

INTRODUCTION

# The ecology of gadid fishes in the circumpolar Arctic with a special emphasis on the polar cod (*Boreogadus saida*)

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In high-Arctic marine ecosystems, the gadids *Boreogadus saida* (Lepechin, 1774) and *Arctogadus glacialis*, hereafter referred to as polar cod and Arctic cod, as respective European common names, are foundation species that make up important links between lower and higher trophic levels of the food web (Bradstreet et al. 1986; Christiansen et al. 2012; Hop and Gjøsæter 2013). Other Arctic gadids considered here are the saffron cod [*Eleginus gracilis* (Tilesius, 1810)], which is endemic to the Pacific Arctic but extends into boreal waters as far south as Japan (Mecklenburg et al. 2002), and its Atlantic sister species, the navaga [*Eleginus navaga* (Walbaum, 1792)], which is limited to European Arctic and subarctic waters of the Barents, White and Kara seas (Cohen et al. 1990). There is a strong imbalance in the scientific literature regarding these species—a search for the words “*Boreogadus*” in Google Scholar (April 2016) resulted in 4010 hits, compared to only 522 hits for “*Arctogadus*,” reflecting a greater emphasis on the more abundant polar cod. The genus “*Eleginus*” resulted in 1480 hits (*E. gracilis*: 1070;

*E. navaga*: 408), reflecting the importance of saffron cod as a subsistence resource in parts of the North Pacific.

While research on *B. saida* has a long history, particularly in Russia (Andriyashev 1954; Rass 1968; Ponomarenko 2000; Boitsov et al. 2013), interest in Arctic marine ecosystems has grown in recent years as summer sea ice cover has diminished and water temperatures have increased (Wang and Overland 2009). Arctic gadids, in particular polar cod, have been a focal point for studies of climate impacts (Fortier et al. 2006; Benoit et al. 2008; Bouchard and Fortier 2008; Renaud et al. 2012) and pollution impacts (Christiansen and George 1995; Nahrgang et al. 2010; Dussauze et al. 2014; Geraudie et al. 2014; Andersen et al. 2015). Yet, our current understanding of these important Arctic species is surprisingly fragmented and inconclusive, leaving major gaps in knowledge that prevent a holistic understanding of the interaction between these species and their environment.

This special issue contains a collection of manuscripts from an international workshop on the ecology of circumpolar Arctic gadids. The workshop was convened during the Ecosystem Studies of the Subarctic and Arctic Seas (ESSAS) Annual Science Meeting, 8–9 April 2014, in Copenhagen, Denmark. Four of the papers in this collection take a comparative approach across species: Bouchard et al. (2016) compare the early life history of polar cod and Arctic cod, Laurel et al. (2016) contrast the growth rates of four gadids in the North Pacific under different temperatures, Kunz et al. (2016) compare growth of polar cod and Atlantic cod (*Gadus morhua*) under different temperatures and CO<sub>2</sub> levels, and McNicholl et al. (2015) compare diets of two potential competitors, polar cod and capelin (*Mallosus villosus*). A single paper focuses on saffron cod, specifically their trophic dynamics as inferred from several trophic biomarkers (Copeman et al. 2016). The remaining

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12 papers describe studies on various aspects of polar cod only. These include studies of ecotoxicology (Bakke et al. 2016), population genetics (Madsen et al. 2016), distribution and habitat use (Astthorsson 2016; Crawford 2016; David et al. 2016; Geoffroy et al. 2016; Kessel et al. 2016; Kono et al. 2016), diets of juveniles and adults (Gray et al. 2016; Majewski et al. 2016; Nakano et al. 2016) and reproductive biology (Nahrgang et al. 2016). Combined, the current special issue is, at least in the western scientific literature, so far the largest single step forward in our understanding of the ecology, life history and distribution of Arctic gadids in a changing Arctic. Below, we present a brief synopsis of papers in the special issue, as well as some context leading up to the work described.

### Distribution in the Arctic and habitat preferences

Polar cod and Arctic cod have a pan-Arctic distribution and are regularly observed in association with Arctic sea ice. Both have antifreeze glycoproteins to survive long periods at sub-zero temperatures (Pörtner and Playle 1998), but neither can be regarded as a primarily ice-associated species. Rather, they should be considered a demersal or semi-pelagic species with a preference for pelagic prey items (Süfke et al. 1998; McNicholl et al. 2015; Gray et al. 2016; Majewski et al. 2016; Nakano et al. 2016). Their distributions overlap, but polar cod extend to lower latitudes than Arctic cod (Mecklenburg and Steinke 2015; Madsen et al. 2016; Bouchard et al. 2016). The latter has a more restricted distribution and appears to be absent from the Central Arctic Basin (Mecklenburg and Steinke 2015). In contrast, polar cod (primarily 1-year-old fish) are ubiquitous under the sea ice throughout the central Arctic Ocean in the Canadian Basin (Melnikov and Chernova 2013) and the Eurasian Basin, where fish in good energetic condition have been observed in relatively high densities up to an estimated 15,920 individuals km<sup>-2</sup> (David et al. 2016). These fish likely originate on the Arctic shelves, and it is unclear how their distribution will be affected by further shortening of the ice-covered season and reduced sea ice extent (David et al. 2016). The vertical distribution of polar cod changes from a strong surface orientation of egg and larval stages (Bouchard et al. 2016; Geoffroy et al. 2016) to deeper waters, including demersal habitats, at the end of their first year (Geoffroy et al. 2016).

The distribution of *Arctogadus* spp. is poorly described, partly because their taxonomy remains uncertain, with some authors distinguishing at least two species [*A. borisovi* (Dryagin, 1932) and *A. glacialis* (Peters, 1872)] in the Atlantic Arctic based on classical taxonomic studies (Natalia Chernova, Russian Academy of Sciences, pers. comm.). Others consider *A. glacialis* to be a single

circumpolar species based on morphology and genetics (Jordan et al. 2003; Aschan et al. 2009; Mecklenburg et al. 2014; Mecklenburg and Steinke 2015). In both the Atlantic and the Pacific Arctic, *A. glacialis* overlaps with *B. saida*, but is generally much less abundant (Madsen et al. 2016; Bouchard et al. 2016). For example, only 8–9 % of larval cod sampled in the Amundsen Gulf were classified as *A. glacialis* (Bouchard et al. 2016). Local exceptions, however, are reported from the Northeast Water Polynya off NE Greenland in 1990 (von Dorrien et al. 1991).

Saffron cod are distributed along the coastlines of the North Pacific Ocean, extending through the Bering Strait northward into the Chukchi, East Siberian and Beaufort seas and as far east as Nunavut (Cohen et al. 1990). In contrast to polar cod and Arctic cod, they primarily inhabit brackish to marine waters at relatively shallow depths up to 75 m (Wolotira 1985). They are often found in areas of tidal influence at the mouths of coastal rivers (Wolotira 1985), where they can reach locally high abundances and serve as an important food for Arctic seabirds and marine mammals (Bluhm and Gradinger 2008). Reflecting their more southern and nearshore distribution, saffron cod are able to grow and store excess lipids at temperatures as high as 20 °C (Copeman et al. 2016; Laurel et al. 2016), suggesting a competitive advantage over polar cod in a warming climate.

The polar cod is the most abundant Arctic gadid and occupies a wide variety of habitats including nearshore waters, semi-enclosed bays, Arctic and subarctic shelves, continental slope regions and the Central Arctic Basin (Drolet et al. 1991; Michaud et al. 1996; Hop et al. 1997; Norcross et al. 2010; Logerwell et al. 2015; Mecklenburg and Steinke 2015; David et al. 2016; Kessel et al. 2016). Relatively large abundances occur in the western Beaufort Sea (Benoit et al. 2008) and in the eastern and northern Barents Sea, where they have supported a modest-sized fishery of up to 50,000 t in recent decades (Hop and Gjøsæter 2013; McBride et al. 2014). More recently, large aggregations of young-of-year polar cod were observed in the northeast Chukchi Sea (De Robertis et al. 2016), but their origin remains unknown. Biomass estimates in the Barents Sea region peaked at 2 million t in 2006, but have declined to less than 300,000 t in 2014 in spite of relatively conservative exploitation rates between 0 and 4 % that are believed to have little impact on stock dynamics (McBride et al. 2014; Havforskningsrapporten 2015; Pavel Krivosheya, PINRO, Murmansk, pers. comm.). Reductions in abundance may be related to increasing abundances of potential competitors such as capelin (Hop and Gjøsæter 2013; McNicholl et al. 2015) or predators such as larger gadids (Nahrgang et al. 2014). However, the distribution of polar cod has recently shifted toward the northeast, into the Russian zone of the Barents Sea, where the survey

coverage has been poorer with no catches in 2014 (Havforskningsrapporten 2015). Thus, some of the apparent decline can likely be explained by a shift in stock distribution. At the very edges of their distribution around Iceland, polar cod have been encountered less frequently in fishery surveys during recent years, which may be related to increasing bottom water temperatures; this may eventually lead to their disappearance from Icelandic waters (Astthorsson 2016). Similarly, the abundances of several Arctic species, including polar cod, decrease in years with reduced sea ice cover in the Bering Sea (Mueter and Litzen 2008) and where the polar frontal zone has retreated in the Barents Sea during recent warm years (Fossheim et al. 2015). Monitoring polar cod using existing fishery surveys therefore provides a good indicator of changes in the sub-Arctic–Arctic ecotone.

### Population genetics

Little is known regarding stock structure in polar cod or the other Arctic gadids. Genetic variation across the broad geographic range occupied by polar cod is relatively low (Nelson and Bouchard 2013; Mecklenburg and Steinke 2015), with some genetic variation at regional scales. Specifically, Madsen et al. (2016) showed significant population differentiation between polar cod inside fjords of northeast Greenland and Svalbard relative to populations on the shelf. The differentiation, albeit weak, was most pronounced between Svalbard and northeast Greenland. The authors speculate that the fjord populations may have become genetically isolated from populations on the shelf during recolonization after the last glacial maximum.

### Life cycle strategies

Knowledge of the life history strategies of polar cod is essential not only for our ability to predict ecological consequences of environmental change in the Arctic, but also for our general understanding of life history adaptations to pronounced seasonality. For polar cod, some life cycle data exist; the species reaches a maximum age of 7–8 years and becomes sexually mature between the age of 2–3 years (Hop and Gjøsæter 2013), although some specimens may reach maturity at age 1 (Nahrgang et al. 2016). Furthermore, males may reach maturity at a younger age and have a shorter life span (Nahrgang et al. 2014). Recent studies suggest that polar cod is an iteroparous species (Hop et al. 1995; Nahrgang et al. 2014) with strong indication of a group-synchronous oocyte development with determinate fecundity (Nahrgang et al. 2016). Polar cod is assumed to be a pelagic broadcast spawner, producing

large floating eggs (Aronovich et al. 1975; Graham and Hop 1995), with spawning reported mainly between January and March (Andriyashev 1954; Rass 1968; Ponomarenko 2000). Polar cod eggs are buoyant and translucent with an approximate diameter of 1.6–1.9 mm (Aronovich et al. 1975; Graham and Hop 1995). Optimal conditions for embryonic development range from 0 to 3 °C and salinity 30–33 (Doroshev and Aronovich 1974; Aronovich et al. 1975; Sakurai et al. 1998). Larval development of polar cod, saffron cod and navaga has been studied experimentally (Doroshev and Aronovich 1974; Aronovich et al. 1975; Dunn and Vinter 1984; Haryu and Nishiyama 1993; Andersen et al. 1994; Sakurai et al. 1998). Bouchard and Fortier (2008, 2011) reviewed hatching time relative to environmental conditions and found that hatching time was extended in seas receiving large river discharges, occurring as early as January. Favorable temperature conditions in these river plumes allow more rapid egg development and help larvae achieve the motility needed for successful first feeding before the ice melts. In regions lacking a river plume, extreme temperatures (about −1.8 °C) appeared to delay hatching until after ice breakup (April–July). This may also be the case in the northern Bering Sea and Chukchi Sea, where larvae are primarily associated with offshore marine waters (De Robertis et al. 2016; Kono et al. 2016).

### Role in food web

Polar cod have long been recognized as a key secondary consumer and important prey for upper trophic level species in the Arctic (Bradstreet et al. 1986; Welch et al. 1992), but little was known about ontogenetic, temporal and spatial variability in their prey. Polar cod appear to be generalists feeding primarily on available zooplankton and prey composition primarily varies with size. Larger fish consume larger prey items and more benthic prey (Walkusz et al. 2013; Gray et al. 2016). The shift to benthic prey presumably reflects ontogenetic shifts in vertical distribution as larger juveniles descend in the water column toward the bottom or to join older fish in an epipelagic layer (Geoffroy et al. 2016). The vertical separation between young-of-year and older fish, and a general increase in body size with depth (Geoffroy et al. 2016), limits cannibalism, which is relatively rare in polar cod in the Pacific Arctic (Rand et al. 2013; Gray et al. 2016; Majewski et al. 2016) compared to other gadids such as walleye pollock (*Gadus chalcogrammus*) in the Bering Sea (Bailey 1989).

Diets of similarly sized polar cod vary among regions and by depth, reflecting regional differences in prey availability (Gray et al. 2016; Nakano et al. 2016; Majewski et al. 2016). For example, pelagic prey, in

particular calanoid copepods, generally dominates the diet of juvenile polar cod. However, fish in the Chukchi Sea ate more benthic prey than those in the Beaufort Sea, likely reflecting higher benthic productivity in the Chukchi Sea (Grebmeier et al. 2006). Diets also changed along a depth gradient from shallow shelf stations to deep slope stations in the Beaufort Sea, although differences in this case were at least partially due to an increase in the size of polar cod with depth (Majewski et al. 2016). Polar cod in the northern Bering Sea and southern Chukchi Sea consumed a high proportion of appendicularians, which were highly abundant near the bottom during the survey period based on video transects (Nakano et al. 2016), further supporting the notion that polar cod are opportunistic feeders.

High dietary overlap has been shown between polar cod and some other forage fish such as saffron cod, juvenile walleye pollock, capelin and, to a more limited extent, Pacific sand lance (*Ammodytes hexapterus*), suggesting a strong potential for interspecific competition if the latter species were to expand their ranges from the subarctic into the Arctic (Hop and Gjøsæter 2013; Falardeau et al. 2014; McNicholl et al. 2015). In addition, polar cod have a cold-water stenothermic response with optimum growth near 5 °C, whereas saffron cod have a much broader temperature range (Copeman et al. 2016) and the Pacific boreal gadids, walleye pollock and Pacific cod (*Gadus macrocephalus*), have much faster maximum growth rates at temperatures above 5 °C (Laurel et al. 2016). Similarly, Atlantic cod outgrow polar cod at 8 °C and have a competitive advantage under future warming and ocean acidification (Kunz et al. 2016). In combination, these observations suggest that polar cod are highly vulnerable to continued climate change in the Arctic marginal seas, particularly in nearshore or shelf areas that already experience considerable warming. This applies in the Chukchi Sea, where summer temperatures can reach as high as 10 °C during summer, as well as in the fjords and on the shelf of western Svalbard, where the water temperature rises above 5 °C during summer. In addition to overlapping distributions between polar cod and other gadids, polar cod and capelin co-occur in these areas, with 80 % dietary overlap (Schoener's Index) in the Canadian Arctic (McNicholl et al. 2015) and 40 % dietary overlap around Svalbard (Dalpadado et al. 2016).

Polar cod and other Arctic gadids also serve as key prey for a wide variety of predators including larger fish, seabirds and marine mammals (Bradstreet et al. 1986; Welch et al. 1992; Bluhm and Gradinger 2008). However, the role of predation in their population dynamics and the impacts of changes in the distribution and abundance of polar cod on predators remain poorly understood. Seasonal migrations of some of these predators may be timed to take advantage of this high-energy fish prey including

piscivorous seabirds feeding on juvenile polar cod in the Chukchi Sea (Kuletz et al. 2015) and beluga whales feeding on polar cod along the Beaufort Sea shelf and slope (Loseto et al. 2009; Hauser et al. 2014). Locally, decreases in the availability of polar cod due to earlier ice retreat can have important consequences for nearshore predators with a restricted foraging range, such as Black Guillemot (*Cepphus grylle mandtii*) at a breeding colony (Divoky et al. 2015). In the Beaufort Sea, Black Guillemot and two other species, feeding primarily on polar cod, ringed seals (*Pusa hispida*) and beluga whales (*Delphinapterus leucas*), have shown declines in condition, growth or production during recent decades, possibly reflecting decreased availability of polar cod (Harwood et al. 2015; Moore and Stabenro 2015). Jellyfish, although an integral part of high-Arctic food webs (Hopcroft et al. 2005), have received less attention as potential predators on Arctic gadids, but Crawford (2016) provides evidence that the scyphomedusa *Cyanea capillata* has the potential to affect the small-scale distribution of polar cod in nearshore areas. Kessel et al. (2016) expand on this work to examine the roles of the environment and predator–prey dynamics on the migration of polar cod into and out of a nearshore area using acoustic telemetry.

## Conclusions

Arctic gadids, in particular the polar cod *B. saida*, play a pivotal role in Arctic marine ecosystems, including those of the broad Arctic shelves and the central Arctic basins. In combination, the papers assembled here suggest that the distribution, growth and abundance of these species are highly sensitive to direct temperature effects and to indirect food web effects associated with climate change. In particular, in areas with increasing summer temperatures several gadid species with a more southerly distribution, as well as capelin and other forage species, are likely to out-compete polar cod and Arctic cod in areas where they currently overlap. We hope that this special issue will contribute to a better understanding of these dynamics as climate change continues to affect marine ecosystems in a rapidly changing Arctic.

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