Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

**Otolith chemistry and redistributions of northern cod:
evidence of Smith Sound-Bonavista Corridor connectivity**

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0357.R1
Manuscript Type:	Article
Date Submitted by the Author:	10-Mar-2018
Complete List of Authors:	Neville, Victoria; Memorial University of Newfoundland, Biology Rose, George; Memorial University of Newfoundland, Biology Rowe, Sherrylynn; Memorial University of Newfoundland, Centre for Fisheries Ecosystems Research Jamieson, Robyn; Department of Fisheries and Oceans, Piercey, Glenn; Memorial University of Newfoundland, Core Research Equipment and Instrument Training Network
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	ISOTOPES < General, OTOLITHS < General, WATER CHEMISTRY < General, GADOID SPECIES < Organisms, MIGRATION < General

SCHOLARONE™
Manuscripts

Otolith chemistry and redistributions of northern cod: evidence of Smith Sound - Bonavista Corridor connectivity

Victoria Neville¹, George Rose^{1,2,3}, Sherrylynn Rowe^{1,4}, Robyn Jamieson⁵ and Glenn Piercey⁶

¹ Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

² NSERC Chair in Fisheries Conservation, Memorial University of Newfoundland, St. John's, NL A1C 5R3, Canada

³ Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

⁴ Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute, Memorial University of Newfoundland, St. John's, NL A1C 5R3, Canada.

⁵ Department of Fisheries and Oceans, PO Box 5667, St. John's, NL A1C 5X1, Canada.

⁶ Core Research Equipment and Instrument Training Network (CREAIT), Bruneau Centre for Research and Innovation, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada.

Corresponding author: vk.neville@mun.ca

Keywords: Stable oxygen isotopes, Atlantic cod, otolith chemistry, migration, isoscapes

Abstract

Stable oxygen isotope assays of otoliths ($\delta^{18}\text{O}_{\text{oto}}$) from migrant Atlantic cod (*Gadus morhua*) that overwintered in Smith Sound, Newfoundland during 1995-2006 differed from those of non-migrating summer residents and cod from Placentia Bay and Halibut Channel, but did not differ from those of cod from the adjacent offshore Bonavista Corridor in summer. All fish sampled were of the 1990-year class (founder of the Smith Sound aggregation) at ages 8-10 years. Hence, overwintering Smith Sound and summering Bonavista Corridor cod likely experienced similar temperatures and salinities in each year of life, representing different migration stages of an

intermixed group. Moreover, predictions of $\delta^{18}\text{O}_{\text{oto}}$ from near-bottom ocean temperatures and salinities differed between inshore and offshore sites and in general matched observed signatures of inshore and offshore cod. The Bonavista Corridor cod, however, were an exception, having $\delta^{18}\text{O}_{\text{oto}}$ signatures suggestive of inshore exposure. Our findings provide direct evidence of metapopulation structure in the Northern cod and are consistent with offshore rebuilding having been spurred by dispersal of cod from inshore Smith Sound.

Introduction

The historic range of the “Northern” cod (*Gadus morhua*) stock extended from the Hamilton Bank region off Labrador, Canada, to the northern Grand Bank occupying Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL (Fig. 1). Long recognized as a stock complex (Lear 1986), the largest components overwintered and spawned offshore in warm ($\sim 2\text{--}4^{\circ}\text{C}$) water on the continental shelf and slope (Templeman 1962; Fitzpatrick and Miller 1979; Hutchings et al. 1993). In spring, cod migrated inshore to feed, primarily on capelin, utilizing several deep channels that undercut the outer parts of the cold Labrador Current (Lear 1984; Rose 1993). The stock complex also included smaller groups of inshore residents that overwintered and spawned in the colder (at times sub-zero) coastal habitats in winter, spring and early summer (Templeman and Fleming 1956; Goddard et al. 1994; Wroblewski et al. 1995; Smedbol and Wroblewski 1997; Rose et al. 2011).

The collapse of Northern cod in the early 1990s coincided with substantial distributional changes (deYoung and Rose 1993; Atkinson et al. 1997; Rose et al. 2000; Ruzzante et al. 2001). In the offshore, cod “hyper-aggregated” in large shoals in their southernmost migration channel, the

Bonavista Corridor, as the stock declined (Rose 1993; Rose and Kulka 1999). By 1993, few cod remained there (Rose et al. 1994), and by 1994, few were evident anywhere within the former Northern cod offshore range (Bishop et al. 1995; Rose 2007).

In the spring of 1995, with offshore components of the Northern cod at their lowest levels in recorded history (Bishop et al. 1995), a relatively large aggregation (10,000 t) appeared inshore in Smith Sound, Trinity Bay, a fjord adjacent to the Bonavista Corridor (Rose 2003; Rose et al. 2011). The majority of individuals in this aggregation were 5 years old (1990-year class), accompanied by some 6-year-olds (1989 year-class), and were likely first-time spawners. By early that summer, most had migrated out of Smith Sound, but they returned each fall for the next decade to overwinter. They spawned both there and during the early phases of the outward migration from Smith Sound (Brattey and Healey 2007; Knickle and Rose 2010; Rose et al. 2011). Smith Sound historically maintained a relatively small number of resident cod year-around, but the overwintering of a large migratory aggregation was unprecedented (Rose et al. 2011). The aggregation grew to >25,000 t by the early 2000s but beginning in 2007 a sharp decline occurred in overwintering biomass (Rose et al. 2011). By 2009, there was little evidence of the overwintering aggregation and it was assumed that the fish had largely dispersed (Brattey et al. 2010; Rose et al. 2011).

The rise and fall of the Smith Sound cod was attributed not to an event isolated from adjacent groups, but to metapopulation dynamics (Rose et al. 2011). In keeping with this notion, the offshore trawl survey conducted by Department of Fisheries and Oceans Canada (DFO) showed unexpected and difficult to explain increases in some year classes during the time the Smith

Sound cod dispersed. Potential links between Smith Sound cod and those inhabiting the offshore were further supported by improvements in the fit of stock assessment models that included the Smith Sound cod as a component of the full Northern cod stock not surveyed by the offshore survey (Cadigan 2016). The improved model fit assumed a lower catchability (q) for the offshore survey until the Smith Sound cod rejoined the offshore. It was apparent, nonetheless, that direct evidence of links between the Smith Sound cod and those from offshore regions was lacking (Rose et al. 2011; Rose and Rowe 2015). As the Northern cod stock rebuilds, connections among inshore and offshore stock components are not yet fully understood. A key question is whether the rebuilding of Northern cod is solely a product of isolated local population growth, or have spatial redistributions within a metapopulation played a role (Rose and Rowe 2015)?

Stable oxygen isotope ($\delta^{18}\text{O}$) signatures in otoliths (hereinafter $\delta^{18}\text{O}_{\text{oto}}$) reflect past ambient environmental conditions (specifically seawater salinity and temperature) and hence have potential to identify annual and seasonal habitats of individuals, when past conditions can be mapped. Notably, $\delta^{18}\text{O}_{\text{oto}}$ has been used to identify habitat changes spanning life stages (Gao and Beamish 2003, Gao et al. 2004, Shephard et al. 2007) and seasons (Weidman and Millner 2000; Gao et al. 2001; Begg and Weidman 2001; Høie and Folkvord 2006). Here, we postulated that $\delta^{18}\text{O}_{\text{oto}}$ signatures of cod from the Smith Sound overwintering aggregation and summer residents would differ, and furthermore, that if overwintering Smith Sound cod had non-local origin, their signatures should be similar, at least in their early years, to cod from a remote site.

In this study, we used $\delta^{18}\text{O}_{\text{oto}}$ signatures to test these hypotheses on the origins of the Smith Sound cod and putative connection with the adjacent offshore Bonavista Corridor and other

remote sites. Specifically, we compared the $\delta^{18}\text{O}_{\text{oto}}$ signatures from cod otoliths from the 1990 founder year-class collected from the winter aggregation with those from the same year-class that remained as summer residents and thought to possibly represent a different ecotype (subgroup that is especially adapted to a particular set of environmental conditions) with different life history and origin. We then hypothesized that the Smith Sound overwintering and Bonavista Corridor summering cod had a similar origin and distributional history over their life, their $\delta^{18}\text{O}_{\text{oto}}$ signatures would be similar, but differ from those from the Halibut Channel and Placentia Bay (Fig. 1). To ensure that isotopic signatures of the sites would be distinguishable, ambient ocean $\delta^{18}\text{O}_{\text{oto}}$ was predicted using available salinity and temperature data for each area (Fig. 2; Fig. 4). We later compared our predicted $\delta^{18}\text{O}_{\text{oto}}$ with the signatures measured in the cod otoliths.

Methods

Otolith collection

Cod were collected during research cruises (CCGS Teleost) conducted during 1998-2000, with the exception of otoliths from Halibut Channel, which were provided by Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, St. John's (Table 1). In Smith Sound, otoliths that were taken from cod caught in January from the main aggregation were most likely those of overwintering migrants, whereas cod caught in June of the same year-class, after the aggregation had migrated beyond the Smith Sound, were more widely dispersed within Smith Sound and will be referred to as residents. In all other regions, cod were caught between May and July from spawning and post-spawning aggregations. In all cases, otoliths were extracted from sampled cod, dried and stored in envelopes.

Initial ageing was conducted by microscopic examination of the annuli (paired translucent and opaque bands) of right-side otoliths that were cracked and examined by an experienced technician (Norm Batten, former chief ageing technician with Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, St. John's). Right otolith age data were used to identify age- and year class information for the sample. For this study, otoliths from a selection of cod (chosen haphazardly based on availability) from the 1990-year class were analyzed (Table 1).

To test if overwintering and resident cod had differing growth patterns, as might be expected if these groups had differing ranges or migratory habits, lengths of aged cod caught with a Campelen 1800 bottom trawl fished from the RV Teleost in winter and summer in Smith Sound from 1996 to 2003 were compared. von Bertalanffy curves (using nonlinear least squares regression) were fit for each group. Using the estimated parameters from these curves we back-calculated length-at-age and tested whether the products of these calculations were different at each age using a Welch's two sample t-test. First, we treated age as a categorical variable, from 1-10. However, this method may have been confounded by the fact that Smith Sound migrants (collected in January-February) were approximately 6 months younger than Smith Sound residents (collected in June). To explore an approximation to the extent of size differences between these groups, we subsequently corrected the age data by accounting for the true age ($\text{Year} + \# \text{ of days}/365$) of individuals. We re-ran the analysis with the age of the fish converted to a decimal age (i.e. 1.43 years old) while assuming a birthdate of 01/Jan.

Otolith preparation and analysis

145 Prior to $\delta^{18}\text{O}_{\text{oto}}$ analysis, intact left otoliths were rinsed with distilled water and 70% ethanol,
146 embedded in hard epoxy resin, and sectioned using an IsoMet Low Speed saw (Buehler Canada,
147 Whitby, Ontario). To collect a 1mm otolith section, the saw was mounted with two IsoMet
148 diamond wafering blades (Beuhler, Illinois USA) separated by a 1mm metal spacer. To ensure
149 that the section contained all annuli from the previously determined age, it was examined under
150 an Olympus SZY16 (Olympus America INC, Pennsylvania, USA) stereoscope in a Petri dish of
151 70% ethanol, and digitally imaged with cellSens imaging software (Olympus America INC,
152 Pennsylvania, USA). The images were enhanced for contrast using Photoshop (Adobe).
153 The section image was examined to identify areas on the otolith to be sampled. Two samples per
154 annulus were collected: one opaque sample and one translucent sample comprising sixteen
155 samples of otolith material for an eight-year-old cod. Opaque regions of the otolith annuli are
156 thick, appear light-coloured under reflected light, and sometimes considered to be the “summer
157 band”. The opaque rings are broken up by thinner translucent bands that appear dark under
158 reflected light and are sometimes referred to as “winter bands.” An automated MicroMill (New
159 Wave Research INC, California, USA) equipped with a 480 μm diameter tungsten bit was used
160 to mill otoliths at the identified sample sites to a depth of 150 μm .
161
162 The drill bit was wider than the otolith bands being sampled, hence except for the first annulus
163 removal of discrete samples required that sample paths were milled by running the drillbit along
164 the edge of the otolith bands following the method of Wurster et al. (1999). Each milled sample
165 of otolith powder was tapped into a separate decontaminated EXETAINER® vial (© Labco
166 Limited). Samples were analyzed for stable oxygen isotope ratio on an isotope ratio mass
167 spectrometer (IRMS) using a GasBench II in stable isotope laboratories at Memorial University

(Delta V Plus) and the University of Arkansas (Delta Plus). Stable oxygen isotope values were reported in δ notation relative to the Vienna Pee Dee Belemnite (VPDB) international standard:

Eq 1.
$$\delta^{18}\text{O} = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} - 1 \right) \times 1000 (\text{‰})$$

where R is the ratio of heavy and light isotopes (^{18}O : ^{16}O) in the sample or standard and values are expressed in per mil (‰) units.

After several batches of samples had been assayed, it was observed that the quality of the $\delta^{18}\text{O}_{\text{oto}}$ sample signal precision began to deteriorate when minute amounts of material were assayed on the IRMS. Specifically, measurements of $\delta^{18}\text{O}_{\text{oto}}$ began to drift when the amount of material assayed produced peaks with an area of less than 2.5 Vs (volts seconds). To ensure best results with minute amounts of material, following the method of Breitenbach and Bernasconi (2011), we proceeded to use smaller EXETAINER® vials (4.5 mL) than the customary (12 mL) ones that had initially been used in this study. The use of smaller vials with decreased headspace enabled smaller samples (range: 10-30 μg) to be analyzed using the GasBench II preparation device and significantly improved the quality of data collected. As a result of this issue, all values below the 2.5 Vs threshold (which reflected failed assays) were removed prior to statistical analysis.

Environmental data

Interpretation of $\delta^{18}\text{O}_{\text{oto}}$ data requires knowledge of the ambient isotopic landscape (or “isoscape”; Bowen (2010), Hobson et al. (2010)) of $\delta^{18}\text{O}$ where the fish live and factors that influence the uptake of isotope signatures into otoliths (fractionation). Oxygen isotope ratios of

seawater ($\delta^{18}\text{O}_{\text{sw}}$) are positively correlated with salinity (Epstein and Mayeda 1953; Craig and Gordon 1965; Tan and Strain 1988; Jamieson 2001) and have been extensively surveyed on the Newfoundland and Labrador shelf (Jamieson 2001). Hence, $\delta^{18}\text{O}_{\text{sw}}$ can be mapped in marine areas where salinities are known. Fractionation of oxygen to otolith from seawater however occurs as an inverse function of ambient temperature (Kalish 1991; Høie et al. 2004; Geffen 2012; Stanley et al. 2015, 2016). Consequently, $\delta^{18}\text{O}_{\text{oto}}$ is the product of environmental $\delta^{18}\text{O}_{\text{sw}}$ combined with the effect of temperature fractionation (i.e., a 1°C temperature adjustment results in a change of -0.2‰ in $\delta^{18}\text{O}_{\text{oto}}$ where an adjustment in salinity of 1 will result in a change of $+0.62\text{‰}$ $\delta^{18}\text{O}_{\text{oto}}$; Jamieson (2001)).

Measured $\delta^{18}\text{O}_{\text{sw}}$

Oceanic $\delta^{18}\text{O}_{\text{sw}}$ data from Jamieson (2001) were collected during an extensive April-July 1998 survey of the spatial variation in $\delta^{18}\text{O}_{\text{sw}}$ across the Newfoundland and Labrador shelf. These data were used to construct a map of real $\delta^{18}\text{O}_{\text{sw}}$ values (Fig. 1) which aided in the interpretation of $\delta^{18}\text{O}_{\text{oto}}$ in this study. Only data from the deepest water sample at each location were extracted for this purpose as these were thought to best represent ambient bottom conditions experienced by cod (mean $\pm$ s.d.; $175.70\text{m} \pm 142.3$). There is likely some uncertainty introduced with this assumption, particularly during spring when cod can undertake extensive vertical migrations (see Rose 2003; 2009; Rose and Rowe 2015) and also as seawater was sampled in April-July only. Water samples were collected alongside temperature and salinity measurements using a rosette sampler fitted with a conductivity, temperature, and depth (CTD) recorder on a Fisheries and Oceans Canada oceanographic survey. In relevant areas where $\delta^{18}\text{O}_{\text{sw}}$ data were not available

from Jamieson (2001), the data were extracted from Tan and Strain (1988) (Accessed from the Global Seawater Oxygen-18 Database <http://data.giss.nasa.gov/o18data/>).

Predicted $\delta^{18}\text{O}_{\text{oto}}$

The oceanic $\delta^{18}\text{O}_{\text{sw}}$ data from Jamieson (2001) and Tan and Strain (1988) illustrate the onshore-offshore trends in $\delta^{18}\text{O}_{\text{sw}}$ but do not predict $\delta^{18}\text{O}_{\text{oto}}$ for the collection locations in this study. To predict $\delta^{18}\text{O}_{\text{oto}}$ values for cod from each area, temperature and salinity data from the Marine Environmental Data Service (MEDS) Canada were used. Only CTD data from the deepest 5m sampled at each location (mean $\pm$ s.d.; $182.0\text{m} \pm 139.8$) were assessed. $\delta^{18}\text{O}_{\text{sw}}$ was predicted using the linear relationship with salinity reported by Jamieson (2001) and salinity records from MEDS (Fig. 2; Fig 3).

Eq 2.
$$\text{Predicted } \delta^{18}\text{O}_{\text{sw}} = 0.65(\text{Salinity}) - 22.61$$

This equation calculated predicted $\delta^{18}\text{O}_{\text{sw}}$ relative to Vienna Standard Mean Ocean Water (VSMOW). Subsequently, we converted the predicted $\delta^{18}\text{O}_{\text{sw}}$ from VSMOW to the Vienna Pee Dee Belemnite (VPDB) carbonate standard (appropriate for otoliths) using the following conversion (Coplen 1995).

Eq 3.
$$\delta^{18}\text{O VPDB} = \delta^{18}\text{O VSMOW} (0.97006) - 29.94$$

Lastly, the predicted $\delta^{18}\text{O}_{\text{oto}}$ was calculated using the predicted $\delta^{18}\text{O}_{\text{sw}}$ with the temperature data from MEDS using a temperature-dependent fractionation equation for cod (Høie et al. 2004)

Eq. 4
$$1000 \text{ Ln } \alpha = 16.75\left(\frac{1000}{T}\right) - 27.09$$

233 where $\alpha = \frac{\delta^{18}\text{O}_{\text{oto}} + 1000}{\delta^{18}\text{O}_{\text{sw}} + 1000}$ and T= temperature in Kelvin

234 *Statistical analysis*

235 To investigate the origin of the Smith Sound overwintering aggregation, a linear model was
 236 applied to test the null hypothesis of no difference in $\delta^{18}\text{O}_{\text{oto}}$ between cod collected in Smith
 237 Sound during winter and those from four potential origin sites (Smith Sound (during summer),
 238 Halibut Channel, Placentia Bay and Bonavista Corridor) for each annulus.

239

240 Eq 5. $\delta^{18}\text{O}_{\text{oto}}[\text{ann}] = \beta_0 + \beta_{\text{Site}}*\text{Site} + \beta_{\text{Season}}*\text{Season} + \varepsilon$

241 Where, $\delta^{18}\text{O}_{\text{oto}}$ is the oxygen isotope ratio of otolith carbonate, ann is the annulus number, Site is
 242 the collection site of the fish (a categorical explanatory variable), Season is the translucent or
 243 opaque band of the fish (a categorical explanatory variable) and ε is residual. This test was
 244 repeated for each annulus. Pair-wise comparisons were calculated using Tukey's post-hoc range
 245 tests. All analyses were undertaken in R (R Core Team 2014).

246 **Results**

247 *Otolith isotopes*

248 For the 87 cod otoliths used in this study, 1423 micromilled powder samples were assayed on the
 249 IRMS. Of these, 1095 samples (77%) satisfied the peak area threshold of 2.5Vs. $\delta^{18}\text{O}_{\text{oto}}$ was
 250 typically, lowest in the first annulus and increased in subsequent annuli (Fig. 4). Differences in
 251 $\delta^{18}\text{O}_{\text{oto}}$ between adjacent opaque and translucent bands were small ($p>0.05$) compared to among
 252 site differences and the ontogenetic trend within otoliths. This effect of season (or difference
 253 between translucent and opaque bands) on $\delta^{18}\text{O}_{\text{oto}}$ was not significant for any annuli ($p's>0.05$)

and was removed from further analyses. The reduced model indicated that collection site had a significant effect on $\delta^{18}\text{O}_{\text{oto}}$ for all annuli ($p < 0.001$).

Smith Sound overwintering and resident cod

The $\delta^{18}\text{O}_{\text{oto}}$ of overwintering and resident cod in Smith Sound differed significantly in annuli 1, 4, 6, 7, and 8 (Fig. 4a; Table 2). Cod sampled in winter (January-February) from the overwintering aggregation were significantly ($p < 0.001$) larger at all ages than resident cod sampled in June (Fig. 5). These differences were highly significant ($p < 0.001$) when age was treated categorically; Smith Sound Winter migrants were ~2 cm larger at all ages (except for age 1; Fig. 5a). Further, when the age data was corrected to include decimal years, the discrepancies between the Smith Sound migrants and residents increased (~5.4 cm, $p < 0.001$; Fig. 5b).

Predictions of $\delta^{18}\text{O}_{\text{oto}}$ from the temperature and salinity data from the Smith Sound area were lower than the predictions for offshore sites (Bonavista Corridor, Halibut Channel; Fig. 3). In general, the measured $\delta^{18}\text{O}_{\text{oto}}$ for Smith Sound residents and migrants were consistent with predictions of lower $\delta^{18}\text{O}_{\text{oto}}$ for Smith Sound and Bonavista Corridor.

The $\delta^{18}\text{O}_{\text{oto}}$ of Bonavista Corridor cod and resident Smith Sound cod differed significantly in annuli 1, 6, 7 and 8 (Fig. 4j; Table 2). In contrast, there was no significant difference between $\delta^{18}\text{O}_{\text{oto}}$ in any annuli, of cod overwintering in Smith Sound and sampled in summer in the Bonavista Corridor (Fig. 4; Table 2).

Halibut Channel

The $\delta^{18}\text{O}_{\text{oto}}$ signatures of cod collected in Halibut Channel were higher than those of any other group (Fig. 4; Table 2) except for annulus 1, which was depleted relative to other annuli and not significantly different from annulus 1 from resident Smith Sound cod (Fig. 4f, h; Table 2). The higher $\delta^{18}\text{O}_{\text{oto}}$ signatures for otoliths from cod in the Halibut Channel were consistent with the higher $\delta^{18}\text{O}_{\text{sw}}$ of the collection site (Fig. 3).

Placentia Bay

The $\delta^{18}\text{O}_{\text{oto}}$ signatures of otoliths from cod collected in Placentia Bay did not differ significantly from those of Smith Sound residents (Fig 4e, Table 2). No consistent patterns of similarity were evident among the $\delta^{18}\text{O}_{\text{oto}}$ signatures of cod from Placentia Bay and other sites, although some similarities existed. The Placentia Bay cod shared similar $\delta^{18}\text{O}_{\text{oto}}$ signatures with cod overwintering in Smith Sound at annuli 3 and 5, and summering in the Bonavista Corridor at annuli 1, 2, 3 and 4 (Fig. 4, Table 2)

Seawater $\delta^{18}\text{O}$

All available data on bottom $\delta^{18}\text{O}_{\text{sw}}$ from waters around Newfoundland and Labrador indicated that low salinity and lower $\delta^{18}\text{O}_{\text{sw}}$ were prevalent in most inshore regions, with both variables increasing with depth toward the offshore (Fig. 1).

Predicted $\delta^{18}\text{O}_{\text{oto}}$

Predicted $\delta^{18}\text{O}_{\text{oto}}$ for each of the origin sites based on ambient temperature and salinity in each area reflected the inshore-offshore trend shown in measured $\delta^{18}\text{O}_{\text{sw}}$ (Fig. 1). The offshore sites Bonavista Corridor and Halibut Channel had the highest predicted $\delta^{18}\text{O}_{\text{oto}}$ values, with Halibut

Channel predicted $\delta^{18}\text{O}_{\text{oto}}$ slightly lower than for the Bonavista Corridor (Fig. 3). By comparison, predicted $\delta^{18}\text{O}_{\text{oto}}$ for the inshore sites Smith Sound and Placentia Bay were 50% lower than for the offshore sites. In general, the measured $\delta^{18}\text{O}_{\text{oto}}$ signatures were congruent with predictions, with the exception of Bonavista Corridor. For this area, observed $\delta^{18}\text{O}_{\text{oto}}$ were less than predicted $\delta^{18}\text{O}_{\text{oto}}$ for this offshore region and similar to predictions and observations for inshore areas.

Discussion

Bonavista Corridor - Smith Sound connection

The results of these otolith assays indicated that cod from the overwintering aggregation in Smith Sound had $\delta^{18}\text{O}_{\text{oto}}$ signatures that were virtually identical to those of the same year-class in the Bonavista Corridor in summer (Fig. 4a). These near-identical $\delta^{18}\text{O}_{\text{oto}}$ signatures held for each year from age 1 (1990) to age 8 (1998), including the 5 years prior to the onset of the aggregation in Smith Sound in 1995. This result suggests that these cod inhabited similar environments from age 1 onward. Furthermore, the low $\delta^{18}\text{O}_{\text{oto}}$ (~ 1.5 ‰ VPDB) suggests that the juvenile habitat was largely inshore. The increase in $\delta^{18}\text{O}_{\text{oto}}$ up to age 5 with relative stability at older ages is consistent with known ontogenic changes of range with age. Northern cod juveniles (1-3) are relatively sedentary in inshore habitats with gradual range and depth increases until a year before maturation (age 4-5) when adult migratory behaviour and range become apparent (Anderson and Dalley 1997). The source of new recruits to Smith Sound and the Bonavista Corridor from 1995-2007 is not known, although Anderson and Rose (2001) linked spawning further north to widespread juvenile presence across much of the Newfoundland Shelf. Knickle and Rose (2010) found that Smith Sound larvae were both retained and subject to drift outside the Sound. The present results indicate that the most likely source of the 1990 year-class, the key founder of the

Smith Sound cod, was the major spawning that occurred in the Bonavista Corridor in 1990 (Rose 1993).

Conventional tagging studies had previously demonstrated that migration of cod from Smith Sound in spring occurred mostly to the north along the coast, but lack of fishing effort precluded any knowledge of potential offshore movements (Bratley 2000). Telemetry studies tracked large cod (>65 cm) solely along the shore (Bratley 2000). Notably, when cod were tagged in the Bonavista Corridor in late winter of 2007 and 2008, there were many captures inshore (Bratley et al. 2010). The present results suggest that the connection between the Smith Sound and Bonavista Corridor cod occurred much farther back, to the founding year-class. Our data suggest that overwintering cod in Smith Sound and those of the same year class in summer in the Bonavista Corridor represented different migration stages of the same group. The $\delta^{18}\text{O}_{\text{oto}}$ signatures of both stages were lower than those from the Halibut Channel, cod not thought to migrate inshore (Healey et al. 2014), despite the Bonavista Corridor site having higher predicted environmental $\delta^{18}\text{O}_{\text{oto}}$ based on temperature and salinity data (Fig 3). The Bonavista Corridor and the adjacent slope waters have relatively stable temperatures (2-4°C) and high salinity (33-34) compared to the inshore, including Smith Sound. The high salinity of the deep Bonavista Corridor area drives the prediction of high $\delta^{18}\text{O}_{\text{oto}}$. That the Bonavista Corridor and overwintering Smith Sound signatures were more consistent with lower predicted $\delta^{18}\text{O}_{\text{oto}}$ for the inshore, and more closely matched the $\delta^{18}\text{O}_{\text{oto}}$ values of cod from the inshore sites (Placentia Bay and Smith Sound residents), suggests that these cod were spending most the year inshore with excursions to the offshore. Vertical movements of migrating cod in spring into the fresher and colder waters of the Labrador Current (Rose 1993, Rose and Rowe 2015) would also lead to

lowered $\delta^{18}\text{O}_{\text{oto}}$ isotope signatures (it was not feasible to take this into account in the present predictions of ambient conditions).

The averaging of translucent and opaque otolith band samples may have contributed to the lack of seasonal differences in $\delta^{18}\text{O}_{\text{oto}}$. Translucent otolith bands are much thinner than opaque bands, hence translucent samples were often contaminated with nearly equal parts adjacent opaque material, and this reduced potential detection of seasonal differences (Høie et al. 2004; Kestelle et al. 2014; Kestelle et al. 2017), and hence the ability to detect seasonal migrations. Secondary Ion Mass Spectrometry enables higher resolution sampling and is suggested as a way to better detect seasonal differences within the otolith (Matta et al. 2013; Darnaude et al. 2014).

Overwintering Smith Sound cod not only had different $\delta^{18}\text{O}_{\text{oto}}$ signatures than residents but were significantly larger ($p < 0.001$). It is noteworthy that the Smith Sound overwintering cod were actually ~6 months younger (when sampled in January-February) than summer residents sampled in June, yet the size differences were still apparent. Seasonally adjusted discrepancies between migrants and residents in Smith Sound increased to ~5.4 cm at all ages ($p < 0.001$; Fig. 5b). Size discrepancies between these groups are consistent with migrants and residents being different ecotypes (Bardarson et al. 2017) occupying different habitats as they mature and likely utilizing different food sources for at least part of the year.

Given similar thermal regimes, migrating cod are likely to have higher growth rates than residents because they access better feeding conditions when they migrate from the overwintering-spawning area (Rose et al. 1994; Atkinson and Sibly 1997). Although the thermal

environments of the sampled cod are not known, migrating offshore in summer would likely lead to a colder not warmer environment than inshore, and hence poorer growth. However, in the years in question, capelin migration from offshore to coastal spawning locations was much delayed from historical norms (Nakashima and Wheeler 2002), and most capelin would have been offshore in June. This differs from historical behaviour, when capelin onshore migration would have been well underway by June. Hence, a possible explanation for cod moving offshore after spawning and into colder waters may be the location of key prey, especially capelin, the historical motivation for the post-spawning migration (Rose et al. 2011). If correct, these cod would have come back inshore in July or August with the late spawning capelin. This hypothesis is consistent with lower $\delta^{18}\text{O}_{\text{oto}}$ signatures than would be predicted by offshore residence.

The closely matching $\delta^{18}\text{O}_{\text{oto}}$ signatures from overwintering Smith Sound and Bonavista Corridor cod differed significantly from those of cod collected at other potential origin sites – including resident Smith Sound cod. The difference between the overwintering Smith Sound cod and those from Halibut Channel and Placentia Bay was not unexpected, as these fish would almost certainly have experienced very different oceanographic (temperature and salinity) conditions.

Cod captured in Placentia Bay in summer had $\delta^{18}\text{O}_{\text{oto}}$ signatures similar to those of Smith Sound residents. Cod are known to spawn in inner Placentia Bay where these cod were captured (Lawson and Rose 2000). Placentia Bay and Smith Sound are separated by only a small isthmus (Fig. 1) and have strong and similar freshwater inputs from adjacent regions; hence the similarity of their inshore signatures was not unexpected. Both inshore groups had $\delta^{18}\text{O}_{\text{oto}}$ signatures that

were lower than Halibut Channel cod that were unlikely to have migrated inshore based on tagging studies (Healey et al. 2014). It remains unexplained, nonetheless, that both of these inshore groups had $\delta^{18}\text{O}_{\text{oto}}$ signatures that were generally higher than those of the overwintering cod in Smith Sound. It might have been expected that inshore residents would exhibit not only different signatures from migrants, as observed, but at lower not higher $\delta^{18}\text{O}_{\text{oto}}$. Increased sea temperatures result in lower $\delta^{18}\text{O}_{\text{oto}}$ as a consequence of temperature-dependant fractionation and year-round residency inshore would almost certainly lead to higher ambient temperatures during the main growth period of summer and fall in this stock, relative to fish that migrated to offshore waters influenced by the cold Labrador Current. This hypothesis might explain the elevated $\delta^{18}\text{O}_{\text{oto}}$ signatures of inshore cod, but requires further investigation.

The predicted isoscape was generally consistent with observed cod $\delta^{18}\text{O}_{\text{oto}}$ measurements, with $\delta^{18}\text{O}_{\text{oto}}$ signatures lower inshore than offshore, based on the Halibut Channel cod being the offshore out-group. These fish had high observed $\delta^{18}\text{O}_{\text{oto}}$ signatures at all ages (except age 1) that were highly congruent with predicted $\delta^{18}\text{O}_{\text{oto}}$ based on ambient salinity and temperature data. In agreement with tagging studies, there was little isotopic evidence of inshore migration from this site to environments with lower ambient $\delta^{18}\text{O}_{\text{oto}}$ (Healey et al. 2014). Despite this, slight offsets (small compared to differences among groups) were evident between predicted and observed $\delta^{18}\text{O}_{\text{oto}}$. Offsets were also reported in a study of plaice (*Pleuronectes platessa*) in the North Sea, in which a hydrographic model was applied to the predictions of $\delta^{18}\text{O}_{\text{oto}}$ (Darnaude et al. 2014). Offsets could be caused by vital (physiological) effects, species specific fractionation or salinity correlation inaccuracies.

Finally, the lowest $\delta^{18}\text{O}_{\text{oto}}$ signatures were commonly observed in the first annulus of the otolith. Two possible scenarios might explain this. Firstly, cod likely occupied shallow nearshore areas at ages 0-1, specifically eel grass (*Zostera marina*) beds (Gotceitas et al. 1997, Laurel et al. 2004, Robichaud and Rose 2006). Nonetheless, first annulus $\delta^{18}\text{O}_{\text{oto}}$ signatures were consistently lower than predictions. One possible explanation is that present predictions of $\delta^{18}\text{O}$ in inshore habitats may have been too high as they were based on measures taken from waters deeper than the fish inhabited. It is also possible that the low $\delta^{18}\text{O}_{\text{oto}}$ observed reflected, at least in part, the pelagic larval phase of Atlantic cod in fresher near surface waters. To test this, it would be necessary to examine the $\delta^{18}\text{O}_{\text{oto}}$ signatures of larval cod which has yet to be assessed in any study of wild Atlantic cod.

In conclusion, the weight of the evidence provided by $\delta^{18}\text{O}_{\text{oto}}$ signatures indicates that cod of the founder year-class (1990) overwintering in Smith Sound in 1998, and those summering in 2000 in the Bonavista Corridor, were part of a single migrating group. These cod apparently experienced very similar environmental conditions throughout their lives. No other group had similar $\delta^{18}\text{O}_{\text{oto}}$ signatures in all annuli. This conclusion is consistent with the hypothesis that the Smith Sound aggregation originated from cod spawning in the Bonavista Corridor in 1990 and rejoined their parent group as the Smith Sound aggregation dispersed post-2007 (Rose 1993; Rose et al. 2011; Rose and Rowe 2015). Finally, an inference from the present study is that these cod belong to a metapopulation (Smedbol and Wroblewski 2002, Rose et al. 2011) with farther spatial expansion possible as the stock rebuilds.

A few comments about the implications of this study to the broader question of the population structure of Northern cod are warranted. Northern cod have long been recognized as a stock

complex. This term was used to describe the composite inshore and offshore overwintering and spawning components that comprised the management unit (based mostly on mark-recapture studies (e.g., Templeman 1962; 1979; Lear 1984). More recently, Smedbol and Wroblewski (2000) modeled the sub-population structure of cod in this region as a metapopulation, employing survey data spanning the range of the stock and beyond to the north (NAFO 2GHJ3KL). These authors reported that cod in most northerly regions (NAFO 2GH) had become commercially extinct prior to the declines farther south, with declines occurring progressively from north to south and the most southerly region of the stock in the Bonavista Corridor remaining strongest (also see Atkinson et al. 1997). Smedbol and Wroblewski (2002) predicted that if the full stock was to rebuild, it would likely be by recolonization rather than local growth. In a follow-up paper, Smedbol et al. (2002) stressed that their definition of a metapopulation did not require local extinction, just major reduction.

Our data suggest that the Smith Sound cod were part of the putative Northern cod metapopulation, as suggested by Rose et al. (2011). It is unlikely that this large overwintering and spawning aggregation of Northern cod was entirely of local origin, and the present data indicate their most likely origin was the adjacent and offshore Bonavista Corridor. The apparent dispersal of the Smith Sound aggregation after 2007, in conjunction with the increase in the Bonavista Corridor, further suggested that the two phenomena were related (Rose and Rowe 2015; Cadigan 2016). If these and the present interpretation of the spatial dynamics linking the coastal area of Smith Sound and the offshore Bonavista Corridor are correct, it is apparent that major changes in distribution can occur quickly. Nonetheless, the data suggest that the links were there all along. Although it was not evident that onshore migration was occurring until tagging

studies were initiated in 2007 (Bratney et al. 2010), the present data suggest it was taking place throughout the 1990s when stock abundance was extremely low. We conclude that although most of the Smith Sound cod remained in the overwintering and spawning aggregation until 2007, venturing out of Smith Sound along the northeast coast in summer (Bratney et al. 2010), some were venturing back to the Bonavista Corridor, perhaps in search of capelin, which would account for the samples taken there of 1990 year-class fish in June of 1998. As a final comment, the increasing spring biomass of cod in the Bonavista Corridor after 2007 and up to 2014 (Rose and Rowe 2015) is thought to enhance the likelihood of further redistribution, especially to former regions of abundance to the north.

Acknowledgments

We thank S. Campana at the University of Iceland for insight and guidance in the methods employed here and for reviewing a version of this MS. Thanks to the at-sea scientists and crew of the Natural Sciences and Engineering Council of Canada (NSERC) Fisheries Conservation Chair at Memorial University and CCGS Teleost, respectively, and Allison Pye from Memorial University's Core Research Equipment & Instrument Training (CREAIT) and Erik Pollock and Lindsey Conaway from University of Arkansas's Stable Isotope Laboratory (UASIL) for performing the assays. We thank Eugene Colbourne and John Bratney of the Department of Fisheries and Oceans Canada for the provision of oceanographic data and otoliths as well as the Marine Environmental Data Service for provision of oceanographic data. Funding was provided by grants and shiptime to G.A. Rose from the Department of Fisheries and Oceans Canada, the former Fisheries Products International, NSERC, the Department of Fisheries and Aquaculture of Newfoundland and Labrador and the Harris Centre of Memorial University, and a Research

and Development Corporation of Newfoundland and Labrador, Ocean Industries Student
Research Award to V. Neville.

Table 1. Age and collection information for otoliths from 1990 year-class cod used in this study
taken from four locations off Newfoundland.

	Smith Sound Winter	Smith Sound Summer	Placentia Bay	Bonavista Corridor	Halibut Channel
N	14	19	10	20	24
Age	10	8	9	8	8
Catch Date	Jan 2000	June 1998	July 1999	June 1998	May 1998

Table 2. P-values of pair wise comparisons calculated using Tukey's post-hoc range test for
linear model comparing potential origin sites: Halibut Channel (HC), Bonavista Corridor (BC),
Placentia Bay (PB), Smith Sound Summer (SSS), Smith Sound Winter (SSW) for each otolith
annulus mean $\delta^{18}\text{O}$. P-values with a significance of $p < 0.05$ are highlighted.

Collection	Annulus							
Sites	1	2	3	4	5	6	7	8
SSW – BC (fig 4a)	0.983	0.769	1.000	0.483	0.504	0.976	1.000	0.585
SSW – SSS (fig 4b)	<0.01	0.116	0.661	<0.01	0.958	<0.01	<0.01	<0.01
SSW – HC (fig 4c)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
SSW – PB (fig 4d)	0.040	<0.01	0.109	0.013	0.361	<0.01	<0.01	<0.01

PB- SSS (fig 4e)	0.658	0.658	0.599	0.992	0.634	1.000	1.000	0.995
PB – HC (fig 4f)	0.417	0.020	<0.01	0.023	0.016	<0.01	0.020	0.038
BC- PB (fig 4g)	0.064	0.079	0.081	0.285	<0.01	0.013	<0.01	<0.01
SSS – HC (fig 4h)	0.989	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.083
BC- HC (fig 4i)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BC- SSS (fig 4j)	<0.01	0.602	0.621	0.330	0.059	<0.01	<0.01	<0.01

494

495 **References**

496
497
498
499

Anderson, J.T., and Dalley, E.L. 1997. Spawning and recruitment of Northern cod as measured by pelagic juvenile cod surveys following stock collapse. Can. J. Fish. Aquat. Sci. Spec. Publ. **54**: 158-167.

500
501
502

Anderson, J.T., and Rose, G.A. 2001. Offshore spawning and year-class strength of northern cod (2J3KL) during the fishing moratorium, 1994-1996. Can. J. Fish. Aquat. Sci. **58** (7): 1386-1394. <https://doi.org/10.1139/f01-068>

503
504
505
506
507

Atkinson, D., and Sibly, R.M. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends in Ecology & Evolution **12**(6): 235-239. doi:10.1016/S0169-5347(97)01058-6

508
509
510
511

Atkinson, D.B., Rose, G.A., Murphy, E.F., and Bishop, C.A. 1997. Distribution changes and abundance of Northern cod (*Gadus morhua*), 1981-1993. Can. J. Fish. Aquat. Sci. **54**(S1): 132-138.

512
513
514
515
516

Bardarson, H., McAdam, B.J., Thorsteinsson, V., Hjorleifsson, E., and Marteinsdottir, G. 2017. Otolith shape differences between ecotypes of Icelandic cod (*Gadus morhua*) with known migratory behavior inferred from Data Storage Tags. Can. J. Fish. Aquat. Sci. **74**:2122-2130. doi: 10.1139/cjfas-2016-0307.

517
518
519
520

Begg, G.A. and Weidman, C.R. 2001. Stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopes in otoliths of haddock *Melanogrammus aeglefinus* from the northwest Atlantic Ocean. Marine Ecology Progress Series **216**: 223–233. doi:10.3354/meps216223

521
522
523

Bishop, C.A., Stansbury, D.E., and Murphy, E.F. 1995. An update of the stock status of Div. 2J3KL cod. DFO Atlantic Fisheries Res. Doc 95/34.

- Bowen, G.J. 2010. Isoscapes: Spatial pattern in isotopic biogeochemistry. *Annu. Rev. Earth Planet. Sci.* **38**: 161-187. doi:10.1146/annurev-earth-040809-152429.
- Bratley, J. 2000. Stock structure and seasonal movements of Atlantic cod (*Gadus morhua*) in NAFO Divs. 3KL inferred from recent tagging experiments. Canadian Stock Assessment Secretariat Res. Doc. 2000/084.
- Bratley, J., Cadigan, N.G., Dwyer, K., Healey, B.P., Morgan, M.J., Murphy, E.F., Maddock Parsons, D., and Power, D. 2010. Assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J+3KL in 2010. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/103.
- Bratley, J., and Healey, B.P. 2007. Exploitation of Atlantic cod (*Gadus morhua*) in NAFO Divs. 3KL: tagging results from the reopened fishery in 2006. DFO Can. Sci. Advis. Sec. Res. Doc. 2007/027.
- Bratley, J., Cadigan, N.G., Dwyer, K., Healey, B.P., Morgan, M.J., Murphy, E.F., Maddock Parsons, D., and Power, D. 2011. Assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J+3KL in 2010. DFO Can. Sci. Advis. Sec. Res. Doc. 2010/103. viii + 108 p.
- Breitenbach, S.F.M., and Bernasconi, S.M. 2011. Carbon and oxygen isotope analysis of small carbonate samples (20 to 100 µg) with a GasBench II preparation device. *Rapid Communications in Mass Spectrometry* **25**(13): 1910-1914. doi:10.1002/rcm.5052.
- Cadigan, N.G. 2016. A state-space stock assessment model for Northern cod, including under-reported catches and variable natural mortality rates. *Canadian Journal of Fisheries and Aquatic Sciences* **73**(2): 296-308. doi: 10.1139/cjfas-2015-0047
- Coplen, T.B. 1995. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Geothermics* **24**(5): 707-712. doi: 10.1351/pac199466020273.
- Craig, H., and Gordon, L.I. 1965. Deuterium and oxygen-18 variations in the ocean and the marine atmosphere, Lischi and Figli, Pisa, pp. 9-130.
- Darnaude, A.M., Sturrock, A., Trueman, C.N., Mouillot, D., EIMF, Campana, S.E., and Hunter, E. 2014. Listening in on the past: What can otolith $\delta^{18}\text{O}$ values really tell us about the environmental history of fishes? *PLOS ONE* **9**(10): e108539.
- deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* **50**(12): 2729-2741. doi: 10.1139/f93-298
- Epstein, S., and Mayeda, T. 1953. Variation of O^{18} content of water from natural sources. *Geochim. Cosmochim. Acta.* **4**: 213-224. doi: 10.1016/0016-7037(53)90051-9
- Fitzpatrick, C., and Miller, R. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. *Fish. Mar. Ser. Tech. Rep.* 905.

- Gao, Y., and Beamish, R.J. 2003. Stable isotopic composition of otoliths from tagged Pacific halibut, *Hippoglossus stenolepis*. *Environ Biol Fish* **67**(3): 253-261. doi: 10.1023/A:1025874110893.
- Gao, Y., Joner, S.H., Svec, R.A., and Weinberg, K.L. 2004. Stable isotopic comparison in otoliths of juvenile sablefish (*Anoplopoma fimbria*) from waters off the Washington and Oregon coast. *Fisheries Research* **68**(1-3): 351-360. doi: 10.1016/j.fishres.2003.11.002
- Gao, Y., Schwarcz, H.P., Brand, U., and Moksness, E. 2001. Seasonal stable isotope records of otoliths from ocean-pen reared and wild cod, *Gadus morhua*. *Environ Biol Fish* **61**(4): 445-453. doi: 10.1023/A:10116544
- Geffen, A.J. 2012. Otolith oxygen and carbon stable isotopes in wild and laboratory-reared plaice (*Pleuronectes platessa*). *Environ Biol Fish* **95**(4): 419-430. doi: 10.1007/s10641-012-0033-2.
- Goddard, S.V., Wroblewski, J.S., Taggart, C.T., Howse, K.A., Bailey, W.L., Kao, M.H., and Fletcher, G.L. 1994. Overwintering of adult Northern Atlantic cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze glycoprotein levels. *Canadian Journal of Fisheries and Aquatic Sciences* **51**(12): 2834-2842. doi: 10.1139/f94-282.
- Gotceitas, V., Fraser, S., and Brown, J.A. 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**(6): 1306-1319. doi:10.1139/f97-033
- Healey, B.P., Murphy, E.F., Bratney, J., Morgan, M.J., Maddock Parsons, D., and Vigneau, J. 2014. Assessing the status of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in 2012. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2013/087.
- Hobson, K.A., Barnett-Johnson, R., and Cerling, T. 2010. Using isoscapes to track animal migration. In *Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping*. Edited by J.B. West, G.J. Bowen, T.E. Dawson and K.P. Tu. Springer Netherlands, Dordrecht. pp. 273-298.
- Høie, H., and Folkvord, A. 2006. Estimating the timing of growth rings in Atlantic cod otoliths using stable oxygen isotopes. *Journal of Fish Biology* **68**(3): 826-837. doi: 0.1111/j.0022-1112.2006.00957.x
- Høie, H., Otterlei, E., and Folkvord, A. 2004. Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). *ICES Journal of Marine Science* **61**(2): 243-251. doi: 10.1016/j.icesjms.2003.11.006.

- Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences **50**(11): 2457-2467. doi:10.1139/f93-270
- Jamieson, R. 2001. Environmental history of Northern cod from otolith isotopic Analysis, Geology, McMaster University, Hamilton, Ontario.
- Kalish, J.M. 1991. ^{13}C and ^{18}O isotopic disequilibria in fish otoliths: metabolic and kinetic effects. Marine Ecology Progress Series **75**: 191-203.
- Kastelle, C., Helser, T., McKay, J., and Anderl, D. 2014 Poster. Age validation of Pacific cod (*Gadus macrocephalus*) using stable oxygen isotopes ($\delta^{18}\text{O}$) In Western Groundfish Conference (18th), Victoria, B.C.
- Kastelle, C., Helser T., McKay, J.L., Johnston C., Anderl D., Matta M., Nichol D. .2017. Age validation of Pacific cod (*Gadus macrocephalus*) using high-resolution stable oxygen isotope ($\delta^{18}\text{O}$) chronologies in otoliths. Fish Res **185**: 43–53.
- Knickle, D.C., and Rose, G.A. 2010. Seasonal spawning and wind-regulated retention-dispersal of early life stage Atlantic cod (*Gadus morhua*) in a Newfoundland fjord. Fisheries Oceanography **19**(5): 397-411. doi: 10.1111/j.1365-2419.2010.00553.x
- Laurel, B.J., Gregory, R.S., Brown, J.A., Hancock, J., and Schneider, D. 2004. Behaviour consequences of density-dependent habitat use in marine fish. Marine Ecology Progress Series **272**: 257-270.
- Lawson, G.L., and Rose, G.A. 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland. Fisheries Research **49**(1): 61-75. doi:10.1016/S0165-7836(00)00187-9.
- Lear, W.H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off Southern Labrador and Eastern Newfoundland, as inferred from tagging studies. Journal of Northwest Atlantic Fishery Science **5**: 143-159.
- Lear, W.H. 1986. The stock complex of Atlantic cod (*Gadus morhua*) in NAFO Divisions 2J, 3K and 3L. NAFO SCR Doc. 86/32.
- Matta, M.E., Orland, I.J., Ushikubo, T., Helser, T.E., Black, B.A., and Valley, J.W. 2013. Otolith oxygen isotopes measured by high-precision secondary ion mass spectrometry reflect life history of a yellowfin sole (*Limanda aspera*). Rapid Communications in Mass Spectrometry **27**(6): 691-699. doi: 10.1002/rcm.6502.
- Nakashima, B.S., and Wheeler, J.P. 2002. Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters—the interaction between beach and demersal spawning. ICES Journal of Marine Science **59**(5): 909-916. doi: 10.1006/jmsc.2002.1261.

- Robichaud, D., and Rose, G.A. 2006. Density-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland. ICES Journal of Marine Science **63**(4): 766-774. doi:10.1016/j.icesjms.2005.12.002.
- Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature **366**(6454): 458-461. doi: 10.1038/366458a0.
- Rose, G.A. 2003. Monitoring coastal Northern cod: towards an optimal survey of Smith Sound, Newfoundland. ICES Journal of Marine Science **60**(3): 453-462. doi: 10.1016/S1054-3139(03)00044-4.
- Rose, G.A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change. ICES Journal of Marine Science **62**(7): 1524-1530. doi: 10.1016/j.icesjms.2005.05.008.
- Rose, G.A. 2007. Cod: the ecological history of the North Atlantic fisheries. Breakwater Books Ltd., St. John's, NL.
- Rose, G.A. 2009. Variations in the target strength of Atlantic cod during vertical migration. ICES Journal of Marine Science **66**(6): 1205-1211. 10.1093/icesjms/fsp085.
- Rose, G.A., Atkinson, B.A., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.
- Rose, G.A., deYoung, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution shifts and overfishing the Northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences **57**(3): 644-663. doi.org/10.1139/f00-004.
- Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the Northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Sciences **56**(S1): 118-127. 10.1139/f99-207.
- Rose, G.A., Nelson, R.J., and Mello, L.G.S. 2011. Isolation or metapopulation: whence and whither the Smith Sound cod? Canadian Journal of Fisheries and Aquatic Sciences **68**(1): 152-169. doi.org/10.1139/f10-135.
- Rose, G.A., and Rowe, S. 2015. Northern cod comeback. Canadian Journal of Fisheries and Aquatic Sciences: 1789-1798. doi:10.1139/cjfas-2015-0346
- Ruzzante, D.E., Taggart, C.T., Doyle, R.W., and Cook, D. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. Conserv Genet **2**(3): 257-269.
- Shephard, S., Trueman, C., Rickaby, R., and Rogan, E. 2007. Juvenile life history of NE Atlantic

- orange roughly from otolith stable isotopes. Deep Sea Research Part I: Oceanographic Research Papers **54**(8): 1221-1230. doi: 10.1016/j.dsr.2007.05.007
- Smedbol, R.K., and Wroblewski, J.S. 1997. Evidence for inshore spawning of Northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991-1993. Canadian Journal of Fisheries and Aquatic Sciences **54**(S1): 177-186. doi: 10.1139/f96-146.
- Stanley, R.R.E., DiBacco, C., Thorrold, S.R., Snelgrove, P.V.R., Morris, C.J., Gregory, R.S., Campana, S.E., and Bradbury, I.R. 2016. Regional variation in otolith geochemistry of juvenile Atlantic cod (*Gadus morhua*) in coastal Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences **73**(10): 1507-1519. doi:10.1139/cjfas-2015-0353
- Stanley, R.R.E., Bradbury, I.R., DiBacco, C., Snelgrove, P.V.R., Thorrold, S.R., and Killen, S.S. 2015. Environmentally mediated trends in otolith composition of juvenile Atlantic cod (*Gadus morhua*). ICES Journal of Marine Science **72**(8): 2350-2363. doi: 10.1093/icesjms/fsv070
- Tan, F.C., and Strain, P.M. 1988. Stable isotope studies in the Gulf of St. Lawrence. In Chemical oceanography in the Gulf of St. Lawrence. Edited by P.M. Strain. Department of Fisheries and Oceans. Canadian Bulletin of Fisheries and Aquatic Sciences, Ottawa, ON. pp. 59-77.
- Team, R.C. 2014. R: A language and environment for statistical computing. In R Foundation for Statistical Computing, Vienna, Austria.
- Templeman, W. 1979. Migrations and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging 1962–1966. Int. Comm. Northwest Atl. Fish. Res. Bull. 14: 5–50
- Templeman, W. 1962. Divisions of cod stocks in the Northwest Atlantic. ICNAF Redbook, III, pp. 79-123.
- Templeman, W., and Fleming, A.M. 1956. The Bonavista longlining experiment, 1950–1953. Bull. Fish. Res. Board Can 109.
- Weidman, C.R., and Millner, R. 2000. High-resolution stable isotope records from North Atlantic cod. Fisheries Research **46**(1–3): 327-342.
- Wroblewski, J.S., Kulka, D.W., Narayanan, S., Oake, A.M., Collier, A.G., and McGrath, B.D. 1995. Winter distribution and movements of Northern Atlantic cod (*Gadus morhua*) along the Newfoundland—Labrador continental shelf edge derived from observations on commercial trawlers. Fisheries Oceanography **4**(2): 128-146. doi: 10.1111/j.1365-2419.1995.tb00067.x.
- Wurster, C.M., Patterson, W.P., and Cheatham, M.M. 1999. Advances in micromilling techniques: a new apparatus for acquiring high-resolution oxygen and carbon stable isotope values and major/minor elemental ratios from accretionary carbonate. Comput. Geosci. **25**(10):1159-1166. doi: 10.1016/s0098-3004(99)00052-7.

Figure 1. $\delta^{18}\text{O}_{\text{sw}}$ (‰ VSMOW) gradients on Newfoundland and Labrador shelves shown as a range of colour from blue to red. Circles represent seafloor bottom data from Jamieson (2001), and squares represent seafloor bottom data from Tan and Strain (1988). Stars indicate the collection locations for Atlantic cod in this study: Bonavista Corridor (BC), Halibut Channel (HC), Placentia Bay (PB) and Smith Sound (SS). Map data ©2018 R package "mapdata" and accompanying "worldhires" function.

Figure 2. Hydrographic data taken from the Marine Environmental Data Service (MEDS) to calculate predicted $\delta^{18}\text{O}_{\text{oto}}$. Map data ©2018 R package "mapdata" and accompanying "worldhires" function.

Figure 3. Mean predicted $\delta^{18}\text{O}_{\text{oto}}$ for Atlantic cod inhabiting Smith Sound (filled squares), Bonavista Corridor (open circles), Placentia Bay (x's) and Halibut Channel (filled triangles). Error bars represent 95% confidence intervals.

Figure 4. Mean $\delta^{18}\text{O}_{\text{oto}}$ signatures of Atlantic cod comparing Smith Sound Winter (SSW; filled squares), Smith Sound Summer (SSS; open squares), Halibut Channel (HC; filled triangles), Bonavista Corridor (BC; open circles) and Placentia Bay (PB; x's). Error bars represent 95% confidence intervals. a) BC and SSW, b) SSW and SSS, c) HC and SSW, d) PB and SSW, e) PB

and SSS, f) PB and HC, g) PB and BC, h) HC and SSS, i) HC and BC and J) BC and SSS.

Draft

Figure 5. Length-at-age and fitted von Bertalanffy curves for overwintering (January-February samples, triangles) and resident Smith Sound cod (June, circles). a) Cod captured in January - June were treated as the same age b) corrected for intra-annual differences in age.