

# First documented large-scale horizontal movements of individual Arctic cod (*Boreogadus saida*)

S.T. Kessel, N.E. Hussey, R.E. Crawford, D.J. Yurkowski, D.M. Webber, T.A. Dick, and A.T. Fisk

**Abstract:** Arctic cod (*Boreogadus saida*) are a key component of the Arctic marine ecosystem. Understanding their movements and distribution is important for predicting future trends in response to climate change. It was commonly assumed that Arctic cod move horizontally throughout the Arctic, but this was so far unproven. In July 2012, 85 Arctic cod were implanted with acoustic transmitters at Resolute Bay, Nunavut, Canada. Five (5.9%) were subsequently detected ~192 km due east along the Barrow Strait, between 67 and 215 days after last detection in Resolute Bay (mean  $\pm$  SE = 161.4  $\pm$  26.7 days). Minimum transition rates ranged between 0.89 and 2.87 km·day<sup>-1</sup> (mean  $\pm$  SE = 1.4  $\pm$  0.4 km·day<sup>-1</sup>). A combination of factors, most notably sea ice extent, make it highly improbable that the detections were representative of predated or scavenged Arctic cod. This represents the first confirmed account of large-scale horizontal movements by this or any Arctic forage fish species. With continuing miniaturization of acoustic telemetry tags, increasing battery life, and expanded receiver coverage, it will be possible to gain a more comprehensive understanding of Arctic cod movements.

**Résumé :** La morue polaire (*Boreogadus saida*) constitue un élément clé de l'écosystème marin arctique. La compréhension de ses déplacements et de sa répartition est importante pour la prédiction des tendances futures en réaction aux changements climatiques. S'il est souvent tenu pour acquis que la morue polaire se déplace horizontalement à la grandeur de l'Arctique, ce postulat n'avait toutefois pas encore été prouvé. En juillet 2012, 85 morues polaires ont été dotées d'émetteurs acoustiques à Resolute Bay (Nunavut, Canada). Cinq (5,9 %) de ces émetteurs ont été subséquemment détectés à ~192 km à l'est, le long du détroit de Barrow, de 67 à 215 jours après la dernière détection dans la baie Resolute (moyenne  $\pm$  ET = 161,4  $\pm$  26,7 jours). Les taux de transition minimums allaient de 0,89 à 2,87 km·jour<sup>-1</sup> (moyenne  $\pm$  ET = 1,4  $\pm$  0,4 km·jour<sup>-1</sup>). Une combinaison de facteurs, notamment l'étendue de la banquise, fait en sorte qu'il est très peu probable que les détections soient représentatives de morues polaires consommées par des prédateurs ou des charognards. Il s'agit du premier signalement de déplacements horizontaux à grande échelle par cette espèce ou tout autre poisson-fourrage arctique. Grâce à la miniaturisation continue des émetteurs acoustiques, la durée de vie accrue des piles et la plus grande couverture des récepteurs, il sera possible d'en arriver à une compréhension plus complète des déplacements de la morue polaire. [Traduit par la Rédaction]

## Introduction

Arctic cod (*Boreogadus saida*) are the primary forage fish in high Arctic marine food webs, facilitating the majority of energy transfer between lower and upper trophic levels (Crawford and Jorgenson 1996; Welch et al. 1992). Despite the challenges associated with conducting research in the high Arctic, Arctic cod have received a reasonable amount of research attention in comparison with other fishes (e.g., Bain and Sekerak 1978; Benoit et al. 2010; Crawford et al. 2012). Understanding the movement ecology of Arctic cod, however, has to date been limited by available methodological approaches that did not permit the spatial monitoring of fish at the individual level (but see Kessel et al. 2016). Given their importance to the Arctic marine ecosystem and the potential ecological and anthropogenic pressures they will encounter in a changing Arctic (Post et al. 2013), improving our understanding of Arctic cod movement ecology is imperative.

The potential for Arctic cod to move horizontally throughout the Arctic region has so far been unknown. Benoit et al. (2010) suggested that Arctic cod are unlikely to undertake long-distance migrations, but noted that due to this species' small size, it had not been possible to track the movements of individuals over time. The majority of research

examining the timing and distribution of Arctic cod has predominantly been investigated through hydroacoustic and net surveys over relatively short time scales. These findings include large winter aggregations at depth (Benoit et al. 2008), lower densities near the surface (David et al. 2016), schooling associated with drifting pack ice (Crawford and Jorgenson 1993) and shallow embayments (Welch et al. 1993), and distribution dictated by water temperature and resource availability (Astthorsson 2016; De Robertis et al. 2016; Geoffroy et al. 2011). As first suggested by Benoit et al. (2010), acoustic telemetry provided the necessary research tools to track individual Arctic cod. Through its use, Kessel et al. (2016) recently demonstrated extended residence of Arctic cod in Resolute Bay across both open water and ice cover periods. Following the residence period, the Arctic cod departed the bay en masse, but neither the scale of the movements outside the bay nor their destination could be immediately ascertained due to limited acoustic receiver coverage. Two years after the completion of that study, through the acoustic array infrastructure of the Ocean Tracking Network (OTN; Cooke et al. 2011), the first documentation of large-scale horizontal movements of Arctic cod has been possible. Here, the events that led to

Received 11 May 2016. Accepted 21 October 2016.

S.T. Kessel, D.J. Yurkowski, and A.T. Fisk. Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Ave, Windsor, ON N9B 3P4, Canada.

N.E. Hussey. Biological Sciences, University of Windsor, 401 Sunset Ave, Windsor, ON N9B 3P4, Canada.

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

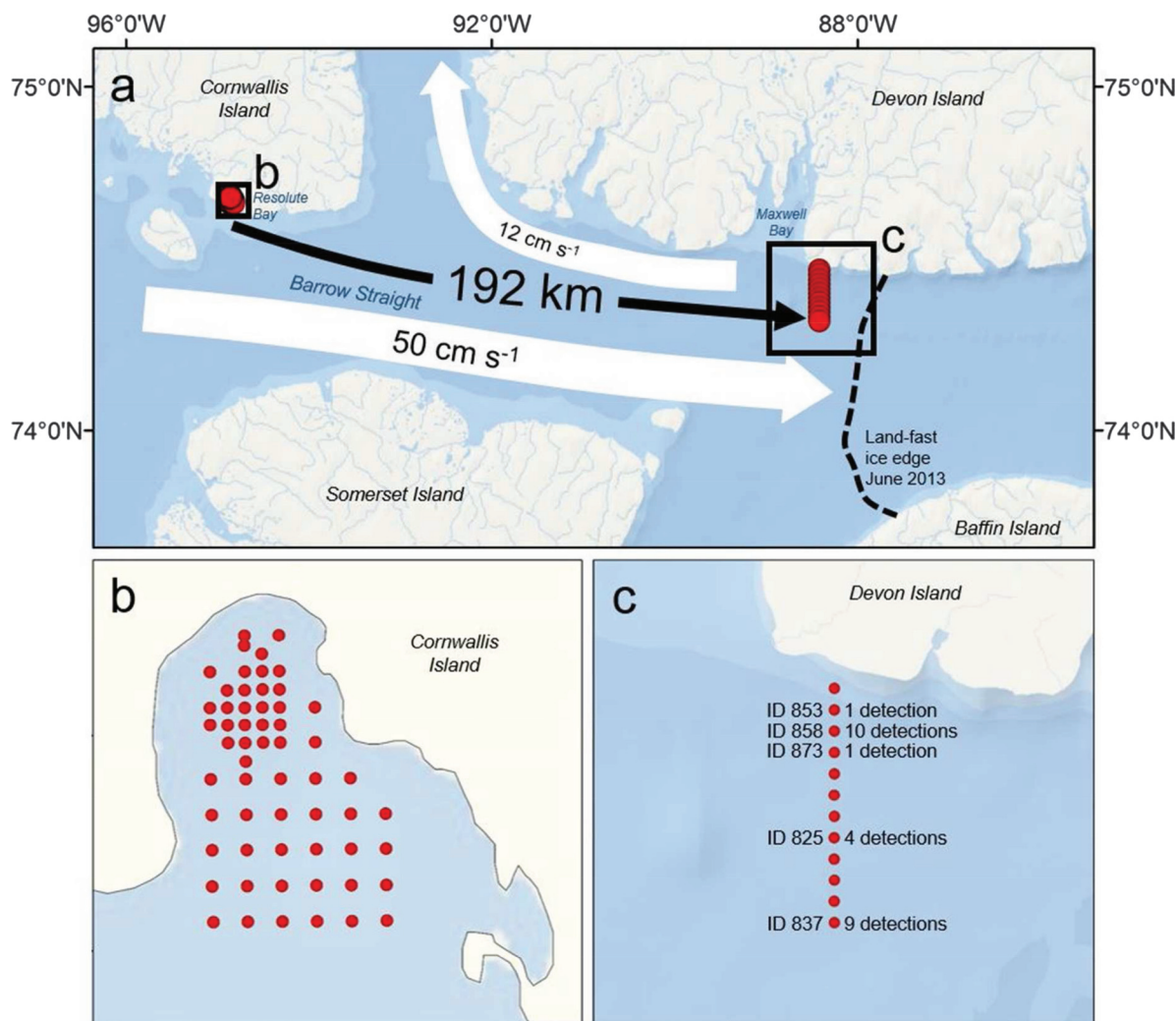
D.M. Webber. VEMCO Ltd., 20 Angus Morton Drive, Bedford, NS B4B 0L9, Canada.

T.A. Dick. Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada.

**Corresponding author:** S.T. Kessel (email: [skessel80@gmail.com](mailto:skessel80@gmail.com)).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](http://RightsLink).

**Fig. 1.** Location of acoustic receiver arrays, showing (a) the transition of Arctic cod from Resolute Bay to the receiver line at Maxwell Bay; (b) the receiver array at Resolute Bay, established in 2012; and (c) the receiver line design adjacent to Maxwell Bay, established in 2011. Red circles represent acoustic receiver deployment locations. In panel (a), the white arrows represent the predominant currents with velocity ( $\text{cm}\cdot\text{s}^{-1}$ ) (Curry et al. 2011; Leblond 1980), and the dashed black line shows the edge of land-fast sea ice (full ice cover to the west and open water to the east) for the month of June 2013, when Arctic cod IDs 853, 858, and 873 were detected at the Maxwell Bay line. During the month of January, at the time of detection of ID 837, the entire area was experiencing full ice cover, and at the time of detection of ID 825 in the month of August, the entire area was open water. Text in panel (c) indicates the receiver each individual was detected on and the number of detections recorded.



this observation are described, and the validity of these observed Arctic cod movements are justified.

## Methods

As a component of the OTN Arctic Arena research program, a study was established to examine Arctic cod residency and spatial use in Resolute Bay, Nunavut, Canada, from 1 August 2012 to 30 April 2013. Resolute Bay is a shallow embayment on the south-eastern shore of Cornwallis Island, ~3 km north to south, ~3.7 km wide at the mouth, and with a maximum depth of ~30 m towards the north of the bay (Figs. 1a and 1b). In July 2012, a split-beam hydroacoustic system (BioSonics DT-X; 200 kHz; 6° nominal beam width) was used to locate Arctic cod within the bay, which were captured using hook and line. After capture, 85 individuals were weighed, measured, and implanted with Vemco V6 180 kHz acoustic transmitters (380 s nominal delay between trans-

missions and an estimated 395-day battery life) following standard procedures (Kessel et al. 2016). An acoustic receiver array was established in Resolute Bay (Fig. 1b) composed of 58 Vemco VR2W 180 kHz receivers. For full Arctic cod capture, tagging procedures, and acoustic array information, see Kessel et al. (2016). As part of the broader OTN Arctic Arena infrastructure, a separate acoustic receiver line was established on 1 September 2011. The line was composed of 12 Vemco VR4 receivers (1975-day battery life), extending from north to south originating at the eastern point of the mouth of Maxwell Bay. This line was located approximately 192 km east of the Resolute Bay array on the south coast of Devon Island (Figs. 1a and 1c). The data from Resolute Bay were analysed and presented in Kessel et al. (2016). Data from the Maxwell Bay receiver line were downloaded on 1 September 2015. Where isolated single detections occurred on the Maxwell Bay receiver line,

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0196>.

**Table 1.** Size (mm) and detection accounts for the five Arctic cod that were detected on the Maxwell Bay receiver line.

| Cod ID | $L_F$ (mm) | Depart RB    | Arrive MB    | Liberty (days) | Min. distance (km) | Rate (km·day <sup>-1</sup> ) | No. detected (MB) |
|--------|------------|--------------|--------------|----------------|--------------------|------------------------------|-------------------|
| 825    | 232        | 10 Jan. 2013 | 13 Aug. 2013 | 215            | 192                | 0.89                         | 4 (2 days)        |
| 837    | 192        | 8 Nov. 2012  | 14 Jan. 2013 | 67             | 192                | 2.87                         | 9 (1 day)         |
| 853    | 195        | 8 Nov. 2012  | 6 June 2013  | 210            | 192                | 0.91                         | 1 (1 day)         |
| 858    | 187        | 8 Jan. 2013  | 8 June 2013  | 151            | 192                | 1.27                         | 10 (2 days)       |
| 873    | 200        | 8 Jan. 2013  | 21 June 2013 | 164            | 192                | 1.17                         | 1 (1 day)         |

Note:  $L_F$  = fork length; RB = Resolute Bay; MB = Maxwell Bay. Rate of transition between Resolute Bay and Maxwell Bay (column 7) is displayed in km per day (km·day<sup>-1</sup>). The total number of detections on the Maxwell Bay line (column 8) is followed in parentheses by the number of days across which the detections were recorded.

further processing was conducted to validate their authenticity (details provided in the online Supplementary Materials<sup>1</sup>).

## Results

Of the 85 Arctic cod tagged with acoustic transmitters in Resolute Bay, five (5.9%) were subsequently detected on the Maxwell Bay receiver line, ~192 km to the east (Fig. 1). The five fish ranged between 187 and 232 mm (mean  $\pm$  SE = 201.2  $\pm$  8.0 mm) fork length ( $L_F$ ), and all were considered adults (Table 1). Prior to departure, all five fish were detected extensively in Resolute Bay; ID 825: 25 870 times, ID 837: 8037 times, ID 853: 12 144 times, ID 858: 26 115 times, and ID 873: 33 585 times (dates of last detection provided in Table 1). The number of detections at Maxwell Bay ranged between 1 and 10 (mean  $\pm$  SE = 5.0  $\pm$  1.9). Only a single detection was recorded on the Maxwell Bay line for Arctic cod IDs 853 and 873. Processing of both raw data files showed only a few pings, but the records were very clear. There were no identifiable noise pings, and in both cases all pings were sourced from a single transmitter (further verification of authenticity of single detections provided in the online Supplementary Materials<sup>1</sup>). Arctic cod ID 825 was detected on receiver M8, 12.5 km from shore; ID 837 detected on receiver 12, 18.8 km from shore; ID 853 detected on receiver M2, 3.4 km from shore; ID 858 detected on receiver M3, 4.9 km from shore; and ID 873 detected on receiver M4, 6.5 km from shore (Fig. 1c). Time at liberty between the last detection in Resolute Bay and the first detection at Maxwell Bay ranged between 67 and 215 days (mean  $\pm$  SE = 161.4  $\pm$  26.7 days), and minimum transition rates ranged between 0.89 and 2.87 km·day<sup>-1</sup> (mean  $\pm$  SE = 1.4  $\pm$  0.4 km·day<sup>-1</sup>; Table 1).

## Discussion

The detection of five Arctic cod on two acoustic receiver arrays separated by ~192 km represent the first confirmed account of large-scale horizontal movements by this species or any Arctic forage fish species. Vertical migrations of Arctic cod schools, during the summer months, have previously been described across depth ranges of 100s of metres (Benoit et al. 2010; Geoffroy et al. 2016). Although widely assumed, in the absence of definitive proof, the potential for individual Arctic cod to undertake large horizontal displacements had only been speculated. For example, Bain and Sekerak (1978) and Craig et al. (1982) inferred biomass displacements from pelagic to coastal waters in the late summer. In the Beaufort Sea, Arctic cod have been documented to migrate to warmer, deeper waters under ice cover, typically below 200 m during the winter months and polar night (Geoffroy et al. 2011). The Barrow Strait is generally shallow to the west where the fish were tagged, rarely exceeding 200 m depth, but increases in depth from west to east, reaching depths >400 m just east of Maxwell Bay. It is possible that the Arctic cod in the Barrow Strait adopt a horizontal displacement to find more favourable habitat in the winter months.

Of the 85 fish initially tagged in Resolute Bay, only five (5.9%) were detected on the Maxwell Bay receiver line. The low number of detections recorded for all five fish indicates that individuals were not residing near the vicinity of the Maxwell Bay receiver

line for extended periods and likely were travelling elsewhere (i.e., swam past the receiver line). No detection range testing was conducted directly on the Maxwell Bay line, so detection range was inferred from the Resolute Bay detection range test results (see Kessel et al. 2016). The conditions along the Maxwell Bay line would have been unlikely to result in close proximity detection interference (Kessel et al. 2015), so an effective detection range of 150 m was assumed. With the receivers spaced at 1700 m, the receiver line (0–19 km from shore) would, therefore, have only experienced 18% effective detection range. In terms of the shortest distance from shore to shore across the Lancaster Sound Channel, only 4% of available area for the Arctic cod to pass through would have received effective acoustic coverage. The low number of detections from each individual and the low number of individuals detected likely reflect the small proportion of the channel monitored by the receiver line. Additionally, if the Arctic cod were continuing to travel west to east, they may well have been favoring the southern half of the channel to take advantage of the predominant current.

Arctic cod ID 837 made the transition to Maxwell Bay in 67 days, less than half the time of the other individuals. This translated to a minimum velocity of 2.87 km·day<sup>-1</sup> or 33 mm·s<sup>-1</sup>. Sustained swimming speed for Arctic cod was estimated at 0.9–1 body lengths·s<sup>-1</sup> (Kessel et al. 2016), translating to 172.8–192 mm·s<sup>-1</sup> for this individual. It is, therefore, completely feasible that this individual made the transition in this amount of time, even if it encountered the countercurrent to the north of the channel of velocity 120 mm·s<sup>-1</sup>. The more probable scenario, however, is that it took advantage of the predominant west-to-east current, with a velocity of 500 mm·s<sup>-1</sup>, to make this transition.

When movements of prey fish are recorded through acoustic telemetry, the potential exists for these movements to be representative of an individual consumed by a predator, thus, the movements of a larger species rather than the originally tagged animal (Thorstad et al. 2011). In the absence of sensor transmitters that can infer predation (Halfyard et al. 2017), it is pertinent to explore whether the detections could represent a transmitter contained in the stomach of a predator. In the high Arctic, the most likely predators that also undertake the documented scale of movement, are toothed whales, pinnipeds, and sea birds. Given the timing of Arctic cod movements during the ice-covered period, it is highly unlikely that these long-distance movements between Resolute Bay and Maxwell Bay resulted from predation by marine mammals or seabirds, which subsequently travelled to Maxwell Bay. The beluga whale (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) migrations in Barrow Strait and Lancaster Sound occur throughout September and early October when individuals travel eastward towards Baffin Bay to their overwintering grounds in the Northwater Polynya and offshore areas of Baffin Bay (Heide-Jørgensen et al. 2003; Richard et al. 1998, 2001; Smith and Martin 1994). In addition, the presence of sea ice limits the ability of long-distance movements for ringed seals (*Pusa hispida*), which have been observed to occupy restricted home ranges during the ice-covered period ranging from <1 to 27.9 km<sup>2</sup> in the high Arctic (Kelly et al. 2010).



The acoustic transmitters were also not likely within the stomach of a marine mammal or avian predator given the time period between the last transmission from Resolute Bay and the initial transmission near Maxwell Bay. The initial defecation time (IDT; time between the initial ingestion and first appearance in the faeces) for pinnipeds and beluga whales is approximately 5 and 4 h, respectively (Helm 1984; Mazzaro et al. 2011). Birds have a slightly slower IDT of approximately 6 h (Helm 1984). Given these IDTs, the likelihood of a transmission from a consumed Arctic cod within the stomach of a predator is very low. Additionally, detections from transmitters expelled from a predator would typically be numerous, as the tag would be stationary; therefore, given the low number of total detections for each individual, it is unlikely that the transmissions were produced from an expelled tag in the detection range of a receiver.

In terms of purely aquatic carnivores, where ice would not impact their spatial and temporal distribution, it is possible that a Greenland shark (*Somniosus microcephalus*) could have consumed the tagged Arctic cod and transited between Resolute and Maxwell bays. Greenland sharks are benthic-pelagic feeders that consume active prey and scavenge carrion (Leclerc et al. 2011; MacNeil et al. 2012). The occurrence of smaller prey fish such as shorthorn sculpin (*Myoxocephalus scorpius*), lumpfish (*Cyclopterus lumpus*), and Atlantic herring (*Clupea harengus*), while reported in stomach content data, represent a minor diet component (McMeans et al. 2010; Nielsen et al. 2013). Considering their smaller size, Arctic cod would be an energetically expensive prey to consume unless Greenland sharks fed on large numbers of individuals while schooling or they scavenged dead individuals. While this is possible, current data on the feeding ecology of Greenland sharks would suggest that consumption of the tagged Arctic cod is unlikely.

Considering all possible factors, it is reasonable to accept these detections as the first documented large-scale horizontal movements of individual Arctic cod. These large-scale horizontal movements have wider implications for the understanding of energy store distributions in the broader Arctic marine ecosystem. In turn, these influence the distribution of large marine predators such as pinnipeds and toothed whales. As tag recapture represents an unfeasible method to document forage fish movements in the high Arctic, the miniaturization of acoustic telemetry systems provides a promising platform for future investigations of large-scale movements, but effective receiver detection range will need to be considered. Additionally, acoustic tracking could be complemented with genetic comparisons between individuals sampled in Resolute Bay and the Maxwell Bay area to increase understanding of spatial connectivity of Arctic cod in the region. Findings such as this highlight the potential of acoustic telemetry in expanding our understanding of aquatic organism ecology and the benefits of the network approach to aquatic research (Hussey et al. 2015). With increased investment in infrastructure in the region, it will be possible to gain a more comprehensive understanding of the timing of the spatial distribution of Arctic cod, a key species in the rapidly changing Arctic marine ecosystem.

## Acknowledgements

Support for this project was provided by funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) and Canada Foundation for Innovation (CFI; International Joint Ventures Fund) through the Ocean Tracking Network (OTN), World Wildlife Fund (WWF), the Polar Continental Shelf Program (PCSP), Environment Canada, and the Arctic Fisheries Alliance. Permissions were obtained from Fisheries and Oceans Canada, Resolute Hunters and Trappers Association, and Government of Nunavut. Field support was provided by Peter and Jeffery Amarualik, Nathaniel Kalluk, Debbie and Brandy Iqaluk, Robert Currie, Emma Murowinski, Amy Tanner, Robert Cook, Jordan Matley, and Duncan Bates. Proof reading was performed by Amanda Swisher. A special

thank you to all the staff at the PCSP Resolute facility, the crew of the FV *Kiviug*, and Joey Angnatok and the crew of the MV *What's Happening* for superb logistical support that made this research possible. We finally thank the editor and two anonymous reviewers for their thorough and constructive comments on an earlier draft of this manuscript, which improved the current version.

## References

- Asthorsson, O.S. 2016. Distribution, abundance and biology of polar cod, *Boreogadus saida*, in Iceland–East Greenland waters. *Polar Biol.* **39**(6): 995–1003. doi:10.1007/s00300-015-1753-5.
- Bain, H., and Sekerak, A. 1978. Aspects of the biology of Arctic cod (*Boreogadus saida*) in the central Canadian Arctic. LGL Limited, Toronto, Ont.
- Benoit, D., Simard, Y., and Fortier, L. 2008. Hydroacoustic detection of large winter aggregations of Arctic cod (*Boreogadus saida*) at depth in ice-covered Franklin Bay (Beaufort Sea). *J. Geophys. Res. Oceans*, **113**(C6): C06S90. doi:10.1029/2007JC004276.
- 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**(11): 1505–1520. doi:10.1007/s00300-010-0840-x.
- Cooke, S.J., Iverson, S.J., Stokesbury, M.J.W., Hinch, S.G., Fisk, A.T., VanderZwaag, D.L., Apostle, R., and Whoriskey, F. 2011. Ocean Tracking Network Canada: A network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. *Fisheries*, **36**(12): 583–592. doi:10.1080/03632415.2011.633464.
- Craig, P.C., Griffiths, W.B., Halderson, L., and McElderry, H. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. *Can. J. Fish. Aquat. Sci.* **39**(3): 395–406. doi: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**(4): 345–357. doi: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**(2): 181–193. doi: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**(2): 179–190. doi:10.1007/s00300-011-1051-9.
- Curry, B., Lee, C., and Petrie, B. 2011. Volume, freshwater, and heat fluxes through Davis Strait, 2004–05. *J. Phys. Oceanogr.* **41**(3): 429–436. doi:10.1175/2010JPO4536.1.
- David, C., Lange, B., Krumpfen, T., Schaafsma, F., Franeker, J.A., and Flores, H. 2016. Under-ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their association with sea-ice habitat properties. *Polar Biol.* **39**(6): 981–994. doi:10.1007/s00300-015-1774-0.
- De Robertis, A., Taylor, K., Wilson, C.D., and Farley, E.V. 2016. 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.
- 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**(12): 1959–1971. doi: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**(6): 1023–1037. doi:10.1007/s00300-015-1811-z.
- Halfyard, E.A., Webber, D., Del Papa, J., Leadley, T., Kessel, S.T., Colborne, S.F., and Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Meth. Ecol. Evol.* [Online ahead of print.] doi:10.1111/2041-210X.12726.
- Heide-Jørgensen, M.P., Dietz, R., Laidre, K.L., Richard, P., Orr, J., and Schmidt, H.C. 2003. The migratory behaviour of narwhals (*Monodon monoceros*). *Can. J. Zool.* **81**(8): 1298–1305. doi:10.1139/z03-117.
- Helm, R.C. 1984. Rate of digestion in three species of pinnipeds. *Canadian J. Zool.* **62**(9): 1751–1756. doi:10.1139/z84-258.
- Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F., Mills Flemming, J.E., and Whoriskey, F.G. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, **348**(6240). doi:10.1126/science.1255642.
- Kelly, B.P., Badajos, O.H., Kunnsranta, M., Moran, J.R., Martinez-Bakker, M., Wartok, D., and Boveng, P. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biol.* **33**(8): 1095–1109. doi:10.1007/s00300-010-0796-x.
- Kessel, S.T., Hussey, N.E., Webber, D.M., Gruber, S.H., Young, J.M., Smale, M.J., and Fisk, A.T. 2015. Close proximity detection interference with acoustic telemetry: the importance of considering tag power output in low ambient noise environments. *Anim. Biotelem.* **3**(1): 5. doi:10.1186/s40317-015-0023-1.
- 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**(6): 1057–1068. doi:10.1007/s00300-015-1723-y.
- Leblond, P.H. 1980. On the surface circulation in some channels of the Canadian Arctic Archipelago. *Arctic*, **33**: 189–197. doi:10.14430/arctic2554.
- Leclerc, L.M., Lydersen, C., Haug, T., Glover, K.A., Fisk, A.T., and Kovacs, K.M. 2011. Greenland sharks (*Somniosus microcephalus*) scavenge offal from minke (*Balaenoptera acutorostrata*) whaling operations in Svalbard (Norway). *Polar Res.* **30**. doi:10.3402/polar.v30i0.7342.
- MacNeil, M.A., McMeans, B.C., Hussey, N.E., Vecsei, P., Svavarsson, J., Kovacs, K.M., Lydersen, C., Treble, M.A., Skomal, G.B., Ramsey, M., and Fisk, A.T. 2012. Biology of the Greenland shark *Somniosus microcephalus*. *J. Fish Biol.* **80**(5): 991–1018. doi:10.1111/j.1095-8649.2012.03257.x. PMID:22497371.
- Mazzaro, L.M., Richmond, J.P., Morgan, J.N., Kluever, M.E., Dunn, J.L., Romano, T.A., Zinn, S.A., and Koutsos, E.A. 2011. Evaluation of an alternative to feeding whole frozen fish in belugas (*Delphinapterus leucas*). *Zoo Biol.* **30**(1): 32–51. PMID:21319209.
- McMeans, B.C., Svavarsson, J., Dennard, S., and Fisk, A.T. 2010. Diet and resource use among Greenland sharks (*Somniosus microcephalus*) and teleosts sampled in Icelandic waters, using  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and mercury. *Can. J. Fish. Aquat. Sci.* **67**(9): 1428–1438. doi:10.1139/F10-072.
- Nielsen, J., Hedeholm, R., Simon, M., and Steffensen, J. 2013. Distribution and feeding ecology of the Greenland shark (*Somniosus microcephalus*) in Greenland waters. *Polar Biol.* **37**: 1–10. doi:10.1007/s00300-013-1408-3.
- Post, E., Bhatt, U.S., Bitz, C.M., Brodie, J.F., Fulton, T.L., Hebblewhite, M., Kerby, J., Kutz, S.J., Stirling, I., and Walker, D.A. 2013. Ecological consequences of sea-ice decline. *Science*, **341**(6145): 519–524. doi:10.1126/science.1235225. PMID:23908231.
- Richard, P.R., Heide, J., Jørgensen, M.P., and St. Aubin, D. 1998. Fall movements of Belugas (*Delphinapterus leucas*) with satellite-linked transmitters in Lancaster Sound, Jones Sound, and Northern Baffin Bay. *Arctic*, **51**(1): 5–16. doi:10.14430/arctic1040.
- Richard, P.R., Heide-Jørgensen, M.P., Orr, J.R., Dietz, R., and Smith, T.G. 2001. Summer and autumn movements and habitat use by belugas in the Canadian High Arctic and adjacent areas. *Arctic*, **54**(3): 207–222. doi:10.14430/arctic782.
- Smith, T.G., and Martin, A.R. 1994. Distribution and movements of belugas, *Delphinapterus leucas*, in the Canadian High Arctic. *Can. J. Fish. Aquat. Sci.* **51**(7): 1653–1663. doi:10.1139/f94-166.
- Thorstad, E.B., Uglem, I., Arechavala-Lopez, P., Okland, F., and Finstad, B. 2011. Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. *Boreal Environ. Res.* **16**(2): 115–120.
- Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., and Hop, H. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. *Arctic*, **45**(4): 343–357. doi: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**(4): 331–339. doi:10.14430/arctic1361.