

Size class segregation of Arctic cod (*Boreogadus saida*) in a shallow High Arctic embayment

S.T. Kessel, R.E. Crawford, N.E. Hussey, S.V. Ivanova, J.P. Holden, and A.T. Fisk

Abstract: Arctic cod (*Boreogadus saida* (Lepechin, 1774)) vertically segregate by size class in deep waters, but such dynamics had not been explored in shallow waters. Spatial distribution of Arctic cod was investigated in Resolute Bay, Nunavut, Canada (74°41N, 94°52W) from 20 July to 5 August 2012, using a combination of hydroacoustic survey and direct capture. Hydroacoustic surveys identified two high concentrations of Arctic cod, with larger individuals detected on the west side, and smaller individuals on the east. Catch data confirmed size segregation, with fish sampled on the west side of the bay significantly larger (mean = 174 mm total length (TL); 35.9 g weight (WT)) than those on the east (mean = 110 mm TL; 9.2 g WT). Fish density on the west was estimated at 3.52 fish·m⁻², extrapolated to the full 0.52 km² of the surveyed shoal to ~1 830 400 fish and 65 711 kg (assuming a 35.9 g mean WT). Smaller fish on the east side were more abundant (9.32 fish·m⁻²; total abundance ~11 836 400 fish or 108 894 kg; mean WT = 9.2 g). Horizontal habitat-partitioning was observed between Arctic cod size classes over a small geographic area (~8 km²), most probably due to partitioned resources and to mitigate predation risk.

Key words: habitat partitioning, hydroacoustics, conspecific predation, Northwest Passage, Resolute Bay, resource competition.

Résumé : La morue arctique (*Boreogadus saida* (Lepechin, 1774)) se sépare verticalement par classe de taille dans les eaux profondes, mais une telle dynamique n'a pas été explorée dans les eaux peu profondes. La distribution spatiale de la morue arctique a été étudiée à Resolute Bay, Nunavut, Canada (74° 41 N, 94° 52 W) du 20 juillet au 5 août 2012, en utilisant une combinaison d'études hydroacoustiques et de captures directes. Les études hydroacoustiques ont permis d'identifier deux fortes concentrations de morue arctique, avec des individus plus grands détectés à l'ouest et des individus plus petits à l'est. Les données de captures ont confirmé la ségrégation des tailles, les poissons échantillonnés sur le côté ouest de la baie étant significativement plus grands (moyenne = 174 mm longueur totale (LT); 35,9 g poids total (PT)) que ceux de l'est (moyenne = 110 mm LT; 9,2 g PT). La densité des poissons à l'ouest a été estimée à 3,52 poissons m⁻², extrapolée à la totalité des 0,52 km² du banc étudié à ~1 830 400 poissons et 65 711 kg (en supposant une moyenne de 35,9 g PT). Les poissons plus petits du côté est étaient plus abondants (9,32 poissons m⁻²; abondance totale ~11 836 400 poissons ou 108 894 kg; poids moyen = 9,2 g).

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S.T. Kessel. Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada; Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, 1200 South Lake Shore Drive, Chicago, IL 60605, USA.

R.E. Crawford.* Department of Biology, East Carolina University, Greenville, NC 27858, USA.

N.E. Hussey. Integrative Biology, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada.

S.V. Ivanova and A.T. Fisk. Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada.

J.P. Holden. Ontario Ministry of Natural Resources and Forestry, 41 Hatchery Lane, RR #4, Picton, ON K0K 2T0, Canada.

Corresponding author: S.T. Kessel (e-mail: skessel@shedd Aquarium.org).

*Deceased.

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Une répartition horizontale de l'habitat a été observée entre les classes de taille de morue arctique sur une petite zone géographique (~8 km²), très probablement en raison de la répartition des ressources et pour atténuer le risque de prédation. [Traduit par la Rédaction]

Mots-clés : partitionnement de l'habitat, hydroacoustique, prédation conspécifique, passage du Nord-Ouest, Resolute Bay, concurrence pour les ressources.

Introduction

Arctic cod (*Boreogadus saida* (Lepechin, 1774)) is a key species for energy transfer in the Arctic marine ecosystem (Welch et al. 1992; Crawford and Jorgenson 1996). Due to logistical difficulties associated with operating in the High Arctic, our knowledge of their spatial ecology has to date been limited. With continuing reductions in sea ice extent associated with climate change, anthropogenic disturbances are increasing in the High Arctic, particularly through increased fishing and shipping (Pizzolato et al. 2014). These evolving impacts on Arctic ecosystems are placing increasing importance on the need to delineate the distribution of marine species, to provide baseline information against which to assess future alterations in response to climate change and increased anthropogenic disturbance, such as shipping, fisheries and resource exploration/extraction.

The horizontal and vertical distribution of Arctic cod has been investigated throughout the Arctic, mainly through scientific fishery captures and hydroacoustic surveys, including those conducted in the Beaufort Sea (Craig et al. 1982; Geoffroy et al. 2011; Benoit et al. 2014; Bouchard et al. 2016), Chukchi Sea (Crawford et al. 2012; Lin et al. 2014; De Robertis et al. 2017), Bering Sea (Eisner et al. 2013; De Robertis et al. 2017), central Canadian Arctic (Bain and Sekerak 1978; Crawford and Jorgenson 1993; Welch et al. 1993), and central Arctic Ocean (Melnikov and Chernova 2013). Several of these studies have noted spatial segregation between schools containing smaller and larger Arctic cod (e.g., Benoit et al. 2014; Geoffroy et al. 2016), with all studies on the vertical distribution of Arctic cod documenting smaller fish in the upper water column, and larger fish at greater depths (Benoit et al. 2010, 2014; Geoffroy et al. 2011, 2016). Multiple drivers for this observed size segregation have been proposed, including resource partitioning, freshwater refuge, and refuge from cannibalistic conspecifics (Christiansen et al. 2012). Deeper depths may also be more favourable for larger cod as they offer protection from predation, particularly from avian predators that have a limited diving range (Matley et al. 2012; LeBlanc et al. 2019). If the latter prediction is true, the observed size segregation by depth would imply that, for smaller Arctic cod, the risk of interspecies predation is outweighed by the risk of intraspecies predation.

In addition to deep water areas, shallow embayments, generally <30 m deep, also provide important habitat for Arctic cod, both during open water and ice cover periods (Crawford and Jorgenson 1993; Welch et al. 1993; Geoffroy et al. 2011; Kessel et al. 2016). Arctic cod captured in shallow embayments are often mature (Crawford and Jorgenson 1996), although it is possible that this is biased by the selectivity of the gear (e.g., gillnets with a particular mesh size) used for capture. Nevertheless, in these shallow embayments, varying size classes of Arctic cod would have less opportunity to stratify vertically, thus, if segregation does occur, it would probably be in the horizontal plane. One such shallow embayment, where Arctic cod have been studied for decades, is Resolute Bay (Welch and Bergmann 1989; Crawford and Jorgenson 1993; Kessel et al. 2016). Given unknowns over the occurrence of size segregation of Arctic cod in shallower water ecosystems, this study used a combination of hydroacoustic surveys and physical capture to quantify the distribution of Arctic cod within Resolute Bay. Specifically, our objective was to determine the horizontal distribution of schools of smaller and larger Arctic cod.

Materials and methods

Study site

The study was conducted from 20 July to 5 August 2012 at Resolute Bay, Nunavut, Canada (74°41N, 94°52W; [Fig. 1](#)). The bay is shallow (predominantly <20 m) with a deeper area towards the head of the bay extending down to ~30 m. There are three freshwater inputs with one small river mouth on the west shore and two on the east. At the north west of the bay, untreated sewage enters through a pipe originating from the hamlet of Resolute Bay, home to ~250 residents.

Hydroacoustic surveys and analysis

Fish abundance and distribution was examined with a split-beam hydroacoustic system (BioSonics (Seattle, Washington, USA) DT-X; 200 kHz; 6° nominal beam width), coupled to a JRC (Houston, Texas, USA) global positioning system (GPS) unit for georeferencing, and recorded to a Panasonic (Newark, New Jersey, USA) Toughbook CF-29 computer. The DT-X was powered by an independent 12 V battery to avoid interference that might affect the hydroacoustic data. A calibration experiment was conducted at the beginning of each transect using a tungsten sphere ([Foote 1987](#); [Demer et al. 2015](#)) to determine a calibration offset that was applied during the post-processing in Echoview (Myriax Inc., Hobart, Tasmania, Australia). A pulse length of 0.4 ms and a pulse rate of 2.5 s⁻¹ were used throughout the survey. Speed of sound was assumed constant throughout the survey at 1445.7 m·s⁻¹ based on an average water temperature of 0.5 °C.

Fish distribution was examined by following an established zigzag transect path previously surveyed in Resolute Bay in the 1980s ([Crawford and Jorgenson 1993](#)). Because this survey pattern was designed to cover the bay proper, coverage of the nearshore region was limited to brief excursions near shore at the terminus of transects. A vessel speed of 8 km·h⁻¹ was maintained throughout the survey.

Acoustic data were processed in Echoview (Myriax Inc.). Previous studies ([Crawford and Jorgenson 1993, 1996](#)) determined that -65 dB was a suitable minimum threshold to apply to single targets and backscatter data to exclude echoes from ctenophores, jellyfish, and other organisms smaller than post-larval Arctic cod. Single targets detection used a pulse length value of 6 dB and a maximum beam compensation of 6 dB using the BioSonics beam compensation model. Targets smaller than the minimum threshold of -65 dB (compensated target strength) were excluded from the analysis. Density was estimated throughout the transect for cells at 40 m distance intervals and 1 m depth bins and aggregated to a regional density using the methods described by [Crawford and Jorgenson \(1993\)](#). Single targets had total lengths estimated based on the target strength where: $TL = 10^{((TS + 72.7)/21.8)}$, a derivation of the target strength relationship derived by [Crawford and Jorgenson \(1996\)](#), where TL is total length, and TS is target strength.

Fish capture and analysis

Schools of Arctic cod were identified with the hydroacoustic system and captured using hook and line, jigging with hook size #5 sabiki rigs. All captured fish were weighed to the nearest 0.1 g, and measured for both fork (FL) and total (TL) length to the nearest mm. For full capture procedures see [Kessel et al. \(2016\)](#). All fish collections occurred while anchored or drifting near the shelf break and waiting for fish to pass beneath (target strength measurements only), rather than when the boat was moving under power. Differences in TL and weight (WT) between the east and west side capture groups were compared using the two-sample *t* test (assuming unequal variances).

Fig. 1. Study site; (a) location of Resolute Bay (Cornwallis Island, Canada) and the surrounding area in the Canadian High Arctic; (b) path of standardized six-legged track of transects run during the hydroacoustic survey; and (c) Resolute Bay bathymetry is dominated by deeper areas in Central Basin and the southeastern Plateau area, showing location of Fig. 2a echogram (i) and Fig. 2b echogram (ii). Maps created in ArcMap 10.

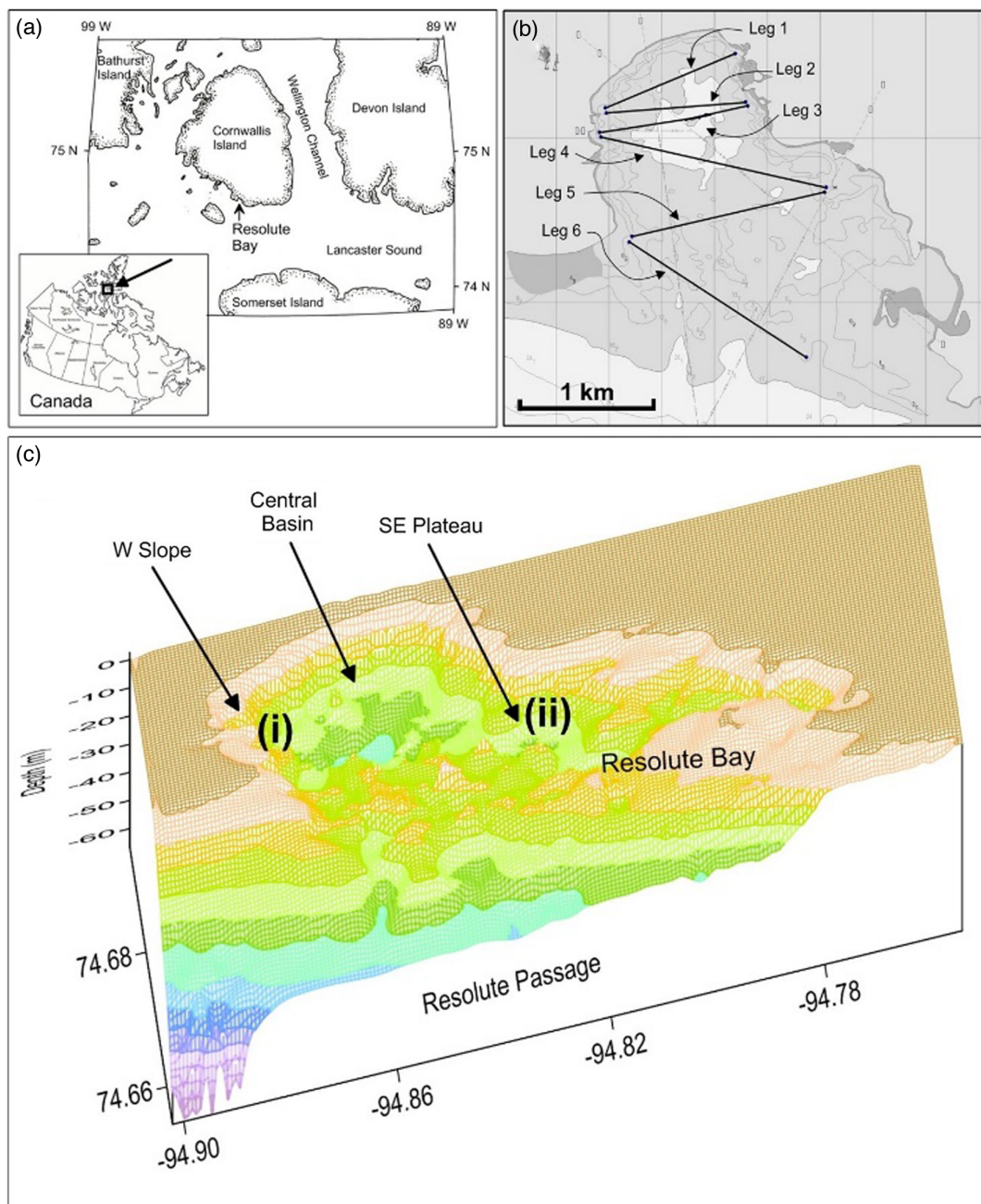
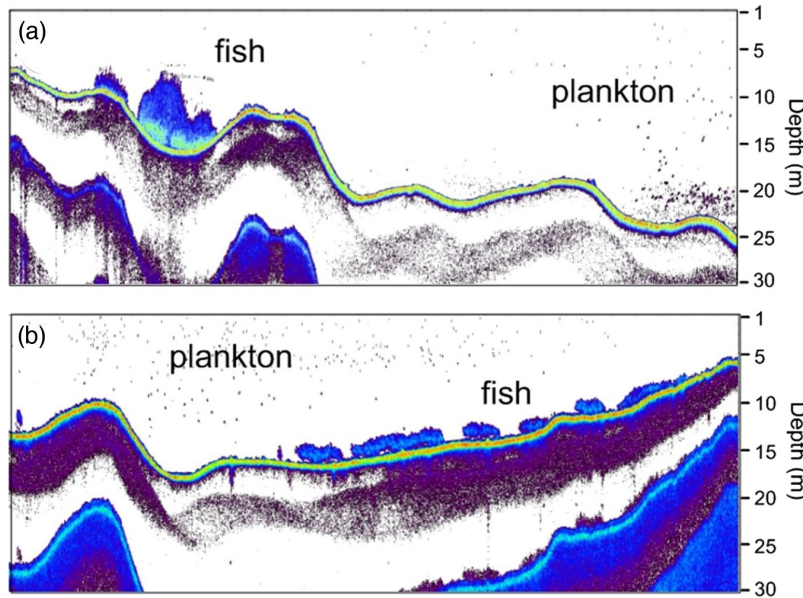


Fig. 2. (a) Echogram of a fish shoal detected on the slope along the west side of Resolute Bay (Fig. 1c (i)); and (b) echogram of a fish shoal detected along the east side of Resolute Bay (Fig. 1c (ii)). As can be seen from both echograms, the fish were easily discernable from the plankton by their size and distribution (as confirmed by fish capture).



Results

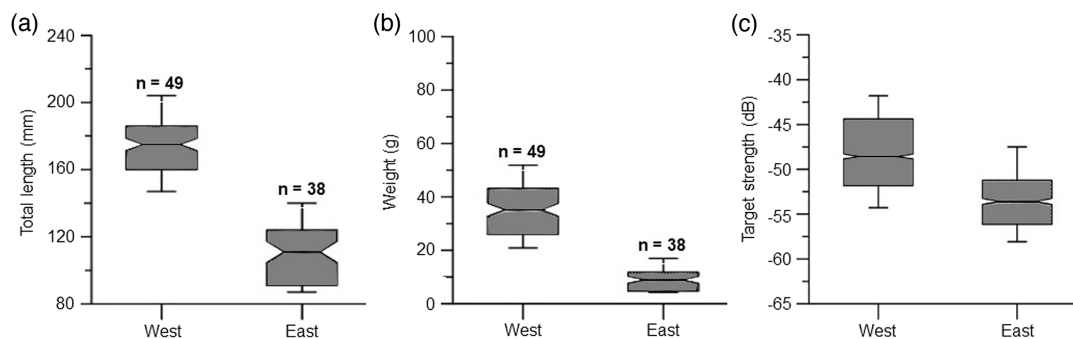
The standardized hydroacoustic surveys identified two high concentration areas of Arctic cod within the bay. These concentrations occurred predominantly along the bay's slope on the west side (Figs. 1c (i) and 2a), and southeast plateau (Figs. 1c (ii) and 2b). No other pelagic fish species have been recorded from scientific fishing gears in Resolute Bay besides Arctic cod, both in this and past studies (Crawford and Jorgenson 1993). As such, it is assumed that all hydroacoustic results that identify fish are Arctic cod. This assumption was further verified through the direct capture of only Arctic cod from hydroacoustic detected shoals. Fish detected on the west side were consistently in a shoal that was detected between surveys appearing to move back and forth along the west side of the bay, from near the bay's mouth to roughly mid-way inside the bay (Figs. 1c (i) and 2a). This area is strongly influenced by sediment deposition at the outflow from Resolute Lake (S.T. Kessel, personal observation, 2012) that has created a shallow "delta" on the shelf forming a unique sheltered habitat in the bay.

Fish captured on the west side of the bay were significantly larger than those captured on the east side, both in terms of TL (west mean = 174 cm; east mean = 110 cm; $T = -18.42$; $df = 84$; $P = 1.54 \times 10^{-31}$; Table 1; Fig. 3a) and WT (west mean = 35.9 g; east mean = 9.2 g; $T = -14.55$; $df = 57$; $P = 7.59 \times 10^{-21}$; Table 1; Fig. 3b). The difference in fish size between the two areas was also reflected in the target strength (TS) distribution (a proxy for fish size distribution) derived from the hydroacoustic surveys for the two areas (Figs. 3c and 4; Table 2). Both data types consequently identified a clear size segregation, with larger fish occurring on the west side of the bay and smaller fish occurring in the east. The density of these larger fish in the west shoal was measured once at $3.52 \text{ fish} \cdot \text{m}^{-2}$ (on the third day of the study), extrapolating to the full 0.52 km^2 of the surveyed shoal yielded $\sim 1\,830\,400$ fish. Given a mean fish weight of 35.9 g for captured individuals on the west shore (Table 1), total

Table 1. Length and weight of live Arctic cod collected in Resolute Bay, located during the hydroacoustic surveys.

Area	Mean total length (mm)	Range total length (mm)	Mean weight (g)	Range weight (g)	N
West	174	121–232	35.9	10.4–82.4	71
East	110	80–149	9.2	3.5–22.9	38

Fig. 3. Box-whisker plots of fish sizes (a) total length (mm); and (b) weight (g); derived from fish caught from the west and east sides of Resolute Bay. Plots display minimum, maximum, median (notched lines), lower quartile, and upper quartile values. See Table 1. (c) A box-whisker plot of target strength measurements obtained from high concentrations of fish at the west and east areas of Resolute Bay, calculated in the linear domain. Plot displays minimum, maximum, median (notched line), lower quartile, and upper quartile values. See Table 1.



biomass of larger size Arctic cod in that shoal would equate to 65 711 kg. In contrast, smaller fish were more widely distributed on the east side (over an area of about 1.27 km²) and were more abundant (9.32 fish·m⁻²; total abundance ~11 836 400 fish or 108 894 kg (mean weight = 9.2 g). The overall movement pattern of smaller cod on the east side was less discernable with the school detected in roughly the same location across surveys (i.e., not an obvious north/south movement as apparent on the west side).

Discussion

Arctic cod exhibit size class segregation on both a large scale by depth in the pelagic environments (Benoit et al. 2010, 2014; Geoffroy et al. 2011, 2016), and, as demonstrated here, on a small scale horizontally in a shallow embayment. Habitat partitioning by size class is commonly observed for fish species when conspecific predation is a known factor (Ross 1986). In the case of Arctic cod, vertical habitat partitioning by depth between smaller and larger Arctic cod has been attributed to several factors including water column characteristics, resource partitioning and predation risk (Geoffroy et al. 2011, 2016; Benoit et al. 2014). In this study, horizontal habitat-partitioning was observed between schools of smaller and larger Arctic cod over a relatively small geographic area (~8 km²). Resolute Bay only contains shallow habitat (~30 m maximum depth), consequently only spatial segregation, which usually occurs in 100s of meters depth, was only possible in the horizontal plane within the study area. The physical conditions in the shallow depths of the bay (10s of meters) between the west and east sides of the bay would have been more similar than those experienced by cod that partition size classes separated by 100s of meters of depth (e.g., Benoit et al. 2010; Geoffroy et al. 2016). Thus, it is hypothesized that resource

Fig. 4. Target strength data collected from the two areas in Resolute Bay where fish were concentrated. The relative abundance of echoes > -48 dB (i.e., larger fish) was much greater in the west area. Histograms display normal fit curves (red lines) for the two distributions, a typical fit model for target strength determinations. West location peak frequency = -48.2 dB; shape parameter = 4.75; goodness of fit = 3.06; $n = 1004$. East location peak frequency = -53.10 dB; shape parameter = 4.29; goodness of fit = 4.29; $n = 279$.

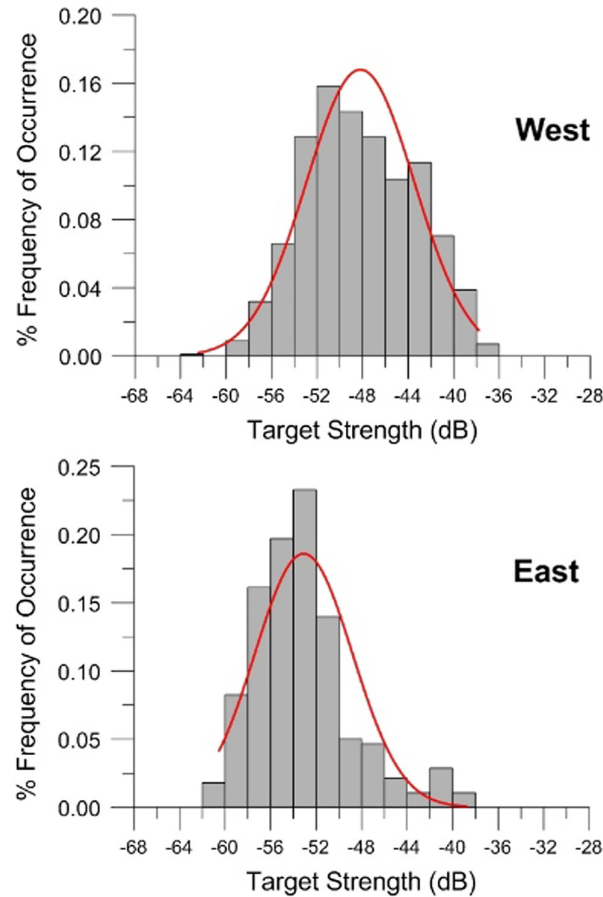


Table 2. Results of hydroacoustic target strength (TS) determinations and echo integration analysis (fish per cubic meter (FPCM) is $\text{fish} \cdot \text{m}^{-3}$) of data collected from the two areas with the highest concentrations of fish in Resolute Bay.

Area	Mean TS (dB)	TS range	FPCM	N
West side	-48.2	-62.43 to -37.77	0.173	1004
East side	-53.1	-62.43 to -38.77	0.542	279

partitioning and intraspecific predation risk were probably the primary factors driving Arctic cod habitat partitioning in the shallow waters of Resolute Bay, but further study is needed.

Ontogenetic diet differences and the distribution of prey items, whereby smaller Arctic cod favour copepod eggs and adults prefer developed zooplankton (Benoit et al. 2014), could

have driven the observed segregation. Nutrient input from untreated sewage at the north of the bay may have also influence productivity, but more investigation into current dynamics would be required to understand its transport to the west and east where the schools were observed. The influence of the lake outflow in the west area of the bay could have resulted in a difference in the prey field between the two areas due to an influx of nutrients. That is, larger prey may have been more abundant on the west side of the bay and they attracted larger fish, which was observed during opportunistic plankton tows in these locations (S.T. Kessel, personal observation, 2012). River mouths as sites of high primary productivity, such as that present on the east side of the bay, have been identified as important habitat for smaller developmental stages of Arctic cod (Bouchard and Fortier 2011). It is possible that the benefits of proximity to the river input to smaller cod, and a potential reduction in predation risk from adult conspecifics (Christiansen et al. 2012), outweighed the alternative predation risk (e.g., avian predators) associated with presence in the shallow water area for the smaller individuals. Whereas the larger individuals have previously been found to favour the deeper area for protection from avian predators (Matley et al. 2012; Kessel et al. 2016). Adult cod in the bay have also been shown to increase spatial habitat use under ice cover, relative to the open water period, further suggesting that predation risk drives adult cod distribution into deeper waters (Kessel et al. 2016).

The finding of horizontal habitat partitioning by size classes of a schooling Gadidae in this study builds on previous research on Arctic cod ecology in Resolute Bay that revealed extended residence of individuals during both open water and ice covered periods (Kessel et al. 2016) and the first documented large-scale horizontal movements of Arctic cod (Kessel et al. 2017). Such information contributes to the body of literature from which predictions of future trends in a changing Arctic climate can be based. Here, smaller and larger size classes of Arctic cod showed demonstrated segregation within a small shallow embayment, indicating they are potentially sensitive to fine scale anthropogenic disturbances.

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References

- Bain, H., and Sekerak, A. 1978. Aspects of the biology of Arctic cod (*Boreogadus saida*) in the central Canadian Arctic. LGL Limited, Toronto, Ont., Canada.
- Benoit, D., Simard, Y., Gagne, J., Geoffroy, M., and Fortier, L. 2010. From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. *Polar Biol.* **33**: 1505–1520. doi: [10.1007/s00300-010-0840-x](https://doi.org/10.1007/s00300-010-0840-x).
- Benoit, D., Simard, Y., and Fortier, L. 2014. Pre-winter distribution and habitat characteristics of polar cod (*Boreogadus saida*) in southeastern Beaufort Sea. *Polar Biol.* **37**: 149–163. doi: [10.1007/s00300-013-1419-0](https://doi.org/10.1007/s00300-013-1419-0).
- Bouchard, C., and Fortier, L. 2011. Circum-Arctic comparison of the hatching season of polar cod *Boreogadus saida*: a test of the freshwater winter refuge hypothesis. *Prog. Oceanogr.* **90**: 105–116. doi: [10.1016/j.pcean.2011.02.008](https://doi.org/10.1016/j.pcean.2011.02.008).
- Bouchard, C., Mollard, S., Suzuki, K., Robert, D., and Fortier, L. 2016. Contrasting the early life histories of sympatric Arctic gadids *Boreogadus saida* and *Arctogadus glacialis* in the Canadian Beaufort Sea. *Polar Biol.* **39**: 1005–1022. doi: [10.1007/s00300-014-1617-4](https://doi.org/10.1007/s00300-014-1617-4).

- Christiansen, J.S., Hop, H., Nilssen, E.M., and Joensen, J. 2012. Trophic ecology of sympatric Arctic gadoids, *Arctogadus glacialis* (Peters, 1872) and *Boreogadus saida* (Lepechin, 1774), in NE Greenland. *Polar Biol.* **35**: 1247–1257. doi: [10.1007/s00300-012-1170-y](https://doi.org/10.1007/s00300-012-1170-y).
- Craig, P.C., Griffiths, W.B., Haldorson, L., and McElderry, H. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. *Can. J. Fish. Aquat. Sci.* **39**: 395–406. doi: [10.1139/f82-057](https://doi.org/10.1139/f82-057).
- Crawford, R.E., and Jorgenson, J.K. 1993. Schooling behaviour of Arctic cod, *Boreogadus saida*, in relation to drifting pack ice. *Environ. Biol. Fishes*, **36**: 345–357. doi: [10.1007/BF00012412](https://doi.org/10.1007/BF00012412).
- Crawford, R.E., and Jorgenson, J.K. 1996. Quantitative studies of Arctic cod (*Boreogadus saida*) schools: important energy stores in the Arctic food web. *Arctic*, **49**: 181–193. doi: [10.14430/arctic1196](https://doi.org/10.14430/arctic1196).
- Crawford, R.E., Vagle, S., and Carmack, E.C. 2012. Water mass and bathymetric characteristics of polar cod habitat along the continental shelf and slope of the Beaufort and Chukchi seas. *Polar Biol.* **35**: 179–190. doi: [10.1007/s00300-011-1051-9](https://doi.org/10.1007/s00300-011-1051-9).
- De Robertis, A., Taylor, K., Wilson, C.D., and Farley, E.V. 2017. Abundance and distribution of Arctic cod (*Boreogadus saida*) and other pelagic fishes over the U.S. Continental Shelf of the Northern Bering and Chukchi Seas. *Deep Sea Res., Part II: Top. Stud. Oceanogr.* **135**: 51–65. doi: [10.1016/j.dsr2.2016.03.002](https://doi.org/10.1016/j.dsr2.2016.03.002).
- Demer, D.A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., et al. 2015. Calibration of acoustic instruments. ICES Cooperative Research Report No. 326. 133 pp. doi: [10.25607/OBP-185](https://doi.org/10.25607/OBP-185).
- Eisner, L., Hillgruber, N., Martinson, E., and Maselko, J. 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biol.* **36**: 87–113. doi: [10.1007/s00300-012-1241-0](https://doi.org/10.1007/s00300-012-1241-0).
- Footo, K.G. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. International Council for the Exploration of the Sea Cooperative Research Report No. 144. pp. 1–69.
- Geoffroy, M., Robert, D., Darnis, G., and Fortier, L. 2011. The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. *Polar Biol.* **34**: 1959–1971. doi: [10.1007/s00300-011-1019-9](https://doi.org/10.1007/s00300-011-1019-9).
- Geoffroy, M., Majewski, A., LeBlanc, M., Gauthier, S., Walkusz, W., Reist, J.D., and Fortier, L. 2016. Vertical segregation of age-0 and age-1+ polar cod (*Boreogadus saida*) over the annual cycle in the Canadian Beaufort Sea. *Polar Biol.* **39**: 1023–1037. doi: [10.1007/s00300-015-1811-z](https://doi.org/10.1007/s00300-015-1811-z).
- Kessel, S.T., Hussey, N.E., Crawford, R.E., Yurkowski, D.J., O'Neill, C.V., and Fisk, A.T. 2016. Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. *Polar Biol.* **39**: 1057–1068. doi: [10.1007/s00300-015-1723-y](https://doi.org/10.1007/s00300-015-1723-y).
- Kessel, S.T., Hussey, N.E., Crawford, R.E., Yurkowski, D.J., Webber, D.M., Dick, T.A., and Fisk, A.T. 2017. First documented large-scale horizontal movements of individual Arctic cod (*Boreogadus saida*). *Can. J. Fish. Aquat. Sci.* **74**: 292–296. doi: [10.1139/cjfas-2016-0196](https://doi.org/10.1139/cjfas-2016-0196).
- LeBlanc, M., Gauthier, S., Garbus, S.E., Mosbech, A., and Fortier, L. 2019. The co-distribution of Arctic cod and its seabird predators across the marginal ice zone in Baffin Bay. *Elem. Sci. Anth.* **7**: 1. doi: [10.1525/elementa.339](https://doi.org/10.1525/elementa.339).
- Lin, L., Chen, Y., Liao, Y., Zhang, J., Song, P., Yu, X., et al. 2014. Composition of fish species in the Bering and Chukchi Seas and their responses to changes in the ecological environment. *Acta Oceanol. Sin.* **33**: 63–73. doi: [10.1007/s13131-014-0490-x](https://doi.org/10.1007/s13131-014-0490-x).
- Matley, J.K., Crawford, R.E., and Dick, T.A. 2012. Summer foraging behaviour of shallow-diving seabirds and distribution of their prey, Arctic cod (*Boreogadus saida*), in the Canadian Arctic. *Polar Res.* **31**: 15894. doi: [10.3402/polar.v31i0.15894](https://doi.org/10.3402/polar.v31i0.15894).
- Melnikov, I.A., and Chernova, N.V. 2013. Characteristics of under-ice swarming of polar cod *Boreogadus saida* (Gadidae) in the Central Arctic Ocean. *J. Ichthyol.* **53**: 7–15. doi: [10.1134/S0032945213010086](https://doi.org/10.1134/S0032945213010086).
- Pizzolato, L., Howell, S.E.L., Derksen, C., Dawson, J., and Copland, L. 2014. Changing sea ice conditions and marine transportation activity in Canadian Arctic waters between 1990 and 2012. *Clim. Change*, **123**: 161–173. doi: [10.1007/s10584-013-1038-3](https://doi.org/10.1007/s10584-013-1038-3).
- Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia*, **1986**: 352–388. doi: [10.2307/1444996](https://doi.org/10.2307/1444996).
- Welch, H.E., and Bergmann, M.A. 1989. Seasonal development of ice algae and its prediction from environmental factors near Resolute, NWT, Canada. *Can. J. Fish. Aquat. Sci.* **46**: 1793–1804. doi: [10.1139/f89-227](https://doi.org/10.1139/f89-227).
- Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., et al. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. *Arctic*, **45**: 343–357. doi: [10.14430/arctic1413](https://doi.org/10.14430/arctic1413).
- Welch, H.E., Crawford, R.E., and Hop, H. 1993. Occurrence of Arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. *Arctic*, **46**: 331–339. doi: [10.14430/arctic1361](https://doi.org/10.14430/arctic1361).