoscandian pike in sub-Arctic lakes from 1965 to 2015 (Braaten et al., 2019). Hudelson et al. (2019) analyzed temporal trends of Hg concentrations in landlocked Arctic char from six lakes near Resolute Bay on Cornwallis Island, Nunavut, in the Canadian High Arctic. The Hg trends differed among lakes, with no change in length-adjusted mean annual Hg concentration in char of three of the lakes and a decreasing trend for the other three lakes over the last two to three decades (Hudelson et al., 2019). The study lakes were in close proximity to each other, and none of the examined climate variables (wind speed, precipitation, air temperature, sea-ice duration, oscillation indices, and snow) consistently explained the length-adjusted Hg concentrations of char. However, in Resolute Bay, the sea-ice duration was positively correlated with char Hg for three of the lakes, which may indicate that longer lake-ice duration is influencing Hg bioaccumulation. Mean length-adjusted Hg concentrations of Arctic char varied several-fold among the study lakes and were best explained by water concentrations of dissolved and particulate organic carbon. Hudelson et al. (2019) concluded within-lake processes had a dominant influence on Hg bioaccumulation in the Arctic char populations based on the association with lake organic carbon and the occurrence of different temporal trends for lakes with the same climate. Together, these studies did not find evidence that climate variables had strongly influenced Hg bioaccumulation in fishes of the Canadian Arctic since the 1990s.

The effects of other climate metrics, such as glacial meltwater inflow, on Hg bioaccumulation were assessed in a well-studied Arctic system, Lake Hazen. This lake is the largest by volume in the Arctic, Lake Hazen, has shown since the mid-2000s an order of magnitude increase in glacial meltwater inflow, greater frequency of ice-free conditions in the summer, and more turbidity of inflow and nearshore waters (Lehnherr et al., 2018). Due to these

pronounced shifts, Hg input into the lake has accelerated (St. Pierre et al., 2019). Landlocked Arctic char are the sole species of fish in Lake Hazen, making them useful sentinels of contaminant bioaccumulation within the Lake. Adult (>200 g) char have been sampled in the summer nearly every year since 1990 (Gantner et al., 2009; Lehnherr et al., 2018; Morris et al., this issue). Over the three decades, the large-scale alterations in the hydrological regime showed no discernible influence on growth rate, body condition, or diet of the Arctic char. The least squares (LS) length-adjusted mean muscle concentrations of Hg, nonetheless, did significantly decline at a rate of 3.4% per year (p < 0.001) over the same time (Fig. 3). This declining trend was not correlated with the increasing glacial melt water inputs; however, a weak relationship with ice-free period was apparent (Fig. 3).

In another study on freshwater systems in the Canadian Arctic, the Cape Bounty Arctic Watershed Observatory on Melville Island (Nunavut, Canada) is home to two physically similar lakes located adjacent to each other (East Lake and West Lake), which have experienced significant changes in Arctic char length-adjusted Hg concentration over the past decade, albeit in opposite directions. Permafrost degradation has occurred in the catchments of both East Lake and West Lake, but several subaqueous slumps (since fall 2008) have also happened in West Lake. These slumps have led to a sustained rise in turbidity and a related decline in the body condition of Arctic char (Roberts et al., 2017). In 2009 after the first subaqueous slump, length-adjusted Hg concentrations started increasing in Arctic char in West Lake (Fig. 4; Burke et al., 2021). In contrast, starting in 2008, length-adjusted Hg concentrations declined in Arctic char in East Lake (Fig. 4; Burke et al., 2021). Fish size-at-age (a proxy for growth) was the strongest predictor of length-adjusted Hg in East Lake char, suggesting a somatic growth dilution effect (Karimi et al., 2007). Elevated growth rates and subsequent growth dilution were probably due to shorter duration of the ice-cover season, leading to higher water temperature and/or more primary production. Unlike in East Lake, carbon and nitrogen stable isotope values were the strongest predictors of length-adjusted Hg-concentrations in West Lake char, consistent with a change in feeding due to the dramatic elevation in turbidity of the lake. This paired-lake research demonstrates how climate change can lead to different proximate drivers of Hg concentrations in lacustrine fish, despite similarity in the lakes and in their locations. These findings underscore how challenging it will be to forecast trends of Hg concentrations in Arctic freshwater fish due to climate change, including influences from permafrost degradation.

3.3. Marine biota

In the Arctic marine environment, studies assessing how climate change-linked variation in diet or food web composition affects Hg (and

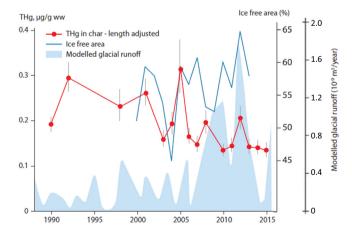


Fig. 3. Temporal trends of least-squares length-adjusted mean total Hg (THg) concentrations (\pm SD) in muscle tissue of adult Arctic char from Lake Hazen (1990–2015) along with ice-free area and modeled glacial runoff, as reported by Lehnherr et al. (2018).

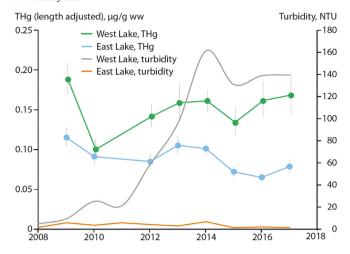


Fig. 4. Length-adjusted (LS mean) log THg concentrations (μ g/g ww, \pm SD) for Arctic char collected between 2008 and 2016 from East Lake (blue line) and West Lake (green line) at the Cape Bounty Arctic Watershed Observatory on Melville Island (Nunavut, Canada). Lake water turbidity in nephelometric turbidity units (NTU) between 2007 and 2016 in West Lake (gray line) and East Lake (orange line).

persistent organic pollutant) levels in biota were reviewed earlier (McKinney et al., 2015). These studies reported on climate change-Hg linkages for marine mammals and seabirds and within the Canadian Arctic, Greenland, and Svalbard, Norway. At that time, no such reports for Hg in any marine invertebrates or fishes had been published, and no data sets from any species were available from the Alaskan or Russian Arctic regions. Since the McKinney et al. (2015) review, there have been several other reports, including in fish, as well as in species from Alaska, in terms of either associations between physical environmental changes or ecologically-based climate changes and biotic Hg concentrations. These studies are detailed below, focusing first on reports in marine fish, followed by seabirds, and then marine mammals.

3.3.1. Marine fish

For marine fish, the concentrations of Hg, as well as multiple organic contaminants (e.g., polychlorinated biphenyls (PCBs) and organochlorine (OC) pesticides), were compared among native and northward redistributing non-native marine prey fishes in the eastern Canadian Arctic (Pedro et al., 2017), with particular attention to the keystone Arctic forage fish, Arctic cod, relative to similar northward range-shifting sub-Arctic species, capelin and sand lance. With the caveat that not every species was collected in each region, native benthic species, specifically sculpin spp. (Cottoidea) and northern shrimp (Pandalus borealis), showed the highest Hg concentrations of all species. Unlike for PCBs and organochlorine compounds, concentrations of Hg were elevated in Arctic cod relative to capelin, and this difference was likely partly due to differences in length between the two species. In a follow-up study, MeHg concentrations in Arctic cod were found to be similar to those in capelin and sand lance (Pedro et al., 2019). For total Hg, a study in northern Hudson Bay similarly reported higher concentrations in Arctic cod relative to capelin (Braune et al., 2014b). These findings together suggest that invading sub-Arctic capelin can have lower Hg and MeHg burdens than native Arctic cod, which may alter Hg exposures for higher trophic level piscivores.

3.3.2. Seabirds

For seabirds within the Low and High Canadian Arctic, links between Hg trends, diets, and sea-ice conditions were investigated for thick-billed murres (Braune et al., 2014a). Increased feeding on fish relative to invertebrate prey has been reported for murres of the High Arctic (Provencher et al., 2012), and here, Hg concentrations rose faster than diet-adjusted trends (based on δ^{15} N). In the Low Arctic, a dietary shift to capelin from Arctic cod has been reported concurrent with declining sea-ice, and here, Hg levels did not show trends, yet δ^{15} N-adjusted trends increased. These

findings may be partly explained by the co-occurring diet change to lower trophic level capelin, but it was suggested that changes in Hg cycles and bioavailability along with other climate change-related factors, may have played an additional role. In a follow-up study that focused on a suite of meteorological and climate variables, Foster et al. (2019) found that Hg concentrations in both fulmar (Fulmarus glacialis) and thick-billed murre eggs were best explained by models that in addition to year and $\delta^{15}N$, also included time-lagged North Atlantic Oscillation (NAO), temperature, and/ or sea-ice variables. This work suggests a combined effect of both physical and ecological influences of climate change on Hg levels in these species. Early results from thick-billed murres that breed in Hudson Bay suggest that higher circulating concentrations of Hg were related to lower circulating triiodothyronine that, in turn, was related to increased time diving under water when foraging for prey; however, these relationships were evident only when sea-ice breakup was earlier (2016, 2017) than the 50-year mean date (1971-2021) when 50% of the sea-ice coverage was gone from Hudson Bay (Esparza et al., 2022).

In East Greenland, a study indicated that little auk (*Alle alle*) diet, derived from $\delta^{15}N$ and $\delta^{13}C$ values, showed only minor inter-annual variation over an eight-year period (Fort et al., 2016). Temporal trends in Hg in little auks were not associated with this minor dietary variation, but rather with contamination in their major zooplankton prey species.

For seabirds at two locations in Svalbard, two time-point comparisons of Hg levels and δ^{15} N ratios (2008 and 2009) were made for black-legged kittiwake (Rissa tridactyla) and little auk (Øverjordet et al., 2015a). For kittiwakes, levels of Hg were lower when they fed at a lower trophic position and showed different feeding habits. The lower trophic position year had reduced ice and thus access to Arctic cod was reduced, and Arctic cod feed at a higher trophic position than other prey. However, Hg was not affected by trophic position in little auks, which exhibit more specialized feeding habits and feed mostly on invertebrates, relative to the more opportunistic feeding behavior exhibited by kittiwakes, which feed on various fish and invertebrates. A seasonal study from Svalbard indicated a decrease in Hg and MeHg from May to July to October in kittiwakes and from May to July in little auks, which coincided with a decline in trophic position (Øverjordet et al., 2015b; Ruus et al., 2015). This led also to lower trophic magnification factors in October than in May and July (Ruus et al., 2015). A separate long-term temporal trend study related Hg concentrations in kittiwakes to climate-induced changes in chlorophyll a (Chl a) concentrations and sea-ice extent in Svalbard (Tartu et al., 2022). Mercury concentrations in chick-rearing kittiwakes captured in Kongsfjorden, Svalbard from 2000 to 2013 declined by 3% per year, after which they increased by 11% per year until 2019. Both Chl a and sea-ice extent showed a U-shaped association with Hg concentrations in kittiwakes. Chl a, but also sea-ice extent, can be used as reliable predictors of shifts in fish communities (Eisner et al., 2013; Mérillet et al., 2020). The blood Hg U-shaped trend is likely due to a shift from polar cod to Atlantic fish species in kittiwake diet, and then likely increased in the later years due to the input of MeHg from Arctic shrinking sea-ice (Schartup et al., 2020; Vihtakari et al., 2018).

3.3.3. Marine mammals

The ringed seal represents a key biomonitoring animal for AMAP for evaluating trends of contaminants in the Arctic. Temporal trends of Hg in ringed seals across different regions of the Canadian Arctic were evaluated for relationships to climate variables, including air temperature, precipitation, ice extend, and climatic indices (Houde et al., 2020). More than 1500 ringed seals from regions of the Beaufort Sea, the central Arctic, eastern Baffin Island, Hudson Bay and Ungava/Nunatsiavut were collected by Inuit communities during their subsistence harvest between 1972 and 2017. Liver Hg concentrations were found to be stable over time in the seals. In contrast, muscle Hg concentrations declined significantly at approximately -1% per year in seals from Hudson Bay and Ungava/Nunatsiavut. In both liver and muscle tissues, concentrations of Hg showed significant increases with $\delta^{15} \mathrm{N}$ values in the ringed seals. Carbon stable isotope ($\delta^{13} \mathrm{C}$) values in the seal muscle declined significantly over time at several locations, suggesting a change in feeding towards more pelagic

and/or offshore prey types (Houde et al., 2020). Variation partitioning analyses across regions indicated that age (7.3% to 21.7%) best explained Hg accumulation in ringed seal livers, while diet (up to 9%) and climate (3.5% to 12.5%) were also significant explanatory variables (Houde et al., 2020). The climate indices, Arctic Oscillation (AO), NAO and Pacific/ North America pattern (PNA), seemed to mainly explain these proportions in comparison to ice coverage and air temperature/precipitation. Correlation analyses between Hg concentrations in seal liver/muscle and environmental variables indicated several significant associations which varied by regions and tissues (Fig. 5). For example, the total precipitation (both rain and snow) was negatively related to Hg muscle concentrations in seals from the Beaufort Sea, the central Arctic and Hudson Bay. Multiple sitespecific relationships were additionally detected between the total annual sea-ice coverage and Hg levels in seals. Moreover, positive correlations between Hg levels and the AO (recorded in the year of seal capture) were observed for several regions and both tissues. Overall, results from this study indicated that environmental factors may be influencing, in a site-specific manner, the accumulation of Hg in ringed seals across the Canadian Arctic.

In central West Greenland, Northwest Greenland (Avanersuaq) and central East Greenland (Ittoqqortoormiit), Hg temporal trends in ringed seal liver were assessed in relation to climate metrics, including water temperature, sea-ice coverage and AO index (Rigét et al., 2012). From the early 1980s to 2010, Hg levels in seal liver rose by 10% and 2% per year in central East Greenland and Northwest Greenland, respectively. Hg levels in all

three regions were explained by the winter AO index, as well as by other variables, including year, age and trophic position. That is, levels of Hg were higher when the AO was higher (i.e., when conditions enhanced transport of air masses from North America and Europe to the region and when precipitation was higher). Rigét et al. (2012) suggested that higher Hg levels may be found in ringed seal livers under climate change due to greater atmospheric and fluvial Hg transport.

The dynamics and sources of Hg were studied in harp seals, hooded seals and ringed seals from Greenland Sea in the light of climate change (Pinzone, 2021). Muscle Hg concentrations were higher in ringed seals sampled on land fast ice in East Greenland than in hooded seals and harp seals sampled offshore on the drift ice in the Greenland Sea and Denmark Straight. Isotopic compositions of Hg, nitrogen, carbon, and sulfur indicated that ringed seals fed in sympagic coastal food webs, and their high Hg exposure was related to local Hg input from land, rivers, and sea-ice, and to high MeHg production in the sympagic coastal system. Hooded seals and harp seals relied on offshore food webs and were exposed to Hg that originated from precipitation of particle-bound Hg. These results highlight the importance of habitat use rather than diet on the Hg exposure in some marine mammals. Pinzone (2021) also investigated Hg sources and bioaccumulation in relation to climate indices over time in ringed seals and hooded seals from the Greenland Sea. In ringed seals, Hg showed a non-significant trend during the study period of 1987-2018. Muscle Hg concentrations were strongly related to muscle $\delta^{15}\mbox{N}$ values. This temporal

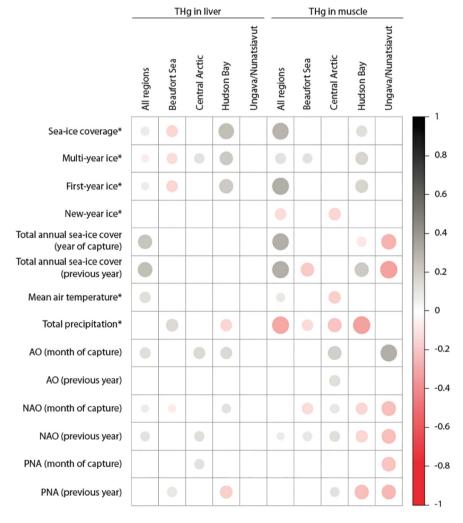


Fig. 5. Correlations between liver and muscle total mercury (THg) concentrations of ringed seals and environmental factors for specific regions of the Canadian Arctic and all regions combined. Circle size depicts the strength of the correlation. Black circles represent positive correlations, while red circles represent negative correlations (p < 0.05). *Based on the available data for the month of capture. AO: Arctic Oscillation; PNA: Pacific/North American pattern; NAO: North Atlantic Oscillation. See Houde et al., 2020 for details.

Hg variation in ringed seal seemed to be more related to the shifts at the base of the food web rather than a change in trophic position. Temporal changes in the ratios of even mass Hg isotope values (represented by δ^{200} Hg) in ringed seals suggested that Hg transport from lower latitudes decreased, and Hg inputs from terrestrial reservoirs increased, during the study period. Hg showed a significant decrease over time (~1.5%/year) in hooded seals, an offshore specialist (i.e., narrow diet and habitat use), which was related to a shift from benthic- to pelagic-dominated prey. Thus, Hg exposure in a coastal generalist may depend on local scale biogeochemical processes, whereas Hg exposure in an offshore specialist may be related to global-scale emissions and shifts in food web structure (Pinzone, 2021).

From the mid-1980s or 1990s to the 2000s in Hudson Bay and Foxe Basin, Canada, levels of Hg declined in beluga whale but not in Atlantic walrus (Odobenus rosmarus) and narwhal (Gaden and Stern, 2010). Values of δ^{13} C also declined in beluga, suggesting possible increases in feeding on prey farther offshore or pelagic-associated prey or habitat, but only weak associations of δ^{13} C values with the NAO index were found. Additionally, no associations were found between $\delta^{15}N$ or Hg with NAO. In another study on beluga whales in the Canadian Arctic, Hg levels increased between 1981 and 2002, but then declined or stabilized between 2002 and 2012 in individuals from the Beaufort Sea (Loseto et al., 2015). Climate indices, such as the Pacific Decadal Oscillation (PDO) with an eight-year time lag, better explained variation in Hg levels than did $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ ratios. Narwhal tusks were used to examine lifelong Hg exposures and suggested that a particular recent rise in Hg may have been due to increased emissions or to sea ice-driven shifts in migration, habitats, or food web linkages (Dietz et al., 2021). Beluga teeth samples from 1854–1905 versus 1985–2000 also showed a recent rise in Hg concentrations, which the authors concluded could have been related to increased primary emissions or remobilization (e.g., from permafrost) (Desforges et al., 2022).

For polar bears from the southern Beaufort Sea region in Alaska, as the sea ice has declined both spatially and temporally, the proportion of the subpopulation spending an extended period of time (>21 days per year) onshore during the melt season has risen (Atwood et al., 2016). While onshore, these polar bears consume the leftover tissues from subsistence-harvested bowhead whales and possibly other prey (Schliebe et al., 2008; Rogers et al., 2015; McKinney et al., 2017a; Bourque et al., 2020a). Levels and trends of Hg in hair were investigated in this polar bear subpopulation

during this time of rising land use from 2004 to 2011 (McKinney et al., 2017a). In spring-sampled polar bears, levels of Hg fell by 13% per year, mainly driven by declines in adult males. Reduced Hg concentrations were related to higher body mass index (BMI) and increased proportional consumption of lower trophic position prey. Trends in Hg, adjusted for BMI, showed non-significant declines, suggesting that altered feeding and better condition, rather than declining environmental concentrations of Hg, were responsible for these short-term declines in Hg concentrations (Fig. 6). As longer-term studies of this polar bear population (Rode et al., 2010, 2014) and some other populations have shown declines in polar bear body condition, McKinney et al. (2017a) suggested climate-driven declines in body condition may, in fact, increase the circulating levels of Hg. A follow-up study reported that top models explaining Hg and other contaminant concentrations in this polar bear subpopulation in 2013 and 2014 included BMI and/or habitat use, and that PCB (but not organochlorine or THg) concentrations influenced plasma concentrations of cytokines, which are small immune signaling proteins (Bourque et al., 2020b).

In a single study of Hg in multiple Hudson Bay wildlife, including polar bears (liver, 2007/08-2015/16), as well as thick-billed murre (eggs, 1993–2015 normalized to the mean $\delta^{15}N = 14.2\%$) and caribou from the Qamanirjuaq herd (kidney, 2006–2015, normalized to the mean age = 6.3 y), the Hg concentrations (µg/g dw) did not change significantly over time (Morris et al., 2022). Hg concentrations in murres were normalized to the mean $\delta^{15}\mbox{N}$ to compensate for the significant decrease observed from 1993 to 2015, as also previously noted at both Coats Island (Akpatordjuark) and High Arctic murre colonies (Braune et al., 2014a). Morris et al. (2022) used general linear models (GLMs) to test the effects of year, climate and weather variables (time-lagged zero to three years), and their interactions on Hg concentrations in the polar bear, thick-billed murre, and caribou populations. First, sea ice exhibited significant relationships with Hg concentrations in caribou and southern Hudson Bay polar bears but not in western Hudson Bay polar bears or murres. More sea ice in the eastern Hudson Bay (later break-up dates, shorter ice-free periods, or greater fall sea-ice coverage) was consistently associated with greater concentrations of liver Hg in southern Hudson Bay polar bears. The two strongest models for caribou found that concentrations of Hg increased when the one year and two-year time-lagged ordinal dates of sea-ice freeze-up were later (calculated based on 50% and 90% coverage, respectively), though some lower ranked models produced conflicting results

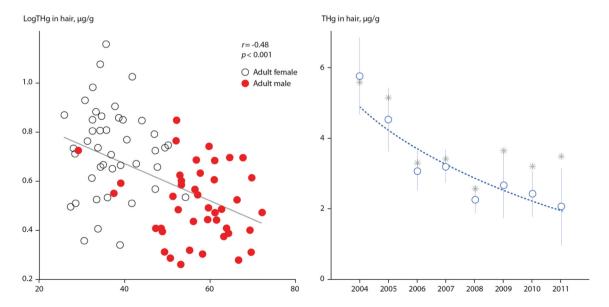


Fig. 6. (Left panel) Correlation between hair log-total mercury (THg) concentrations in adult female polar bears (white circles) and adult male polar bears (red circles) and body mass index (BMI); (right panel) time trends in median hair THg concentrations (\pm SE; blue open circles, dashed line) from adult polar bears (males and females combined) for 2004–2011 in the southern Beaufort Sea. Log-linear declining trends were significant (-13% per year, $r^2 = 0.84$, p = 0.002). Annual medians adjusted to the covariate body mass index (BMI) are also shown (asterisks, no line). Log-linear trends in these adjusted means were not significant (-6.6% per year, $r^2 = 0.41$, p = 0.08). Raw medians, not log-transformed values, are shown for ease of visualizing the concentration changes. Figure modified from McKinney et al. (2017a).

with sea ice. Compensating for the freeze-up date one year prior to sampling also produced a significant trend with year (4.4% per year) in the multivariate model with sea ice in caribou. Greater ice coverage, shorter ice-free periods and later break-up times allow polar bears to effectively hunt high trophic level prey, such as seals, for longer periods of time (Derocher et al., 2004). Macdonald et al. (2005) also hypothesized that more sea ice would limit Hg volatilization and increase bioavailability to the marine food web, both of which could increase levels of Hg as observed in Morris et al. (2022). That later freeze-up dates (i.e., more open water) were related to greater Hg levels in caribou (Morris et al., 2022) agrees with previous observations that longer open water periods lead to greater bioaccumulation in coastal lichens (St Pierre et al., 2015) and that bioaccumulation in lichens impacts uptake and levels in caribou (Gamberg, 2015).

In the same Morris et al. (2022) study, lower concentrations of Hg in murre eggs and caribou were related to June and summer AO+ values three years prior to sampling, and Hg levels in western Hudson Bay polar bears were related to time-lagged annual, fall and summer NAO + /NAO + values. The latitude of the Hudson Bay study sites situates them between zones of influence of the oscillation indices and directly in the latitude of the westerly winds and the jet stream, which strengthen under AO + conditions. Foster et al. (2019) found that greater Hg concentrations in seabird eggs were associated with NAO+/AO+ conditions in long time-series (~40 years), but when the time-series were shortened to a comparable length, some inverse relationships were observed as in Morris et al. (2022). The results of several studies (e.g., Foster et al., 2019; Houde et al., 2020; Morris et al., 2022) now suggest that time-series of different lengths may track climate and weather patterns differently with long and short datasets often exhibiting opposite relationships, which is an important consideration for climate-related analyses (Morris et al., 2022).

In murre eggs (Morris et al., 2022), higher annual sea level pressures one year prior to sampling were associated with higher Hg concentrations, corroborating the June AO model, as in the AO - phase, sea-level pressure is greater at higher latitudes, and Hg concentrations tended to be greater in that phase of the AO. In addition, greater precipitation levels in the summer or fall one or two years prior to sampling resulted in greater tissue residues of Hg in polar bears and caribou, which is a logical result of greater atmospheric scavenging and deposition associated with more precipitation (Macdonald et al., 2005). Greater fall and annual wind speeds (with a three-year time lag) were related to lower egg Hg concentrations in murres, but greater winter wind speeds (with no time lag) were associated with higher concentrations in western Hudson Bay polar bear livers. Differences in time lags, wind direction and the status of the seasonal oscillation indices would all affect how contaminants are delivered or dispersed by greater wind speeds depending on the source region, which may explain these differences between the species.

In another study, significant annual increases in hair Hg of Northwest Greenland polar bears were found from 1892 and 2008 were analyzed for Hg concentrations, with the two most recent median concentrations in 2006 and 2008 being 23- to 27-fold higher respectively than the preindustrial levels from 1300 CE previously reported for polar bears in the same region, Nuullit (Dietz et al., 2011). The authors found a significant negative correlation (p=0.048) between Hg and δ^{13} C, which could be interpreted as an influence of diet or food web variation. This interpretation was also used to explain higher Hg in ringed seals linked to shorter ice-free periods in the western Canadian Arctic (Gaden et al., 2009) and rising trends in Northwest Greenland ringed seals from 1984 to 2008 (Rigét et al., 2012) and means that climate may have contributed to the observed increases of Hg in ringed seals and in polar bears from Northwest Greenland (Dietz et al., 2011; Rigét et al., 2012).

Temporal trends of Hg in relation to variation in dietary carbon, nitrogen and sulfur were investigated in 199 hair samples from adult female polar bears sampled on Svalbard from 1995 to 2016 (Lippold et al., 2020). Temporal decline in hair $\delta^{13} C$ and $\delta^{34} S$ values indicated that the importance of land-based foods in the summer diets of these polar bears diet has increased with time. Alternatively, changes in $\delta^{34} S$ are hypothesized to reflect a higher sulfate reduction rate linked to higher Hg methylation

in the environment (Elliott and Elliott, 2016); however, this relationship is often too confounded by dietary source to clearly quantify the importance of sulfate reduction in Hg levels in biota. Hg concentrations increased with increasing $\delta^{13}C$ and $\delta^{34}S$ values, which suggested that polar bears with a more mixed diet were exposed to less Hg than those with a solely marine diet. Concentrations of Hg increased between 1995 and 2016, with a steeper increase after 2000, which may have been related to re-emissions from thawing sea ice, glaciers, and permafrost due to climate change. When Hg concentrations were adjusted for $\delta^{13}C$ or $\delta^{34}S$ variation, the increase in the later period was slightly steeper, but the trends were not significantly different. This suggests that the diet change towards more terrestrial food items exposed polar bears to lower Hg concentrations; nonetheless, the temporal trend of Hg in these polar bears is not vet significantly affected by dietary changes. A further study on spatial variation in Hg concentrations in relation to diet in Svalbard and Russian Arctic polar bears indicated that spatial variation in Hg concentrations was minor and not explained by variation in $\delta^{13}C$ and $\delta^{15}N$ values (Lippold et al., 2022).

The presence of sea ice likely influences the exposure of polar bears to Hg. A circumpolar study on polar bears investigated how liver concentrations of Hg were related to lipid and carbon sources inferred from fatty acids composition and $\delta^{13} C$ (Routti et al., 2012). Concentrations of Hg were positively related to proportions of fatty acids abundant in sea ice-associated copepods, suggesting that Hg levels are higher in polar bear food webs rich in sea ice associated copepods. This finding is in agreement with high MeHg concentrations below the productive surface layer in the marginal sea-ice zone, which likely enhances uptake and bioavailability of MeHg in food webs (Heimbürger et al., 2015). The polar bear study also concluded that Hg accumulates to a larger degree in polar bears that feed in regions with elevated fluvial inputs of terrestrial carbon versus those that feed in regions of lower freshwater inputs (Routti et al., 2012).

There is a strong predator-prey relationship between polar bears and ringed seals, and both species are experiencing loss of sea-ice habitat and exposure to Hg and other pollutants via their diets (Yurkowski et al., 2020). The ice-covered springtime is critical for polar bears and ringed seals; polar bears rely on the sea ice to hunt from prior to sea-ice breakup, and ringed seals need the ice at this time for pupping and molting prior to extensive feeding during the subsequent open-water period. Both species are opportunistic foragers and consume varied previtems. A recent study investigated how similarly polar bears and ringed seals within the same region are responding to ecosystem changes by investigating temporal patterns of their Hg concentrations, niche dynamics and body fat condition (Yurkowski et al., 2020). Polar bear hair and adipose samples as well as ringed seal muscle were collected between 2003 and 2016 in southwestern Hudson Bay. Inter-annual fluctuations in $\delta^{15}N$ values of polar bears were highly correlated with those of ringed seals, indicating that temporal variation in polar bear $\delta^{15} \text{N}$ values depends on ringed seal $\delta^{15} \text{N}$ values. This finding suggests that mechanisms that affect inter-annual variability in food web dynamics in the lower part of the food web may similarly influence both polar bears and ringed seals. In ringed seals, declining Hg concentration of 3.8% per year, and of $\delta^{13} C$ values of 1.5% over 13 year period, suggested shifting feeding habits and increased reliance on phytoplankton carbon versus benthic or sympagic carbon; however, these changes did not occur for polar bears. Additionally, three-dimensional niche size, based on Hg, δ^{13} C, and δ^{15} N, decreased in polar bears but not in ringed seals. The δ^{13} C range also declined in polar bears, but significantly increased in ringed seals. These contrasting patterns suggest that the two species are likely responding in different ways to primary production changes between pelagic, sympagic and benthic pathways, as well as to inter-annual changes in prey availability. Finally, a \sim 1.5-fold increase in δ ¹³C spacing between the species niches suggested species-specific responses to changing sympagic-pelagic carbon source production. The changing foraging ecologies for both species suggest a diminishing of their predator-prey relationship; while polar bears continue to rely mainly on the sympagic food web (~80%; Brown et al., 2018), ringed seals are increasingly reliant on the pelagic food web (Yurkowski et al., 2020). Similar climate changeinduced weakening of the polar bear-ringed seal relationship has also been shown in East Greenland (McKinney et al., 2013; Dietz et al., 2018) and in Svalbard (Hamilton et al., 2017). These trends are expected to continue, given a lack of reductions in greenhouse gas emissions, which are the cause of the continued loss of sea ice habitat for polar bears and ringed seals (Castro de la Guardia et al., 2013).

Across Arctic regions, marine mammals go through seasonal changes in their stores of body fat. For example, polar bears generally feed extensively in the spring to early summer when ringed seals are pupping and molting on sea ice. During sea-ice free periods, polar bears have reduced, if any, access to food and therefore they fast. Pregnant females spend winter in the den, and thus may fast for up to eight months in a row. As discussed in their Alaskan polar bear study, McKinney et al. (2017a) suggested that hair MeHg accumulation may increase in fasting polar bears that catabolize proteins and thus mobilize MeHg into the blood circulation. This is supported by findings of a negative, although non-significant, trend between body condition and hair Hg in female polar bears from Svalbard (Lippold et al., 2020). However, temporal changes in polar bear body condition did not affect temporal trends of Hg in Svalbard polar bears. Similar to the polar bear studies, feather Hg concentrations were negatively related to body condition in little auks from East Greenland (Amélineau et al., 2019), yet an opposite relationship was found for blood Hg concentrations and body condition in common eider ducks (Somateria mollissima; Provencher et al., 2016). Liver concentrations of Hg in Arctic foxes were not related to their body fat (Hallanger et al., 2019). Blévin et al. (2017) hypothesized that Hg, among other pollutants, would affect metabolic rate through changes in thyroid hormone levels in kittiwakes from Svalbard. The results showed, however, that Hg was not related to metabolic rate in either male or female birds.

4. Conclusions and recommendations

4.1. How has climate change affected Arctic ecosystems?

- Arctic marine biota are responding to climate change either directly, associated with thermal or acidity tolerance, or indirectly, in relation to other species' ranges or populations, including northward range shifting boreal species. Food web responses may be particularly important and include bottom-up effects from changing prey and top-down effects from changing predators.
- 2. Terrestrial monitoring and experimental studies in the circumpolar Arctic suggest that both grass and grass-like plants and shrubs respond positively to warming and their abundance is likely to increase over time, while warm spells in winter and rain-on-snow events have been shown to negatively affect reproduction and survival of High Arctic tundra herbivores, but these effects may be compensated by a longer summer season.
- Warmer-adapted terrestrial and aquatic species are extending their range and abundance into the Arctic and will likely alter food web structure and function.
- 4. Carbon and nutrient leaching from catchments, driven by climate change, increases the overall productivity of freshwater ecosystems. Lower visibility in murky lakes from organic carbon loading (browning) promotes pelagic primary and secondary production over benthic production. Increased productivity of lakes can promote anoxic conditions, especially in winter.

4.2. How has climate change altered mercury exposures in Arctic biota?

5. Climate and weather variables, including sea-level pressure oscillations and sea-ice patterns, sometimes with single- or multi-year time lags, have been linked to spatial and temporal variation in tissue Hg concentrations in some Arctic marine and terrestrial species. These findings suggest that variation and change in wind, precipitation and the cryosphere affecting the atmospheric and aquatic transport of Hg may, in turn, be impacting Hg exposures in Arctic biota.

- Changing species interactions due to northward range shifts of sub-Arctic marine and terrestrial species, may alter Hg exposures in Arctic biota.
- 7. Several studies have shown higher Hg concentrations in marine animals with low body condition, suggesting that, all else being equal, climate-related decreases in body condition may lead to higher Hg exposure in some Arctic species.
- Climate-change related Hg remobilization (e.g., from permafrost, sea ice, and glaciers) may have led to increased Hg concentrations in certain hiota.
- Climate-related variation in food accessibility (terrestrial vs. iceassociated) can alter Hg concentrations in terrestrial predators.
- 10. Climate-influenced processes, such as food web exposure to MeHg, shifts in dominant energy pathways of food webs, condition, and growth dilution, have been shown to affect Hg bioaccumulation in Arctic freshwater fish. The importance of climate change in affecting these processes remains unclear and likely varies due to species- and site-specific conditions.
- 11. Multi-decadal time series of Hg concentrations in Arctic freshwater fishes have been examined for influences of climate change on bioaccumulation. Based on several studies and fish species, it is clear the effects of climate change on fish Hg concentrations are complex, difficult to predict, and are often species-, lake-, and region-specific.

4.3. Recommendations

Climate change may affect Hg levels in Arctic biota in myriad ways, including numerous physical changes impacting Hg transport and deposition as well as complex biological and ecological changes impacting Hg uptake and fate in organisms and trophic transfer through food webs. Due to a limited number of populations and species examined for Hg-climate change linkages within marine and, in particular, terrestrial and freshwater systems to date, further study of the relative importance of climate change factors and how they may vary through space and time, which would require broader geographic coverage, is needed to determine the key drivers and net impacts of climate change on biotic Hg concentrations in Arctic ecosystems.

Long-term pan-Arctic Hg monitoring programs on Arctic biota should consider ancillary datasets on climate and weather, as well as Hg deposition, MeHg production, and DOC release (Chételat et al., 2022). These programs should also develop complementary ecological and physiological datasets by merging traditional metrics with modern methods. For example, improved understanding of Hg uptake related to movement or along migratory routes could be gained from using animal tracking datasets. Bulk isotopes in addition to nitrogen and carbon (e.g., sulfur), compound-specific stable isotopes analysis, and fatty acid signature analysis can provide detailed insight into habitat and diet influence on Hg concentrations in biota (McKinney et al., 2017a; Elliott et al., 2021). Amino acid nitrogen isotopes, for instance, may provide trophic estimates un-confounded by spatial variation in baseline nitrogen isotope values. Such approaches could advance interpretation of spatial variation and temporal trends in Hg in Arctic biota in relation to climate change.

CRediT authorship contribution statement

Melissa A. McKinney: Conceptualization, Writing – original draft, Writing – review & editing. John Chételat: Conceptualization, Writing – original draft, Writing – review & editing. Samantha M. Burke: Writing – original draft. Kyle H. Elliott: Writing – original draft, Writing – review & editing. Kim J. Fernie: Writing – original draft. Magali Houde: Writing – original draft. Kimmo K. Kahilainen: Writing – original draft, Writing – review & editing. Robert J. Letcher: Writing – original draft. Adam D. Morris: Writing – original draft. Derek C.G. Muir: Writing – original draft. Heli Routti: Writing – original draft, Writing – review & editing. David J. Yurkowski: Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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