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EDITORIAL

# Arctic gadids in a rapidly changing environment

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This special issue originated from an international workshop on the *Biology and Ecology of Arctic Cods* convened in Fairbanks, Alaska, in June 2018 as part of the Ecosystem Studies of the Subarctic and Arctic Seas (ESSAS) Annual Science Meeting. This followed an earlier ESSAS workshop on Arctic gadids held in Copenhagen, Denmark, in April 2014 (Mueter et al. 2016). The aim of both workshops was to synthesize recent advances in our understanding of the biology, ecology, and dynamics of Arctic gadids around the circumpolar North in the context of a rapidly changing Arctic marine environment. Changes in the structure of Arctic marine ecosystems with direct effects on humans have been particularly pronounced on the major Arctic inflow shelves (Fig. 1), including the Northern Bering Sea and Chukchi Sea (Huntington et al. 2020) and the Barents Sea (Skern-Mauritzen et al. 2018; Haug et al. 2020), where the majority of the contributed papers are focused. The growing interest in the Arctic, combined with increased accessibility of formerly ice-covered regions within these major gateways to the Arctic, has led to a proliferation of research in Arctic seas over recent decades, including research on Arctic gadids (Fig. 2).

The strong focus on the polar cod (*Boreogadus saida*) throughout these papers reflects the central role of this species in Arctic marine ecosystems (Bradstreet et al. 1986; Hop and Gjøsæter 2013), as well as its circumpolar distribution (Mecklenburg et al. 2011). The importance of polar cod as prey for seabirds and marine mammals is consistent with estimates of very high natural mortality rates in the Chukchi Sea (Marsh et al. 2020). In addition to a number of regional studies of polar cod, contributions include circumpolar studies on diets (Bouchard and Fortier 2020) and genetics (Nelson et al. 2020) of polar cod and laboratory studies comparing aspects of polar cod with other Subarctic and Arctic gadids (Copeman et al. 2020; Leo et al. 2020; Spencer et al. 2020). Only two studies primarily focus on other species, namely the navaga (*Eleginus nawaga*) (Maznikova and Orlov 2020) and the saffron cod (*Eleginus gracilis*) (Smé et al. 2020). These congeners are limited to relatively nearshore waters in the White, Barents, and Kara seas, and in the Pacific Arctic, respectively. Few studies on navaga are available outside the Russian literature, and the synthesis of their biology and distribution in the White Sea by Maznikova and Orlov (2020) makes much of what is known about this true Arctic gadid more widely available.

The first main theme in this special issue is the population structure of polar cod and other Arctic gadids. Population genetic structure is evident in polar cod collections from around the Arctic, suggesting the existence of at least four major groups in the Alaskan Arctic (northern Bering Sea to western Beaufort Sea), western Canadian waters (Beaufort Sea and Amundsen Gulf), eastern Canadian waters (Resolute Bay to Gulf of St. Lawrence), and European waters including the Greenland, Iceland and the Laptev Sea (Nelson et al. 2020). The differentiation between the Alaskan and western Canadian groups is consistent with an earlier regional study that found small-scale geographic partitioning in the transition zone between these groups (Wilson et al. 2019). However, the mitochondrial genome suggests little population-level structure but high levels of genetic diversity in polar cod from the northern Bering Sea to the Canadian Beaufort Sea, suggesting the potential for local differentiation (Wilson et al. 2020). Population differentiation in the Pacific Arctic is supported by a distinct gap in the distribution of juvenile polar cod between the western Beaufort Sea, which is contiguous with the Chukchi Sea, and the eastern Alaskan

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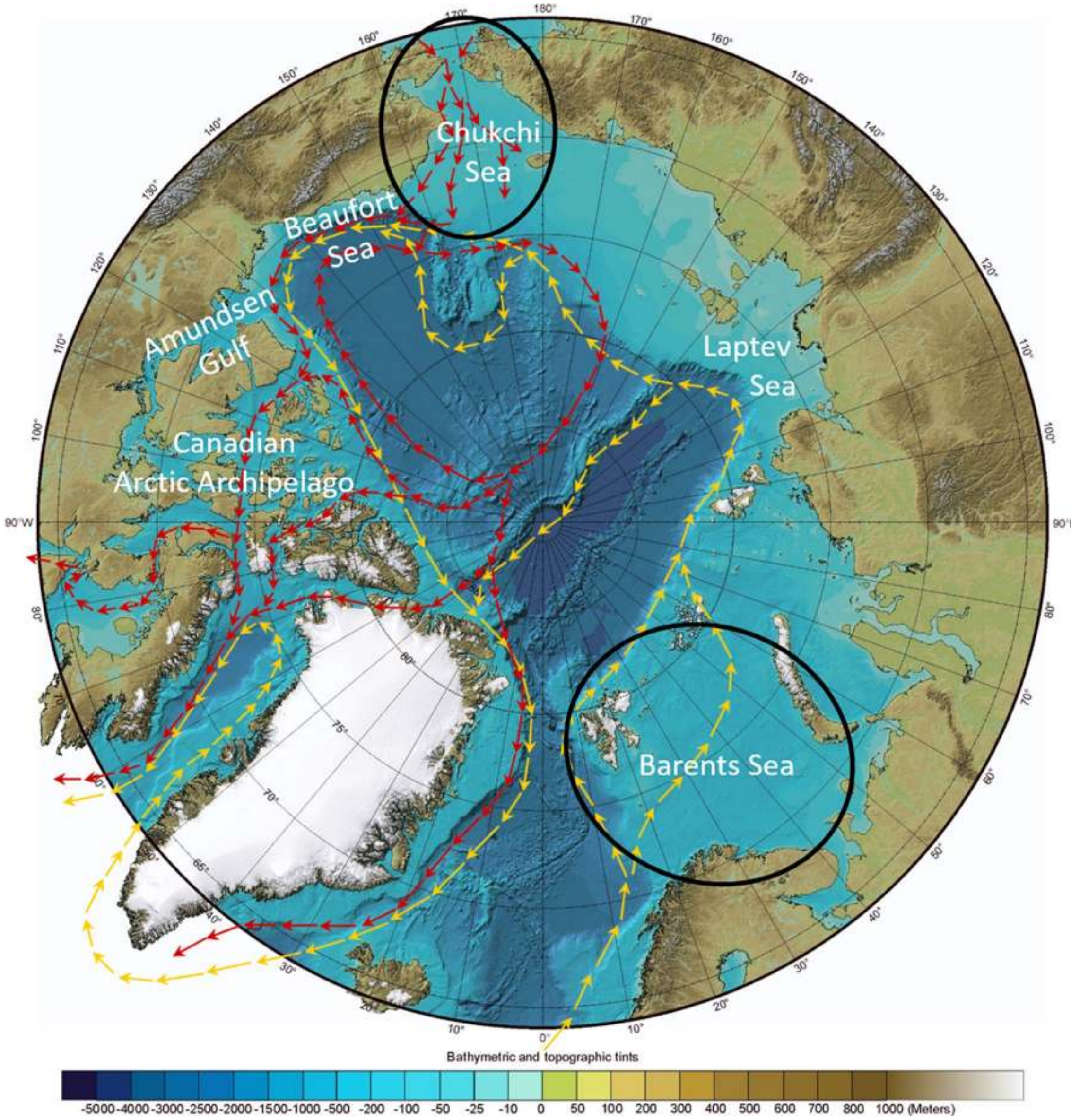


**Fig. 1** Arctic Ocean with major currents indicating flows of deep waters originating in the Atlantic (yellow) and surface waters origination in the Pacific (red). Currents compiled from various sources. Black ovals indicate the major Arctic inflow shelves with other study regions indicated. Base map from Arctic Council Conservation of Arctic Flora and Fauna Working Group (2000)

Beaufort Sea, which is contiguous with the Canadian Beaufort Sea (Forster et al. 2020).

The genetic population structure in the Northeast Atlantic remains unclear, as Nelson et al. (2020) did not have samples from the Barents Sea. There is evidence of two distinct spawning populations in the southeastern Barents Sea (Pechora Sea) and in the northwestern Barents Sea east of Svalbard, respectively, supported by distinct distributions of eggs and larvae (Boitsov et al. 2013) and by biophysical modeling studies (Huserbråten et al. 2019; Eriksen et al. 2020). Hypothesized spawning sites to the south, east, and north of the Svalbard Archipelago are consistent with the observed distribution of age-0 polar cod in the northwest Barents Sea (Eriksen et al. 2020). In contrast, particles released in the western fjords were largely retained in the fjords, consistent with previously reported fine-scale genetic structure differentiating fjord populations in western Svalbard and eastern Greenland from open ocean populations (Madsen et al. 2016). To what extent Barents Sea populations are connected with the Russian Siberian shelf to the east remains unresolved (Chernova 2018).

Relatively small-scale population structure is also evident in the navaga, with three distinct populations in the White Sea (Maznikova and Orlov 2020), as well as in the saffron

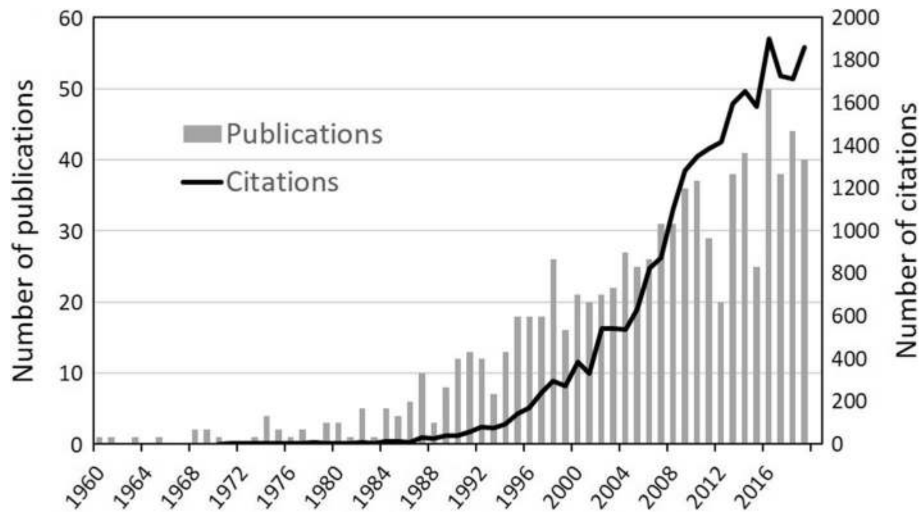


**Fig. 2** Number of publications and number of citations related to Arctic gadids from 1960 to 2019. Search terms in Scopus: TITLE-ABS-KEY (Boreogadus OR Arctogadus OR "Arctic cod" OR "polar cod" OR navaga OR "Gadus ogac" OR Eleginus OR "saffron cod")

cod in the Pacific Arctic. The latter displays limited genetic variation within the northern Bering and Chukchi seas, but shows evidence of distinct Subarctic populations in the Gulf of Alaska and in the Sea of Okhotsk, with the Gulf of Alaska population forming a divergent lineage (Smé et al. 2020; Wilson et al. 2020). These patterns likely reflect the expansion of saffron cod into the Bering Strait and Chukchi Sea regions as sea levels rose after the last glacial maximum (Smé et al. 2020).

The second major theme aims to understand how environmental changes drive the growth and survival of polar cod in the Arctic and their ability to adapt to sea ice loss and rising ocean temperatures. Polar cod can be considered a sentinel species for Arctic changes as the southern limits of their distribution are closely tied to variations in temperature (Marsh and Mueter 2020) and variability in early survival is linked to the timing of sea ice retreat (Bouchard et al. 2017; Gjøsæter et al. 2020; LeBlanc et al. 2020). Bouchard et al. (2017) suggest that polar cod, which are adapted to a narrow range of temperatures, will initially benefit from rising temperatures, but will ultimately be replaced by more southern species as ocean temperatures continue to increase. This hypothesis is supported by LeBlanc et al. (2020), who show that an earlier ice breakup in the Canadian High Arctic is associated with an earlier bloom, higher zooplankton abundances in August and a higher biomass of young polar cod. However, they found no evidence that zooplankton or cod biomass experienced additional benefits from ice retreating prior to June.

In contrast to the Canadian High Arctic, young polar cod at the southern edge of their distribution on both the Pacific and Atlantic inflow shelves can encounter temperatures well above those associated with maximum growth in the laboratory, which occurs at 5–7 °C (Kunz et al. 2016; Laurel et al. 2016; Koenker et al. 2018). Age-0 polar cod in the Chukchi Sea are most likely to occur at the coldest temperatures, but abundances peak near the temperature of maximum growth and decline rapidly at higher temperatures (Marsh et al. 2020). Acoustic surveys suggest large interannual variability in abundance (De Robertis et al. 2017), but the effects of interannual variability in environmental conditions in the Chukchi Sea on the abundance of polar cod have not yet been examined. Young polar cod in the Barents Sea typically encounter temperatures well within their physiological tolerance (< 6 °C), but individual-based models suggest that an earlier ice melt, reduced summer ice, and the increasing influence of warmer Atlantic waters negatively affect the survival of polar cod larvae from the major spawning aggregations in the southeast Barents Sea (Gjøsæter et al. 2020). The Barents Sea stock is one of the main stocks of polar cod in the Arctic and has long supported an important fishery in the Russian part of the Barents Sea (Boitsov et al. 2013; Hop and Gjøsæter 2013). The abundance of this stock has fluctuated widely, is currently at low levels, and is expected to further decline under continued warming (Gjøsæter et al. 2020).

The mechanisms regulating the abundance of polar cod at the end of their first summer are likely tied to the effects of sea ice and temperature conditions on the quantity and quality of prey. Larval polar cod are highly specialized predators on large calanoid copepods (Bouchard and Fortier 2020), which tend to be replaced by smaller, less lipid-rich species under warmer conditions (Aarflot et al. 2018; Kimmel et al. 2018; Møller and Nielsen 2020). Reduced abundances of large calanoid copepods, in turn, impact the ability of young polar cod to store lipids (Copeman et al. 2020), which may result in a reduced transfer of energy to higher trophic levels and may affect their overwinter survival. While variability in the survival of polar cod during their first winter has not been estimated to our knowledge, mortality rates are thought to be high (Marsh et al. 2020) and are likely affected by pre-winter condition. For example, the survival of Subarctic walleye pollock (*Gadus chalcogrammus*) in the Bering Sea from spawning to recruitment at age 1 is substantially lower if young pollock fail to store sufficient lipid reserves prior to their first winter (Heintz et al. 2013).

A key uncertainty in a changing climate is the ability of a species to adapt physiologically to changing conditions through phenotypic plasticity or genetic variation. Laboratory experiments indicate that eggs are very temperature-sensitive (Laurel et al. 2018), but Spencer et al. (2020) indicate that polar cod larval stages are more resilient to changes in salinity than other Subarctic gadids. Wilson et al. (2020) suggest that polar cod may be able to evolutionarily adapt to a changing environment due to large population sizes combined with high levels of diversity in the mitochondrial genome, which plays a key role in aerobic metabolism and energy balance. On the other hand, laboratory studies suggest that enzymes involved in mitochondrial respiration in the hearts of polar cod have very limited phenotypic plasticity (Leo et al. 2020), limiting the ability of polar cod to overcome their adaptation to a very narrow thermal range. In contrast, Atlantic cod (*Gadus morhua*), acclimated to similarly cold temperatures, show high plasticity in enzyme activity and appear to be much more resilient to variable temperature conditions (Leo et al. 2020). This suggests that Atlantic cod will outperform polar cod as temperatures increase in the areas of overlap between these two species and may explain the negative relationship between local abundances of Atlantic cod and polar cod on the Newfoundland/Labrador shelf (Marsh and Mueter 2020). Atlantic cod and haddock (*Melanogrammus aeglefinus*) have already expanded north to the margins of the Arctic Ocean, likely resulting in increased competition and predation on polar cod (Renaud et al. 2012; Ingvaldsen et al. 2017). Negative relationships between polar cod and walleye pollock abundances in the Bering Sea suggest that similar mechanisms may be at play in the Pacific Arctic (Marsh and Mueter 2020).

In summary, the available evidence suggests that a combination of bottom-up processes, the lack of phenotypic plasticity, and competitive interactions with other species will result in declining abundances of polar cod populations at or near the southern limits of their range, and increasingly at higher latitudes. Earlier ice retreat and warmer summer temperatures directly and indirectly affect growth and condition of young polar cod. Direct effects result from temperature-dependent effects on physiological rates, while indirect effects are mediated by prey availability, likely limiting survival at the larval and juvenile stages beyond a critical temperature threshold. Furthermore, competitive interactions with sympatric or Subarctic species that are more resilient to higher temperatures limit the southern extent of polar cod and may result in the replacement of this key forage species in many regions. The replacement of polar cod by other species will have unknown consequences for seabirds, marine mammals and ultimately people living in Arctic and Subarctic regions where cultural identity, food security and socioeconomic systems are closely linked with marine ecosystems.

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