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REVIEW

The circumpolar impacts of climate change and anthropogenic stressors on Arctic cod (*Boreogadus saida*) and its ecosystem

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Arctic cod (*Boreogadus saida*) is the most abundant forage fish in the Arctic Ocean. Here we review Arctic cod habitats, distribution, ecology, and physiology to assess how climate change and other anthropogenic stressors are affecting this key species. This review identifies vulnerabilities for different life stages across the entire distribution range of Arctic cod. We explore the impact of environmental (abiotic and biotic) and anthropogenic stressors on Arctic cod with a regional perspective in a scenario up to the year 2050 and identify knowledge gaps constraining predictions. Epipelagic eggs and larvae are more vulnerable to climate change and stressors than adults. Increased water temperatures, sea-ice decline, altered freshwater input, acidification, changing prey field, increased interspecific competition, new predators, and pollution are the principal stressors that will affect Arctic cod populations. Detrimental effects are likely to be greater in regions characterized by the advection of warmer Atlantic and Pacific waters. In contrast, Arctic cod may benefit from ocean warming in colder areas of the High Arctic. The risk from fisheries is moderate and primarily limited to bycatch. Overall, a decrease in suitable habitat and an associated decline in total

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Arctic cod biomass are predicted. In most Arctic seas, the relative abundance of Arctic cod within the fish community will likely fluctuate in accordance with cold and warm periods. A reduced abundance of Arctic cod will negatively affect the abundance, distribution, and physiological condition of certain predators, whereas some predators will successfully adapt to a more boreal diet. Regional management measures that recognize the critical role of Arctic cod are required to ensure that increased anthropogenic activities do not exacerbate the impacts of climate change on Arctic marine ecosystems. Ultimately, the mitigation of habitat loss for Arctic cod will only be achieved through a global reduction in carbon emissions.

Keywords: Arctic cod, Polar cod, Climate change, Borealization, Circumpolar, Risks

1. Introduction

The Arctic is warming nearly four times faster than the rest of the planet (Rantanen et al., 2022). Both sea surface and deeper water temperatures are increasing in Arctic regions (Meredith et al., 2019). In all Arctic seas, the sea-ice cover is decreasing in extent and thickness, and the ice-covered season is shortening because of earlier spring breakup and later autumn freeze-up (e.g., Notz and SIMIP Community, 2020; Crawford et al., 2021). Earth system models project that by the mid-21st century, the Arctic will become episodically ice-free in summer under all plausible future emission scenarios (Overland and Wang, 2013; Notz and Stroeve, 2018). These environmental changes have, and will continue to have, a strong impact on Arctic endemic species, such as Arctic cod (*Boreogadus saida*), which are adapted to sub-zero temperatures, extreme light regimes, and pulsed peaks in primary production (Wassmann et al., 2011). Moreover, the reduced extent of sea ice and the lengthening of the ice-free season are facilitating access to the Arctic, favoring the expansion of human activities such as mining, oil and gas exploration, transport, and fisheries (Meredith et al., 2019).

Arctic cod, often referred to as “polar cod” in Europe, has a circumpolar distribution and occurs in virtually all arctic and subarctic marine habitats, from shallow coastal shelf waters to epi- and mesopelagic layers over the continental slope and the deep central Arctic Ocean, as well as in under-ice surface waters (Coad and Reist, 2018 and references therein; **Figure 1**). Arctic cod is the most abundant forage fish in the Arctic seas (e.g., Benoit et al., 2008; Dolgov et al., 2011; Geoffroy et al., 2016; Kono et al., 2016). In some regions, Arctic cod transfers more than 70% of the energy between zooplankton and piscivorous fish, marine mammals, and seabirds (Bradstreet and Cross, 1982; Welch et al., 1992; Darnis et al., 2012; Steiner et al., 2019). Similar to temperate and tropical forage species, this short-lived (usually <7 years; Cohen et al., 1990), small fish (adult body length generally ≤ 25 cm) forms dense aggregations targeted by top predators (Welch et al., 1993; Benoit et al., 2010; Coad and Reist, 2018). Early life stages of Arctic cod are found mainly near the surface in ice-covered and open waters, whereas adults are more common in either deeper layers (>100 m) or close to the seafloor (Matley et al., 2013; Geoffroy et al., 2016; Kessel et al., 2016). Juvenile and immature Arctic cod are also commonly observed just beneath the sea ice or in cracks, wedges, and cavities within the ice (Andriashev, 1954;

Andriashev et al., 1980; Bradstreet, 1982; Lønne and Guliksen, 1989; Gradinger and Bluhm, 2004; Melnikov and Chernova, 2013; David et al., 2016). Arctic cod is a key species in all Arctic marine ecosystems; providing meaningful predictions of ecosystem states requires a clear understanding of how climate change and other anthropogenic stressors affect its different life stages and habitats.

The cumulative impacts of climate change and amplified anthropogenic stressors on the population dynamics of Arctic cod are predicted to cascade through food webs and modify the ecosystem services supported by Arctic cod (**Figure 2**). Warmer ocean temperatures and reduced sea-ice extent allow boreal species to extend their distributions northward, increasing the risks of competition with and predation on endemic Arctic fish fauna, including Arctic cod (Wassmann et al., 2011; Darnis et al., 2012; Renaud et al., 2012; Fossheim et al., 2015; von Biela et al., 2023). A borealization of the marine ecosystem coupled

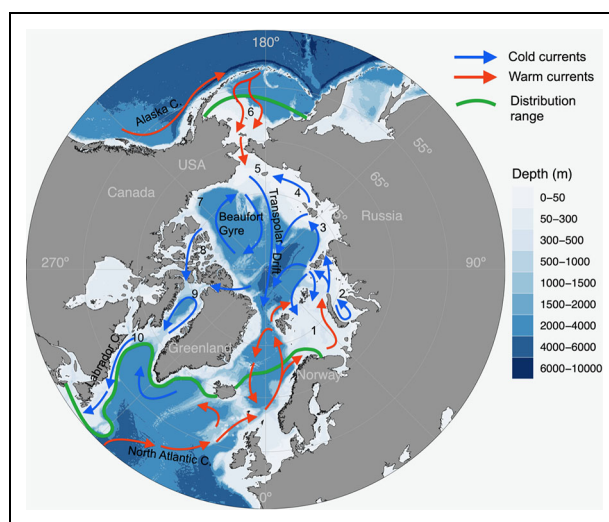


Figure 1. Southern distribution of Arctic cod (after Mecklenburg et al., 2018). The limits of Arctic cod distribution (green line), with cold Arctic currents (blue arrows) and warmer Atlantic and Pacific currents (red arrows), reproduced from Arctic Monitoring and Assessment Programme (AMAP, 2018), and marine areas indicated by number: Barents Sea (1); Kara Sea (2); Laptev Sea (3); East Siberian Sea (4); Chukchi Sea (5); Bering Sea (6); Beaufort Sea (7); Canadian Archipelago (8); Baffin Bay (9); and Labrador Sea (10).

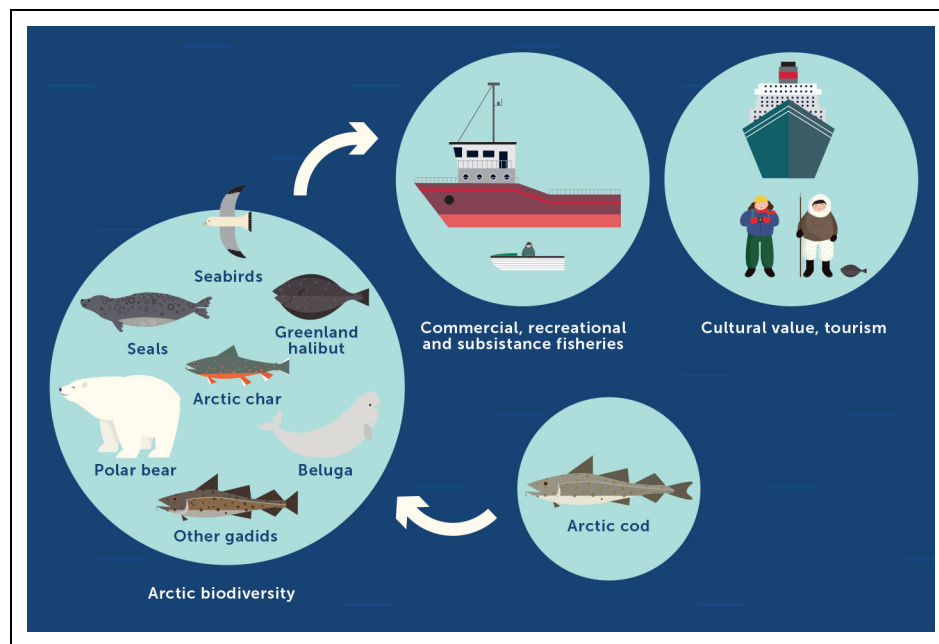


Figure 2. Schematic representing the ecosystem services supported by Arctic cod. Ecosystem services supported by Arctic cod are related to their role in maintaining biodiversity.

with changes in the distribution and abundance of Arctic cod can have detrimental effects on the populations of top predators, such as seabirds and marine mammals, on which depend hunters from northern communities and the growing Arctic tourism industry. Several larger fish species, targeted by both subsistence and commercial fisheries, also forage on Arctic cod (Darnis et al., 2012; Steiner et al., 2019; Tai et al., 2019; Steiner et al., 2021; **Figure 2**).

The impacts of climate change on the ecology of Arctic cod differ among regions. Along the southern boundary of its range—in the Bering, Labrador, and Barents seas—Arctic cod is already coping with boreal conditions at the limit of its tolerance range (Fossheim et al., 2015; Marsh and Mueter, 2020). Anthropogenic stressors are also more prevalent in these regions known as Arctic gateways. In contrast, populations in the High Arctic, such as the Canadian Arctic Archipelago, the Siberian Arctic, and the Arctic Basin, currently experience low levels of anthropogenic impacts (Steiner et al., 2019). Thus, realistic projections of climate change effects on Arctic cod require a comprehensive understanding of such regional differences.

The overarching objective of this narrative review is to assess the vulnerability of Arctic cod to climate change and other stressors, either directly or indirectly through habitat alterations and modified trophic interactions. We first describe the impacts of all stressors on the physiology and survival of each life stage of Arctic cod. We then compare the effects and risks of these stressors for each life stage and for all Arctic regions in a scenario up to the year 2050. This risk assessment is based on a rigorous expert judgment procedure, following the example of the IPCC Oceans and Cryosphere report (Pörtner et al., 2019). Expert judgment is a powerful tool for assessing complex problems across disciplinary boundaries and communicating societally important questions (Mach et al., 2017). This

assessment, which covers a wide range of ontogenetic and geographical perspectives, was undertaken by all coauthors according to the following roadmap (Supplementary Text S1): (1) A detailed literature research, as presented in this review; (2) assessment of the potential effects of stressors on the different life stages of Arctic cod, taking into account the variability in the geographical distribution of these life stages; (3) evaluation of the potential effects of stressors on the population level within various large marine ecosystems (LMEs; Conservation of Arctic Flora and Fauna [CAFF], 2017), considering the different distributions of life stages among these LMEs; (4) scoring the confidence associated with points 2 and 3, taking into account the evidence and consensus in the scientific literature (Mach et al., 2017); and (5) calculation of the median of all scores, which approximates the consensus of most coauthors.

This review provides a comprehensive overview of Arctic cod habitat, distribution, and biology to assess how climate change and anthropogenic stressors affect this Arctic key species and the ecosystem that it supports. We identify the knowledge gaps that constrain current predictions and assess cascading impacts on higher trophic levels. We conclude by reviewing the management and stewardship approaches required to monitor and protect Arctic cod and its ecosystem.

2. Direct impacts of climate change on Arctic cod physiology and survival

In this review, we consider the life cycle of Arctic cod over five different stages: (1) eggs; (2) larvae from hatching until metamorphosis into juveniles; (3) juveniles from metamorphosis until the end of their first year of life; (4) immatures from age-1 until sexual maturity; and (5) adults. Given that habitat preferences and the effects of

Table 1. Physiological optimum temperature range and distribution relative to sea ice of Arctic cod life stages

Life Stage, Age	Physiological Optimum Temperature Range (°C)	Association With Sea Ice	Distribution and Habitat
Egg, 35–79 days	–1.5 to 2	Spawning generally in ice-covered areas in winter but has never been observed directly	Buoyant, passive, just under the ice or at the surface
Larva, months	–1 to 5	Larvae found near the surface in both ice-covered and ice-free areas	Buoyant and passive, generally within the top 30 m
Juvenile, <1 year	–1 to 9	Juveniles found in the water column (pelagic) in both ice-covered and ice-free areas or at the surface under the sea ice and in water wedges or cavities in sea ice (sympagic)	Sympagic or pelagic, down to 100 m
Immature, 1–2 years	–1.8 to 6	Immatures found in the water column (pelagic) in both ice-covered and ice-free areas or at the surface under the sea ice and in water wedges or cavities in sea ice (sympagic)	Sympagic to mesopelagic, down to 400 m but generally <250 m
Adult, 2–7 years	3 to 10	Adults generally not associated with sea ice	Mainly demersal–pelagic and remain deeper (>100 m) than younger stages; often in Atlantic offshore waters and fjords

environmental changes and anthropogenic stressors differ among life stages (**Table 1**), we must understand the mechanisms on a life-stage basis, taking into consideration any fine-scale ontogenetic differences when required, for example, early- versus late-stage larvae.

2.1. Eggs

Egg development rate and hatching success are temperature-dependent, with winter and spring temperatures playing an important role in egg survival (Sakurai et al., 1998; Laurel et al., 2018). The eggs develop normally between –1.5°C and 3.0°C (Sakurai et al., 1998). However, a precipitous decline in hatching success occurs at temperatures above 2.0°C (Dahlke et al., 2018; Laurel et al., 2018). Time to hatch (incubation time) decreases as temperatures warm, ranging between 79 days at –1.5°C and 29 days at 3.8°C (Aronovich et al., 1975; Altukhov, 1981; Graham and Hop, 1995; Sakurai et al., 1998; Laurel et al., 2018; Bender et al., 2021). However, in natural environments, disentangling the effect of temperature on survival from other temperature-mediated factors is difficult. For example, Arctic cod embryos experience a narrowing of their optimal thermal range and increased mortality under ocean acidification scenarios (Dahlke et al., 2018). These pelagic eggs are positively buoyant (density of 1.022–1.024 g cm^{–3}) and come into direct contact with the underside of the sea ice in ice-covered areas (Ponton and Fortier, 1992; Spencer et al., 2020). The low relative density of Arctic cod eggs floating at the surface makes them prone to wind-driven advection in ice-free areas (Eriksen et al., 2020; Spencer et al., 2020), and they could potentially be transported outside of suitable nursery areas when floating in open waters. Eggs range from 1.5 mm to 1.8 mm in diameter, have a smooth, thin, single

chorion, and lack pigmentation (Sakurai et al., 1998). As sea-ice cover declines, the unpigmented Arctic cod eggs will experience greater exposure to temperature variation, turbulence from mechanical wave action, and UV radiation, all of which may negatively affect egg survival (Altukhov, 1981; Borkin et al., 1987b; Dahms et al., 2011; Christiansen, 2017; Laurel et al., 2018; Spencer et al., 2020; Bouchard et al., 2021). Conversely, with slightly warmer surface waters, the eggs could develop faster at temperatures closer to their optimal temperature range (Laurel et al., 2018).

2.2. Larvae

Arctic cod larvae can tolerate higher temperatures than their eggs. Laboratory experiments and inferences from in situ studies suggest high mortality rates and poor development below –1°C and above 5°C (Kashkina, 1962; Rass, 1968; Altukhov, 1981; Fortier et al., 2006; Koenker et al., 2018a; Koenker et al., 2018b). Size-at-hatch ranges between 3.5 mm and 7 mm standard length (e.g., Graham and Hop, 1995; Ponomarenko, 2000b; Bender et al., 2021) and, as shown in laboratory experiments, decreases with increasing temperatures between –0.4°C and 3.8°C (Laurel et al., 2018). A larger size-at-hatch is often linked to improved survival through enhanced swimming and foraging capabilities, particularly during the critical period of yolk exhaustion and the onset of exogenous feeding. A positive relationship between size-at-hatch and survival is supported by the in situ observations by Bouchard et al. (2013), who found evidence of selection for large size-at-hatch in the southeastern Beaufort Sea.

In addition to size-at-hatch, temperature variability within the thermal tolerance range of Arctic cod also affects individual growth trajectories (e.g., Rass, 1968;

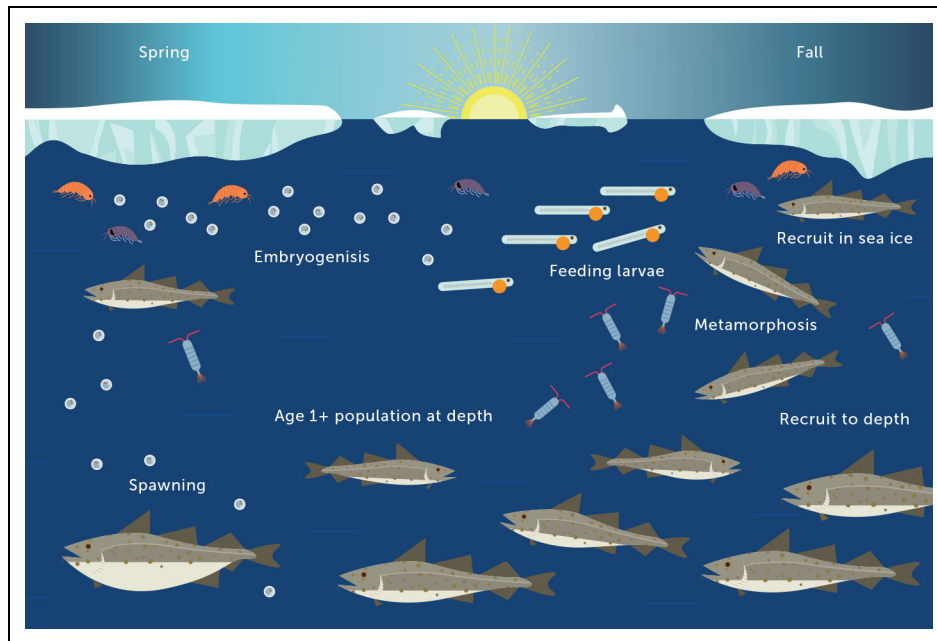


Figure 3. The life cycle of Arctic cod in Arctic seas over a full year. Spawning occurs between September and April. The positively buoyant eggs rise to the surface, generally in ice-covered waters. The temperature-dependent embryogenesis lasts 29–79 days. Hatching occurs between January and July. The larvae hatch with a large yolk sac, which completely resorbs after 18–28 days depending on temperature. Exogenous feeding can start before complete yolk sac resorption. Newly hatched larvae feed mostly on copepod eggs and nauplii, whereas late-stage larvae also prey on copepodites and various zooplankton prey. Metamorphosis into juveniles occurs when individuals reach approximately 30 mm standard length. Juveniles continue to feed in surface waters until reaching 30–55 mm, and, in the fall, they either recruit in the sea ice or descend deeper in the water column to spend the winter. Adults (age-1+) found at depth segregate vertically by size, with smaller individuals at shallower depths than larger individuals.

Koenker et al., 2018b). In most rearing experiments, the optimal temperature for growth was close to the upper thermal limit but was associated with elevated mortality rates. For example, Koenker et al. (2018b) reported an optimal temperature for growth ranging between 5°C and 7°C but recorded an optimal temperature for survival at 2°C. Similarly, Bender et al. (2021) reported faster growth but lower survival at 3°C than at 0°C because the larvae that hatched were less developed. The advantages associated with fast growth are likely offset by increased metabolic demand at higher temperatures (David et al., 2022). In natural environments, however, fast growth under relatively high temperatures seems to provide a survival advantage. Physiological models based on field observations from the Northeast Water and North Water polynyas in the 1990s demonstrated the existence of strong growth-dependent mortality favoring fast-growing individuals, which suggests that warmer temperatures and growth rate could enhance overall survival (Thanassekos et al., 2012). This discrepancy between experiments and in situ observations likely results from the range of temperatures at which the field observations were conducted. In the High Arctic, a slight increase in sea surface temperature (SST) in the short- to mid-term is predicted to benefit Arctic cod recruitment transiently (Bouchard et al., 2017). In contrast, along the southern margins of Arctic cod distribution, the survival of larvae is currently threatened, as summer SSTs now frequently

exceed the thermal tolerance limits of larvae (Huserbräten et al., 2019; Marsh and Mueter, 2020; Bouchard et al., 2021; Deary et al., 2021).

Arctic cod larvae are euryhaline and are thus well adapted to habitats where ice melt and river discharge can rapidly modify salinity (Spencer et al., 2020). Their low density (1.024 g cm⁻³; Spencer et al., 2020) implies that, except in low salinity areas, they are generally distributed near the surface at depths as shallow as the upper 0.5 m of the water column and mostly in the top 30 m (Shleinik, 1970; Belikov et al., 1991; Bouchard et al., 2016; Spencer et al., 2020; **Figure 3**). In regions highly influenced by riverine input, such as the Beaufort Sea, the Laptev Sea, and Hudson Bay, brackish water from river plumes increases the freezing point of under-ice water in winter and spring. This effect provides a thermal refuge against lethally cold temperatures and allows early-hatching larvae to survive winter, grow at faster rates, and benefit from a longer growth season than late hatchers (Bouchard and Fortier, 2008; Bouchard and Fortier, 2011; Schembri et al., 2021). Similarly, in some coastal areas, the presence of less-dense glacial meltwater in summer causes larvae to remain in colder and deeper waters, where they are neutrally buoyant, a mechanism that can provide larvae a thermal refuge against lethally warm surface waters (Bouchard et al., 2021). Hence, increased meltwater in fjord ecosystems could counterbalance some of the egg and larval mortality associated with high summer SSTs and

increased exposure to UV radiation, thereby limiting recruitment failure.

Some studies have documented relationships between sea-ice parameters (concentration, coverage, timing of breakup) and larval feeding success, growth, and survival (e.g., Borkin et al., 1987b). In general, a strong correlation between sea-ice conditions and temperature prevents any conclusion regarding the role of sea ice alone in regulating larval population dynamics (Michaud et al., 1996; Bouchard et al., 2017; Gjøsæter et al., 2020). In the northern Canadian Archipelago, year-round low temperatures of approximately -1.8°C below multiyear ice strongly compromise the growth and survival of Arctic cod, and the presence of sea ice and associated cold temperatures limit population connectivity between the western and eastern Canadian Arctic (Bouchard et al., 2018). In ice-covered regions, primary production shifts from sea ice to the pelagic system in spring–summer (Leu et al., 2015). If the food supply remains sufficient because of increased primary production, larvae may thrive for a transient period in these more productive waters (Bouchard et al., 2017; Lewis et al., 2020).

2.3. Juveniles

Arctic cod juveniles (age-0) are characterized by a broad thermal tolerance and can survive at temperatures between -1°C and 12°C , although their growth rates decrease above 9°C (Laurel et al., 2017). In the Chukchi Sea, juvenile Arctic cod are most abundant at intermediate temperatures (5°C – 6°C) and high salinities (>28 , with peak density at 31; De Robertis et al., 2017; Vestfals et al., 2019; Marsh et al., 2020). In laboratory experiments where Arctic cod juveniles have been reared at constant temperatures (3°C or 7°C) from hatching to metamorphosis at approximately 30 mm standard length (Ponomarenko, 2000b), they have exhibited isometric growth but allometric lipid storage because of the rapid increase in lipids per weight when the juveniles reach >35 mm standard length (Copeman et al., 2020). In open water, larvae and juveniles feed on a variety of prey, including copepods, amphipods, rotifers, bivalves, and echinoderm larvae (Walkusz et al., 2011). Modifications to the quantity and the quality of food available to juveniles and the temperature of their habitat will likely affect the recruitment success from juveniles to immatures. Copepodite stages and adults of the calanoid copepod *Calanus glacialis* are the main source of carbon used by juvenile Arctic cod to accumulate large reserves of lipids in their liver and muscle to survive the winter (Bouchard and Fortier, 2020; Copeman et al., 2020). Climate change-induced reductions in the abundance of lipid-rich Arctic mesozooplankton and alterations of their phenology are expected to affect Arctic cod juveniles negatively (Copeman et al., 2022a).

Reductions in sea-ice cover and duration likely have a more limited impact on juveniles than on eggs and larvae. Juvenile Arctic cod descend deeper in Pacific and Atlantic water masses once they reach 30–55 mm at the end of their first summer (Borkin et al., 1987b; Ponomarenko, 2000b; Bouchard and Fortier, 2011; Benoit et al.,

2014; Geoffroy et al., 2016; Majewski et al., 2016). Yet, an unknown proportion of juveniles and immature Arctic cod remain ice-associated, that is, sympagic (Lønne and Gulliksen, 1989; David et al., 2016; **Figure 3**). Late hatchers have been suggested to remain sympagic at the start of winter to avoid predation from adults (cannibalism) in deeper waters or avoid competition with older, larger individuals from the same hatching year and only descend to deeper layers upon reaching sexual maturity at age-2 or age-3 (Craig et al., 1982; Geoffroy et al., 2016). A shorter sea-ice season will likely enhance the exposure of juveniles to visual predators (Varpe et al., 2015; LeBlanc et al., 2019). Furthermore, the rapid decline of multiyear ice coverage observed in the Arctic Ocean over the last 2 decades may have affected ice-dwelling Arctic cod by reducing habitat complexity and the structural refuges provided by this older sea ice (Gradinger et al., 2010; Kacimi and Kwok, 2022).

2.4. Immatures

Immature Arctic cod (age-1 or age-2) exposed to temperatures $>6^{\circ}\text{C}$ over the long-term experience a decreased growth performance, reduced food conversion efficiency, and elevated standard metabolic rates (Kunz et al., 2016; Laurel et al., 2016; Laurel et al., 2017; Kunz et al., 2018). High temperatures (10°C – 12°C) result in negative growth and increased mortality (e.g., Laurel et al., 2016). Furthermore, there is some evidence that the negative effect of higher temperatures can be exacerbated by ocean acidification (Kunz et al., 2016). Immature Arctic cod can be found either under the sea ice, where they feed at least partly on sympagic prey (Lønne and Gulliksen, 1989; David et al., 2016; Kohlbach et al., 2017), or at mesopelagic depths in ice-free waters, where they feed mainly on copepods and, to some extent, on a broad range of organisms, including amphipods, rotifers, bivalves, and echinoderm larvae, in the water column or near the seafloor (Orlova et al., 2009; Walkusz et al., 2011; Hop and Gjøsæter, 2013; Nahrgang et al., 2014; Geoffroy et al., 2019). A decline in sea-ice age and concentration or a delay in ice freeze-up may be associated with reduced habitat for a portion of the immature population, including a lower abundance of their sympagic prey (Kohlbach et al., 2017; Hop et al., 2021a). Ultimately, reduced sea-ice cover could lead to a decrease in the survival of immature Arctic cod or an increase in the proportion of immature individuals dwelling in the water column or near the seafloor (e.g., Borkin et al., 1987a; Dupont et al., 2021).

2.5. Adults

Adult Arctic cod can be found in water temperatures up to 13.5°C (Craig et al., 1982) and have a physiological optimum between 3°C and 10°C (Drost et al., 2016; Kunz et al., 2016; Laurel et al., 2017; Leo et al., 2017; Koenker et al., 2018a; Koenker et al., 2018b). At the southern limit of the species' range, higher temperatures are associated with lower abundances of adult populations (Eriksen et al., 2015; Marsh and Mueter, 2020; Chawarski et al., 2022). Most adult Arctic cod continue to descend deeper as they grow and become demersal–pelagic (**Figure 3**). Typically,

adult Arctic cod reside in the deeper layers of the water column, offshore, and in fjord systems (Falk-Petersen et al., 1986; Wathne et al., 2000; Christiansen et al., 2012; Geoffroy et al., 2016; Majewski et al., 2016; Forster et al., 2020). On some occasions, Arctic cod also form mass aggregations near the surface (e.g., Crawford and Jorgenson, 1996). Such near-surface aggregations of immature and adult Arctic cod (1–4+ years) have been recorded in coastal and ice-free areas and along the ice edge in the Siberian Arctic (Andriashev et al., 1954; Moskalenko, 1964; Andriashev et al., 1980; Melnikov and Chernova, 2013) and the Canadian Arctic (Welch et al., 1993; Hop et al., 1997). Moreover, aggregations of adult Arctic cod can occur in relatively shallow embayments (<30 m bottom depth), and size-class segregation can occur horizontally in these cases (Kessel et al., 2020). These near-surface aggregations provide easily available prey to top predators, but the frequency of occurrence and the exact mechanisms behind the formation of these aggregations remain unknown.

Sea ice does not seem to be an important habitat for adult Arctic cod. The abundance of adult Arctic cod is either not significantly or negatively associated with sea ice in the Barents Sea (Dupont et al., 2021) and the Canadian Arctic (Bouchard et al., 2018). Moreover, growth is negatively associated with sea ice in the Barents Sea, which could result in size-related mortality (Dupont et al., 2020).

2.6. Spawning

Arctic cod has multiple reproductive cycles over the course of its lifetime (Hop et al., 1995; Nahrgang et al., 2014). The spawning season varies regionally but generally occurs between September and April, with a peak in January–February (Ponomarenko, 1964; Shleinik, 1973; Graham and Hop, 1995; Ponomarenko, 2000a; Boitsov et al., 2013). Although few direct observations of spawning have been reported in the wild, several spawning locations have been proposed across the circumpolar Arctic. In the Barents Sea and Siberian Arctic, spawning has been suggested to occur southeast of Svalbard, around the Severnaya Zemlya archipelago, and in the Kara and Pechora seas (Huserbråten et al., 2019; Aune et al., 2021; Chernova et al., 2021; and references therein). In the Canadian Arctic, dense winter aggregations at depths >140 m in Franklin and Darnley bays have been hypothesized to be related to spawning events (Benoit et al., 2008). In the Pacific Arctic, spawning has been suggested in the northern Bering Sea, the southern Chukchi Sea, and Kotzebue Sound (Deary et al., 2021; Vestfals et al., 2021). Uncertainties around the location of potential spawning grounds remain high because most are based on modeling or the sampling of larvae and recently spawned adults (rather than eggs or direct observations of spawning). The ubiquity of early-stage larvae in Arctic seas during the spring and summer further suggests that several spawning areas remain undocumented.

Little is known about the potential effects of climate change on Arctic cod spawning. In a modeling study, Dahlke et al. (2018) predicted a reduction in spawning

habitat of between 20% and 80% in the European Arctic on the basis of proposed climate and ocean acidification scenarios. Among several fish species, the spawning adult stage, along with the egg stage, has the narrowest thermal tolerance (Dahlke et al., 2020; Laurel and Rogers, 2020; Côté et al., 2021). In the northwestern Barents Sea, Arctic cod originating from regions influenced by warmer Atlantic water had a lower fecundity (i.e., number of eggs in females) and matured at an earlier age and smaller size than fish from regions having cold Arctic water masses (Nahrgang et al., 2014). Moreover, if sea ice forms later in the autumn, the timing of optimal spawning of Arctic cod may shift. This shift may lead to a potential mismatch between larval development and the phenology of food availability (Daase et al., 2013; Dahlke et al., 2018; Huserbråten et al., 2019).

2.7. Overwintering

The overwintering physiology of juvenile Arctic cod remains a major knowledge gap that hampers our capacity to make informed predictions about the annual survival success of Arctic cod in the face of intense summer–fall warming. Although the summer habitat of Arctic cod is rapidly changing, overwintering conditions will remain long, dark, cold, and typified by low or zero primary productivity. Generally, small fish are more vulnerable to overwintering starvation and predation than larger fish (Sogard and Olla, 2000; Hurst, 2007). Fish that overwinter for extended periods at sub-zero temperatures (Benoit et al., 2008; Geoffroy et al., 2011) reduce their metabolic energy demand to a minimum to survive periods of starvation (Hop and Graham, 1995; Hop and Tonn, 1998). During early spring, Arctic cod benefit from prey arriving with the seasonal upward migration of zooplankton (Daase et al., 2013; Hop et al., 2021b). Furthermore, the extreme seasonality in food production requires Arctic cod to accumulate energy reserves rapidly during late summer, prior to entering an extended overwintering period. As a strategy to deal with short, cold summer growing conditions, Arctic cod juveniles generally enter winter at a smaller size but with much higher tissue lipid concentrations compared with boreal species (Copeman et al., 2017; Brewster et al., 2018; Dissen et al., 2018; Copeman et al., 2020). Currently, we know little about how their autumn size or energy storage will be affected by both the direct physiological (e.g., response to temperature) and indirect food web effects of the continued warming and loss of spring–summer sea ice. Additional fall blooms resulting from longer open-water periods might increase secondary production and the abundance of prey before winter (Tremblay et al., 2012; Ardyna et al., 2014). In contrast, if juvenile Arctic cod have reduced lipids at the onset of winter, their specialized ability to survive long periods of severe wintering conditions will likely be affected negatively (Copeman et al., 2022b).

Our understanding of Arctic marine ecosystems during winter continues to evolve. Previous research on this topic has shown that Arctic cod exhibited unexpected levels of biological activity during the polar night (Berge et al., 2015) and continued to feed to some extent (Cusa et al.,

2019; Geoffroy and Priou, 2020). Moreover, prey for larval Arctic cod, such as *Calanus* spp., may have flexible overwintering strategies and exit diapause early or skip diapause entirely to adapt to changing environmental conditions (Hobbs et al., 2020), further modifying their timing and availability as prey for Arctic cod.

3. Impacts of environmental and anthropogenic stressors on the future of Arctic cod and its ecosystem

The main environmental (abiotic and biotic) and anthropogenic stressors for Arctic cod have been identified in a scenario up to the year 2050. These stressors are described below and were scored in a risk assessment based on a rigorous expert judgment process by the coauthors (Mach et al., 2017; Text S1 and Data S1). Although we assessed each stressor individually, most stressors interact and may amplify the risk to Arctic cod through cumulative impacts. However, the exact effects and interactions of cumulative impacts are poorly documented. Potential geographic and ontogenetic biases in this assessment have been minimized by the broad scope of geographic and ontogenetic perspectives of the 38 coauthors who participated in the assessment. Relying on the state of knowledge presented in this review, we scored the impact of nine environmental stressors on (a) the different life stages of Arctic cod and (b) in the eight LME of the Arctic Ocean (CAFF, 2017) in an online survey according to the established scoring system of the IPCC, ranging from “0” (no measurable impact) to “3” (very high impact; Pörtner et al., 2019; Text S1). When scoring for the different life stages, each coauthor considered the potential negative effect of each stressor on the survival of each life stage of Arctic cod in 2050 integrated across the species’ entire distribution range, that is, considering the potential geographic variability of impact in relation to their spatial distribution. When scoring for the populations in different LMEs, the potential negative impact of each stressor on the Arctic cod populations within each LME by 2050 was integrated across all life stages; that is, the impact on the different life stages and their relative share of the population may vary between LMEs (Text S1). Moreover, each coauthor scored the confidence of the impact assessment for each life stage and population in the various LMEs on a scale from 1 (low confidence) to 4 (high confidence), taking into consideration evidence and the degree of scientific consensus in the literature (Mach et al., 2017; Pörtner et al., 2019; Text S1).

3.1. Environmental stressors

3.1.1. Sea-ice decline

Although little evidence suggests that Arctic cod depends directly on sea ice in terms of temperature-dependent development, including for early life-history stages, reduced ice cover is nevertheless likely to affect the distribution and total biomass of Arctic cod (e.g., Borkin et al., 1987b; Huserbråten et al., 2019). Sea-ice decline will likely reduce spawning habitat and egg survival and affect food availability and quality (Wassmann et al., 2006; Søreide et al., 2010; Dahlke et al., 2018; Hop et al., 2021b). A reduced

sea-ice extent will increase egg exposure to predators, as the under-ice habitat refuge becomes more limited. The effect of a reduced sea-ice extent will vary among ontogenetic stages (**Table 1**). Larvae, juvenile (after ice formation in autumn), and some immature Arctic cod can be associated with sea ice (Gradinger and Bluhm, 2004; David et al., 2016). In the Arctic Basin, ice-associated Arctic cod feed predominantly on sympagic fauna or zooplankton that obtain their carbon from sympagic production (Kohlbach et al., 2017). Younger stages and adults have aggregations segregated spatially and vertically, as observed in the Kara Sea (Borkin, 2008; Dolgov et al., 2011), the Laptev and East Siberian seas (Glebov et al., 2016), and the Beaufort Sea (Geoffroy et al., 2016). The importance of the under-ice habitat for feeding, protection, and energy maintenance is lower for older immatures and adults, which are generally found in aggregations in the open ocean (Hop and Gjøsæter, 2013) and in deeper waters (Benoit et al., 2008; Benoit et al., 2010; Geoffroy et al., 2011; Benoit et al., 2014; Geoffroy et al., 2016). Nonetheless, adults occasionally stay below sea ice in coastal areas, where they are less subject to predation (Crawford and Jorgenson, 1990; Crawford and Jorgenson, 1993; Kessel et al., 2016; Kessel et al., 2017). Without the protective cover of sea ice, those adults schooling in coastal areas are more exposed to predation from marine mammals and seabirds (Welch et al., 1993; Crawford and Jorgenson, 1996). The overall reduction in sea ice and snow cover will also lead to increased underwater light (Nicolaus et al., 2012; Lannuzel et al., 2020; Castellani et al., 2021), which in turn will modify the vertical positioning of zooplankton prey and require adaptive foraging behavior by Arctic cod (Hobbs et al., 2020). Increased underwater light will improve the visual range for planktivorous species such as Arctic cod but also improve visibility for their predators (Varpe et al., 2015; Langbehn and Varpe, 2017).

Sea-ice decline is particularly noticeable along the shelf and slope regions of the Arctic Ocean, where a large part of the Arctic cod stock resides. In the Canadian Arctic, the disappearing multiyear ice will favor potential genetic exchanges between the eastern and western populations (Bouchard et al., 2018). However, sea ice can also act as a transport vector for juvenile and immature individuals recruiting under the ice, facilitating gene flow among populations (David et al., 2016; Maes et al., 2021). Increasingly, the Transpolar Drift will be disconnected from ice formation over the Siberian Shelf (Krumpen et al., 2019), which will affect the transport of sympagic biota across the central Arctic Ocean, including Arctic cod (David et al., 2015; Kiko et al., 2017; Ehrlich et al., 2020).

We consider the added risk of sea-ice decline by 2050 as very high for the survival of eggs, high for larval and juvenile Arctic cod, and moderate for immatures and adults. From the available information, our confidence is high for eggs and larvae, medium for juveniles and immatures, and low for adults (**Figure 4a**).

3.1.2. Ocean warming and dynamics

Arctic cod is retreating northward with increased ocean warming, as observed in the Barents and Bering seas

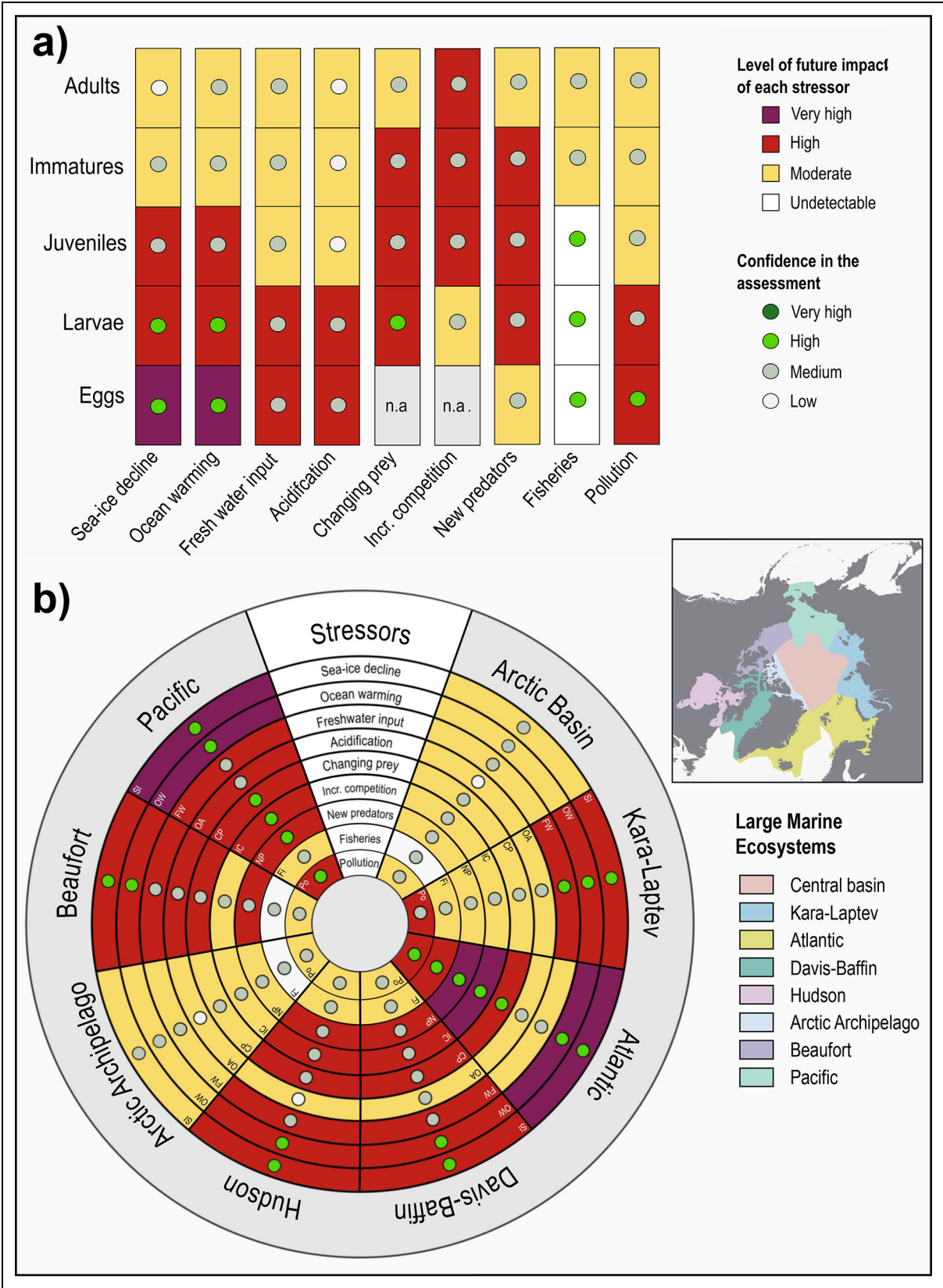


Figure 4. Expected impacts on Arctic cod within large marine ecosystems of the Arctic Ocean by 2050. Expected impacts of changing environmental variables and confidence levels in the assessment on (a) Arctic cod life stages and (b) Arctic cod populations. Large marine ecosystems are indicated in the insert map adapted from CAFF (2017).

(Fossheim et al., 2015; Baker, 2021). Adult Arctic cod may prefer moderate temperatures up to about 10°C when no competitors are present (Table 1). In the presence of subarctic competitors and predators, however, Arctic cod retracts to cooler waters where it has a growth advantage over boreal species (Laurel et al., 2017; Marsh and Mueter,

2020). In the presence of boreal competitors, the temperature range causing a northward retreat lies at approximately 5.5°C in the Barents Sea (temperature within the upper 50 m; Eriksen et al., 2015) and approximately 2°C in the Bering Sea and Newfoundland–Labrador region (bottom temperature; Marsh and Mueter, 2020). In the southern part of the distribution range of Arctic cod, particularly in the Pacific and Atlantic gateways, ocean temperatures are thus increasingly advantageous to boreal species, at the expense of Arctic cod, and the upper thermal tolerance limits of immature Arctic cod (6°C; **Table 1**) could be reached before 2050 (Slagstad et al., 2015; Drost et al., 2016; Kunz et al., 2016; Laurel et al., 2016; Laurel et al., 2017). Embryos will be affected sooner through increased mortality above 2°C (Dahlke et al., 2018).

Toward the mid-21st century, ocean warming is expected to contribute to a decreased abundance of Arctic cod (Steiner et al., 2019) and will lead to a latitudinal compression of its distribution because of a northward shift of the southern boundary of the thermal habitat for this species. Arctic cod populations at higher latitudes and in specific regions may benefit from a certain level of ocean warming. In regions experiencing a moderate temperature increase, warmer water initially may be positive for the growth and survival of larvae and juvenile Arctic cod (Bouchard and Fortier, 2011; Dupont et al., 2020). However, over the longer term, additional stressors, such as changing prey composition, increasing interspecific competition, predation pressure, and winter mortality, may outweigh these positive effects (Bouchard et al., 2017; Dupont et al., 2021). In most Arctic seas, the relative abundance of Arctic cod within the fish community will likely fluctuate in accordance with colder and warmer periods, as observed in the Bering, Labrador, and Barents seas (Eriksen et al., 2015; Vihtakari et al., 2018; Marsh and Mueter, 2020).

Therefore, given the relatively narrow Arctic temperature tolerance for the early life stages of Arctic cod (**Table 1**) combined with additional stressors inseparably linked to ocean warming, we conclude that ocean warming will be associated with a very high added risk for the survival of eggs in the future Arctic Ocean, a high risk for larvae and juveniles, and a moderate risk for immature and adult Arctic cod. Because of the broad knowledge base from both experimental and empirical field studies, the confidence in this risk assessment is considered high for eggs and larvae, and medium for juveniles, immatures, and adults (**Figure 4a**).

3.1.3. Changes in freshwater inputs

The Arctic marginal seas are strongly influenced by freshwater, and global warming is resulting in important changes in all freshwater components, notably increased precipitation within the drainage basins of Arctic rivers, increased glacial meltwater input, and increased river runoff (e.g., Peterson et al., 2002; Hanna et al., 2008; Bintanja and Selten, 2014; Tedesco and Fettweis, 2020). Climate models project by the end of the century a 30% increase in Arctic runoff, an earlier onset of the spring freshet, and greater winter runoff, resulting in a reduced seasonality of

freshwater discharge (Nummelin et al., 2016; Stadnyk et al., 2021). Changes in freshwater inputs could benefit larval Arctic cod in some regions by improving the survival of winter hatchers (see Section 2.2). On the other hand, increased river runoff and surface freshening can also induce stronger currents close to river mouths and along the coastal areas of the Arctic Ocean (Spall, 2013; Whitefield et al., 2015), which would affect Arctic cod movement and carry eggs and larvae out of nursery grounds. Greater river runoff would also increase turbidity (Doxaran et al., 2015) and negatively affect larvae, which are visual predators and avoid highly turbid waters (Ponton and Fortier, 1992). Greater river runoff can also increase pollutant levels (Harms et al., 2000) with consequences for Arctic cod at different life stages (see Section 3.2.2). Heightened glacial meltwater could have both local and larger-scale effects on Arctic cod, notably on egg and larval survival. A fresher and thicker surface layer will cause eggs and larvae to sink in the water column until they reach neutral buoyancy, where they are less subject to predation from the surface and UVB damage (Bouchard et al., 2021). Changes in freshwater inputs are associated with changes in stratification and mixed-layer depth (e.g., Oliver et al., 2018; Yamaguchi and Suga, 2019; Hordoir et al., 2022), which could affect primary production and cascade up to affect Arctic cod. Subregions of the Arctic Ocean, however, vary considerably in glacial and riverine inputs, making it difficult to generalize their impacts on Arctic cod across all regions.

We consider the impact of changes in freshwater inputs as high for the survival of egg and larval Arctic cod in the future and moderate for juveniles, immatures, and adults. From the available information, we consider the confidence as medium for all life stages (**Figure 4a**).

3.1.4. Ocean acidification

Ocean acidification is faster in the Arctic than in most other oceans because of the loss in sea-ice cover limiting atmospheric exchanges, coupled with increased inflow of glacier meltwater with lower alkalinity. With an estimated 0.02 unit decrease in pH per decade, pH would decrease 0.08 units by 2050 (AMAP, 2018; Pörtner et al., 2019). Ocean acidification effects, compounded by temperature and freshwater input (i.e., lower alkalinity; Semiletov et al., 2016), impair larval fish sensory abilities, affect the morphology of otoliths, cause tissue damage and behavioral changes, and increase embryo mortality (Dahlke et al., 2018). Studies on juvenile and immature Arctic cod show that although effects appear limited at the cellular and whole-body level, the combined effect of ocean acidification and ocean warming negatively affects fitness and reduces the competitive strength of Arctic cod (Kunz et al., 2016; Leo et al., 2017; Leo et al., 2020). Some regions, such as the Beaufort, Kara, and Laptev seas, are already frequently or permanently undersaturated in aragonite, affecting marine calcifiers such as pteropods (Mortenson et al., 2020; Niemi et al., 2021). Whereas early life stages of Arctic cod might be more affected, the consequences of ocean acidification on adults appear minimal, as reported in a recent modeling study (Steiner et al., 2019).

We conclude that the added impact of ocean acidification on eggs and larvae is high, whereas it is moderate for juvenile, immature, and adult Arctic cod. Given the limited information on the exact future acidification rate and, in particular, the effects on older life stages, the confidence for this assessment is medium for eggs and larvae and low for juveniles, immatures, and adults (**Figure 4a**).

3.1.5. Changing prey field

Arctic cod larvae mainly consume eggs, nauplii, and copepodites of the genera *Calanus* and, to a lesser extent, *Pseudocalanus* (Bouchard et al., 2016; Bouchard and Fortier, 2020; Bouchard et al., 2022). Juveniles also eat large numbers of calanoid nauplii but positively select *Calanus* copepodites, their main source of carbon (Walkusz et al., 2011; Bouchard and Fortier, 2020; Table S1). Although pelagic zooplankton remain the dominant prey in most regions (e.g., Renaud et al., 2012; Table S1), juvenile and immature Arctic cod residing underneath the sea ice in the Eurasian Basin of the Arctic Ocean depend strongly on carbon originating from ice algae because they feed mainly on ice-associated species such as the amphipod *Apherusa glacialis* and the harpacticoid copepod *Tisbe* spp. (Lønne and Gulliksen, 1989; Kohlbach et al., 2017).

Marked effects on larval and juvenile survival may result indirectly from the regulation of prey availability. The timing of sea-ice breakup dictates the timing of the phytoplankton bloom and subsequent secondary production (Leu et al., 2011). Higher food availability because of earlier ice melt promotes the growth and survival of age-0 fish in the Canadian High Arctic (LeBlanc et al., 2020). However, very early or late ice breakup may produce a mismatch between larval emergence and the availability of their prey (Søreide et al., 2010). The declining availability of sea-ice algae and a modified timing between sea-ice algae productivity and the pelagic phytoplankton bloom affect the ontogeny, survival, and energy content of *Calanus glacialis* (Søreide et al., 2010; Wassmann and Reigstad, 2011; Tedesco et al., 2019), a key prey of Arctic cod (e.g., Bouchard and Fortier, 2020). In years of temporal mismatch with their preferred prey, Arctic cod larvae switch to other available prey, and their survival can be maintained by increasing their prey spectrum (Borkin, 2013). For example, ice algae made up 40% of stomach contents in ice-associated individuals collected in February (Pechenik et al., 1973; Aune et al., 2021). Nonetheless, decreased large and ice-associated zooplankton (Balazy et al., 2018; Lannuzel et al., 2020), the advection of smaller temperate taxa into the Arctic, for example, the proportional replacement of *C. glacialis* by *C. finmarchicus* in some regions (Beaugrand et al., 2013; Aarflot et al., 2018; Spear et al., 2019), and the reduced lipid content of *Calanus* spp. (Møller and Nielsen, 2020) are expected to lead to long-term negative effects on the growth and survival of Arctic cod larvae and juveniles (David et al., 2022). Synergistic effects of temperature and food abundance on the energetic condition of Arctic cod have been measured in laboratory experiments. A higher sensitivity to changes in food quantity occurs at warmer temperatures (5°C) than at their lower end of the thermal range (2°C) in late larval stages

because of elevated metabolic rates at higher temperatures (Koenker et al., 2018b).

Immature and adult Arctic cod feed opportunistically on benthic, pelagic, and ice-associated prey (Hop and Gjøsaeter, 2013; Walkusz et al., 2013; Dalpadado et al., 2016; Majewski et al., 2016; Kohlbach et al., 2017; Cusa et al., 2019). Their diet varies among regions, habitats, seasons, and body size, with calanoid copepods and hyperiid amphipods, such as *Themisto libellula*, being recurrent prey items. Krill (e.g., *Thysanoessa inermis*), benthic amphipods, appendicularians, chaetognaths, polychaetes, mollusks, shrimp, mysids, barnacle larvae, and other fish—including the cannibalism of juveniles—are other regionally important prey items of immature and adult Arctic cod (Bradstreet and Cross, 1982; Gray et al., 2016; McNicholl et al., 2016; Prokopchuk, 2017; Table S1). Recently, a diet composition study using molecular markers indicated that fish larvae and soft-bodied invertebrates are more common prey than previously assumed (Maes et al., 2022). The diet composition has been found to vary both at a regional (Renaud et al., 2012) and more localized scale (Ajiad and Gjøsaeter, 1990). In the Barents Sea, for example, a seasonal shift in prey dominance occurs when, during winter, the relative contribution of benthic crustaceans to diet increases (Ponomarenko, 2000a; Cusa et al., 2019). Because of their broad prey spectrum, immatures and adults are expected to be less vulnerable to changes in the prey field than younger stages. However, the extent of this dietary flexibility remains unknown, and there is considerable uncertainty regarding the effects of an altered plankton community on Arctic cod diet and fitness.

In some regions, sea-ice decline and ocean warming are associated with a marked increase in zooplankton biomass (Dalpadado et al., 2020). A higher total biomass is generally linked to increased dominance of boreal *Calanus* spp. having shorter life cycles, which could result in higher total lipid availability, albeit with reduced lipids per individual prey (Renaud et al., 2018; Møller and Nielsen, 2020). Because boreal competitors such as capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus*) are adapted to feed on smaller and more abundant zooplankton, they are more likely to benefit from this zooplankton surplus than Arctic cod (Steiner et al., 2019; Stige et al., 2019). The benefits of increased secondary productivity to counterbalance the negative effects of diminishing Arctic prey thus depend on the ability of Arctic cod to exploit their new prey field effectively.

We assess the overall added risk of changing prey field on the survival of larvae, juveniles, and immatures as high but moderate for adults. This assessment has a high confidence for larvae, which have a narrow prey spectrum and are susceptible to mismatch dynamics. Given the uncertainties regarding the ability of Arctic cod to adapt to a new prey field, the confidence level is medium for all older life stages.

3.1.6. Increased competition

The northward expansion of boreal fishes in some Arctic regions heightens the risk of competition with Arctic cod populations (Fossheim et al., 2015; Fall et al., 2018; Côté

et al., 2021; Levine et al., 2023). In the Barents Sea, boreal capelin, Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) have extended their ranges northward into areas historically dominated by Arctic cod (Renaud et al., 2012; Hop and Gjosæter, 2013; Fossheim et al., 2015). In the Kara Sea, the highest similarity in diet composition occurs between mature Arctic cod and capelin, Atlantic herring, the boreal spotted barracudina (*Arctozenus risso*), as well as benthic sculpins and snailfishes (Dolgov, 2016). So far, the abundance of these other fishes in the Kara Sea remains low relative to that of Arctic cod. In North America, boreal forage fish species, for example, capelin, Pacific sand lance (*Ammodytes hexapterus*), and saffron cod (*Eleginus gracilis*), have increased their range and abundance northward and occupy a similar dietary niche as Arctic cod (Falardeau et al., 2014; Ulrich and Tallman, 2021; von Biela et al., 2023). They could thus actively compete with Arctic cod for prey (McNicholl et al., 2016; McNicholl et al., 2018; Pedro et al., 2020). In the eastern Chukchi Sea, a high degree of similarity prevails among the diets of juvenile Arctic cod, juvenile sand lance, and saffron cod, suggesting the potential for interspecific competition (Kuznetsova, 2018).

The risk of interspecific competition varies among the different life stages. Overall, juveniles are likely more vulnerable to competition than larvae because their diet overlaps with that of other species for a longer period (several months; e.g., Persson, 1988). Arctic cod larvae generally hatch in high densities in spring, earlier than most boreal species (Bouchard and Fortier, 2011; Chapman et al., 2023), which likely limits the risk of competition for larval stages. Furthermore, Bouchard et al. (2022) demonstrated that in the Greenland Sea, resource partitioning can limit competition between early life stages of Arctic cod and bigeye sculpin (*Triglops nybelini*), gelatinous snailfish (*Liparis fabricii*), and ice cod (*Arctogadus glacialis*), at least under current abundances. In contrast, a dietary overlap occurs between Arctic cod and ice cod in West Greenland fjords, with Schoener's indices of 0.64–0.70 (Christiansen et al., 2012). A greater dietary overlap (Schoener index of 0.80) with a potential for competition between age-1 Arctic cod and age-2+ capelin was suggested in the western Canadian Arctic, where both species feed on calanoid copepods and amphipods (McNicholl et al., 2016; McNicholl et al., 2018).

Although the diets of Arctic cod and boreal fish overlap (e.g., Hop and Gjosæter, 2013), this overlap does not necessarily result in increased competition. For example, Panasenkov and Soboleva (1980) concluded from stomach content analyses that the prey of capelin and Arctic cod were abundant and that their diet overlap probably did not lead to severe competition for food in the Barents Sea. In contrast, Orlova et al. (2009) reported competition for copepods between immature capelin and Arctic cod in northern feeding areas. Stomach content and stable isotope analyses revealed less than 40% dietary overlap between the diet of mature Arctic cod and juvenile specimens of similarly sized Atlantic cod and haddock where they overlapped (Renaud et al., 2012). The risk of interspecific competition among these gadids is thus relatively

low. Furthermore, studies from the Bering and Labrador seas suggest a positive association between capelin and Arctic cod abundance, possibly because high abundance of capelin reduces the predation pressure on Arctic cod by common generalist predators, such as Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*), and Atlantic cod (Marsh and Mueter, 2020).

The added risk of increased competition is considered high for juveniles, immatures, and adults but moderate for larvae. Because most studies reporting the risk of interspecific competition between Arctic cod and boreal species compare diet overlap and do not measure competition directly and there is considerable uncertainty as to how interspecific relationships will develop in the future Arctic ecosystem, our assessment has medium confidence for all life stages (**Figure 4a**).

3.1.7. New predators

In regions of advanced warming, the abundance of endemic Arctic predators, for example, Mandt's black guillemot (*Cepphus grylle mandtii*; Divoky et al., 2015), beluga whale (*Delphinapterus leucas*; O'Corry-Crowe et al., 2016), and ringed seal (*Pusa hispida*; Hamilton et al., 2015), is expected to diminish. Conversely, new boreal predators are expanding their foraging range into the distribution area of Arctic cod. Thus, the demise of some Arctic predators could partly be outbalanced by a greater predation pressure from new boreal and temperate predators.

Because of their small size, juvenile, immature, and adult Arctic cod are susceptible to predation by boreal fishes expanding into the Barents and Kara seas, mainly adult Atlantic cod, haddock, wolffishes (*Anarhichas* spp.), redfishes (*Sebastes* spp.), and Atlantic mackerel (*Scomber scombrus*) (Berge et al., 2015; Eriksen et al., 2015; Dolgov and Benzik, 2017; Haug et al., 2017; Ingvaldsen et al., 2017), and Arctic cod larvae may be caught by Scyphomedusae, which are extending their range northward (Crawford, 2016; Geoffroy et al., 2018). In the Pacific Arctic, Pacific cod, walleye pollock, and pink salmon (*Oncorhynchus gorbuscha*) have also expanded northward, potentially increasing predation pressure on Arctic cod (Huntington et al., 2020). Larger gadids not only prey on early life stages of Arctic cod, but they also feed on immatures and adults. Bogstad et al. (2015) hypothesized that Atlantic cod are outcompeting marine mammals in the Barents Sea for access to dominant prey species, including Arctic cod. Moreover, immature and adult Arctic cod fall within the prey spectrum of northward-expanding seabirds, for example, red-legged kittiwake (*Rissa brevirostris*) in the Bering Sea (Robinson et al., 2019), and marine mammals, for example, harp seals (*Pagophilus groenlandicus*) and minke whales (*Balaenoptera acutorostrata*) in the Barents Sea (Haug et al., 2017). Orcas (*Orcinus orca*) are also expanding their range into the Canadian Arctic (Higdon and Ferguson, 2009; Darnis et al., 2012). However, these species are specialized predators, and whether they target Arctic cod is unknown.

Overall, we consider the added risk of the new predators for larvae, juveniles, and immatures as high and moderate for eggs and adult Arctic cod. The magnitude of this

impact is difficult to predict, and we therefore have medium confidence for all life stages for this assessment (**Figure 4a**).

3.2. Stressors from increased anthropogenic activities

Global warming and, in particular, the retreat of sea ice is leading to a marked increase in anthropogenic activities in the form of fishing, shipping activities, oil and gas extraction, and tourism (Kaiser et al., 2016). These activities bring new or intensified chemical and physical ecosystem disturbances, including pollution by contaminants, noise, and light, which all could affect Arctic cod populations.

3.2.1. Fisheries

Although Arctic cod has never been a major target species for fisheries, it was commercially harvested by Norway and Russia in the Barents Sea between the 1930s and 2012. Norway halted the Arctic cod fishery in 1975, with a small exception of 100 tonnes in 1981. The Russian fishery continued until 2012 in the eastern Barents Sea (Novaya Zemlya Archipelago), with average landings of 22.3 thousand tonnes per year from 1992 to 2011 (Boitsov et al., 2013). As with other forage fish, the Arctic cod stock in the Barents Sea is characterized by large interannual variations in recruitment and high mortality by predation. Fisheries between 1969 and 1985 had a large and negative impact on this stock, resulting in the suspension of the Russian fishery between 1977 and 1980 and again between 1989 and 1992 (Boitsov et al., 2013). A fishery for Arctic cod was also conducted in the Chukchi Sea in 1970 (Glebov et al., 2016), and small directed bait fisheries for Arctic cod occur in some regions of Greenland (Bouchard et al., 2023). Currently, there are no commercial fisheries for Arctic cod in Canada or the United States. Arctic cod are unlikely to be targeted by large-scale fisheries in Arctic seas in the near future because of the relative remoteness of fishing grounds from major fishing ports and low landing prices for the species.

Despite negligible targeted fisheries, Arctic cod is caught as bycatch in other fisheries. In the Barents Sea, the only major bottom trawl fisheries conducted in northern regions where Arctic cod is found are fisheries for northern shrimp (*Pandalus borealis*; Jacques et al., 2019). All bycatch must be landed if it constitutes >10% of the shrimp catch. No Arctic cod have been landed in recent years in the Barents Sea, implying that large bycatches of Arctic cod have not been taken in the region. In the eastern Canadian Arctic and western Greenland, Arctic cod are caught as bycatch in bottom trawls used for commercial fisheries of Greenland halibut (*Reinhardtius hippoglossoides*) and northern and striped shrimp (*Pandalus montagui*). The total annual bycatch of Arctic cod in each of these fisheries is generally <50 tonnes, with a maximum of 143 tonnes in 1993 (Treble and Nogueira, 2020; Walkusz et al., 2020).

At present, fishing is the major maritime activity in Arctic seas, and fishing activities are concentrated primarily in the Barents Sea and, to a lesser extent, in the southern part of the Pacific Arctic, Baffin Bay, and western

Greenland (Aastrup et al., 2018; Protection of the Arctic Marine Environment [PAME], 2020). Because of climate change, however, the vast shelves under national jurisdiction will be ice-free for a longer period of the year, opening access to northward-expanding commercial species, such as redfish, Atlantic cod, haddock, and Greenland halibut on the Atlantic side, and walleye pollock, Pacific cod, and saffron cod on the Pacific side (Haug et al., 2017; Mecklenburg et al., 2018; Smé et al., 2020). In the eastern Chukchi Sea, for example, pollock recently expanded its distribution onto northern shelves (Orlov et al., 2021), and Russia authorized a fishery. This scenario has raised concerns that the fishing industry will follow the northward expansion of their boreal target species over Arctic shelves, increasing fishing mortality via bycatch for Arctic native fish (Christiansen et al., 2014). Nonetheless, the expected fishery expansion will be limited to shelves and slopes, where bottom trawling is possible. In the future Arctic Ocean, Arctic cod will most likely be a bycatch species, mainly in shrimp and Greenland halibut fisheries, and fishing mortality will disproportionately affect immatures and adults rather than the younger stages because of the size selectivity of commercial fishing trawls and the deeper distribution of older life stages.

Considering these uncertainties, we evaluate the added risk of an expanding Arctic fishery on the survival of eggs, larvae, and juvenile Arctic cod as undetectable and on immatures and adults as moderate. This assessment has a high confidence for eggs, larvae, and juveniles, and a medium confidence for immatures and adults (**Figure 4a**). However, the population dynamics of Arctic cod and fishing activities both need to be monitored continuously.

3.2.2. Pollution

3.2.2.1. Contaminants

Arctic cod is exposed to a wide range of contaminants, including legacy persistent organic pollutants (POPs; e.g., polychlorinated biphenyls [PCBs] and dichlorodiphenyltrichloroethane [DDT]), trace metals (especially mercury and its organic form methyl-Hg), pesticides currently in use (e.g., endosulfan), polycyclic aromatic hydrocarbons (PAHs), and Arctic emerging contaminants (e.g., perfluoroalkylated substances [PFAS]; Haukås et al., 2007; Morris et al., 2016; Pedro et al., 2017; Gopakumar et al., 2021; Spataro et al., 2021). These contaminants do not have significant local sources; rather, they are transported to the Arctic from industrial and other anthropogenic sources in temperate regions through atmospheric, oceanic, and riverine currents (Macdonald et al., 2000). Once in Arctic marine environments, the long-range transported contaminants bioaccumulate in biota. Some contaminants biomagnify, that is, they increase in concentration within the upper levels of the food web (Atwell et al., 1998; Hop et al., 2002; Borgå et al., 2004). Arctic cod is exposed to these contaminants mainly through ingesting contaminated prey. Depending on the properties of the contaminant, Arctic cod exposure can be influenced by fish size, spatial differences in feeding, and potential source inputs of contaminants (Loseto et al., 2008; Pedro et al., 2017;

Gopakumar et al., 2021). Overall, contaminant levels in Arctic cod are low relative to higher trophic level taxa, such as marine mammals (e.g., Atwell et al., 1998; Borgå et al., 2004). Therefore, most contaminant studies have primarily focused on the role of Arctic cod as a contaminant vector in food webs and whether Arctic cod exposure to these contaminants, despite being low, leads to deleterious biological effects (Dietz et al., 2019). In an attempt to establish Arctic cod as a bioindicator species for the environmental monitoring of PAHs, some studies have characterized biomarker responses of PAH exposure (biotransformation enzymes, biliary metabolites) and effects (e.g., DNA damage) in wild-caught specimens to show varying levels across seasons (Nahrgang et al., 2010) and regions (Jonsson et al., 2010; Tomy et al., 2014; Vieweg et al., 2017). These baseline variations are attributed, however, to biological factors, for example, reproductive status and feeding activity, rather than biomarker induction from PAH exposure.

The retreat of summer sea ice in the Arctic favors an increase in pan-Arctic shipping activities (Melia et al., 2016; PAME, 2019). The northward expansion of shipping also contributes to the continuous release of contaminants such as PAHs and antifoulants (Svavarsson et al., 2021). Furthermore, exploration and operational activities linked to undiscovered oil and gas resources involve potential effects from seismic and drilling activities, operational discharges of produced water, and accidental discharges of petroleum (Beyer et al., 2020). Because most anthropogenic activities are currently delimited to the southern areas of the Arctic shelf seas, associated risks to Arctic cod populations are limited to these areas, although northward expansion will become possible by 2050.

The effects of acute oil spills and petroleum-related mixtures (e.g., crude oil, produced water) on Arctic cod have been studied extensively in experimental settings since the mid-1990s. These studies showed that the early life stages of Arctic cod are the most sensitive to crude oil exposure: for instance, early life stages experience reduced survival and growth and greater deformities (Nahrgang et al., 2016; Laurel et al., 2019). These effects are exacerbated by increased temperatures (Bender et al., 2021). The fitness (e.g., growth) of adults is lowered when exposed to crude oil (Christiansen and George, 1995; Bender et al., 2018; Nahrgang et al., 2019), and poorer body condition or physiological traits may amplify adverse responses (Christiansen et al., 1996; Nahrgang et al., 2019). Crude oil exposure can advance the spawning period over the season with effects on gamete quality and early life stages (Strople et al., 2023).

A few experimental studies have conducted acute toxicity testing of crude oil on Arctic cod to generate data for environmental risk assessments (Gardiner et al., 2013; Camus et al., 2015; Bejarano et al., 2017). However, these studies do not provide an appropriate time frame to detect significant sublethal effects for individual fitness, especially for cold-water species. Modeling approaches have also assessed the potential effect of oil spills (Gallaway et al., 2017; Nevalainen et al., 2017; Fahd et al., 2019;

De Vries et al., 2021) but have not found significant effects at the local population level (Gallaway et al., 2017). However, these models considered only acute mortality data for the most vulnerable life stages and disregarded trophic interactions. Unknown is whether the effects of pollution reported at individual levels can have consequences for Arctic cod populations over the long term. Evaluating long-term effects requires population models that consider the entire life cycle of Arctic cod and include the synergetic effect of several biotic and abiotic stressors (Langangen et al., 2017; Arrigo et al., 2020; Dupont et al., 2021). Arctic cod sensitivity to individual stressors depends on stock health (Durant and Hjermann, 2017) and the intensity of the stressors (Dupont et al., 2021). Localized oil pollution may not affect sufficient numbers of fish to impact populations; however, the combined effect of oil pollution and climate warming may produce a stronger effect, especially on early life stages (De Vries et al., 2021).

Arctic cod is also exposed to microplastics through ingestion, as reported for juvenile and immature Arctic cod caught in the central Arctic Ocean and Svalbard Shelf, and adult Arctic cod from northeast Greenland (Kühn et al., 2018; Morgana et al., 2018) and Beaufort Sea (Moore et al., 2022). Microplastics are small synthetic polymer particles of <5 mm in size that originate from plastic manufacturing, wastes, and personal care products. The biological effects of this plastic debris in aquatic organisms remain poorly understood but can include physical damage and physiological alterations. In addition, plastics can act as vectors of toxic additives and adsorbed chemicals (Diepens and Koelmans, 2018; Halsband and Herzke, 2019).

3.2.3. Other stressors

Increasing human activity, in particular maritime shipping and oil and gas exploration (e.g., seismic airguns, drilling activities), can alter the underwater soundscape and lead to physical, behavioral, and physiological effects on marine species, depending on the characteristics of the noise and the distance to the source (reviewed by Carroll et al., 2017; PAME, 2019). A recent analysis of the marine soundscape in the Northwest Territories, Canada, reported significantly higher sound pressure levels during the summer months because of increased wind, waves, and vessel traffic (Halliday et al., 2020). Only one study has investigated the effects of the presence of marine vessels on the swimming behavior of Arctic cod, revealing that Arctic cod detected and reacted to the presence of vessels by horizontal movements away from vessels and a reduction in explorative behavior (Ivanova et al., 2020). The consequences of these effects are unknown, but Arctic cod is known to produce underwater sounds (Riera et al., 2018), and Ivanova et al. (2020) suggest potential energetic implications when these disruptions occur during feeding periods.

Increased human presence and activity will inevitably also increase light pollution (commonly referred to as artificial light at night or ALAN) in the Arctic Ocean, especially during the polar night. Light influences marine

organisms in several ways, and ALAN may affect the behavior of demersal–pelagic organisms such as Arctic cod (Davis et al., 2020; Geoffroy et al., 2021). Recent studies have documented that light from a research vessel may affect fish, including Arctic cod and zooplankton, down to >200 m depth (Ludvigsen et al., 2018; Berge et al., 2020). For Arctic cod, ALAN has mainly an indirect effect by modifying the temporal and spatial availability of prey. Because Arctic cod feed predominantly on pelagic organisms known to perform diel vertical migration (DVM) even during the polar night (Berge et al., 2009), feeding opportunities might be affected by light-disrupted DVM patterns. However, the impacts of artificial light are most likely local and concentrated near light sources.

High levels of toxicity from harmful algal blooms have recently been reported at the Pacific Arctic gateway, including in zooplankton that are prey for Arctic cod (Anderson et al., 2021). These harmful algal blooms have been linked to anomalously warm ocean conditions (Lefebvre et al., 2022). Although the effects on Arctic cod at the population level are unknown, they likely contribute to cumulative impacts on Arctic cod in a warming ocean.

If the pollution footprint continues at present-day levels, we consider the added risk of pollution for eggs and larvae as high and for all older life stages of Arctic cod as moderate. Given the susceptibility of eggs to pollutant uptake in surface waters, we consider the confidence of this assessment as high. As there are uncertainties in regard to future pollutant sources and because most studies have focused on specific life stages (e.g., adults), we only have medium confidence in our assessment for all older life stages (larvae to adults; **Figure 4a**).

3.3. Future risk for Arctic cod populations in Arctic LMEs

The authors evaluated the levels of added risk of each climate change-related stressor on Arctic cod populations by the year 2050 in various LMEs (CAFF, 2017): the Arctic Basin, Kara–Laptev seas, Atlantic Arctic, Davis Strait–Baffin Bay, Hudson complex, Arctic Archipelago, Beaufort Sea, and Pacific Arctic (**Figure 4b**). The use of LMEs provides predefined and objective boundaries and allows our assessment to be compared with previous studies that have used the same regions. However, strong latitudinal gradients in environmental conditions and considerable subregional structure can occur within these regions. Intraregional differences are greater in the Atlantic and Pacific Arctic, where frontal structures separate boreal and Arctic water masses, both influenced differently by climate and anthropogenic stressors.

3.3.1. Genetic exchange

Patterns of genetic diversity are linked intrinsically with fitness, stress resistance, as well as evolutionary and adaptive potential. These patterns and forcings have important implications for the resilience of the various Arctic fish populations in a changing Arctic (Wilson et al., 2018). Genetic markers can be used to distinguish species, particularly morphologically similar species, such as Arctic cod and ice cod. Polymorphic microsatellite

markers have been used to separate these two species with >96% certainty (Madsen et al., 2009; Nelson et al., 2013) and have also been used to separate larva and juveniles of both species (Bouchard et al., 2013). Further genetic separation has been made between saffron cod and other cod species (Smé et al., 2017). All species consist of many populations, and their genetic structure can provide insights into distinct spawning populations as well as interpopulation genetic exchange, and thus genetic structure can serve as the basis for establishing meaningful management areas.

Populations of Arctic cod have been sampled around the Arctic to assess the circumpolar population structure by means of microsatellite DNA loci (Madsen et al., 2009; Nelson et al., 2020; Maes et al., 2021; Quintela et al., 2021). Many distinct genetic groups, which may include one or more populations, have been identified: European (Greenland, Iceland, and Barents seas), Canada East (Resolute Bay to the Gulf of St. Lawrence), Canada West (Canadian Beaufort Sea and Amundsen Gulf), US–Alaska (North Bering, Chukchi, and western Beaufort seas), and East Siberia (East Siberian and Laptev seas). Little genetic differentiation exists within identified groups, and there was no differentiation between the Kara and Svalbard/Barents seas (Quintela et al., 2021), which is supported by the seasonal migratory pattern outlined in Aune et al. (2021) and the transpolar drift hypothesis (David et al., 2016). Genetic studies also suggest fjord and oceanic mixing for Arctic cod in Svalbard and northeast Greenland (Madsen et al., 2016). A more complete understanding of Arctic cod genetics, migrations, larval drift, and connectivity patterns is needed to provide insights into the potential resilience of Arctic cod populations and to help guide management and conservation actions that avoid the loss of genetic diversity. Currently, the genetic methods are not sufficiently refined to address these issues. Further genetic subdivision—to determine genetic structure within groups (e.g., European and Canadian) or identify populations—is limited by the spatial coverage of samples, and results are therefore genetically homogeneous rather than distinct. However, northern localities with Arctic cod tend to show higher genetic diversity, which may be influenced by population dispersal (Wilson et al., 2020). Greater numbers of markers and deeper genomic coverage are needed to further exploit connections between distinct populations and determine whether populations with high levels of genetic diversity are better able to respond to changing environmental conditions. The risk of genetic separation is considered moderate to low, although highest in the Atlantic sector where populations may become isolated geographically (e.g., within deep, cold-water layers in fjords) because of warming-related habitat loss (e.g., Christiansen and Fevolden, 2000).

3.3.2. Arctic Basin

Despite the ongoing sea-ice decline and warmer conditions, persistent sea ice and cold, deep waters still characterize the Arctic Basin (Wassmann et al., 2020). No reproducing populations of Arctic cod have been

documented in the region. The impacts of sea-ice decline, ocean warming, and changes in freshwater inputs on Arctic cod in the Arctic Basin are thus considered moderate. Similar to the Arctic Archipelago, Arctic cod in colder areas of the Arctic Basin may experience positive effects of warming, as rising temperatures improve physiological conditions, and increased prey abundance compensates for higher metabolic rates. Risks from ocean acidification are considered moderate, albeit at low confidence (Steiner et al., 2014; AMAP, 2018; Mortenson et al., 2020). The effects of the changing prey field, increased competition, and the arrival of new predators are considered moderate, with more limited impacts in areas characterized by inflow from the Atlantic and Pacific (Ershova et al., 2021). In addition to varying regionally, the impact of new predators on Arctic cod in the Arctic Basin will vary seasonally. Recent catches of Atlantic cod (32–68 cm) in the Arctic Basin show that boreal predators are already present in ice-covered waters, although still probably at a very low abundance (Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023). Boreal predators could be transient and only expand their range northward during the ice-free season. The ongoing moratorium on fisheries prevailing in the central Arctic Ocean since June 2021 and the limited shipping activities result in undetectable future impacts from fisheries and moderate pollution effects (Stevenson et al., 2019). This risk for all these stressors is assessed at a medium confidence (**Figure 4b**).

3.3.3. Kara–Laptev seas

The impacts of sea-ice decline and ocean warming on Arctic cod populations in the Kara–Laptev seas are considered high with a high degree of confidence. Risks are greater along the Siberian coast, where sea ice is declining faster, and along the north slope, where the inflow of warmer Atlantic waters increases (Tepes et al., 2021). Impacts from altered freshwater inputs are considered high because of the vast watershed of the region (Osadchiv et al., 2020). Ocean acidification is advanced in this region (Semiletov et al., 2016; AMAP, 2018; Mortenson et al., 2020); hence, associated risks are moderate at a medium level of confidence. The effects of the changing prey field, increased competition, and the arrival of new predators will also vary regionally, being a moderate risk in the Atlantic waters along the slope because of the connectivity with the Barents Sea and a lower risk in the more remote areas elsewhere. Our level of confidence is medium for these stressors. The change in prey assemblages will depend on the future intensity and seasonal phenology of primary and secondary production. New competitors may penetrate from the Barents Sea into the Kara Sea and from the east into the East Siberian and Laptev seas. Risks from fisheries are moderate at a medium level of confidence. With increased shipping and oil transportation along the Northern Sea Route, along with runoff from large rivers in the region, the risk of pollution in Kara–Laptev seas is high and expected to increase; however, we currently have medium confidence in this assessment (Harms et al., 2000; **Figure 4b**).

3.3.4. Atlantic Arctic

The inflow regions (i.e., Atlantic Arctic and Pacific Arctic) have the highest expected cumulative risks for Arctic cod populations. Whereas ice and cold water flowing out of the Arctic Basin and south along the east coast of Greenland characterize the western part of the Atlantic Arctic region, the eastern part is an inflow region for the entire Arctic Ocean, which is experiencing rapid borealization (Maslowski et al., 2004). Sea-ice decline and ocean warming are greatest in the Atlantic Arctic, where associated ecosystem changes influencing Arctic cod have been documented (Aune et al., 2021). The effects of sea-ice decline and warming will be highest in areas important for recruitment and where ocean warming exceeds the thermal optimum for Arctic cod early life stages. Moreover, some of the presumed spawning areas, for example, southern Barents Sea (Huserbråten et al., 2019; Gjøsæter et al., 2020), may also be affected by sea-ice loss and warmer temperatures. At the population level, the added risk of sea-ice decline and ocean warming for Arctic cod is considered very high in the Atlantic Arctic. Risks of ocean acidification and changing freshwater input are moderate because in the Atlantic inflow region these factors remain less strong relative to elsewhere in the Arctic (AMAP, 2018; Mortenson et al., 2020). The effects of the changing prey field, increased competition, and the arrival of new predators are also expected to be high to very high in the Atlantic Arctic because of the increased advection of boreal species. The risk resulting from fisheries is considered high in the Atlantic Arctic, where commercial fisheries already concentrate (Ellis and Brigham, 2009). Risks from oil pollution are also high because of ongoing increases in oil exploration and shipping. The relatively good documentation of changes in the Atlantic Arctic justifies a medium to high confidence for this assessment (**Figure 4b**).

3.3.5. Davis Strait–Baffin Bay

The northward inflow of warm Atlantic water on the eastern side and the outflow of cold Arctic water on the western side characterize currents in the Davis Strait–Baffin Bay area (Rysgaard et al., 2020). We consider the cumulative impacts of sea-ice decline, ocean warming, and changing freshwater input to be high because of the strong reduction in sea ice and the melting of the surrounding glaciers (Rudels, 2011). The effects of the changing prey field, increased competition, and the arrival of new predators on Arctic cod populations are high because of the increased advection of boreal species by the West Greenland Current (Møller and Nielsen, 2020). Boreal predators could be transient and only expand their range northward during the ice-free season, especially in the northern areas (Hornby et al., 2021). Risks from ocean acidification are considered moderate (Steiner et al., 2014; AMAP, 2018; Mortenson et al., 2020) as are risks resulting from fisheries because of the ongoing commercial fisheries for Greenland halibut and shrimp (e.g., Anderson et al., 2018). Shipping, mining activities, and tourism are also increasing rapidly in Davis Strait–Baffin Bay, where pollution risks are considered moderate because of both local activities

and transported pollutants, in particular mercury (Dawson et al., 2018; Mosbech et al., 2018; AMAP, 2021). The high risks for Arctic cod from sea-ice decline and ocean warming also come with a high confidence in this assessment; all other risks for this region are of medium confidence (**Figure 4b**).

3.3.6. Hudson complex

The Hudson Bay is a sentinel for the changes to come in other Arctic areas because it is highly sensitive to climate variability, and ecosystem changes are already occurring (Kuzyk et al., 2009; Macdonald and Kuzyk, 2011). The cumulative risks from ongoing sea-ice decline and ocean warming are thus considered high. Because of the large watershed and the many regulated rivers surrounding the bay, the impacts from earlier and increased freshwater inputs on Arctic cod ecology are also considered high (Schembri et al., 2021). Given the ongoing undersaturation of aragonite and calcite, risks from ocean acidification are considered moderate, although at low confidence because this assessment relies on few studies (Azetsu-Scott et al., 2014). The risks from changing prey fields, increased competition, and new predators are considered high because of the increasing abundance of capelin, which has replaced Arctic cod as the dominant forage fish in parts of Hudson Bay since the mid-1990s and early 2000s (Gaston et al., 2003; Chambellant et al., 2013; Gaston and Elliott, 2014). Risks from fisheries are considered moderate, and potential effects from pollution are also considered moderate because of an established shipping route in the region (Copland et al., 2021). The well-documented ongoing changes in the Hudson Bay region allow us to consider the high risk of sea-ice decline and ocean warming at a high confidence. We have medium confidence in our assessment of the risks for Arctic cod from the other stressors, the exception being ocean acidification (low confidence).

3.3.7. Arctic Archipelago

Although ice cover is decreasing in the Canadian Arctic Archipelago, the region remains characterized by cold-water conditions and is ice-covered for a large part of the year. The northern areas also host some of the last multi-year ice of the Arctic Ocean (Lange et al., 2019). The cumulative impacts of sea-ice decline, ocean warming, and changes in freshwater inputs on Arctic cod ecology are thus considered moderate. Colder areas may experience positive (at least in the short term) effects of warming as a rise in temperature will improve physiological conditions, and sufficient prey abundance is expected to compensate for higher metabolic rates. Risks from ocean acidification are considered moderate because of low saturation states, but this assessment is of low confidence because of regional and seasonal variations in pH (Steiner et al., 2014; AMAP, 2018; Mortenson et al., 2020). The effects of the changing prey field, increased competition, and the arrival of new predators are considered moderate because the sea-ice extent and cold-water conditions limit the expansion of boreal species. Commercial fisheries are not expected in the archipelago given the remaining

difficulties of access and the limited fish stocks; the future impacts from fisheries are therefore expected to be undetectable. Pollution effects are considered moderate because shipping activities in the summer–fall are increasing in the region (Copland et al., 2021). Because of a low amount of data from this remote region, we evaluate the impact of all stressors, except ocean acidification, in the Arctic Archipelago at a medium confidence (**Figure 4b**).

3.3.8. Beaufort Sea

Sea-ice cover in the Beaufort Sea has reduced drastically over the past decades, and water temperatures are increasing (Smith et al., 2018). Freshwater discharge from the Mackenzie River strongly influences the sea's hydrography, particularly over the shelf and slope. The cumulative risks of sea-ice decline, ocean warming, and change in freshwater input from the Mackenzie River (Ahmed et al., 2020) on the population of Arctic cod are thus considered high. Risks from ocean acidification are higher in the Beaufort Sea than in the surrounding regions because $p\text{CO}_2$ concentrations are expected to reach high levels coupled with a low pH, potentially affecting eggs and larvae (Steiner et al., 2014; AMAP, 2018; Mortenson et al., 2020; Niemi et al., 2021). The impacts of the changing prey field, increased competition, and the arrival of new predators are considered moderate to high because Arctic cod still dominates the demersal–pelagic assemblage in the region (e.g., Geoffroy et al., 2016), but Pacific species are expanding their range northward. Future impacts from fisheries are expected to be undetectable because of the prevailing moratorium on commercial fisheries; however, the impacts of pollution are considered moderate on the basis of the known oil and gas resources in the region (Durell and Neff, 2019). The assessments for the Beaufort region are of high confidence for sea-ice decline and ocean warming and medium confidence for all other stressors (**Figure 4b**).

3.3.9. Pacific Arctic

Similar to the Atlantic Arctic, this inflow region shows high expected cumulative risks for Arctic cod populations. The risks from sea-ice decline and ocean warming are considered very high in the Pacific Arctic (Svendsen et al., 2018; Woodgate, 2018; Danielson et al., 2020) at a high confidence. Changes in freshwater inputs from the Alaskan Coastal Current through the Bering Strait are considered high with medium confidence (Woodgate, 2018). The effects are expected to be stronger where ocean warming exceeds the thermal optimum for the early life stages of Arctic cod (Vestfals et al., 2019). As in the Beaufort Sea, the risks of ocean acidification are considered high (AMAP, 2018; Mortenson et al., 2020), although our confidence in this risk is medium. The effects of the changing prey field, increased competition, and the arrival of new predators are also high in the Pacific Arctic at a high confidence because of the increased advection of boreal species through the Bering Strait (Huntington et al., 2020; Spear et al., 2020; Levine et al., 2023). Risks resulting from fisheries are moderate at a medium level of confidence.

Risks from pollution are high, as is the confidence level for this risk, because of ongoing oil exploration, tourism, and shipping activities (Suprenand et al., 2020; **Figure 4b**).

3.4. Models and scenarios

Our evaluation is coherent with models developed for different Arctic regions that associate past fluctuations in Arctic cod biomass with changes in climate to predict future biomass distribution (Hoover et al., 2013; Steiner et al., 2019; Hoover et al., 2021). These models predict that Arctic cod biomass will increase at higher latitudes, accompanied by a decrease at lower latitudes because of a northward distribution shift (Steiner et al., 2019). In the Beaufort Sea, these models estimated past increases of up to 28% in Arctic cod biomass from 1970 to 2012, driven by a longer open-water season and an increased zooplankton biomass (Hoover et al., 2021). Overall, however, in a high carbon emissions scenario, modeling shows a future decrease in Arctic cod biomass of more than 17%, resulting from increased temperatures and the deterioration of sea-ice habitats (Steiner et al., 2019). An ecosystem model for Hudson Bay, at the southern limit of the distribution range of Arctic cod, estimated a past decrease of <25% in Arctic cod biomass from 1970 to 2009 and a decline of 8%–27% of total fish biomass over the same period (Hoover et al., 2013). Business-as-usual climate change scenarios (RCP 8.5) for the Hudson Bay region predict reductions of over 75% in Arctic cod biomass by 2100 (Hoover et al., 2013). Yet, several knowledge gaps need to be addressed to improve the reliability of the models and scenarios (**Table 2**).

4. Cascading impacts on higher trophic levels

Given the high concentration of lipids in Arctic cod, several predators rely on this species as their main prey and source of energy (Welch et al., 1992; Darnis et al., 2012; Sora et al., 2022; Pedro et al., 2023). The aggregation behavior of Arctic cod makes them an ideal target for upper trophic level predators. Arctic cod has been reported as a locally or regionally dominant prey of Atlantic cod, Arctic char (*Salvelinus alpinus*), Greenland halibut, and other piscivorous fish (e.g., Bowering and Lilly, 1992; Gjøsæter et al., 2009; Dolgov, 2016; Chernova, 2017; Dolgov and Benzik, 2017; Giraldo et al., 2018; Marsh and Mueter, 2020). It also represents an abundant prey for seabirds, including thick-billed murre (*Uria lomvia*), black guillemot (*Cepphus grylle*), common murre (*Uria aalge*), northern fulmar (*Fulmarus glacialis*), black-legged kittiwake (*Rissa tridactyla*), ivory gull (*Pagophila eburnea*), and glaucous gull (*Larus hyperboreus*; e.g., Bradstreet and Cross, 1982; Mosbech and Johnson, 1999; Karnovsky et al., 2008; Gaston and Elliott, 2014; LeBlanc et al., 2019; Strøm et al., 2020). Endemic Arctic marine mammals that prey on Arctic cod include ringed seal (*Pusa hispida*) and beluga whale (*Delphinapterus leucas*), which are circumpolar in distribution, and harp seal (*Pagophilus groenlandicus*) and narwhal (*Monodon monoceros*), which have a restricted distribution (e.g., Bradstreet and Cross, 1982; Welch et al., 1992; Mehlum and Gabrielsen, 1993; Ajiad et al., 2011; Matley et al., 2012; Borkin, 2013). The relative

importance and contribution of Arctic cod to predator diets vary with habitat, accessibility, season, and the demographics of predator populations (**Table 3**).

4.1. Changing diets and diet energetic value

The impacts of changing environmental conditions are often transmitted to top predators through the population dynamics of Arctic cod (**Figure 5**). Changes in the availability of Arctic cod, for example, have already led to shifts in the diets of some predators, such as beluga whale, ringed seals, and seabirds, with a reduced contribution of Arctic cod coupled with a greater contribution of other available prey fish (Marcoux et al., 2012; Provencher et al., 2012; Chambellant et al., 2013; Divoky et al., 2015; Choy et al., 2017; Lowther et al., 2017; Vihtakari et al., 2018; **Table 3**). In some cases, these shifts were linked to concurrent declines in the body condition of predators (Gaston et al., 2003; Provencher et al., 2012; Divoky et al., 2015; Harwood et al., 2015; Vihtakari et al., 2018; Choy et al., 2020). Yet, on the basis of nutritional value, many fish species serve as comparable substitutes for Arctic cod. For example, the energetic density of coastal and offshore fish along the coast of Newfoundland and Labrador range from 4.2 kJ g⁻¹ (Atlantic cod) to 9.4 kJ g⁻¹ (Atlantic herring) with Arctic cod valued at 4.4 kJ g⁻¹ (see table 2 in Lawson et al., 1998). Noticeably, capelin has become more available to Arctic cod predators within several High Arctic seas and has a similar energetic value and nutritional composition (Brekke and Gabrielsen, 1994; Hop and Gjøsæter, 2013; Pedro et al., 2019).

The impacts of a shift in prey availability are not fully understood for all predators and will likely depend on the availability and quality of replacement species. Observed shifts from Arctic cod to capelin in the diet of thick-billed murres at Coat's Island demonstrated that although this shift is energetically sufficient, the average weight of an Arctic cod is roughly three times greater than capelin (Gaston and Hipfner, 2000); the delivery of one fish at a time to chicks results in a higher energetic demand because of more frequent feeding trips (Gaston et al., 2005). Beyond calorific value and body mass, the shape and digestibility of fish prey are also important. A shift by black guillemots in the western Beaufort Sea between 1975–1984 and 2003–2012 from Arctic cod to sculpins for feeding their chicks led to nestling starvation and a reduced body condition probably associated with greater difficulty swallowing and digesting a spiny, bony fish such as sculpin (Divoky et al., 2015).

The spatiotemporal availability of prey is an important factor for both long-distance migratory species (e.g., marine mammal and bird migrations) and local timing of predator lifecycles (e.g., bird nesting and chick fledging). Disconnected time–space links between Arctic cod and their predators can affect the reproductive timing and success of some seabird populations, with colony-based seabirds being more impacted by changing prey conditions than migratory species (Kuletz et al., 2020). In certain areas, new prey sources have become available, as observed for the thick-billed murre in Hudson Bay and kittiwake in Kongsfjorden (Gaston et al., 2003; Gaston et

Table 2. Main knowledge gaps at a circumpolar level in relation to the principal stressors affecting Arctic cod and how these gaps limit the reliability of predictions for future Arctic cod populations

Subject or Stressor	Knowledge Gap
Abundance, distribution, and movement	Abundance values in most Arctic areas except in the ice-free areas of the Barents, Kara, and Chukchi seas Spawning migrations and locations in most Arctic areas Genetic plasticity and population connectivity
Sea-ice decline	Relative proportion of juvenile and immature Arctic cod associated with the sea-ice habitat The significance of sea-ice drift for recruitment and genetic exchange among Arctic cod populations around the Arctic Ocean Mechanisms contributing to an increased mortality of eggs and larvae because of reduced sea ice, for example, increased turbulence because of greater wave activity and storms, UV damage How changes in winter sea-ice dynamics, such as increases in polynya openings, will affect survival
Ocean warming and dynamics	Changes to the phenology of Arctic cod in response to ocean warming and how this driver interacts with other environmental cues, for example, light levels, to modulate key life-history milestones such as spawning and development Connectivity and larval drift between spawning and nursery areas given changing flow regimes
Changes in freshwater input	Effect of increased and earlier river discharge and glacial meltwater on freshwater refuges and the regional survival of early life stages Effect of regional increases in stratification on the dynamics of early life stages, including drift patterns
Acidification	Exact physiological tolerance of the egg and larval stages to ocean acidification Carry-over effects from early exposure to ocean acidification and ramifications for feeding success, competition, and predation at later stages
Changing prey	Interaction of ocean warming and a changing prey field (smaller, less lipid-rich zooplankton prey) on the metabolic demands of larval and juvenile Arctic cod
Competitors	Magnitude and dynamics of the spatial and temporal expansion of boreal competitors into Arctic cod habitats
Predators	Occurrence and rate of predation by boreal predators as they expand into Arctic cod habitats Seasonal and geographic patterns of exposure of the different life stages to boreal predators
Fisheries	Future distribution of shrimp and Greenland halibut fisheries in relation to Arctic cod distribution and bycatch levels
Pollution	Susceptibility of early life stages to increased pollutants, including petrochemical contaminants, mercury, other emerging contaminants, and microplastics Effects of increased shipping and industrialization on Arctic cod, which will increase the potential for accidents, toxic spills, as well as noise and light pollution during critical periods
Cumulative effects	Relative importance of cumulative stressors and their synergistic effects

al., 2005; Vihtakari et al., 2018). In other areas, prey availability and quality are severely reduced, for example, for black guillemot on Cooper Island (Divoky et al., 2015; Divoky et al., 2021; **Table 3**). Furthermore, even when new energy-rich food items become available within the foraging distance of colonies, time is required to adjust breeding phenology and foraging to take advantage of these new opportunities.

Theoretically, generalists have a greater chance of successfully switching to different prey species that can provide a similar functional role and dietary nutrition in the absence of familiar species. For example, Arctic cod frequently dominates the diet of Greenland halibut, but this species is also considered a generalist that feeds

opportunistically on the most abundant prey available (Chernova, 2017; Dolgov and Benzik, 2017; Giraldo et al., 2018). Capelin has partly replaced Arctic cod in the diets of Greenland halibut in Cumberland Sound (Canadian Arctic; Yurkowski et al., 2018). In the Beaufort Sea, capelin are typically found outside the depth range of Greenland halibut and are not common in halibut diet (Giraldo et al., 2018), whereas the depths of these two species often overlap off Labrador and Newfoundland, where capelin can dominate the diet (Bowering and Lilly, 1992).

A greater availability of forage fish, such as capelin and herring, characterized by a more pelagic ecology than demersal–pelagic/sympagic Arctic cod, could coincide with a switch in predator behavior from benthivorous to

Table 3. Examples involving Arctic cod as a key species within a documented trophic cascade

Impacted Species	Location	Trophic Cascade Overview ^a	Reference(s)
Thick-billed murre	Northern Hudson Bay, Canada	Climate change-linked shifts in chick diet (reduced Arctic cod) led to modified breeding timing and chick growth rates	Gaston et al. (2003), Gaston et al. (2009), and Gaston and Elliott (2014)
Thick-billed murre	Arctic wide	Declines in colony-specific populations linked to SST changes and large variations in key prey availability (e.g., Arctic cod)	Irons et al. (2008)
Black-legged kittiwake	Kongsfjorden, Svalbard	Atlantification and dietary shift from Arctic cod to Atlantic species (capelin, herring, Atlantic cod, and haddock) linked to an increased kittiwake population size	Vihtakari et al. (2018)
Mandt's black guillemot	Cooper Island, Alaska	Dietary shift from Arctic cod to sculpin in nestling chicks led to slower growth rates and higher mortality	Divoky et al. (2015, 2021)
Narwhal	Baffin Bay and northern Hudson Bay, Canada	Changes in narwhal migration and foraging areas linked to changes in sea ice and dietary markers (showing less Arctic cod and increased capelin)	Watt and Ferguson (2015)
Ringed seal	Western Hudson Bay, Canada	Ringed seal dietary shifts linked to bottom-up processes. Overall dietary shift from Arctic cod to capelin linked to reduced sea-ice extent	Chambellant et al. (2013)
Beluga	Eastern Beaufort Sea	Worsening body condition indices linked to a shift in diet from Arctic cod to capelin and sand lance	Loseto et al. (2018), Ostertag et al. (2018), Choy et al. (2020), and Quakenbush et al. (2015)
Multispecies: Arctic char, ringed seal ^b	Beaufort Sea, Canada	Increases in Arctic char abundance, growth rates, and body size along with declines in ringed seal body condition and reproduction, linked to variable sea-ice dynamics and reduced Arctic cod in diets (i.e., shift from Arctic cod and invertebrates to capelin and sand lance)	Harwood et al. (2015)

^aThese case studies and trophic cascades have been simplified to highlight the roles of environmental or trophic impacts involving Arctic cod; full descriptions can be found in Table S2.

^bBeluga and black guillemot chicks were also included in this example but have been covered in the case studies above.

pelagic piscivorous (Orlova et al., 2005; Frainer et al., 2017). Arctic cod was found to occur in Atlantic cod stomachs at a much higher proportion in years when capelin biomass was low with the opposite pattern for capelin when Arctic cod were low in abundance (i.e., asynchronous; Gjøsæter et al., 2009; Hop and Gjøsæter, 2013; Eriksen et al., 2017; Dupont et al., 2021). For endemic marine mammals that have the potential to be generalists, for example, beluga, foraging on pelagic versus demersal–pelagic prey can offer benefits in terms of the energetic costs of diving. Beluga likely target Arctic cod during deep dives in the Beaufort Sea, Arctic Archipelago, and the Arctic Basin (Martin and Smith, 1992; Storrie et al., 2022). Consequently, a reduced diving depth would be energetically favorable should they have access to similar but shallower swimming prey resources. However, evidence to date indicates that decreasing Arctic cod biomass is leading to the reduced condition of belugas (Loseto et al., 2018). In contrast, Harwood et al. (2015) found that a switch in diet toward boreal pelagic species improved

the body condition of more omnivorous predators, such as bowhead whales (*Balaena mysticetus*).

4.2. Changing contaminant levels

Given biomagnification and the variation in contaminant levels among prey species and regions, dietary shifts from Arctic cod to other species can also lead to changes in the accumulation of environmental contaminants in Arctic predators. For example, higher levels of total mercury (THg) in Arctic cod relative to capelin in Hudson Bay may have resulted in modified THg levels in thick-billed murres from 1993 to 2013, a period during which the birds were shifting their diet. If thick-billed murres had maintained a diet dominated by Arctic cod, their THg concentrations would have continued to increase. However, the decline in trophic position was likely associated with their feeding on other prey, such as capelin, and THg levels remained stable over those years (Braune et al., 2015; Florko et al., 2021).

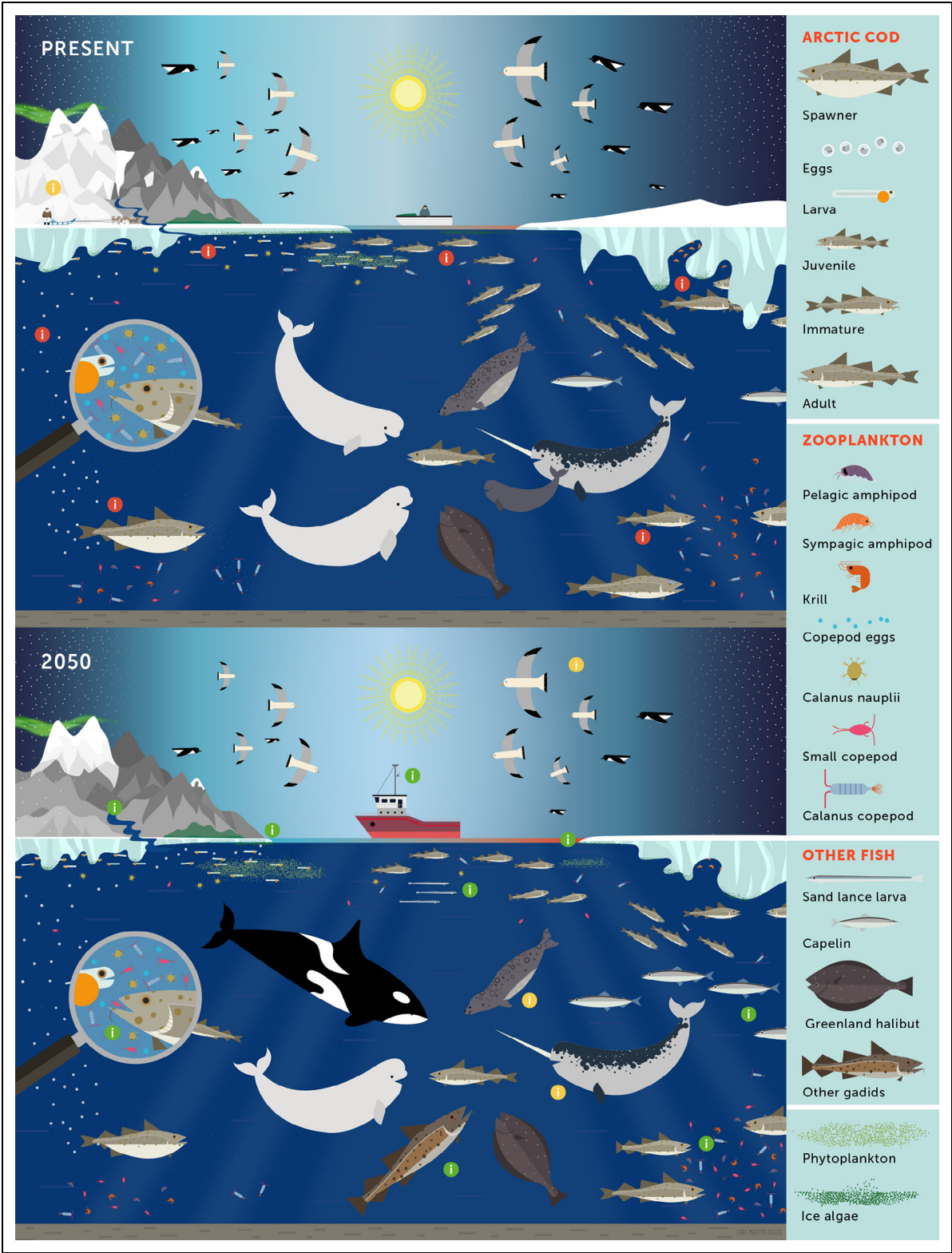


Figure 5. The Arctic marine ecosystems in the present and in 2050. The schematic depicts winter spawning, buoyant eggs and larvae, a long hatching season, and recruitment close to sea ice or at depth in the fall. Anticipated changes in Arctic cod habitat by 2050 include decreased sea-ice extent, increased ocean temperatures and freshwater input, an altered prey field, increased competition, and new predators. An increase in human activities, such as fisheries and tourism, will bring both opportunities for economic development and new pressures, for example, pollution, on the Arctic cod ecosystem. A decrease in Arctic cod populations could have cascading effects on the condition, reproduction, and population size of some predators. Ecosystem services associated with the biodiversity maintained by Arctic cod will be negatively affected. An interactive version of this figure providing additional information about future changes is provided in Supplementary Figure S1.

4.3. Impacts on human populations and ecosystem services

Because Arctic cod are not generally harvested directly by humans, the main ecosystem services they support are related to their role in maintaining biodiversity, that is, as prey for top predators and larger fishes (**Figure 2**). Inuit subsistence, tied to cultural heritage in the North, relies on marine mammals, seabirds, fish, and marine invertebrates as sources of food (Egeland et al., 2009). Top predator migrations are linked to the pulse of feeding that occurs at the ice edge in early spring, with seabirds, beluga whale, narwhal, and harp seal timing their arrival at higher latitudes to take advantage of ice-edge productivity and the associated biomass of Arctic cod (Bradstreet and Cross, 1982; Tynan and DeMaster, 1997). Climate change impacts on the spatial distribution of Arctic cod are modifying these marine mammal migration patterns (Hauser et al., 2014) and, indirectly, access to fish, marine mammals, and seabirds by northern communities. Moreover, modified migrations of marine mammals may lead to the decoupling of interactions with prey or, alternatively, to longer residency periods in summering grounds to exploit Arctic cod. Apart from a bait fishery in Greenland (Bouchard et al., 2023), Arctic cod are seldomly harvested and consumed by Inuit, but the Arctic cod predators (e.g., Arctic char, Greenland halibut, belugas) are widely harvested in the Arctic (Deutch et al., 2007; Gagne et al., 2012). Hence, although the direct impact of changing Arctic cod dynamics and distribution on northern communities will be relatively low, Inuit will be indirectly affected through changes in the distribution, abundance, and, potentially, the quality of the top predators they exploit.

Both the northward retreat of Arctic charismatic megafauna associated with Arctic cod and the modified migration timings of these species could also affect tourism. Tourism is viewed as one possibility for generating important revenue for Arctic communities to address socioeconomic challenges (Maher et al., 2014; Stewart et al., 2015). However, the predictability of megafauna observations may limit its development or may attract tourism agencies further north, where the navigation risks and potential for accidents are higher, increasing the risk of pollution release. Moreover, changes in the distribution and abundance of piscivorous fish feeding on Arctic cod, for example, Greenland halibut in Baffin Bay and Atlantic cod in the Barents Sea (e.g., Giraldo et al., 2018; Holt et al., 2019), could impact their stocks and, in turn, commercial fisheries.

5. Management and environmental stewardship measures for Arctic cod and its ecosystem

Given the strong linkages of Arctic cod to both the physical environment and to other species, the development of monitoring strategies that inform management at the ecosystem level, including in the Arctic Basin, is essential (e.g., Van Pelt et al., 2017; Eriksen et al., 2018). Overall, there is a need for ecosystem-based management in the Arctic (Diamond, 2010). Understanding and communicating the regional occurrence, biomass, and physiological thresholds of Arctic cod are critical for their adequate inclusion

in the species distribution, habitat suitability, and food web models used in ecosystem-based management. Such models are becoming more common in supporting management measures, including marine spatial planning such as marine protected area (MPA) designations. The limited information related to these parameters is a common source of uncertainty in models and restricts their usefulness and applicability. Physiological metrics can be determined through controlled experimental testing in laboratories and aquatic facilities and through ecophysiological monitoring. Steiner et al. (2018) provide an example of a database of physiological limits for aquatic species.

5.1. Fisheries management

In the Barents Sea, annual ecosystem studies comprise the monitoring of commercial and non-commercial species, including Arctic cod. The Russian and Norwegian fisheries for Arctic cod were largely unregulated until the 1970s. The Russian fishery in the period since has been regulated by total allowable catch or, since the late 2000s, recommended catch on the basis of a national stock assessment and quota advice. In addition, constraints are applied to fish length (minimum of 13 cm since 2001), mesh size in trawls (24 mm since 2007), and bycatch of small-sized individuals in a catch (maximum 20% of fish number). Since 2015, the recommended catch values have also been evaluated for Arctic cod in the Kara Sea; however, no commercial fisheries are conducted there. Because Arctic cod has been listed as an endangered species since 2016 on the Norwegian red list for species (The Norwegian Biodiversity Information Centre, 2021), no targeted fishery for this species is allowed in Norwegian waters. In Baffin Bay, bottom trawl fisheries targeting Greenland halibut and shrimp implemented a “move-away” provision in the fishing licenses, which requires boats to move a minimum of 10 nm (18.52 km) from any coordinate during the last tow if the amount of groundfish bycatch, which includes Arctic cod, exceeds either 2.5% of the total catch weight or 100 kg (Department of Fisheries and Oceans, 2018).

Currently, fisheries in the Beaufort Sea are exclusively for subsistence purposes because of a U.S. fishing moratorium implemented in 2009 and the development of Canada's Integrated Fisheries Management Plan, which bans all commercial fishing until more information related to the marine ecosystem is made available (Tai et al., 2019). Fisheries regulations within a country's jurisdiction are determined by the respective country; however, there is no joint governance mechanism for the Arctic region to create and implement protection outside national jurisdictions (Hosain and Czarski, 2018). As a temporary measure, the *International Agreement to Prevent Unregulated Fishing in the High Seas of the Central Arctic Ocean* prohibits vessels from commercially fishing in the central Arctic Ocean, an agreement that highlights the role of science-based management (Vylegzhanin et al., 2020).

5.2. Shipping

Shipping restrictions are often related to marine mammal migration routes, identified feeding hotspots, and bird

sanctuaries (e.g., McWhinnie et al., 2018). Given that many Arctic marine mammals rely to some degree on Arctic cod as a key prey item (Steiner et al., 2021), measures to protect these predator species also require the protection of Arctic cod. The potential for noise impacts on Arctic cod distribution and condition (Ivanova et al., 2020) and increasing sound levels in the Arctic (Halliday et al., 2020) also require consideration in regions where high Arctic cod biomass occurs and in known priority habitats.

5.3. Stewardship and protection

The key role of Arctic cod in transferring energy between lower and higher trophic levels suggests that the conservation of Arctic cod habitats and nurseries are instrumental for protecting higher trophic level species and maintaining the integrity of Arctic food web linkages. In their sea-ice ecosystem services assessment, Steiner et al. (2021) highlighted that whereas conservation measures can assist species conservation, the key mitigation measure for slowing the rate of climate change impacts and reducing overall loss of habitat and diversity is reducing carbon emissions.

The Arctic Council has adopted a framework for a pan-Arctic network of MPAs (PAME, 2015; PAME, 2017) with the goal of developing networks of MPAs and other area-based conservation measures within the national jurisdictions of Arctic states to improve resilience to climate change and other hazards (see figure 2a of Steiner et al., 2021, for a map of Arctic MPAs). Recent designations of marine conservation areas (MCAs) and MPAs by several countries indicate positive progress. Canada has established two MCAs and two MPAs in its Arctic territories, designated with the conservation objective of maintaining habitat and supporting marine mammal and piscivorous fish populations. These conservation objectives encompass maintaining key forage species that support these predator populations, including Arctic cod. In Norway, some Arctic marine areas have received protection status through general environmental measures such as the Svalbard Environmental Protection Act, which explicitly includes marine species and habitats. Norway has also protected the marginal ice zone by excluding new petroleum activities in areas where sea ice is found on 15% of the days in April (Anonymous, 2020). In Greenland, all marine areas have been protected from petroleum activities since 2021 after the government called a halt to future exploration. In the Russian Federation, 47 MPAs have been selected as a priority for the conservation of wildlife in the Arctic (Spiridonov et al., 2017; Spiridonov et al., 2020). For the central Arctic Ocean, the Arctic Council, the International Council for the Exploration of the Seas (ICES), and the North Pacific Marine Science Organization (PICES) are leading an effort to establish an integrated ecosystem assessment as a foundation for an integrated assessment plan. This effort, led through a joint working group (the Working Group on Integrated Ecosystem Assessment for the Central Arctic Ocean, WGICA), also highlights the specific threats to Arctic cod and its ecological role in the Arctic Basin.

Climate change impacts are both observed and felt directly by the Inuit (ICC-Canada, 2008; Eicken, 2010; Huntington et al., 2016; Aastrup et al., 2018; Flora et al., 2018). Hence, the recognition and inclusion of Indigenous knowledge in scientific research and conservation planning are essential. Within Indigenous communities, expanding community-based monitoring efforts, including oceanographic measurements and species observations, is a key contribution to research and provides a critical tool in understanding climate change impacts on Arctic cod and marine ecosystems (e.g., Berkes et al., 2007; Steiner et al., 2019).

6. Conclusions

This narrative review demonstrates that the impacts of climate change and anthropogenic stressors on Arctic cod vary among life stages and regions. Early life stages are more vulnerable to climate change than their older conspecifics because of their selective diet, narrower range of temperature tolerance, ice association, low motility, and distribution near the surface where most ocean-atmosphere interactions occur. The general distribution of the adult stages in deeper waters and their broader temperature tolerance suggest a certain degree of resilience to environmental change. Hence, vulnerability to climate change for Arctic cod lies in the survival and recruitment of its early life stages.

We identified ocean warming, sea-ice decline, increased freshwater input, acidification, changing prey field, increased competition, new predators, and pollution as the main factors affecting Arctic cod ecology (**Figure 4a**). The effects are stronger in Arctic gateway regions where advection of Atlantic and Pacific waters results in a more intense borealization of the ecosystem and as regions where anthropogenic activities are concentrated. The risk from fisheries is moderate and mainly limited to bycatch in region-specific bottom trawl fisheries. The current northeast Atlantic Arctic region experiences the greatest pressure on the Arctic cod ecosystem because of climate change (**Figure 4b**). To a lesser extent, the Pacific Arctic, Hudson complex, and Davis Strait-Baffin Bay also experience a transition toward a borealized ecosystem where the ecological importance of Arctic cod diminishes and the co-distribution with boreal species, such as capelin and sand lance, increases. This transition modifies trophic interactions to the advantage of increasingly abundant competitors. In contrast, Arctic cod may benefit from ocean warming by enhanced growth and survival in some colder areas of the Arctic Archipelago, Kara-Laptev seas, and the Arctic Basin. Nonetheless, models project an overall decrease in Arctic cod biomass over the long term. Moreover, the component of the population associated with the ice cover will likely decline because of the melting of sea ice, which could contribute to reducing their current abundance, for example, through increased intra-specific competition. Overall, in a future High Arctic, the relative abundance of Arctic cod within the fish community will likely mirror currently observed fluctuations at the southernmost range of their distribution, with a lower

abundance during warm periods and a higher abundance during colder phases.

Changes in Arctic cod ecology impact marine mammals, seabirds, and humans, albeit with different consequences depending on the affected species and areas. In general, the potential effects of lower Arctic cod abundance in Arctic seas for top predators and the overall food web remain unclear and depend on the potential for individual predator species to substitute Arctic cod with boreal prey. Lower lipid concentrations or a smaller size of some boreal prey species could be compensated by a higher abundance of such prey, although there would be higher energetic costs because of an increased foraging effort. Cascading effects on food webs from climate-driven changes in Arctic cod ecology will ultimately depend on multiple simultaneous, interacting factors, including the altered distributions of new competitors and predators.

Despite the remoteness of the Arctic Ocean and persisting knowledge gaps, Arctic cod is generally well studied relative to other Arctic fishes. The species is linked to a habitat that is rapidly shrinking. This combination makes Arctic cod an ideal species to guide protection measures, such as the implementation of MPAs and the regulation of transport and tourism to limit noise and contaminant pollution. Robust international management procedures must be developed and enforced in collaboration with northern Indigenous governance structures and through consultation with local communities. The designation of conservation areas and constraints on shipping can help alleviate climate change impacts on Arctic cod by limiting pollution and protecting key habitats. Arctic MPA management plans should include protection for Arctic cod as a recognized key food source for higher trophic levels. Ultimately, however, the mitigation of habitat loss for Arctic cod will only be achieved through a global reduction in carbon emissions.

Data accessibility statement

Results from the scoring assessment are available in Data S1.

Supplemental files

The supplemental files for this article can be found as follows:

Table S1. Summary of Arctic cod diet studies. (PDF)

Table S2. Examples involving Arctic cod as a key species within a documented trophic cascade (summarized in Table 3). (PDF)

Text S1. Procedure for the assessment of the future impact of climate change and anthropogenic stressors on Arctic cod. (PDF)

Data S1. Detailed scoring results for the risk assessment. (.xlsx)

Figure S1. Interactive schematic of the Arctic marine ecosystems in the present and in 2050. (PDF)

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Competing interests

The authors declare no competing interests.

Author contributions

MG led the organization and writing of the manuscript. CB, HF, and DR contributed to structuring and orienting the manuscript and each co-led one section. HG, CH, HH, NEH, JN, and NS each co-led a section of the manuscript. Other coauthors contributed to writing one or more sections or of the manuscript. All coauthors contributed to writing, reviewed, and approved the manuscript and participated in scoring the risk levels and uncertainties related to environmental and anthropogenic stressors.

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