The Arctic Cod (*Boreogadus saida*) Ecosystem Under the Double Pressure of Climate Change and Industrialization (Arctic Cod)

Project Leader

Louis Fortier (Université Laval)

Network Investigators

Yvan Simard (Université du Québec à Rimouski); Jean-Eric Tremblay (Université Laval)

Collaborators

Alexandre Forest, Dominique Robert (Université Laval)

Post-Doctoral Fellows

Keita Suzuki (Université Laval)

PhD Students

Caroline Bouchard, Gerald Darnis, Maxime Geoffroy, Jordan Grigor, Moritz Schmid (Université Laval)

MSc Students

Marianne Falardeau-Cöté (Université Laval)

Undergraduate Students

Mathieu Leblanc (Université du Québec à Rimouski); Marianne Caouette, Salomé Mollard, Vicky St-Onge, Ariane Marais, (Université Laval)

Technical Staff

Cyril Aubry (Université Laval)

Abstract

The Arctic cod (*Boreogadus saida*), also known as the polar cod in Europe, is a key component of the Arctic Ocean pelagic ecosystem that effects up to 75% of the energy transfer between the plankton and the vertebrate fauna (fish, seals, whales and marine birds). Being an hyper-specialist adapted to life in ice-covered seas, Arctic cod is likely to be displaced by southern generalists such as the capelin and the sandlance as the ice regime becomes less severe. This project collaborates closely with 'Hotspots', 'Moorings' and 'Sea-ice' to map the distribution and migrations of Arctic cod populations in the Canadian Arctic, and to measure variations in hatching season and early growth in relation to annual changes in ice regime, surface temperature, and zooplankton prey abundance. In partnership with the Department of Fisheries and Oceans, and the Department of Aboriginal Affairs and Northern Development (Beaufort Regional Environmental Assessment program), we assess the general distribution and reproduction of Arctic cod in the Beaufort Sea and its response to climatic and anthropogenic pressures.

Key Messages

- Thanks to recent progress in automated computer identification of the images provided by the Lightframe On-sight Keyspecies Investigation System (LOKI), we are close to achieve for mesozooplankton a sampling capacity and a spatio-temporal resolution similar to those provided by the CTD-rosette for phytoplankton studies.
- The wide-ranging seasonal vertical migrations (SVM) of the large copepod *Calanus hyperboreus* appears to play a crucial role in structuring the arctic marine ecosystem by dictating the vertical distribution and life strategy of several other copepods and the seasonal migrations of the Arctic cod.

- The summer 2007 record low ice cover in the Beaufort Sea boosted egg production in the large herbivorous copepod *Calanus hyperboreus* but the survival of the nauplii hatched from these eggs was low, perhaps because of predation by the omnivorous copepod Metridia longa.
- Arctogadus glacialis represents ca. 8% of
 the larval and early juvenile cod complex
 (Arctogadus glacialis + Boreogadus saida)
 sampled in the Beaufort Sea, a crucial result that
 confirms that our understanding of the ecology of
 Boreogadus saida based on previous studies that
 did not discriminate the two species in plankton
 collections remains essentially valid.
- The hatching season of both Arctic cod Boreogadus saida and ice cod Arctogadus glacialis is centered on the bloom of ice microalgae.
- True arctic fish such as the Arctic cod and the ice cod share a protracted hatching period from January to early July and slow growth during the larval stage. By contrast, the Pacific sand lance *Ammodytes hexapterus*, an invading species newly recorded in the ichthyoplankton of the Beaufort Sea, hatch during a short period in late July and August and grow explosively before the winter cooling.
- As already seen in Hudson Bay, increasingly warm and ice-free surface waters at the end of the summer will favour the integration of this and other subarctic invaders in the Beaufort Sea ecosystem.
- The lack of regional models and scenarios of the future ocean climate in the Canadian Western Arctic weakens our capacity to forecast precise milestones in the ineluctable transition of the arctic marine ecosystems of the Western Arctic towards boreal marine ecosystems.
- There is an acute need for a synthesis of knowledge about the marine ecosystems of the Kitikmeot.

Objectives

- Assess regional and interannual (2002-2018) variations in the prey field and food intake of larval and juvenile Arctic cod in the Beaufort Sea and North Water:
- Describe annual and decadal variations (2002-2018) in the absolute and relative abundance of the main arctic copepods and their predators (Arctic cod, chaetognaths, and the hyperiid amphipod *Themisto libellula*) in the Beaufort Sea;
- Correlate decadal variations (2002-2018) in the hatch date frequency distribution of Arctic cod to variations in sea ice cover and surface temperature in the Beaufort Sea;
- Track the vertical distribution and migration of the large calanoid copepods *Calanus glacialis* and *C. hyperboreus* and their lipid reserves in relation to the underice phytoplankton bloom using the new LOKI in-situ image profiler;
- Determine the fall migration of arctic cod juveniles from the surface layer to the deep overwintering grounds over the slope;
- Describe the summer distribution of adult and juvenile Arctic cod and their marine mammal predators in southeastern Beaufort Sea;
- In the longer term, document the vertical and horizontal distribution of Arctic cod and zooplankton under the ice cover of the Canadian Arctic Ocean using sonars carried by an Autonomous Underwater Vehicle (AUV).

Introduction

The pelagic ecosystem of the Arctic Ocean provides local communities with many goods and services that include traditional food (fish, marine mammals and birds), "traditional" health (omega-3, selenium, etc.), furs and leather, heating oil, substrates for sculpture (e.g. bones and ivory), inspiration for the arts, social cohesion, intergenerational bonding, spiritual comfort,

and life fulfilling. As the sea-ice cover of Arctic seas shrinks and their surface layer warms up, signs of the expected replacement of the unique Arctic pelagic ecosystem by North-Atlantic and North-Pacific ecosystem types are increasingly detected (e.g. Tynan and Demaster 1997; Gaston et al. 2003; Grebmeyer et al. 2006; Falardeau et al. 2013). The atlantification/pacification of the Arctic pelagic ecosystem threatens the services rendered to northern communities, and harbingers a shift to different ecosystem services that will benefit primarily southern industries: for instance, access to oil and other mineral resources, new shipping lanes, fish stocks of commercial interest, and ecotourism.

The objective of ArcticNet IRISes is to provide Inuit communities, the private sector, and governments with the relevant scientific information to formulate the policies, adaptation strategies, and decisions that will shape the response of Canada to climate change and modernization in the Arctic. As far as marine ecosystem services are concerned, anticipating the rate and timing of the expected transformation of the pelagic Arctic ecosystem is a crucial element of all four IRISes. The Arctic cod (Boreogadus saida) is a key component of the relatively simple Arctic Ocean pelagic ecosystem. This small forage fish channels up to 75% of the energy transfer between the plankton and the fish, seals, whales and marine birds that supply many ecosystem services (Welch et al. 1998). A hyper-specialist adapted to life in ice-covered seas, Arctic cod is likely to be rapidly displaced by southern generalists as the ice regime becomes less severe. In northern Hudson Bay where ice decline is intense, capelin and sand lance have replaced Arctic cod as the main prey brought back to the nest by thick-billed murres to feed their young (Gaston et al. 2003). Similarly, in the Beaufort Sea where ice retreat is also severe, our own studies of the ichthyoplankton assemblage indicate the recent intrusion of the Pacific sand lance in the offshore distribution area of juvenile Arctic cod. We believe that changes in the ecology of Arctic cod, including its displacement by boreal forage fishes, are likely among the most powerful indicators of the transition of the Arctic Ocean pelagic ecosystem to a new equilibrium.

The Arctic Cod project collaborates closely with the "Hotspots" and "Moorings" projects to map the distribution of Arctic cod in the Canadian Arctic, to measure variations in its hatching season and early growth in relation to annual changes in ice regime, surface temperature, and zooplankton prey abundance, and to monitor changes in the ichthyoplankton assemblage to which it belongs. In partnership with the Oil Exploration sector, the Department of Fisheries and Oceans, and the Department of Aboriginal Affairs and Northern Development (Beaufort Regional Environmental Assessment program), we contrast the abundance and reproduction of Arctic cod among different regions of the Beaufort Sea, including the edge of the continental shelf where oil exploration rights have been awarded, so as to assess the potential risks of exploration drilling on the Arctic cod ecosystem. Again in 2013, we collaborated with the Department of Fisheries and Oceans to acquire acoustic data validated by trawling in the Beaufort Sea.

Activities

Time frame and study area.

The first leg of the 2013 mission of the *Amundsen* was highly successful and allowed us to fulfill our objectives for the Eastern Arctic and the North West Passage. In addition to the regular sampling of zooplankton and ichthyoplankton, these included the systematic deployment of the LOKI zooplankton imager at most stations; a study of the importance of the Labrador and Baffin fjords as nursery areas for fish larvae; and the successful deployment of the Remotely Operated Vehicle for visual examination of the macrozooplankton community near the seafloor and around an iceberg (Peterman Ice Island).

Sampling activities in 2013 were curtailed by the tragic crash of the helicopter of the CCGS *Amundsen*. The second leg of the 2013 mission corresponding to planned work in the Beaufort Sea was cancelled. This severely impacted most of our scientific objectives for this region. As for 2012 when the icebreaker was

out of commission for the replacement of engines, we could not complete the *Amundsen*-based planned survey of the inshore distribution of fish as part of the BREA-funded acoustic study of the summer distribution of Arctic cod in the Beaufort Sea. Again this year, to compensate in part the absence of the *Amundsen*, we deployed our acoustic instruments in the Beaufort Sea from the trawler M/V Frosti chartered by DFO as part of BREA.

Research activities in 2013-2014:

As announced in the previous report, we initiated a promising collaboration with Dr. Xie (UQAR) on the distribution and extent of the underwater methane plume in Baffin Bay. The EK60 and Multibeam sonars, methane detectors and the ROV were successfully deployed to characterized the vertical and horizontal distribution of the gas and to confirm that its sources are gas hydrates outcrops on the Canadian side in northern Baffin Bay.

Acoustic surveys of fish and sampling of zooplankton from the M/V Frosti in the offshore Beaufort Sea in collaboration with DFO at the Freshwater Institute (Jim Reist). Forty-four days (July 31 – September 12) of continuous multifrequency (38, 120, 200 kHz) echo sounder data during the ice-free season. Validation of echoes with ichthyoplankton nets, mesopelagic and benthic trawls.

Successful deployment of the Lightframe On-sight Keyspecies Investigation System (LOKI), an in situ profiling mesozooplankton imager, in Baffin Bay. Further development of a computer-assisted identification protocol.

We completed an in depth comparison of the early life history of the morphologically identical larval and juvenile stages of Arctic cod (*Boreogadus saida*) and Ice cod (*Arctogadus glacialis*) in the Beaufort Sea.

Presenting our results in Norway in January 2013 resulted in an invitation to prepare a manuscript contrasting the ecology of larval and juvenile Arctic

cod and Pacific sand lance in the offshore Beaufort Sea in summer for publication in the prestigious ICES Journal of Marine Science. The paper was prepared in record time and is now published.

We pursued our comparison of the diet of chaetognaths between Svalbard and the Beaufort Sea.

We completed a first draft of the Marine Ecosystems chapter for the IRIS-1 Assessment and coordinated several meetings with collaborators for the preparation of the Fisheries chapter for the IRIS-2 Assessment.

Ploughing through the red tape jungle of the Quebec provincial administration, we pursued our efforts to secure funding for the acquisition of a HUGIN 1000 Autonomous Underwater Vehicle that would create a whole new research capacity for the *Amundsen* and enable us to develop new expertise in arctic marine geophysics and the study of the under-ice ecosystem.

Two Ph. D. theses and one Master's thesis were completed this year:

- Gérald Darnis. 2013. Zooplankton vertical migration and respiratory carbon flux in the Beaufort Sea (Canadian Arctic). Ph. D. Thesis. Université Laval.
- Caroline Bouchard. 2013. *Boreogadus saida* and *Arctogadus glacialis*: larval and juvenile life of two gadids sharing the Arctic Ocean. Ph. D. Thesis, Université Laval.
- Marianne Falardeau-Côté. 2013. The invasion of the Beaufort Sea by the Pacific sand lance: impacts on Arctic cod and its ecosystem. M. Sc. Thesis. Université Laval.

Results

In the relatively simple ecosystem of the Arctic Ocean, copepods and the Arctic cod channel most of the carbon and energy from ice algae and phytoplankton (the primary producers) to the vertebrate fauna (fish,

marine mammals, marine birds) that provide services to communities. The magnitude and efficiency of this trophic flux of carbon is strongly influenced by physical conditions such as sea-ice regime, temperature, wind mixing, and the upwelling of nutrients. The "Moorings" and "Hotspots" projects examine how physical processes control primary production and the vertical flux of carbon (the fraction of primary production that ends up sequestered at depth). In close collaboration with these projects, the Arctic Cod project focuses in addition on the trophic flux of carbon that underpins ecosystem services.

The Lightframe Onsight Key-species Investigation System (LOKI) yields the first results for Baffin Bay.

The LOKI in-situ mesozooplankton imager was successfully deployed at several stations in Baffin Bay and the Northwest Passage. Thousands of images of single organisms or particles were obtained on each haul, with corresponding data for depth, temperature, salinity, and chlorophyll fluorescence (Figure 1).

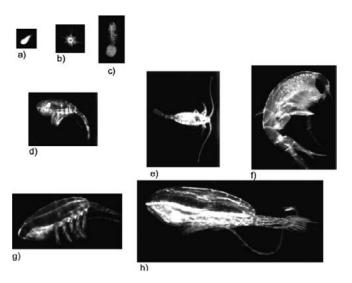


Figure 1. High resolution images of Arctic zooplankton showing structures that are often not visible when sampling with nets because they are too fragile (e.g. egg sacs). Images:
a) Triconia borealis, b) Radiolaria, c) Pseudocalanus sp. female with eggs, d) lateral view of Metridia longa, e) dorsal view of Metridia longa, f) Themisto libellula, g) and h) Calanus glacialis.

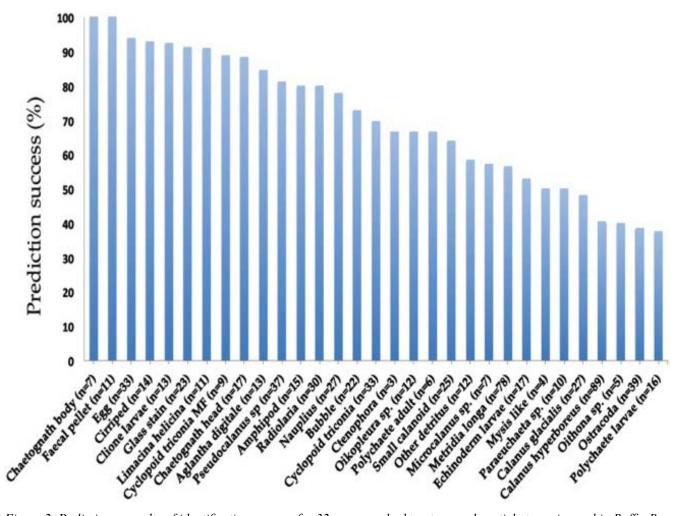


Figure 2. Preliminary results of identification success for 32 mesozooplankton taxa and particle types imaged in Baffin Bay and identified using the Random Tree algorithm.

A machine-learning algorithm (Random Tree) was selected among 5 others to automatically identify and classify the organisms and particles in broad categories validated by visual inspection of the images. With a larger calibration set, we expect to increase identification success (aka recall rate) to 80% for all major taxa (Figure 2).

The LOKI will provide an unprecedented resolution of the vertical distribution of zooplankton organisms that should enable us, for example, to elucidate the fine-scale co-distribution of herbivorous copepods and phytoplankton in the sub-surface chlorophyll maximum or to characterize the diel vertical

migrations of dominant species under the midnight sun.

Life strategy and reproduction of the arctic copepod Calanus hyperboreus during a year of record-low ice cover in the southeastern Beaufort Sea

The life cycle and reproduction of *Calanus hyperboreus* were studied from October 2007 to July 2008 during a period of record low ice cover in the southeastern Beaufort Sea. Stages CIV, adult females and CV dominated the overwintering population, suggesting a 2- to 3-year life cycle. These stages

overwintered at depth until April and made a fast ascent to the surface before the May ice melt and phytoplankton bloom, one month earlier than usual. Within two months, females filled their energy reserves and initiated their downward seasonal migration in July. From February to March, vigorous reproduction (20-65 eggs f-1 d-1) brought numerous eggs (28.863 \pm 23,310 eggs m-2) and nauplii NI-NIII (17,097 \pm 12,257 ind. m-2) in the water column. However, CI recruitment in May, coincident with the phytoplankton bloom, was modest (13-21% of copepodites) in Amundsen Gulf compared to sites outside the gulf (>75%). Consequently, C. hyperboreus abundance and biomass stagnated throughout summer in Amundsen Gulf. As a mismatch between the first-feeding stages and food was unlikely under the favorable feeding conditions of April-May 2008, predation on the young stages in late winter presumably limited subsequent recruitment and population growth. Particularly abundant in Amundsen Gulf, the copepod Metridia longa was likely a main consumer of *C. hyperboreus* eggs and nauplii. With the ongoing climate-driven lengthening of the ice-free season, an intensification of top-down control of C. hyperboreus recruitment by thriving populations of mesopelagic omnivores like

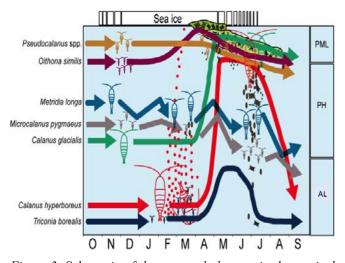


Figure 3. Schematic of the seasonal changes in the vertical distribution and trophic interaction among ice algae, the phytoplankton sub-surface maximum, and the seven copepods that dominate the mesozooplankton community of Arctic seas (PML: Polar Mixed Layer; PH: Pacific Halocline; AL: Atlantic Layer.

M. longa could counteract the potential benefits of increased primary production over the Arctic shelves margins (Figure 3).

Contrasting the early life stages of Boreogadus saida and Arctogadus glacialis, two gadids that share the Arctic Ocean

The larvae and early juvenile stages of polar cod Boreogadus saida and ice cod Arctogadus glacialis co-occur on Arctic shelves and are morphologically undistinguishable. The two species were sampled in southeastern Beaufort Sea from April to August of 2004 and 2008. A stratified subset of 2126 of the 10565 gadids collected were identified to species by genetics and/or the size of the nucleus of the lapillar otolith. Identified A. glacialis were longer at hatch (6.9 vs 5.5 mm in 2004; 6.2 vs 4.9 mm in 2008) and consistently larger than B. saida from April to June. Based on size in month of capture, 8.0% of the overall cods were assigned to A. glacialis in 2004 and 8.7% in 2008. The two species shared the same hatching season from February to July, peaking in April-May during maximum production of ice microalgae. Under the ice in April and May, A. glacialis was associated with the ice-water interface while B. saida avoided the interface. In partially ice covered and open waters from June to August, both species were distributed primarily from the surface to 40 m and exhibited a small-amplitude diel vertical migration (DVM) between 0-5 m at night 5-10 m during daytime. The summer spatiotemporal distribution of B. saida and A. glacialis in the Beaufort Sea was similar with both species occurring at 77% of 96 stations. At lengths <15 mm, B. saida preyed primarily on Pseudocalanus nauplii, and A. glacialis on cyclopoid nauplii. At lengths >25 mm, the two species shared the same wide spectrum of prey, the calanoids Calanus glacialis and C. hyperboreus providing >50% of the carbon intake. Growth rates ranged from 0.161 to 0.176 mm d-1 and were not significantly different between species. Slopes of the catch-at-age regressions indicated a higher mortality rate in B. saida than in A. glacialis. A larger size at age from hatching to metamorphosis may provide A. glacialis with some survival advantage over B. saida (Figure 4).

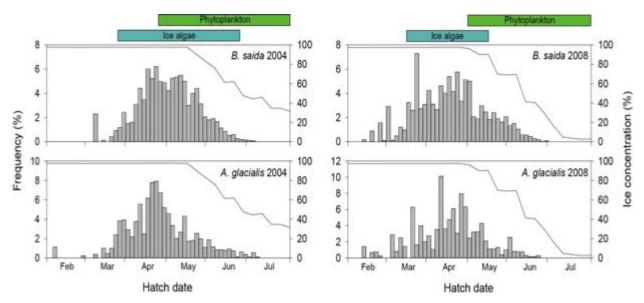


Figure 4. Hatch date frequency distributions corrected for mortality for all Boreogadus saida and Arctogadus glacialis collected in the Beaufort Sea in 2004 and 2008 after species redistribution. The black line indicates weekly ice concentration in the study area. The timing of ice algae and phytoplankton production in Franklin Bay (2004) and Amundsen Gulf (2008) are indicated above each panel.

Could the planktonic stages of polar cod and Pacific sand lance compete for food in the warming Beaufort Sea?

The boreal Pacific sand lance (*Ammodytes hexapterus*) was recently detected in southeastern Beaufort Sea (Canadian Arctic), numbering as the second most abundant ichthyoplankton species after the polar cod (*Boreogadus saida*) in 2011. We contrast the hatching periods, growth, prey selectivity, and feeding success of the planktonic stages (10 to 60 mm in length) of the two species. Polar cod hatched from January to mid-July and sand lance from mid-July to early

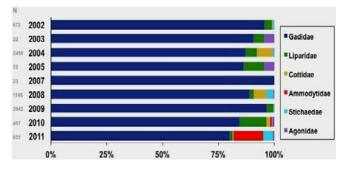


Figure 5. Ichthyoplankton composition by year in the offshore Beaufort Sea in summer.

September, precluding any competition among the larval stages. By weight, sand lance larvae grew 3.7 times faster than polar cod larvae. The co-occurring juveniles of both species fed primarily on copepods and to a lesser extent on bivalve larvae, shifting to larger prey with growth. The feeding success of both species appeared limited by the availability of their preferred prey. A significant diet overlap in juveniles > 25 mm (Schoener Index = 0.64) suggested potential competition for Pseudocalanus spp., Calanus spp. and bivalve larvae. However, sand lance strongly selected for nauplii while the more diversified diet of polar cod comprised mainly the copepodites of these species. Interspecific competition for food is unlikely at this time but is predicted to amplify with a climate-related reduction in the size of zooplankton prey and an increase in the abundance of sand lance (Figure 5).

Pre-winter distribution and habitat characteristics of Arcticcod (Boreogadus saida) in southeastern Beaufort Sea

Arctic cod was shown to form dense under-ice winter aggregations at depth in Amundsen Gulf (southeastern

Beaufort Sea). In this paper, we verify the premises of the aggregation mechanism by determining the distribution and habitat characteristics of Arctic cod prior to the formation of winter aggregations. Multifrequency split-beam acoustic data collected in October-November 2003 revealed that age-0 Arctic cod formed an epipelagic layer between 0 and ~60 m depth over the entire region. In contrast, adult Arctic cod tended to distribute into an offshore mesopelagic layer between ~200 - 400 m and shoaling into a denser (1 to 37 g m-2) bentho-pelagic layer on sloping bottoms (between 150-m and 600-m isobaths) along Mackenzie shelf and into Amundsen Gulf basin. Concentrations peaked in Amundsen Gulf where estimated total biomass reached ~250 kt. Both age-0 and adult Arctic cod distributed in the warmer waters (> -1.4°C). Arctic cod concentration over slopes is likely governed by the combined actions of 1) local currents concentrating both depth-keeping zooplankton and polar cod at the shelf-break and basin slopes, and 2) trophic association with these predictable topographically-trapped aggregations of zooplankton prey. During freeze-up, these slope concentrations of Arctic cod are thought to constitute the main source of the observed dense under-ice winter aggregations. The hypothesis of active short-distance displacements combined with prevailing mean currents is retained as the likely aggregation mechanism.

Arctic Change: Impacts on Marine Ecosystems in the Canadian High Eastern Arctic

In collaboration with the "Hotspots" and "Marine Mammals" projects, we drafted the Marine Ecosystems chapter of ArcticNet Integrated Regional Impact Assessment for the Canadian Eastern High Arctic. The pelagic (open water) and benthic (seafloor) marine ecosystems of the Western Canadian Arctic provide Inuvialuit and Nunavummiut of the Kitikmeot with many services. With climate warming and a shift in sea-ice regime, these ecosystems are likely to transform into somewhat richer subarctic/boreal ecosystems over the present century. Presently, the pelagic and benthic ecosystems of the Western Canadian Arctic are still essentially intact except

for the first symptoms of the expected invasion by animals from the North Pacific. However, studies in the Bering Sea indicate that a spectacular shift in the relative importance of the pelagic and benthic ecosystems can occur in less than 20 years. Recent scientific studies in the area point to the following potential transformations: (1) increased penetration of light in the surface layer of the ocean, and increased upwelling of nutrients by wind from the deep layer to the surface layer; (2) reduced production of ice algae and increased production of phytoplankton; (3) enrichment of the pelagic ecosystem to the detriment of the benthic ecosystem; (4) initial improvement of conditions for key arctic specialists such as the large copepod Calanus glacialis, the Arctic cod and several seabirds until mid-century; (5) a decline in the abundance and health of resident ice-dependant seals and polar bears after mid century; and (6) significant changes in the migration patterns of migratory species such as the beluga, the bowhead whale and the killer whale. The lack of regional models and scenarios of the future ocean climate in the Canadian Western Arctic weakens our capacity to forecast precise milestones in the ineluctable transition of the arctic marine ecosystems of the Western Arctic towards boreal marine ecosystems. Oil exploration leases overlap with the distribution of Arctic cod. There is an acute need for a synthesis of knowledge about the marine ecosystems of the Kitikmeot.

Discussion

Although much remains to be elucidated, our continuing studies of Arctic cod and its ecosystem in the Beaufort Sea are yielding an increasingly clear picture of the life cycle of this key species, and of its potential response to the on-going reduction of the seaice cover and warming of the surface layer of Arctic seas. Starting with the ice formation in October, Arctic cod 1 year and older aggregate on the continental slope within the lower part of the Pacific Halocline and the Atlantic Water (Geoffroy et al. 2012). Spawning probably takes place at this time in early winter. The aggregations tend to move to deeper regions over

the winter, perhaps to avoid predation by the ring seal and other diving predators. Entrainment by the circulation of the deep Pacific Halocline may result in the concentration of the fish into extremely dense schools at depth under the ice of coastal embayments (Benoit et al. 2010). During the winter months, the vounger Arctic cod migrate on a diel basis into the cold intermediate arctic layer (100-140 m) most likely to feed on copepods, while the larger adults sporting large liver reserves remain at depth to limit predation by seals (Benoit et al. 2011). With the ice break-up, the winter aggregations of Arctic cod were observed to disperse, most likely into the surface layer to follow the upward migration of their copepod prey as the spring bloom unfolds (Benoit et al. 2010, Geoffroy et al. 2012).

Previous studies in the Alaskan sector of the Beaufort Sea reported significant concentrations of Arctic cod in the nearshore zone in summer (REF). The non-availability of the Amundsen in 2012 and 2013 thwarted our plans to confirm the inshore summer distribution of the Arctic cod and other fishes in the Canadian Beaufort Sea. However, work from the Frosti n collaboration with DFO confirmed that significant numbers of Arctic cod remain on the slope in summer. Combining American observations and our results strongly suggests that inshore and offshore populations of Arctic cod exist, a phenomenon reported for other species of cod. From a management point of view and to foresee the impacts of an eventual oil spill on the ecosystem, elucidating the population structure of Arctic cod in the Beaufort Sea is of the utmost importance.

The hatching season of the Arctic cod and the Ice cod is centered on the bloom of ice algae, a new result that raises many questions on the importance of the ice ecosystem for the early feeding and survival of fish (Bouchard and Fortier 2011; Bouchard et al. submitted). But some eggs of both species hatch starting as early as January months before any microalgal production, whereas hatching continues until the first weeks of July during the phytoplankton bloom. Early hatching in winter under poor survival

conditions guarantees a large size at the end of summer, which increases chances of surviving the first winter. But what are the preys of the first-feeding larvae in winter remain an intriguing mystery. Late hatching in early summer ensures optimal temperature and feeding conditions for the larvae, which however may not attain a sufficient pre-winter size (Bouchard et al. 2011). Winter/spring cohorts of Arctic cod larvae have been observed to nearly vanish in years when ice breakup is delayed. Hence, from an evolutionary point of view, late spawning and hatching resulting in small pre-winter size is perhaps maintained to avoid the lost of an entire year class (Bouchard et al. submitted). By late summer, the 0+ juveniles are distributed in the surface 0-100 m layer while the 1+ start to aggregate on the slope (Benoit et al. 2014). And the annual cycle starts all over again.

As the ice cover regresses in the Beaufort Sea, indications are that increased light availability and the upwelling of nutrients in the surface layer, which fuel the primary production that sustains the production of the prev of Arctic cod, are increasing (e.g. Rysgaard et al. 1999; Tremblay et al. 2006, 2011). Hence, conditions for Arctic cod survival, especially during the larval and juvenile stages, may improve in the coming decades as the severity of the ice regime abates. In the medium term however (mid-century?), milder temperatures and sea ice regimes may favour the replacement of the typical arctic zooplankton assemblage by more diversified assemblages, and the invasion of arctic seas by less specialized fish from the boreal and subarctic Atlantic and Pacific Oceans (Babaluk et al., 2000; Beaugrand et al., 2002; Gaston et al., 2003; Perry et al., 2005; Hunt and Megrey 2005; Barber et al. 2008; Stephenson and Hartwig 2010). Although longer time series of observations are needed, the first signs of an invasion of the Beaufort Sea by the Pacific sand lance (Falardeau et al. 2014) and of Hudson Bay by the capelin (Gaston et al. 2003) may have been detected. Presently, the ecological consequences of these invasions are debated: will invading species displace arctic species or simply integrate the ecosystem, adding biodiversity and services, without necessarily outcompeting the arctic

specialists? Whatever indication we have from Hudson Bay suggests that a shift in dominant forage fish from the Arctic cod to sand lance or capelin harbingers a profound transformation of the prevailing low-diversity and low productivity arctic pelagic marine ecosystem to a more productive ecosystem typical of the north Atlantic. And a transition from the unique and exotic ecosystem services presently provided to local populations to a set of more mundane services. An important issue at this time is the extent to which these new forage fish are exploited by seabirds and seals, and what are the potential impacts of a transition from Arctic cod to sand lance on the lipid spectrum of seals and the physiology of seal predators including polar bear and Inuit.

Conclusion

Impacts of the proposed research

As with previous arctic work by my team, several components of the research help inform policy, decisions, and adaptation strategies of stakeholders (e.g. Inuit, Federal departments, Oil Exploration sector) in the rapidly changing and developing Canadian Arctic. Examples of the significance of the research include:

- Our work on the present and future services provided by pelagic arctic marine ecosystems is being incorporated into ArcticNet's Integrated Regional Impact Assessments for the Canadian Western High Arctic and Eastern High Arctic;
- Our study of the summer offshore distribution of Arctic cod in southeastern Beaufort Sea is part of the Beaufort Region Environmental Assessment (BREA) of Aboriginal Affairs and Northern Development Canada;
- In addition to its contribution to the BREA, the annual survey of the southeastern Beaufort Sea pelagic ecosystem provides the regional background necessary to assess the ecological importance of the exploration claims acquired by

- Imperial Oil Limited and BP at the edge of the Mackenzie Shelf:
- All data sets generated by my arctic research program are integrated into the Polar Data Catalogue developed jointly by ArcticNet and the Canadian Cryospheric Information Network;
- The expertise of my team on arctic zooplankton and fish is in demand by other parties, for example the Oil Exploration sector (IOL, BP); the Nunatsiavut and Royal Military College joint program on the ecology of Labrador Fjords; the Institute of Marine Sciences at the University of Alaska, Fairbanks; and the Census of Marine Life.

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