International workshop on the ecology of Arctic gadids

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An international workshop on the ecology of circumpolar Arctic gadids (*Boreogadus saida* and *Arctogadus* spp.) was convened during the ESSAS Annual Science Meeting on April 8-9 in Copenhagen, Denmark, with over 60 scientists from 10 countries. A total of 10 poster and 17 oral presentations highlighted recent advances in our understanding of the ecology of these important species, which occupy a central role in Arctic marine food webs. All references in this article refer to workshop presentations (Appendix 1); abstracts and selected presentations will be available at the ESSAS website (http://www.imr.no/essas). While research on *B. saida* has a long history, particularly in Russia (Karamushko and Christiansen), interest in Arctic marine ecosystems has grown in recent years as summer sea ice cover has diminished and water temperatures have increased.

Both *Boreogadus saida*, hereafter referred to as Polar cod, and *Arctogadus* spp. are cold-adapted and have antifreeze glycoproteins, which are required to survive long periods at sub-zero temperatures but come at a metabolic cost (Karamushko and Christiansen). The geographic distribution of *B. saida* extends throughout the Arctic and into the subarctic seas (Figure 1), while *Arctogadus* spp. are restricted to higher latitudes (Madsen et al., Bouchard et al.). The distribution of *Arctogadus* spp. is poorly described, in part because their taxonomy remains uncertain with at least two species (*A. borisovi, A. glacialis*) distinguished in the Atlantic Arctic (Chernova). In both the Atlantic and the Pacific Arctic, *A. glacialis* overlap with *B. saida,* but are much less abundant (Madsen et al., Bouchard et al.). For example, only 8-9% of larval cod sampled in the Amundsen Gulf were classified as *A. glacialis* (Bouchard et al.).

Figure 1: The Polar cod (Boreogadus saida), also known as Arctic cod, has a circumpolar distribution extending into the marginal seas. Photo credit: Sheiko and Mecklenburg. Map from Mecklenburg & Mecklenburg (http://www.arcodiv.org/Fish/Boreogadus_saida.html).

There is considerable genetic structure in the population of *B. saida* at both large (1000s of km) and smaller geographic scales (Nelson et al., Præbel et al.). Analysis of microsatellite DNA suggests that populations in eastern Canada and West Greenland are distinct from those in the

Pacific Arctic, with smaller-scale structure separating populations in the Chukchi and US Beaufort Sea from those in the Canadian Beaufort Sea and Amundsen Gulf (Nelson et al.). Population divergence seems to be occurring in some isolated (silled) fjords in East Greenland, while no population structure was evident in shelf populations from East Greenland to Svalbard (Præbel et al.).

Polar cod occupy a wide variety of habitats including nearshore, shallow waters, Arctic and subarctic shelves, continental slope regions and the central Arctic basin. The largest abundances have been observed in the eastern and northern Barents Sea, where they have supported a modest-sized fishery of up to 50,000 t in recent decades (Krivosheya). Biomass estimates in the region peaked at 2 million t in 2006, but have declined to less than 400,000 t in 2013 in spite of relatively conservative exploitation rates from 0 to 4% (Krivosheya). Reductions in abundance may be related to increasing abundances of potential competitors such as capelin or predators such as *Gadus* spp. (Hop and Gjøsæter).

High abundances of *B. saida* have also been observed along the outer shelf and slope of the Canadian Beaufort Sea and Amundsen Gulf (Majewski et al., Geoffroy et al.), where peak abundances typically occur below cold Pacific waters in a layer of slightly warmer Atlantic water (350-500 m). Young-of-the-year cod occupy the fresher surface layer (Marsh et al, Geoffroy et al.), while larger fish occupy deeper waters, thereby limiting cannibalism. Mean size generally increases with depth, suggesting an ontogenetic movement towards deeper waters (Geoffroy et al.). Polar cod also range into subarctic waters including the Bering Sea and Iceland, where they expand during cool periods such as those associated with extensive ice cover in the Bering Sea (Marsh et al.) and with the intrusion of polar water masses onto the shelf north of Iceland (Astthorsson).

Nearshore aggregations of *B. saida* are found in the fjord systems of East Greenland (Madsen et al.), Svalbard (Nahrgang et al., Larsen et al.), the Canadian Archipelago (Crawford), and the Beaufort Sea (Divoky & Tremblay). Nearshore distributions are highly dynamic and respond to variability in small-scale oceanographic features such as tidal fronts that can interact with topography to provide shelter from jellyfish predators (Crawford). In nearshore waters of the Beaufort Sea, *B. saida* are closely associated with sea ice and have become less available to coastal predators such as shallow-diving seabirds during recent years when sea ice has retreated earlier in the season (Divoky and Tremblay).

Recent advances in under-ice sampling have also confirmed that *B. saida* are ubiquitous under first year ice in the Arctic basin, where they occur in relatively low densities and presumably feed on sea-ice associated amphipods such as *Apherusa glacialis* (David et al.). Total under-ice biomass of *B. saida* in the Eurasian Basin was estimated at 38,000 tons (David et al.).

Spawning of *B. saida* occurs primarily in shallow, nearshore areas as inferred from the distribution of larvae. Known spawning concentrations in the Atlantic occur during winter along the east coast of Novaya Zemlya in the Kara Sea, in the southeast Barents Sea, and around Svalbard (Krivosheya, Hop & Gjøsæter). High larval concentrations imply that spawning concentrations in the Pacific Arctic occur in the eastern Chukchi Sea (Marsh et al.) and in the southeast Beaufort Sea (Bouchard et al.).

B. saida and *A. glacialis* differ in their growth and reproductive characteristics. For example, *A. glacialis* hatch at a larger size, have a larger size at least through metamorphosis, achieve a larger size overall, have a longer life span, and mature later than *B. saida* (Bouchard et al.). Under laboratory conditions, *B. saida* at very low temperatures (0°C) grow much faster than other gadids such as Pacific cod or walleye pollock (Laurel et al.). Optimal growth under unlimited food conditions occurs at ~5°C but decreases rapidly at higher temperatures (Laurel et al, Kunz et al.). Growth rates in the ocean can vary substantially among regions, as evident in a much larger mean size at-age in the Barents Sea compared to the Kara Sea (Raskhozheva). Around Svalbard, Polar cod in both an Arctic-type and a warmer Atlantic-type fjord grew to a very similar size by age-1, but the size-at-age of older fish, as well as their fecundity, was considerably larger in the colder, Arctic fjord (Nahrgang et al.). In the Arctic domain, female Polar cod also grow to a larger size, mature later, and have a longer life expectancy than males (Nahrgang et al.).

The population dynamics of *B. saida* are poorly understood and the only the Barents Sea stock is regularly surveyed. The estimated production to biomass ratio ranges from 0.6 to 1.1 and has increased between 1969-1981 and 1986-2008, associated with a younger age structure (primarily 2-3 year old fish) and earlier maturation in recent decades (Raskhozheva). Abundances have fluctuated widely since the 1960s, which cannot be attributed to fishing alone (Krivosheya). Models to simulate the future dynamics of Polar cod under climate change are currently under development (Duarte et al.).

Polar cod have generally been recognized as a key link between lower trophic levels and higher tophic levels such as seabirds and mammals. Diet composition varies among regions, but diets are typically dominated by calanoid copepods and hyperiid amphipods, in particular *Themisto* spp. Larval *B. saida* feed almost exclusively on calanoid copepods or their nauplii in the Beaufort Sea (Bouchard et al.) and in the Chukchi Sea (Marsh et al.). The diet of demersal *B. saida* in the Beaufort Sea varies with depth and is dominated by *Calanus hyperboreus* and *C. glacialis* on the shelf (Majewski). The proportion of *T. libellula* in the diet, as well as their abundance in the water column, increase with depth and *T. libellula* dominate on the lower slope. These three prey species, along with *T. abyssorum*, make up over 90% of *B.saida* diets in the Canadian Beaufort Sea. Similarly, *T. libellula* dominates diets in the Kara Sea (Orlova et al.). In contrast, larger (> 60mm) Polar cod in the Chukchi Sea (Marsh et al.) and in the Barents Sea (Orlova et al.) consumed a much larger variety of prey items, including fish (10-20%). The proportion of copepods decreases and the proportion of fish and amphipods typically increases with size (e.g. Orlova et al.). A shift to feeding at higher trophic levels with increasing size is also confirmed by isotopic analyses. Cannibalism has been reported but was relatively rare in the Barents & Kara Sea (< 1.4% frequency of occurrence), although it can account for up to 8% of diets by weight (Orlova et al.). Cluster analyses suggest that diets of *B. saida* in the Barents Sea overlap most strongly with capelin, while there was very little overlap with the diets of *A. glacialis*.

Polar cod are vulnerable to temperature fluctuations and long-term trends in the marine environment, which affects their distribution (Marsh et al., Astthorsson), growth (Laurel et al., Nahrgang et al., Hop & Gjøsæter), and fecundity (Nahrgang et al.). Due to their important trophic role in the Arctic marine ecosystem, such effects may alter ecosystem structure and functioning in the Arctic, hence Polar cod in the marginal seas of the Arctic may be replaced by boreal species such as capelin under global warming (Hop & Gjøsæter). Moreover, Polar cod in the Arctic Ocean may be impacted by ocean acidification resulting from increased levels of atmospheric CO_2. Under CO_2 levels expected by the end of the century, Polar cod in the laboratory had reduced growth rates and exhibited behavioural changes (Kunz et al., Schmidt et al., Storch et al.). Transcriptomic studies are underway to determine the capacity of Polar cod to adapt to changing temperatures and CO_2 levels (Windisch et al.)

The goal of the workshop was to bring together scientists from around the circumpolar Arctic to focus exclusively on the ecology of Arctic Gadids and, by all accounts, it was an unqualified success thanks to the thoughtful contributions of all presenters and other participants. We thank the POLARISATION project (Research Council of Norway) and the International Arctic Science Committee for providing generous travel support and the Natural History Museum of Denmark, University of Copenhagen, for hosting the workshop.

Appendix I: Workshop Presentations

Oral Presentations

Kim Præbel, Matias Langgaard Madsen, Jørgen Schou Christiansen and Svein-Erik Fevolden: *On the doorstep to a deeper understanding of population divergence in highly mobile Arctic gadoids: examples from sympatric* Arctogadus glacialis *and* Boreogadus saida

R. John Nelson, C. Bouchard, A. Majewski, M. Madsen, J. Reist, L. Fortier, J. Christiansen, S-E. Fevolden, S. Talbot, R. Crawford, D. Archambault, T. Siferd, S. Palsson, G. Rose, K. Dunton, G. Divoky, and Kim Præbel:
Molecular Genetics of Arctic Cod

Olafur S. Astthorsson: *Distribution, abundance, and biology of polar cod,* Boreogadus saida*, in Icelandic Sub-Arctic waters*

Pavel Krivosheya: *Review of Russian investigations of polar cod (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*) in the Barents and Kara Seas*

Andrew Majewski, Wojciech Walkusz, Jane Eert, James Reist, and Sheila Atchison: *Distribution of Arctic (Polar) Cod,* Boreogadus saida*, in the Canadian Beaufort Sea relative to key prey items and oceanographic parameters*

Maxime Geoffroy, Andrew Majewski, Stéphane Gauthier, Mathieu LeBlanc, Wojciech Walkusz, James D. Reist, and Louis Fortier: *Vertical distribution and migrations of Arctic cod (*Boreogadus saida*) in the Canadian Beaufort Sea from spring to fall*

Carmen David, Hauke Flores, Benjamin Lange and Doreen Kohlbach: *Under-ice distribution of polar cod* Boreogadus saida *in the Central Arctic Ocean and its association with sea ice habitats properties*

Richard E. Crawford: *Occurrence of a gelatinous predator (*Cyanea capillata*) affects Arctic cod habitat utilization in High Arctic coastal waters*

Haakon Hop and Harald Gjøsæter: *Polar cod (*Boreogadus saida*) in a warmer and more competitive Arctic environment*

George Divoky[1] and Yann Tremblay[2]: *Decadal, annual and seasonal variation in Arctic Cod (*Boreogadus saida*) abundance in the nearshore Beaufort Sea: the effects of decreasing sea ice and increasing SST*

Daniela Storch, Flemming Dahlke, and Jasmine Nahrgang: *Effects of ocean acidification and warming on the embryonic development of Polar cod* Boreogadus saida

Benjamin J. Laurel, Mara Spencer, and Louise A. Copeman: *Temperature-dependent growth, condition and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids*

Caroline Bouchard, Salomé Mollard, Dominique Robert, Keita Suzuki, and Louis Fortier: *Comparing the early life history of sympatric* Boreogadus saida *and* Arctogadus glacialis *in the southeastern Beaufort Sea*

Jasmine Nahrgang, Øystein Varpe, Ekaterina Korshunova, Svetlana Murzina, Ingeborg G. Hallanger, Ireen Vieweg, and Jørgen Berge: *Gender specific reproductive strategies of an Arctic key species (*Boreogadus saida*) and implications of climate change*

Larisa I. Karamushko and Jørgen S. Christiansen: *Bioenergetic adaptations in polar cod* Boreogadus saida *(Lepechin, 1774)*

Jennifer M. Marsh and Franz J. Mueter: *Distribution and trophodynamics of Arctic cod (*Boreogadus saida*) in the eastern Chukchi and northeastern Bering Seas*

Emma V. Orlova, Andrey V. Dolgov, Irina P. Prokopchuk, Valentina N. Nesterova: *Diet of polar cod (*Boreogadus saida*) in the Barents and Kara Seas*

Poster presentations

Natalia V. Chernova: *Polymorphism of* Arctogadus*, an alternative point of view*: A. borisovi *is a valid species*

Emma V. Orlova, Andrey V. Dolgov, Valentina N. Nesterova, Anna S. Orlova, Irina P.Prokopchuk, Aleksander N. Bensik: *Food supply of polar cod in the Barents Sea in recent warming period - changes in the meso- and macroplankton communities.*

Pedro Duarte, Haakon Hop, Harald Gjøsæter, Jasmine Nahrgang: *Population dynamics modelling of polar cod* (Boreogadus saida).

Kristina Kunz, Rainer Knust and Felix C. Mark*: Effects of ocean acidification and warming on growth and food consumption of juvenile Polar cod,* Boreogadus saida.

Lars-Henrik Larsen, Sam Newby, Torstein Pedersen, Morgan Bender, Stig Falk-Petersen: *Distribution of fish in Kongsfjord, Svalbard during polar night.*

Matias Langgaard Madsen, Raul Primicerio, Michael Greenacre, Kim Præbel, Svein-Erik Fevolden, Oleg V. Karamushko, Jørgen Schou Christiansen*: Spatial distribution and abundance of* Arctogadus glacialis *and* Boreogadus saida *in NE Greenland.*

Evgeniia Raskhozheva: *Growth and production of polar cod* Boreogadus saida *(Lepechin) in the Barents and Kara Seas.*

Matthias Schmidt, Christian Bock, Hans-Otto Pörtner, Daniela Storch: *Effects of ocean acidification and warming on the behaviour of Polar cod* Boreogadus saida.

Tomáš Tyml and Oleg Ditrich: Gadimyxa sphaerica*, a myxosporean parasite found in Polar cod (*Boregadus saida*) and its life cycle in Billenfjorden, Svalbard.*

Heidrun Windisch, Magnus Lucassen, and Stephan Frickenhaus: *Comparative transcriptomics in* Gadus morhua *and* Boreogadus saida *under different temperatures and* PCO_2 *levels.*