

# Larval and adult fish assemblages along the Northwest Passage: the shallow Kitikmeot and the ice-covered Parry Channel as potential barriers to dispersal

Caroline Bouchard, Maxime Geoffroy, Mathieu LeBlanc, and Louis Fortier

**Abstract:** Climate warming and sea ice decline are expected to increase fish population movements in the circumpolar Arctic, including across the Canadian Arctic Archipelago (CAA). Knowledge gaps on present distribution, habitat uses, barriers to dispersal, and population connectivity along the Northwest Passage (NWP) limit science-based management of fish in the North American Arctic. Pelagic trawl, bottom trawl, and ichthyoplankton net collections from the US Beaufort Sea to Baffin Bay between 2005 and 2017 are used to map fish distribution along the NWP and identify potential zoogeographic barriers. In the Kitikmeot (southern CAA), the combination of shallow depths, sub-zero temperatures and slow water circulation may represent a physical barrier reducing the dispersal of marine fish between western and eastern regions. In contrast, the Parry Channel (northern CAA) may exemplify a disappearing sea ice barrier as climate warming unfolds and allow new genetic exchanges.

*Key words:* Arctic cod, polar cod, fish larvae, Canadian Arctic Archipelago, spatial connectivity.

**Résumé :** On s'attend à ce que le réchauffement climatique et la baisse de la glace de mer causent l'augmentation des mouvements de population de poissons dans l'Arctique circumpolaire, y compris à travers l'archipel Arctique canadien (AAC). Les lacunes au niveau des informations à jour sur la répartition, les utilisations d'habitat, les barrières à la dispersion et la connectivité de population le long du passage du Nord-Ouest (PNO) limitent le système de gestion scientifique des poissons dans l'Arctique de l'Amérique du Nord. Le chalut pélagique, le chalut de fond et les collectes d'ichthyoplankton au filet de la mer de Beaufort aux États-Unis jusqu'à la baie de Baffin entre 2005 et 2017 sont utilisés pour dresser la carte de la répartition des poissons le long du PNO et pour établir les barrières zoogéographiques potentielles. Dans le Kitikmeot (l'AAC au sud), la combinaison de faibles profondeurs, des températures au-dessous de zéro et de la circulation d'eau lente peuvent représenter une barrière physique réduisant la dispersion de poissons marins entre les régions occidentales et orientales. Au contraire, le chenal Parry (l'AAC au nord) peut donner un exemple d'une barrière de glace de mer disparaissant à mesure que le réchauffement climatique évolue et permettre de nouveaux échanges génétiques. [Traduit par la Rédaction]

*Mots-clés :* morue arctique, morue polaire, larve de poisson, archipel Arctique canadien, connectivité spatiale.

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**C. Bouchard,\* M. LeBlanc, and L. Fortier.** Québec-Océan, Département de Biologie, Université Laval, Québec, QC G1V 0A6, Canada.

**M. Geoffroy.** Centre for Fisheries Ecosystems Research, Marine Institute of Memorial University of Newfoundland, St. John's, NL A1C 5R3, Canada.

**Corresponding author:** Caroline Bouchard (e-mail: [cabo@natur.gl](mailto: cabo@natur.gl)).

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## Introduction

In the ocean, identifying barriers to dispersal and patterns of population connectivity is often challenging. Yet, understanding how populations are connected is crucial to manage fisheries resources and to predict the response of marine ecosystems to climate change and other anthropogenic disruptions (e.g., [Carvalho and Hauser 1994](#); [Gerber et al. 2014](#)). Habitat fragmentation is one of the main types of physical barriers, and it can create population discontinuities even on short geographical distances (e.g., [Blanco Gonzalez et al. 2016](#)). In Arctic seas, sea ice acts as a barrier to the dispersal of many marine mammal species, and a diminishing ice cover results in increased hybridization between subspecies and closely related species ([Kelly et al. 2010](#)).

Warmer temperatures and reduced ice cover, by favoring the northward range expansion of boreal fish species, are expected to increase the interchange of fish populations between the Atlantic and the Pacific via the Northwest and Northeast Passages ([Wisiz et al. 2015](#)). The Canadian Arctic Archipelago (CAA) connects the Pacific-influenced waters of the Beaufort Sea with the Atlantic-influenced waters of Baffin Bay ([Fig. 1a](#)) and will be at the forefront of this interchange. However, our knowledge of fish population structure, habitat use, and larval ecology for the region is limited ([Fortier et al. 2015](#)). For instance, despite its dominance of the pelagic fish assemblage ([Benoit et al. 2008](#)) and its pivotal role in arctic marine ecosystems ([Welch et al. 1992](#)), the different habitat uses of Arctic cod (*Boreogadus saida*) and their relative importance remain debated. Immature Arctic cod colonize anfractuosités in the ice pack (e.g., [David et al. 2016](#)) and sometimes form dense surface schools in shallow embayments (e.g., [Welch et al. 1992](#); [Matley et al. 2013](#); [Drost et al. 2014](#)). In the North American Arctic, mature individuals concentrate over the continental slope in the relatively warm Atlantic waters at depth >200 m (e.g., [Benoit et al. 2008](#); [Geoffroy et al. 2011](#); [Parker-Stetter et al. 2011](#)).

Shallow regions of the Kitikmeot (e.g., Queen Maud Gulf, max. depth ca. 100 m; [Fig. 1a](#)) may represent a suboptimal habitat for mature Arctic cod and some barrier to dispersal and gene fluxes across the CAA. Dispersal could be possible further north through the deeper western Parry Channel ([Fig. 1a](#)). Yet, extreme environmental conditions in the central and northern Archipelago, including a frequent ice cover, low SSTs and absence of freshwater input may shorten the hatching season and limit the early survival of Arctic cod ([Bouchard and Fortier 2008](#); [Bouchard and Fortier 2011](#); [Bouchard et al. 2017](#)). The genetic population structure of Arctic cod, showing a phylogenetical break between the Beaufort Sea and Baffin Bay (R.J. Nelson, Fisheries and Oceans Canada, unpublished data), also suggest the presence of barriers to dispersal in the CAA. Several benthic arctic fish of the families Stichaeidae, Cottidae, Liparidae, Agonidae, and Ammoditidae, typical of shallow waters ([Fortier et al. 2015](#)), are less mobile as adults than the pelagic Arctic cod and depend on their planktonic larvae for dispersal. The harsh environment of the central and northern CAA may also reduce connectivity among populations of these species.

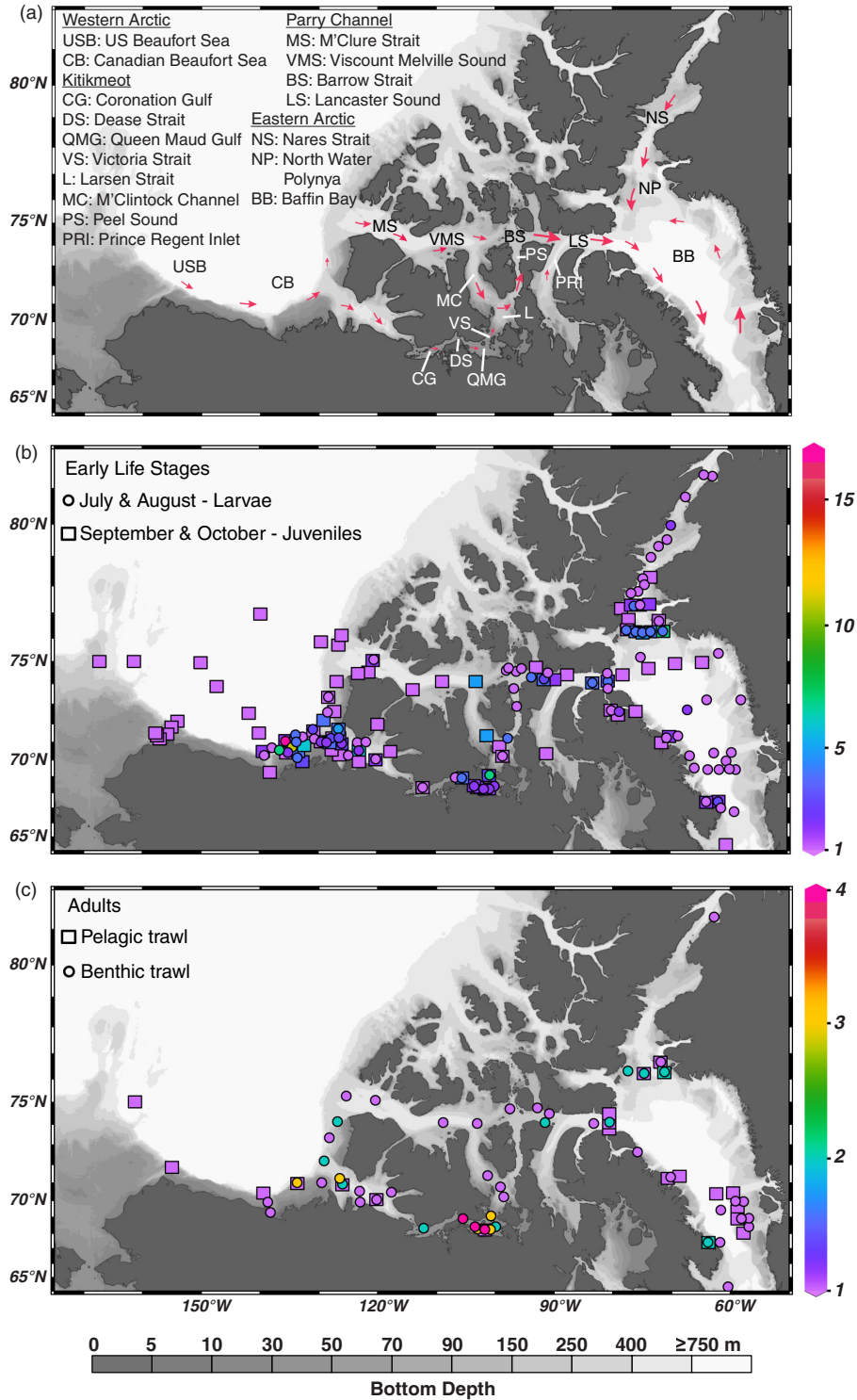
In the present study, we document larval and adult fish assemblages along the Northwest Passage (NWP) and explore possible barriers to dispersal of fish populations between western and eastern regions. In particular, we test the hypothesis that the Kitikmeot represents a zoogeographical barrier for Arctic cod, a key species in arctic marine ecosystems.

## Materials and methods

### Study areas

The NWP links the Beaufort Sea to Baffin Bay and is composed of two main waterways: (1) the Parry Channel, which runs from M'Clure Strait to Lancaster Sound in a

**Fig. 1.** Bathymetric maps showing (a) a schematic of surface currents strength and direction (red arrows, adapted from Canadian Ice Service (2012), Leblond (1980), and Wang et al. (2012)), the four areas and regional subdivisions used in the study; (b) sampling locations for ichthyoplankton in July and August (circles) and September and October (squares); and (c) sampling locations for benthic (circles) and pelagic (squares) fish. The color scale indicates the number of times a location was sampled from 2005 to 2017.



relatively straight line, and (2) the Kitikmeot formed of complex coastlines and heterogeneous bathymetry from the Amundsen Gulf to Lancaster Sound, via M'Clintock Channel or Peel Sound (Fig. 1a). Both waterways are relatively contrasted in terms of fish habitats. The Parry Channel is deep (maximum of ~700 m), generally ice covered and receives very little coastal freshwater. The Kitikmeot is shallower (<100 m in the southern waterways of Dease Strait and Queen Maud Gulf and <350 m in the northern waterways of Larsen Sound, M'Clintock Channel and Peel Sound), has longer ice-free seasons and receives freshwater from numerous rivers. For the analyses, the general study area was divided into four areas: the Western Arctic, the Parry Channel, the Kitikmeot, and the Eastern Arctic, each of them composed of several geographical regions (Fig. 1a).

#### Oceanographic data

Data collected with a SBE-911 plus<sup>®</sup> conductivity, temperature, and depth probe (CTD) deployed from the research icebreaker CCGS *Amundsen* at 11 stations along the NWP from the Amundsen Gulf to Baffin Bay in July and August 2015 were used to illustrate the water masses in the study area. Atlantic water masses were distinguished with the 0 °C isotherm at depths >200 m (Carmack and Macdonald 2002).

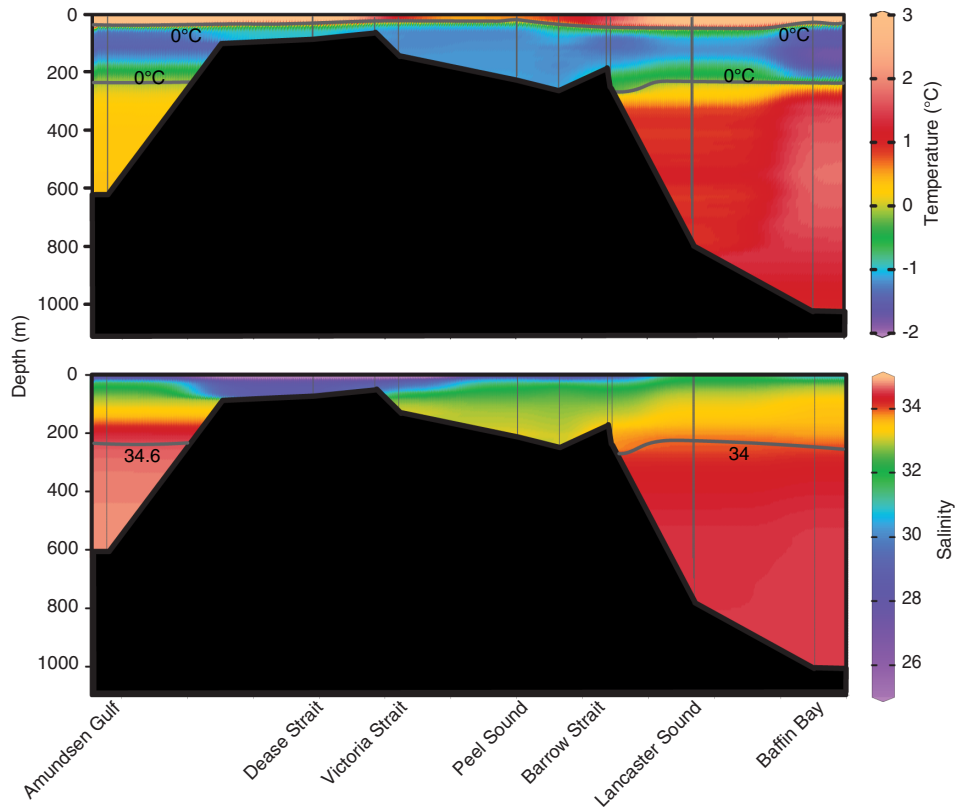
#### Ichthyoplankton sampling

Ichthyoplankton samples were collected between 2005 and 2017 from the *Amundsen* at different stations over the study area (Fig. 1b). A double square net (DSN) carrying two 1 m<sup>2</sup> aperture nets (mesh size 500 and 750 µm) was deployed obliquely at maximum sampling depths of ca. 90 m (or 10 m above the bottom at shallower stations) and at a ship speed of two knots. The duration of the DSN tow averaged 14.6 ± 4.6 min (mean ± standard deviation) and varied between 4.3 to 36.7 min. Larval and juvenile fish were sorted out and individually preserved in 95% ethanol. Back in the laboratory, all individuals were identified to the family. Catch per unit effort (CPUE in fish min<sup>-1</sup>) was calculated by dividing the number of larval and juvenile fish from each family by the DSN deployment duration. To account for the intense mortality occurring in larval fish populations during their first few months in the plankton, ichthyoplankton abundances were estimated separately for collection dates in July–August and September–October. The CPUE values were then averaged for each region.

#### Adult fish sampling

Pelagic fish were sampled with an Isaacs-Kidd Midwater Trawl (IKMT, rectangular 9 m<sup>2</sup> mouth aperture net with mesh size of 11 mm in the first section and 5 mm in the last section) deployed between June and October from 2014 to 2017 (Fig. 1c). The IKMT was lowered in the mesopelagic sound scattering layer visible on the scientific echosounder of the ship. Demersal and benthic fish were sampled with a benthic beam trawl (headline = 4.27 m, footrope = 4.27 m, 9.5 mm codend mesh) (Fig. 1c). The IKMT and the benthic beam trawl were towed at 2–3 knots for 10–20 min. We determined sampling duration for both of trawls using the total period during which the trawl was stabilized at the sampling depth (i.e., winch stopped, constant cable length), with the assumption that a limited amount of fish was collected during lowering and retrieval of the trawls. Sampling depth was estimated using cable length and its angle on the horizon for the IKMT, and a cable length corresponding to 2.5 times the bottom depth for the benthic beam trawl. All adult fish were identified to the family before being frozen at -20 °C. CPUE values were averaged for each region.

**Fig. 2.** Time-distance sections of temperature (top panel) and salinity (bottom panel) along the Northwest Passage in July and August 2015. Vertical lines indicate the location of the conductivity, temperature, and depth profiles.



### Hydroacoustic data

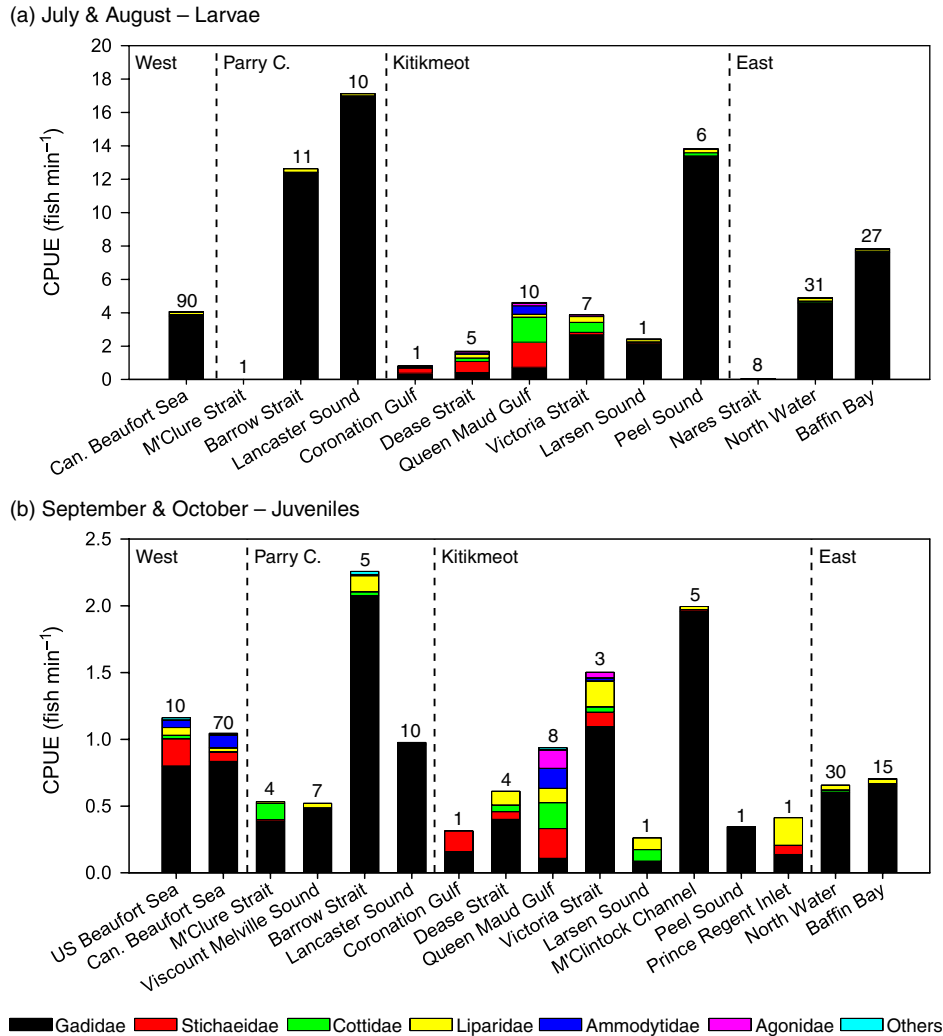
Hydroacoustic data were collected between 16 July and 2 October 2014 along the CCGS *Amundsen's* route across the NWP using a multifrequency echosounder (sampling and processing details in Bouchard et al. 2017). To cover the regions not visited in 2014, acoustic data for the same period of the year were used for Viscount Melville Sound (7 to 11 September 2013), M'Clure Strait (1 to 8 September 2015) and M'Clintock Channel (22 to 23 September 2015). Acoustic signal of fish was discriminated from that of zooplankton using the difference in mean volume backscattering strength (i.e., minimum and maximum thresholds of  $\Delta MVBS_{120-38}$  were respectively set to  $-10$  and  $5$  dB; Benoit et al. 2010; Geoffroy et al. 2016). The nautical area scattering coefficient ( $S_A$  in unit  $m^2 nmi^{-2}$ ; Simmonds and MacLennan 2005) of fish was integrated along the transects to document their spatial distribution with a horizontal resolution of 0.25 nautical miles. In addition, we calculated averaged profiles of  $S_A$  with a vertical resolution of 5 m to compare the vertical distribution of pelagic fish within each area.

### Results

#### Water masses

Atlantic water was present at depths  $>200$  m at both ends of the NWP, with  $T > 0$  °C and  $S > 34.6$  in the Amundsen Gulf, and  $T > 0$  °C and  $S > 34$  in Baffin Bay (Fig. 2). In the Kitikmeot, water masses were fresher ( $S < 34$ ) and sub-zero temperatures prevailed at depths  $> 20$  m. The surface layer above 20 m was generally warmer ( $>2$  °C), but remained around 1 °C in Barrow and Victoria straits.

**Fig. 3.** Ichthyoplankton assemblages and abundances collected between 2005 and 2017 in different regions of the North American Arctic in (a) July and August and (b) September and October. Number of stations sampled indicated above each bar. The category “Others” includes Clupeidae, Osmeridae, Pleuronectidae, and unidentifiable.



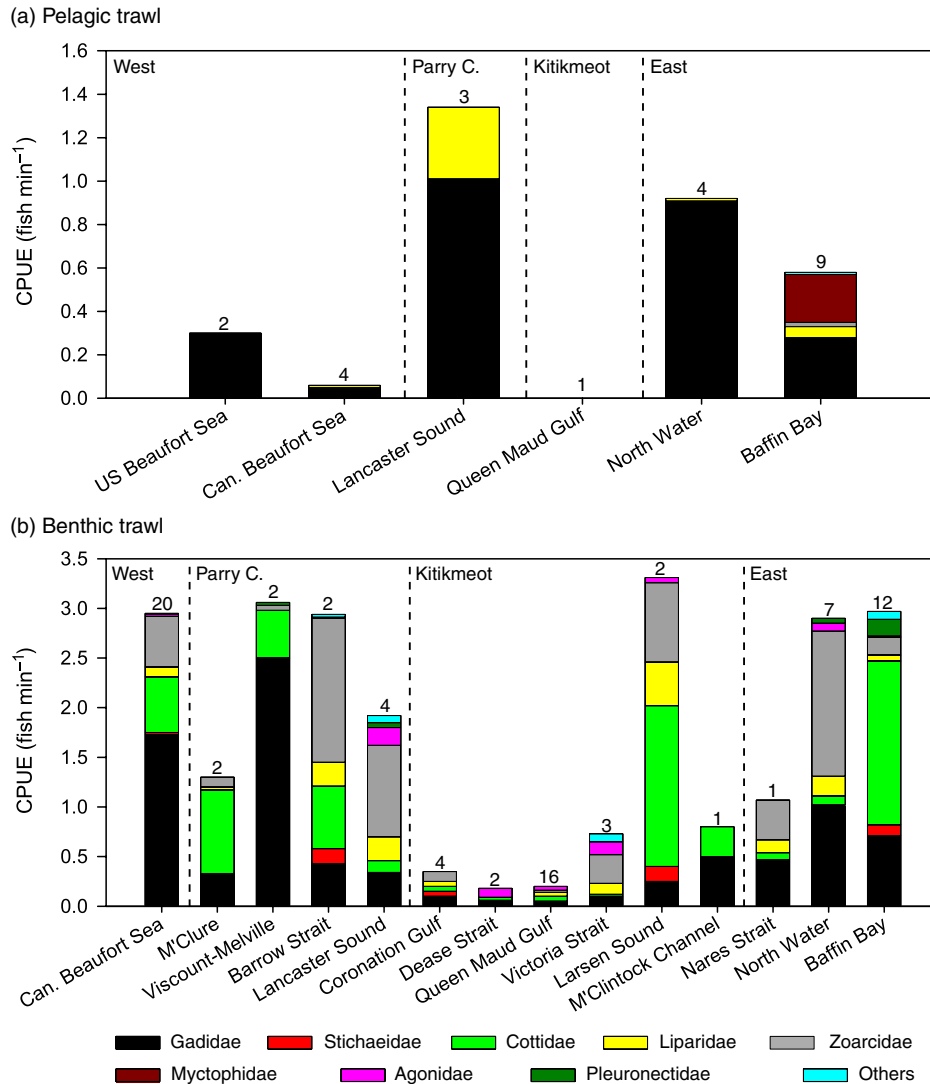
### Ichthyoplankton assemblages and abundances

In July and August, Gadidae dominated (69%–100%) larval fish assemblages in all regions except Coronation Gulf, Dease Strait, and Queen Maud Gulf (Fig. 3a). These regions of the Kitikmeot were characterized by very low number of Gadidae but relatively high number of larvae from other families. These three regions together accounted for only 2% of the Gadidae, but 60% of the Agonidae, 61% of the Cottidae, 87% of the Stichaeidae, and 92% of the Ammodytidae collected between 2005 and 2017 over the entire study areas. Larval Gadidae mostly comprised Arctic cod (Bouchard and Fortier 2011; Bouchard et al. 2016) and were found in high densities in the eastern Parry Channel and Peel Sound (Fig. 3a).

As expected from high mortality during larval life in marine fish, juvenile fish abundances were approximately one order of magnitude lower in September and October than the abundances of larval fish in July and August (Fig. 3b). In September and October, Gadidae



**Fig. 4.** Adult fish assemblages and abundances collected between 2005 and 2017 in different regions of the North American Arctic in (a) the pelagic trawl and (b) the benthic trawl. Number of stations sampled indicated above each bar. The category “Others” includes Cottidae and Macrouridae for the pelagic trawl and Anarhichadidae, Cyclopteridae, Macrouridae, Myctophidae, Psychrolutidae, Rajidae, Stomiidae, and unidentifiable for the benthic trawl.



dominated the ichthyoplankton assemblages (68%–98%) everywhere except in four regions of the Kitikmeot (Fig. 3b). Compared with other regions, Queen Maud Gulf had one of the lowest abundance of juvenile Gadidae in September and October but ranked first for the abundance of Stichaeidae, Cottidae, Ammoditidae, and Agonidae (Fig. 3b).

#### Adult fish assemblages and abundance

Pelagic fish were more abundant in Lancaster Sound and the eastern area (North Water Polynya and Baffin Bay) than in the western area (Beaufort Sea) and the Kitikmeot (Fig. 4a). In the Kitikmeot, shallow depths or ice cover prevented deploying the pelagic trawl most of the time, and only one deployment was made. This cast in Queen Maud Gulf yielded

no fish (Fig. 4a). Gadidae dominated the pelagic fish assemblages in all regions sampled (48%–100%).

Benthic fish were abundant in the western regions, Parry Channel, Larsen Sound, and the eastern regions south of Nares Strait (CPUE > 2.5 fish min<sup>-1</sup>, Fig. 4b). In contrast, abundances were the lowest in the southern Kitikmeot (CPUE < 0.5 fish min<sup>-1</sup>, Fig. 4b). Cottidae were abundant and dominated the assemblages in M'Clure Strait, Larsen Sound and Baffin Bay (49%–65%). Zoarcidae were abundant and dominated the assemblages in Barrow Strait, Lancaster Sound, and North Water Polynya (48%–51%). Gadidae were abundant in the Canadian Beaufort Sea and Viscount Melville Sound, but not in the Kitikmeot and in intermediate abundance elsewhere (Fig. 4b). The lowest abundance of Gadidae (CPUE = 0.05 Gadidae min<sup>-1</sup>) was found in Queen Maud Gulf, representing 32, 19, and 13 times less cod than in the Canadian Beaufort Sea, the North Water Polynya, and Baffin Bay, respectively.

#### Hydroacoustic densities

Fish backscatter from the surface to 100 m was high ( $S_A > 10$  dB re 1 m<sup>2</sup> nmi<sup>-2</sup>) in the US and Canadian Beaufort Sea, M'Clure Strait, Viscount Melville Sound, Prince Regent Inlet, Lancaster Sound, North Water Polynya, and Baffin Bay (Fig. 5a). Fish backscatter in the top 100 m was low ( $S_A < 10$  dB) in Coronation Gulf, Dease Strait, Queen Maud Gulf, and Nares Strait (Fig. 5a). Below 100 m, fish backscatter was high ( $S_A > 10$  dB) in part of the US Beaufort Sea, M'Clure Strait, Viscount Melville Sound, Lancaster Sound, and the North Water Polynya (Fig. 5b). In the present study, different years were used to cover as much waterways of the CAA as possible and give a large-scale overview of fish abundance in the North American Arctic. Interannual variabilities obviously occur within the different regions. However, our long-term dataset shows that most large-scale patterns are relatively stable in time. Importantly for this study, the southern Kitikmeot had lower juvenile fish backscatter than Beaufort Sea and Baffin Bay for all years studied between 2010 and 2017 (LeBlanc et al. unpublished data). The vertical profiles further demonstrate that fish backscatter in the first 100 m (likely from juvenile Arctic cod) was high in the western Arctic, Parry Channel, and the eastern Arctic, and lower in the Kitikmeot (Fig. 6). Fish backscatter between 250 and 400 m (likely from age-1+ Arctic cod) was also lower in the Kitikmeot than in the other areas and higher in the Parry Channel and the eastern Arctic (Fig. 6).

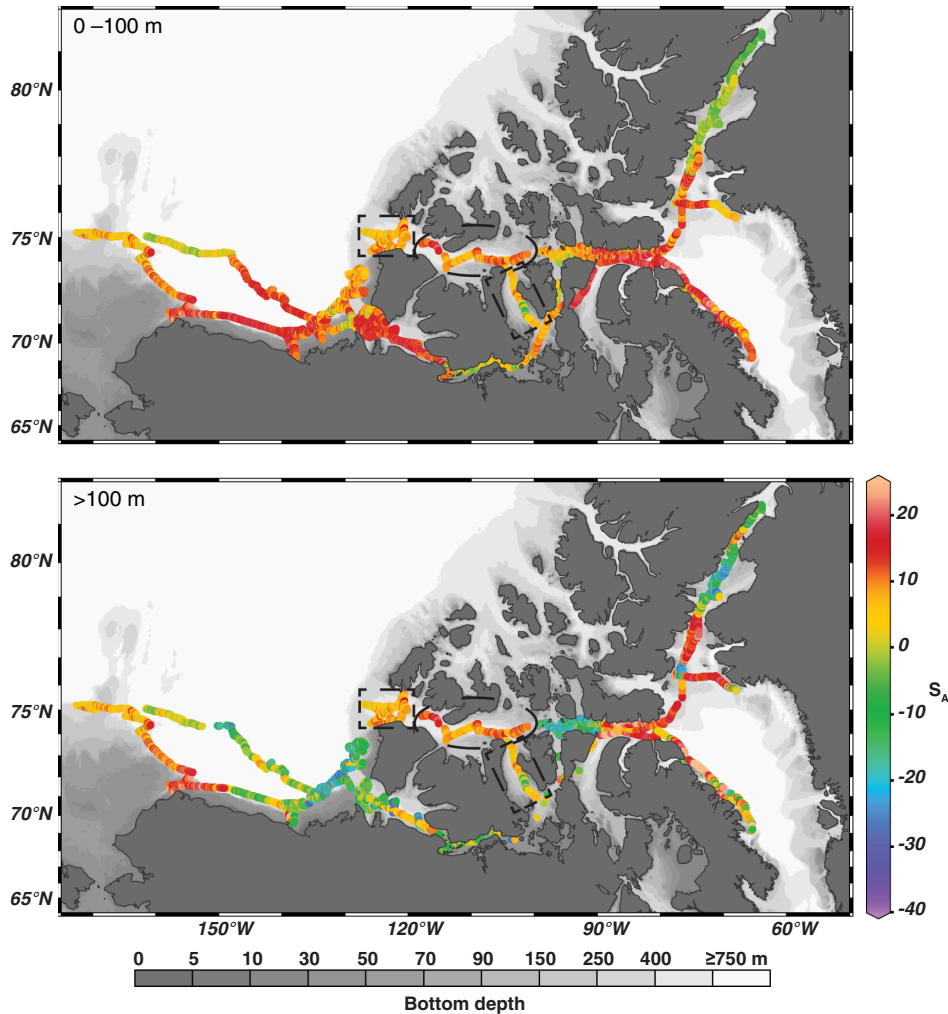
## Discussion

### The shallow and slow-flowing Kitikmeot: a barrier to fish dispersal

The striking paucity of Arctic cod in the southern Kitikmeot suggests that this area acts as a barrier to dispersal between populations in the Beaufort Sea and Baffin Bay. Adult Arctic cod generally avoid the top 100 m to escape predation by seals and, when possible, remain in the relatively warm Atlantic layer located >200 m (Benoit et al. 2010; Geoffroy et al. 2016). The shallow and cold Kitikmeot, especially Dease Strait and Queen Maud Gulf (<100 m), does not contain Atlantic water and likely represents a suboptimal habitat for Arctic cod. Furthermore, biomasses of the calanoid copepods *Calanus hyperboreus*, *C. glacialis*, and *Metridia longa* and of the amphipod *Themisto libellula*, which constitute most of the diet of adult Arctic cod (McNicholl et al. 2016), are lower in the Kitikmeot than in the western and eastern Arctic (G. Darnis, Université Laval, unpublished data). Low number of *Calanus* copepods in the southern Kitikmeot also deprives Arctic cod larvae and juveniles from their most energetic prey (Bouchard et al. 2016). The quasi absence of Arctic cod in this region could also explain the absence of some of its predators. Belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and northern fulmars (*Fulmarus glacialis*) are all absent from the southern Kitikmeot region, but they can be found in the eastern and/or western



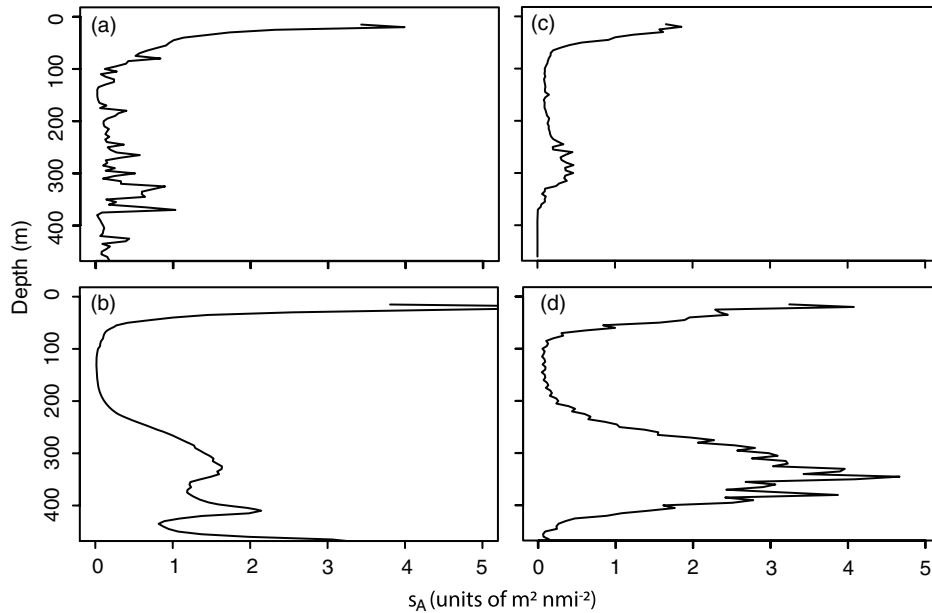
**Fig. 5.** Bathymetric maps indicating integrated fish backscatter ( $S_A$  in  $\text{dB re } 1 \text{ m}^2 \text{ nmi}^{-2}$ ) along the CCGS *Amundsen*'s route in 2013 (inside dashed circle), 2014 (outside dashed regions), and 2015 (inside dashed rectangles) for (a) the top 100 m and (b) the water column below 100 m.



Canadian Arctic (Parks Canada 2006; Wong et al., 2014). Adults Stichaeidae, Cottidae, Liparidae, Zoarcidae, and Agonidae were also uncommon in Coronation Gulf, Dease Strait, and Queen Maud Gulf, presumably due to the scarcity of zooplankton prey (G. Darnis, Université Laval, unpublished data). Hence, the southern Kitikmeot may also act as a significant barrier to dispersal for these benthic fish.

With the exception of Zoarcidae, which have demersal eggs and larvae, the pelagic early life stages are the main vector of dispersion for all fish captured during this study. In principle, the planktonic eggs, larvae, and juveniles could thus contribute to significant connectivity between western and eastern populations via the southern Kitikmeot. However, the region is characterised by slow water circulation, which could greatly limit the potential for dispersion (Michel et al. 2006; Wang et al. 2012; Wekerle et al. 2013). The scarcity of adult fish in Coronation Gulf, Dease Strait, and Queen Maud Gulf suggests that the larvae and juveniles collected in these regions have most likely hatched in the western Arctic and

**Fig. 6.** Average profiles of fish backscatter ( $S_A$  coefficient in units of  $\text{m}^2 \text{nmi}^{-2}$ ) along the CCGS *Amundsen's* route in 2013, 2014, and 2015 in (a) the western Arctic, (b) the Parry Channel, (c) the Kitikmeot, and (d) the eastern Arctic.



drifted slowly in the Kitikmeot with surface currents. Furthermore, convergent currents may retain fish larvae in Queen Maud Gulf as the maximal abundance of larvae and/or juveniles of four fish families were located in this region, despite hosting very few adults. Modelled (e.g., Wang et al. 2012) and observed (e.g., Leblond 1980, Canadian Ice Service 2012) currents in the CAA support this hypothesis (Fig. 1a). In contrast with the shallow southern Kitikmeot, some deeper regions of the northern Kitikmeot had high densities of Arctic cod larvae (Peel Sound) or juveniles (M'Clintock Channel), and although we cannot know their exact origin, we speculate that they originated from the Parry Channel.

#### The ice-covered Parry Channel: a melting barrier between western and eastern Arctic fish populations?

According to the 1981–2010 climatology, M'Clure Strait and Viscount Melville Sound used to be heavily ice-covered areas where sea ice concentration rarely reached <60%, and even then, just a few weeks annually (Canadian Ice Service 2012, 2018). Until recently, the western Parry Channel thus represented a stretch of at least 700 km with high sea ice concentrations between the Beaufort Sea shore lead polynya and the Viscount Melville Sound polynya located at the confluence of M'Clintock Channel (Barber and Massom 2007). However, considerably relaxed sea ice conditions were observed in the area in recent years. Since 2007, mean weekly sea ice concentration in summer dropped below 50% most years, and even reached <10% in 2015 (Canadian Ice Service 2018). The past conditions in western Parry Channel must have considerably limited — if not completely precluded — larval fish survival in the area, and acted as another dispersal barrier between western and eastern populations in the CAA. Indeed, the permanent ice cover and absence of significant rivers in western Parry Channel mean that surface waters must have been around  $-1.8\text{ }^{\circ}\text{C}$  all year round, a temperature strongly compromising the growth and survival of Arctic cod early life stages (Fortier et al. 2006, Bouchard and Fortier 2011; Laurel et al. 2017) and most likely that of other fish species. The absence of polynyas, which play a key role for Arctic cod

larvae by providing prey and the light necessary to hunt them, could have contributed to a very low larval survival in the area until recently (Bouchard and Fortier, 2008).

High densities of juvenile fish (i.e., high acoustic backscatter from 0 to 100 m) were recorded in M'Clure Strait (2015) and Viscount Melville Sound (2013). The abnormally low sea ice concentrations in western Parry Channel over the last decade may have favoured larval fish survival, hence weakening that zoogeographic barrier. M'Clure Strait and Viscount Melville Sound are sufficiently deep to contain Atlantic waters, and thus represent a possible habitat for Arctic cod, which explains why high abundance of adult fish were acoustically detected in the area (i.e., high acoustic backscatter from 100 to the bottom). Although low sample sizes imply precautionous interpretation, Cottidae were also relatively abundant in the trawls. These fish may provide a local supply of pelagic larvae, which can potentially drift with the relatively strong surface currents flowing eastward when ice conditions allow them to survive (e.g., Wekerle et al. 2013, Canadian Ice Service 2012). In the future, larval dispersion through the Parry Channel over single or multiple seasons may result in new connection between the western at the eastern North American Arctic. Similarly to what happened during interglacial periods within the past few million years (Rose 2005) and with marine mammals in the past decade (Kelly et al. 2010), the diminishing sea ice cover may be transforming the Arctic into a region of increased population connectivity and hybridization among fish.

## Conclusion

For Arctic cod, the shallow Kitikmeot may represent a relatively immutable barrier to dispersal due to suboptimal habitat offered by low water depths, sub-zero temperatures, and scarcity of prey. In addition, slow water circulation in the southern Kitikmeot may represent a barrier to dispersal for fish species with pelagic larvae. In contrast, the sea ice barrier in the western Parry Channel may already be fading away with climate change. Unfavorable conditions for the survival of Arctic cod and other pelagic larvae may have greatly limited the connection between western and eastern populations until recently, but ice concentrations now <50% in summer could allow new genetic exchanges through the northernmost waterway of the NWP.

## Conflict of Interest

The authors have no conflicts of interest to report.

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