

# Does redistribution or local growth underpin rebuilding of Canada's Northern cod?

George A. Rose and Sherrylynn Rowe

**Abstract:** The stock structure of Canada's Northern cod (*Gadus morhua*), the largest of many depleted groundfish stocks having multiple spawning areas, is rebuilding by redistribution and not solely by local population growth. In 2007–2008, late winter acoustic surveys suggested initial rebuilding in the southern-most part of the offshore range (Bonavista Corridor, NAFO Divisions 3KL), likely including fish dispersing from the inshore. Thereafter, acoustically determined biomass increases averaged 30% per annum (to near 240 000 t in 2014). In contrast, formerly dominant stock areas farther north retained few fish, mostly juveniles. In 2015, however, biomass in the northern stock range (NAFO Division 2J) reached 65 000 t and mid-north Notre Dame Channel (3K) reached 101 000 t, with Bonavista Corridor declining to 136 000 t. Biomass pooled over all surveyed regions totaled 302 000 t, consistent with sustained 30% growth. Latitudinal gradients in cod size, age distributions, and individual growth existed both historically and recently, but not in 2015. The evidence suggests that the rapid increases of depopulated northern groups resulted from redistribution from the south within a metapopulation.

**Résumé :** La structure du stock de morues (*Gadus morhua*) du nord du Canada, le plus grand de nombreux stocks de poissons de fond en déclin caractérisés par de multiples aires de frai, se reconstitue non seulement par la croissance démographique locale, mais également par l'entremise de la redistribution. En 2007–2008, des relevés acoustiques menés à la fin de l'hiver indiquaient une reconstitution initiale dans la portion la plus méridionale de l'aire de répartition au large (corridor Bonavista, divisions 3KL de l'OPANO), incluant vraisemblablement des poissons dispersés à partir de zones littorales. Par la suite, la biomasse établie par des méthodes acoustiques a connu une augmentation moyenne de 30 % par année (pour atteindre près de 240 000 t en 2014). En comparaison, moins de poissons, et principalement des juvéniles, demeuraient dans les régions auparavant dominantes du stock situées plus au nord. En 2015, la biomasse dans l'aire septentrionale du stock (division 2J de l'OPANO) atteignait toutefois 65 000 t, alors que dans la région du centre-nord du chenal Notre-Dame (3K), elle atteignait 101 000 t, et dans le corridor Bonavista, elle était réduite à 136 000 t. La biomasse cumulative pour toutes les régions évaluées totalisait 302 000 t, ce qui concorde avec une croissance annuelle soutenue de 30 %. S'il existait historiquement et plus récemment des gradients latitudinaux de la taille, de la répartition des âges et de la croissance individuelle des morues, il n'y en avait pas en 2015. Les observations semblent indiquer que les augmentations rapides des groupes septentrionaux dépeuplés sont le résultat d'une redistribution en provenance du sud au sein d'une métapopulation. [Traduit par la Rédaction]

## Introduction

It has long been known that many fish stocks have multiple spawning and aggregation areas (Hjort 1914; McKenzie and Smith 1955; Templeman 1966; Brander 1994). Spawning area occupation may change as a result of environmental changes or the impacts of harvesting (Sundby and Nakken 2008; Dragesund et al. 2008; Opdal 2010). In species that aggregate, changes in abundance typically do not occur uniformly over the stock area as a result of density-dependent range expansion (e.g., MacCall 1990), but perhaps of key importance, depleted stocks often become concentrated in fewer areas (Atkinson et al. 1997; Ames 2004; Fox et al. 2008; Dragesund et al. 2008). Restoring productivity in these depleted stocks may require repopulation of diminished spawning sites and capacity; hence, management is predicated on how rebuilding might occur, or indeed if it is possible.

The Northern cod (*Gadus morhua*) off the northeast coast of Newfoundland and Labrador (Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL) was historically the largest of many depleted cod stocks having multiple spawning areas (e.g., Ames

2004; Rose 2007; Fox et al. 2008). After almost two decades of depletion, recent increases in the Northern cod have been evident, offering the opportunity to study how rebuilding might occur (Rose and Rowe 2015). It was evident that increases were first evident in the southern region, termed the Bonavista Corridor (overlaps NAFO Divisions 3KL boundary), first in 2007 and then more substantially in 2008 (Mello and Rose 2008, 2009). This was the same area that held the last large concentrations of fish in the early 1990s (Rose 1993). By 2015, increases in biomass and age structure were also evident in the northern reaches of the stock in the Hawke Channel and outer portions of the Belle Isle and Hamilton Banks (NAFO 2J; Rose and Rowe 2015; DFO 2016; Kincaid and Rose 2017). A key question posed by Rose and Rowe (2015) concerned the origin and ontogeny of the fish that formed these increasing aggregations and their latent spawning capacity, in particular those in the banks to the north (Templeman 1966). In essence, were these increases solely a result of local population growth or were redistributions occurring?

Received 29 September 2017. Accepted 12 March 2018.

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How the Northern cod might rebuild, or indeed if it would, has been debated since its collapse. It was argued early on that expansion and recolonization was possible within a putative metapopulation in which subgroups had been depleted (Smedbol and Wroblewski 2002; Smedbol et al. 2002). If the Northern cod comprised a metapopulation, fostering growth in extant groups, particularly but not exclusively the Smith Sound group, was of paramount importance (Anderson and Rose 2001; Rose 2003; Rose et al. 2011). On the other hand, some genetic studies suggested that redistribution from the inshore was unlikely and that offshore rebuilding, if it occurred at all, was more likely to result from local production of what were thought to be functionally distinct, if near extirpated, groups (Ruzzante et al. 1996; Beacham et al. 2002; Lilly et al. 2005). Such reasoning influenced management decisions to reopen inshore fisheries in the 1990s. More recently, new evidence has suggested that redistribution from the inshore to offshore has taken place. The Smith Sound cod comprised the largest known extant spawning biomass of the Northern cod complex during 1995–2006 (Rose 2003), but dispersed thereafter concurrent with a sudden and unexpected increase in the offshore biomass in the adjacent Bonavista Corridor (Rose et al. 2011; Rose and Rowe 2015; Cadigan 2016). Nonetheless, it remained uncertain whether or not larger-scale redistribution within the offshore could occur, particularly to the north in the region around the Hawke Channel and surrounding banks where formerly large components of the Northern cod overwintered and spawned (May 1966; Templeman 1966; Lear 1984; Rose 2007). We hypothesized that the observed abundance of adult fish in the northern regions (Rose and Rowe 2015) resulted at least in part not from local stock growth but from redistribution within a putative metapopulation (Smedbol and Wroblewski 2002; Rose et al. 2011). According to this hypothesis, increases in the north resulted from redistribution of the increasing numbers of cod present in the southern range of the stock since 2007 (Mello and Rose 2009; Rose and Rowe 2015; DFO 2016, 2017).

Regaining a broad northern range distribution is key to recovery of this once great stock and hence to management. The importance of northern spawning to production and recruitment has been postulated for many years, as a consequence of the strong southerly flows of the Labrador Current over the continental shelf (Templeman 1966; deYoung and Rose 1993; Davidson and deYoung 1995). An oceanographic drifter study showed that northern spawning would enable transport of reproductive products southward and shoreward to the shelf and northeast coast of Newfoundland (Pepin and Helbig 1997). Empirical evidence that followed demonstrated the link between northern spawning in and around the Hawke Channel and juvenile cod distribution and abundance to the south across a wide region of the northeast Newfoundland Shelf and coastal areas (Anderson and Rose 2001).

The objectives of this paper are to test several demographic and life history expectations of the redistribution hypothesis. Of key diagnostic importance, after a decade of stock growth at a rate approaching 30% (Rose and Rowe 2015; DFO 2016), biomass in the Bonavista Corridor should have declined, or at least slowed if redistribution had occurred. In addition, the strong year classes known to be present in the Bonavista Corridor should be prominent in the north. Also, the historically consistent differences in size at age and individual growth rates between the southern and northern regions (Ruivo 1957; Fleming 1960; Templeman 1966; Sherwood et al. 2007; Morgan et al. 2017) should not be evident. These traits were thought to be diagnostic of residency history and thus provide means to either advance or reject the redistribution hypothesis.

## Methods

Acoustic surveys of the Northern cod were conducted in March of 2007 and 2008 and May of 2012 to 2015, using trawling to con-

firm biological characteristics of acoustic backscatter, based on methods developed in spring surveys since 1990 (e.g., Rose 1993; Rose and Rowe 2015). These surveys were designed to coincide with the time of maximum cod aggregation, as cod (mostly age 4+ years) overwintered near the shelf break (Kulka et al. 1995) then spawned in shallower waters on the shelf (Rose 1993). Aggregations during this period are typically contracted laterally but expanded vertically, at times to >100 m off bottom, and only rarely mixed with other species, making delineation of cod on echograms relatively simple and detection rates high. These factors make Northern cod highly amenable to acoustic-trawl survey methods at this time of year (Fig. 1 shows echograms of aggregations in 2008—the first such large aggregations encountered since 1992 and a sign that the potential for rebuilding was latent).

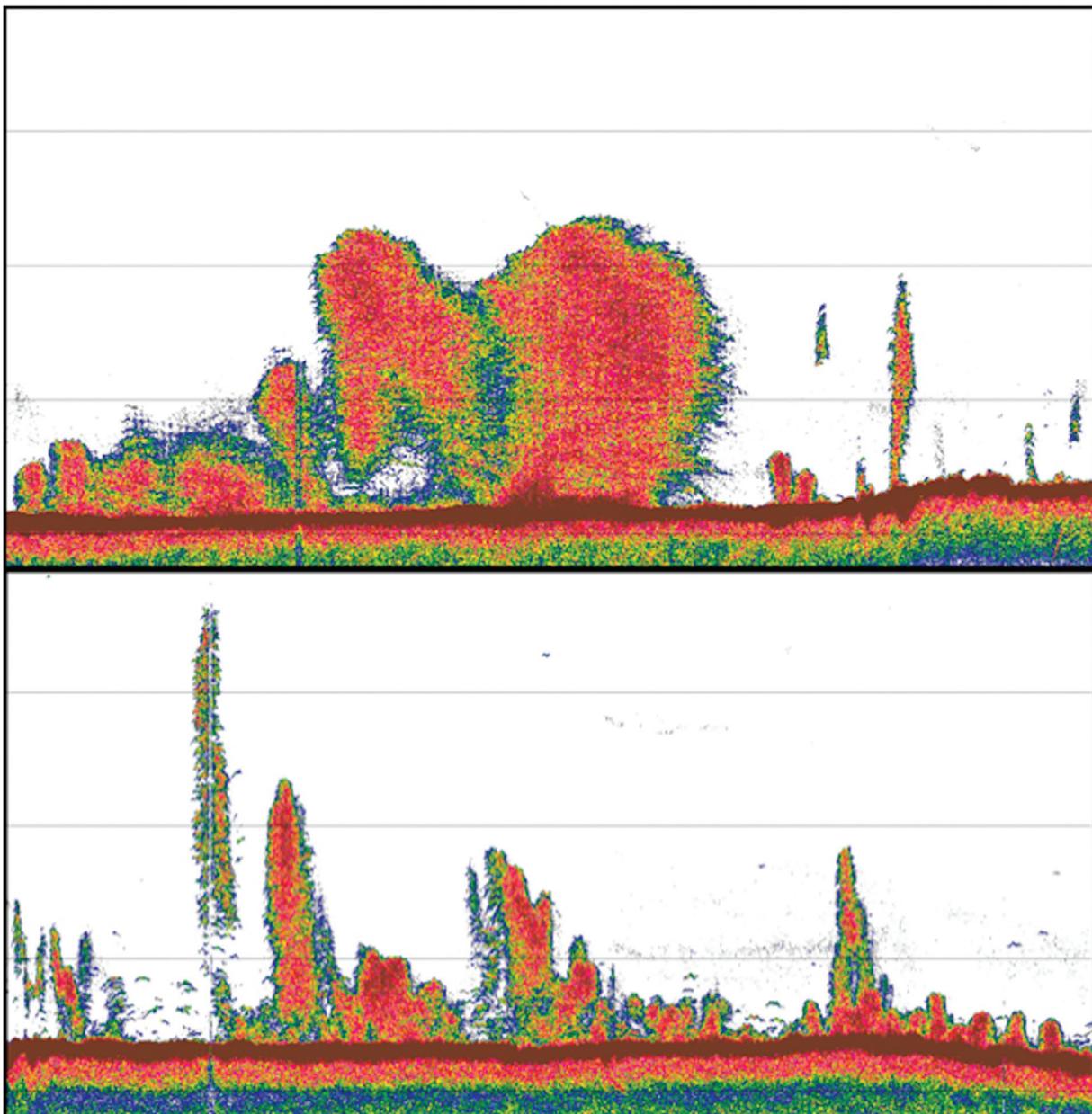
In March of 2007 and 2008, acoustic-trawl surveys were run along the outer part of the northeast Newfoundland and Labrador Shelves from the North Cape of the Grand Bank to the Hawke Channel and southern edge of the Hamilton Bank on the research vessel CCGS *Teleost* (Mello and Rose 2008, 2009; Fig. 2a shows 2008 and 2007 distributions were similar but densities much lower). Coverage was based on research suggesting that in winter cod would most likely be concentrated near the shelf break (Wroblewski et al. 1995; G.A. Rose, unpublished data).

Based on these surveys and the notion of latent rebuilding after more than a decade of little growth, more extensive acoustic-trawl systematic surveys were conducted in May of 2012–2015 from the RV *Celtic Explorer*, a research vessel that for acoustic surveys meets internationally accepted noise standards of the International Council for the Exploration of the Sea (Mitson 1995). These surveys attempted to span the continental shelf each 5 or 10 nautical miles (1 n.m. = 1.852 km) from the shelf break at 500 m depth to 200 m on the banks, at 8–10 knots (1 knot = 1.852 km·h<sup>-1</sup>). Cod were known to aggregate there prior to and during spawning and at the onset of onshore migration (e.g., Rose 1993; Wroblewski et al. 1995), nominally from 49°N to 54°N in NAFO Divisions 2J3KL. The presence of sea ice and limited ship time restricted shoreward and northward coverage to the Bonavista Corridor in 2012 and 2014 (Rose and Rowe 2015), but more complete latitudinal coverage was achieved in 2013 and 2015 (Figs. 2b, 2c). Survey coverage was thought adequate to interpolate densities (kg·m<sup>-2</sup>) to biomass (t) in the southern region each year (coverage was similar in 2012 and 2014 as in 2013 and 2015 in the Bonavista Corridor at latitudes <51°N), but in the northern regions coverage was adequate to assess biomass only in 2015. All biomass estimates should be regarded as minimal for the full stock.

Vessels were equipped with an EK echosounder (Kongsberg Simrad, Horten, Norway). Surveys from the CCGS *Teleost* used only 38 kHz, whereas on the RV *Celtic Explorer*, several frequencies were employed simultaneously (18, 38, and 120 kHz). In all cases, calibrations were conducted prior to each survey with standard spheres (Foote et al. 1987). The 38 kHz signal was used in these analyses, as it has high signal to noise ratios at all depth ranges surveyed and the acoustic properties and target strength of cod at this frequency are well known (e.g., Rose and Porter 1996; Ermolchev 2009; Rose 2009).

Standard methods of acoustic integration of 38 kHz signals were employed (Simmonds and MacLennan 2006) as in previous reports (e.g., Mello and Rose 2009; Rose and Rowe 2015). Initially, all data were edited for any extraneous noise and bottom removal, then the identified cod signal was integrated in 1 nautical mile bins employing Echoview V6 (Myriax, Hobart, Australia). All cod signal had been verified and sampled with fishing sets (see below). The procedure is straightforward — to confirm the biological characteristics of the acoustic backscatter (only cod is reported here) at the various densities identified on the echograms at sea, the backscatter is “targeted”, with the sets considered as random samples of that signal and the catch considered to represent the assigned integrated echogram backscatter. Sets targeted at cod during these surveys near invariably caught almost 100% cod, as a

**Fig. 1.** Echograms of cod in March 2008 in the Bonavista Corridor, northeast Newfoundland Shelf (38 kHz, threshold -75 dB) from CCGS *Teleost*. Seafloor is dark red, one dropped ping shows in the high column in the bottom panel. Horizontal lines are 50 m from surface, approximately 175 m from bottom shown. Top panel spans approximately 2500 m, bottom panel approximately 4000 m. Densities in these aggregations scaled by the target strength model in Rose (2009) exceeded 0.1 fish·m<sup>-3</sup> and areal biomass of 5 kg·m<sup>-2</sup>. Catch was virtually 100% cod.

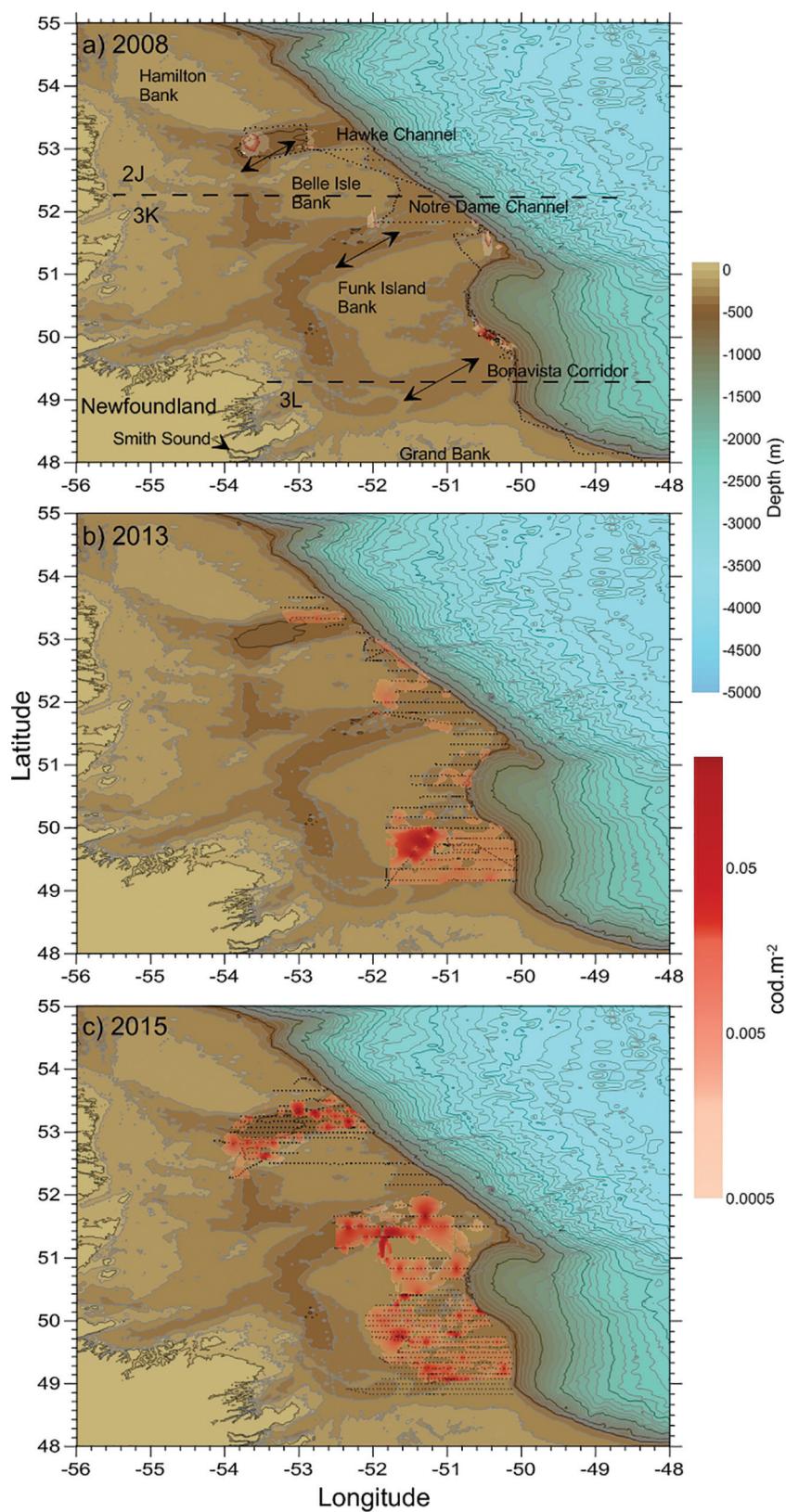


consequence of their aggregative behaviour at this time of year (e.g., Fig. 3). Only in 2008 did catch of other species approach 10%, in the other years <5%, and of these, only redfish (*Sebastodes* spp.) has a target strength comparable to cod (Gauthier and Rose 2001). Overall, the contributions of other species to the total cod-identified backscatter were thought to be minor, and a small correction was made only in 2008. A linear seafloor dead-zone correction was made based on the mean backscatter in the bottom 5 m (Ona and Mitson 1996) but seldom surpassed 15% of the total integrated backscatter from cod from the RV *Celtic Explorer* and only slightly higher from the CCGS *Teleost*. A length-based target strength model ( $TS_{dB} = 20 \log_{10} \text{length} - 67.5$ , after Rose 2009), based on mean length of cod in the catch, was used to convert backscatter to cod densities. Mean densities were determined by a bootstrapping procedure

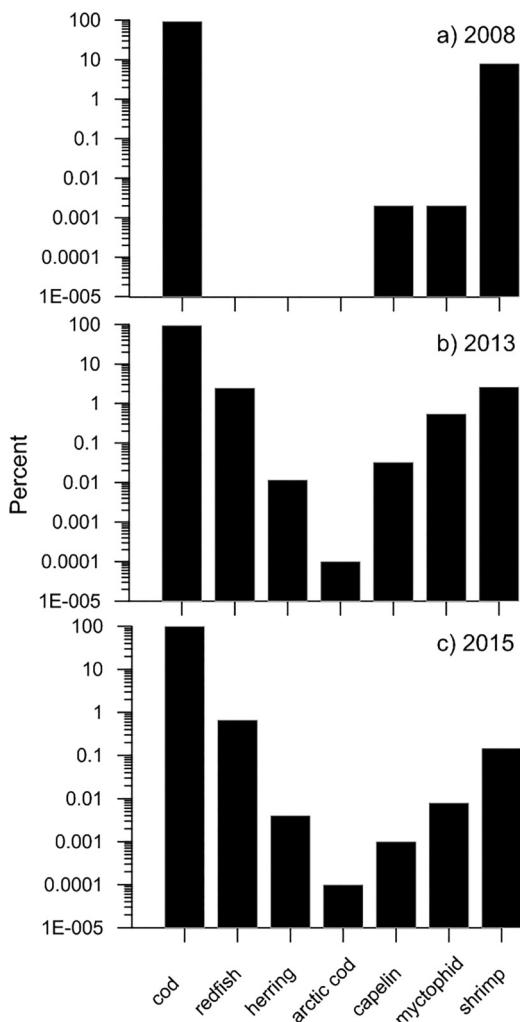
(1000 times) with  $n$  equal to the number of nonoverlapping survey measures (1 nautical mile integrated densities). Confidence intervals (95%) were determined by dropping the largest and smallest estimates (2.5% each). Biomass was calculated based on densities, mean mass of sampled fish, and the area surveyed. We note that geostatistical measures based on an equivalent area block design were also computed and gave similar but more precise results, but were not used in this work to enable direct comparisons with earlier surveys in which these methods were not feasible.

The fishing sets used to support the acoustic surveys were of short duration (5 to 15 min) using a Campelen 1800 research trawl. Experimentation with this trawl using methods developed by Walsh (1992) has shown a near-constant selectivity by length for cod >30 cm (S. Walsh, Fisheries and Oceans Canada (DFO), unpublished

**Fig. 2.** Cod density ( $\text{kg} \cdot \text{m}^{-2}$ ) in (a) March of 2008 and May of (b) 2013 and (c) 2015 and bathymetry of the northeast Newfoundland and Labrador Shelf and Banks, based on kriging of densities. Black dots represent sampling transects.



**Fig. 3.** Catch mass of species caught in trawl sets targeted at cod in March 2008 (a) and May 2013 (b) and 2015 (c). Log<sub>10</sub> scale was used to show minor components of catch. Species are Atlantic cod (*Gadus morhua*), redfish (*Sebastes* spp.), Atlantic herring (*Clupea harengus*), Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*), Myctophids, and shrimp (primarily *Pandalus borealis*).



data). Two sets made in 2012 used the larger Grande Ouverture Verticale (GOV) trawl, whose length selectivity for cod is not known but has been shown to be similar to that of commercial nets (Reid et al. 2012). Any bias introduced by using GOV data is thought to be small relative to the range of our results. All sets reported here targeted cod at various densities and were standardized to 15 min duration (Fig. 3). All fish caught were measured for total length, and a sample was selected for collection of otoliths and determinations of sex, maturity status, masses, and other measures. Age was estimated by microscopic examination of annuli of cracked otoliths using standard procedures employed by experienced cod agers approved by DFO. Comparisons of the proportions of length and age compositions were made using Wilcoxon paired rank sum tests on logit transformations (Baum 2008). von Bertalanffy models and parameters were estimated using individual measures of age and length for fish from each region during 2015 and also for fish sampled from the same regions from 1996 to 2014. Computational and statistical analyses of both acoustic and catch data employed Systat (San Jose, USA), and R (R Core Team 2014). All graphics were done in Grapher and Surfer software (Golden Software, Colorado, USA).

## Results

### Distribution

In March of 2008, for the first time since 1992, dense concentrations of cod were located in the northern part of the Bonavista Corridor around 50°N and 50°W near the shelf edge (Figs. 1, 2a, and 4a). This distribution was similar to that encountered in March of 2007 (not shown), but densities (kg·m<sup>-2</sup>) were much higher in 2008. Much lower densities were found farther north along the shelf edge in both years. Although coverage was highly restricted during these years, few cod were located anywhere else or in the comings and goings of the survey vessel from the surveyed area.

By May 2013, the distribution and relative densities of cod had increased substantially in the Bonavista Corridor and also, but to a lesser extent, farther north in the Notre Dame and Hawke channels (Figs. 2b and 4b). Fish were located primarily on the edges of the major banks that extend to the deeper waters of the channels.

In May 2015, distributions and relative densities had increased substantially in the Notre Dame Channel and in the Hawke Channel – Hamilton Bank and Belle Isle Bank region, but had declined in the Bonavista Corridor (Figs. 2c and 4c).

### Biomass

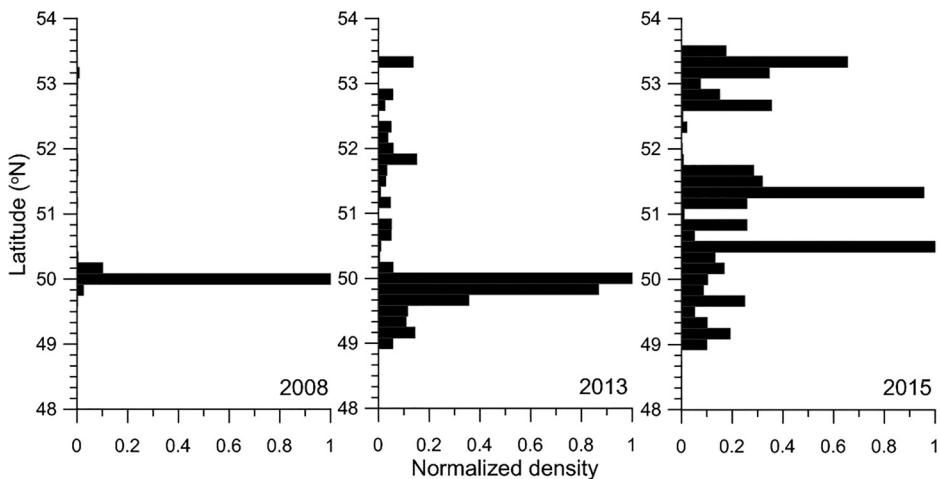
The estimated biomass in the Bonavista Corridor grew from <20 000 t in 2007 to near 240 000 t in 2014 at a rate of approximately 30% per year (Fig. 5). If stock growth had continued at the same rate without emigration, then the biomass would have reached approximately 310 000 t in 2015, but biomass declined sharply from 2014 to 2015 to 136 000 t (95% CI 93 000 – 193 000 t) (Fig. 5). In the northern areas in 2015, biomass was approximately 101 000 t (69 000 – 139 000 t) in the Notre Dame Channel and 65 000 t (31 000 – 106 000 t) in the Hawke Channel – Hamilton Bank and Belle Isle Bank region, which far exceeded expectations based on the observations made in 2008 and 2013 (no comparable biomass estimates can be made for those years as a result of diminished coverage). Of key importance, the total surveyed biomass over the range of the stock in 2015 was approximately 302 000 t (193 000 – 438 000 t), similar to that expected if growth rates in the Bonavista Corridor had been sustained.

### Size and growth

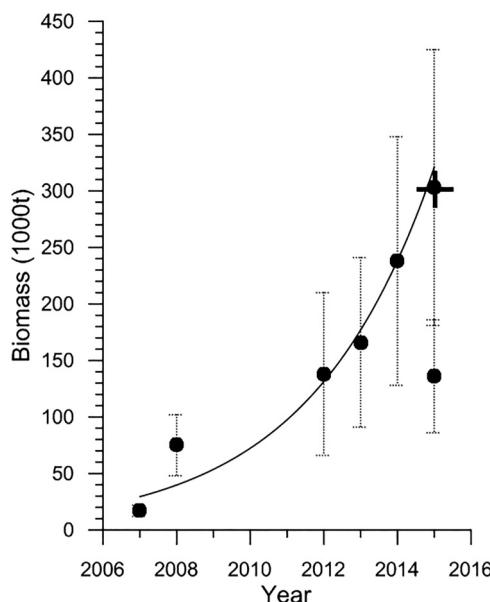
In 2008, larger cod (>60 cm) were much more common in the Bonavista Corridor than they were farther north (Figs. 6a, 6b, 6c). Nonetheless, length distributions did not differ among groups (Wilcoxon paired rank sum tests, P values > 0.05), although the Bonavista Corridor and Hawke Channel – Hamilton Bank and Belle Isle Bank groups differed at the 10% level (P = 0.09). By 2013 there had been a slight shift towards larger fish farther north, but the larger fish remained concentrated around 50°N in the Bonavista Corridor (Figs. 6d, 6e, 6f). Length distributions in 2013 differed between the Bonavista Corridor and Hawke Channel – Hamilton and Belle Isle Banks region (P < 0.05), but not between Bonavista Corridor and the Notre Dame Channel. In 2015, however, larger cod were numerous in all regions, and the size distributions among these groups did not differ (P values > 0.05; Figs. 6g, 6h, 6i).

In the years between the late 1990s and 2014, the von Bertalanffy growth parameters (Table 1) indicate larger size at age of cod in the Bonavista Corridor, especially after age 5, compared with those from Hawke Channel – Hamilton Bank and Belle Isle Bank region (Fig. 7). As a result, cod aged 9 years, the oldest located in the northern region during those years, were approximately 7 cm shorter than those in the Bonavista Corridor (Fig. 7). In the Bonavista Corridor, parameters from cod sampled in 2015 did not differ from those sampled in the earlier years (Table 1; P > 0.05). For the Hawke Channel – Hamilton Bank and Belle Isle Bank region, however, both parameters differed significantly from those measured in the earlier years (P < 0.05) and became similar to those in the Bonavista Corridor (P > 0.05; Table 1). In 2015, cod

**Fig. 4.** Relative latitudinal distributions of Northern cod during late winter – early spring in 2008, 2013, and 2015. Data were normalized to counter bias from interannual variation in sampling intensity.



**Fig. 5.** Biomass of cod in the Bonavista Corridor from 2007 to 2015 with 95% CIs (solid circles with vertical lines). Power curve represents best fit from 2007 to 2014, projected to 2015. The total biomass measured in 2015 is shown with a crossed circle.



of all ages were indistinguishable by size at age in the north and south of the stock range (Fig. 7). The Notre Dame Channel size at age data in 2015 were not significantly different from those from the other regions or years (Table 1) and were in the middle of the von Bertalanffy curves (Fig. 7), but there is greater uncertainty about that model fit, as the sample size was relatively low, with fewer larger fish, compared with the other groups. No data from the earlier period for this region were available for comparison.

#### Age classes

The progression of the relative abundance of age classes present in the Bonavista Corridor was roughly consistent during 2012–2015, with the 2004 and 2002 year classes, 8 and 10 years old in 2012, relatively strong (Figs. 8a, 8b, 8c, 8d). In 2014 and 2015, the 2011, 2009, and 2008 year classes, ages 3, 5, and 6 years, respectively in 2014, were relatively strong in the Bonavista Corridor (Figs. 8c, 8d) and also in the Hawke Channel – Hamilton Bank and Belle Isle Bank region in 2015 (Fig. 8f). In 2015, the 2011 and

2009 year classes in the Notre Dame Channel were also well represented, and, overall, the age structures did not differ among the three regions (Wilcoxon paired rank sum tests,  $P$  values  $> 0.05$ ). It is noteworthy that the age structures in the Bonavista Corridor and Hawke Channel – Hamilton Bank and Belle Isle Bank region were particularly well aligned (Figs. 8d and 8f).

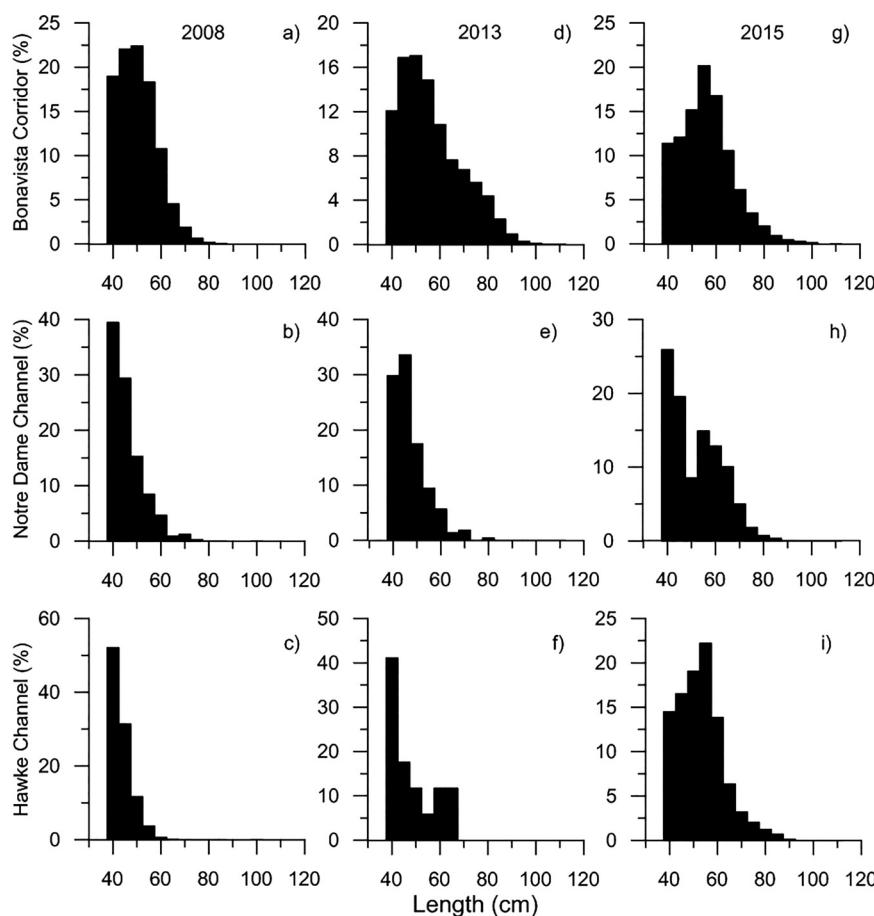
Instantaneous mortality rates ( $Z$ ) estimated for cod of ages 5–12 years in the Bonavista Corridor were low from 2012 to 2013 and from 2013 to 2014 (Fig. 9). From 2014 to 2015, however,  $Z$  became extremely high relative to those in the earlier years. If fish in the Notre Dame Channel were pooled with those in the Bonavista Corridor,  $Z$  was lower, and if fish from all surveyed regions were pooled,  $Z$  approached those measured in the Bonavista Corridor in the earlier years (Fig. 9).

#### Discussion

Several lines of evidence support the hypothesis that the aggregations of cod located in the Hawke Channel – Hamilton Bank and Belle Isle Bank region and Notre Dame Channel in the spring of 2015 were an outcome of a northward redistribution from the Bonavista Corridor, the region of initial rebuilding (Rose and Rowe 2015), and were not solely a product of local production.

A compelling line of evidence comes from data on biomass distribution. After nearly a decade of rapid annual growth at a rate approaching 30% (Rose and Rowe 2015; DFO 2016, 2017), biomass declined in the Bonavista Corridor in 2015, with concomitant increases in both the Notre Dame Channel and Hawke Channel – Hamilton Bank and Belle Isle Bank region. Moreover, a sum of the biomass in all three regions is consistent with a continuance of the growth rates evident from 2007 to 2014 in the Bonavista Corridor. In addition, the increases in size and age of fish comprising the biomass in the north are difficult to explain solely by local population growth. The older year classes present in relatively large numbers in 2015 were concentrated in the Bonavista Corridor in previous years, and with particular reference to the Bonavista Corridor and Hawke Channel – Hamilton Bank and Belle Isle Bank region, the relative size and year-class distributions were similar in 2015 after being disparate both historically and recently. Finally, low  $Z$  values assessed from 2007 to 2014 in the Bonavista Corridor are consistent with those from the DFO fall survey data (DFO 2016), but the highly negative  $Z$  between 2014 and 2015 suggests emigration and not mortality. The fishery likely had little influence on this high  $Z$ , as reported landings in 2014 and 2015 were less than 5000 t, excluding the recreational fishery. Even if these reported landings are underestimates, the fishery is highly unlikely to have been responsible for the >100 000 t decline in the

**Fig. 6.** Length frequency percentages from catches of cod in 2008, 2013, and 2015 in the Bonavista Corridor, Notre Dame, and Hawke Channel – Hamilton and Belle Isle Bank regions.



**Table 1.** von Bertalanffy parameters estimated from individual length and age data for cod from 1998 to 2014 and in 2015 from the Bonavista Corridor (BC) and 1996–2013 and 2015 from the Hawke Channel – Hamilton Bank and Belle Isle Bank region (HC) and for the Notre Dame Channel (NDC) in 2015.

Year-region	$L_{\text{inf}}$ (95% CI)	K (95% CI)	$A_0$	N
1998–2014 BC	112.2 (110.2–114.2)a	0.117 (0.113–0.121)a	0.009 (0.008–0.010)a	10 398
2015 BC	113.8 (109.7–117.9)a	0.130 (0.120–0.140)ab	0.468 (0.348–0.587)	1 284
1996–2013 HC	98.5 (88.5–108.6)b	0.128 (0.107–0.149)b	-0.098 (-0.230–0.034)a	5 369
2015 HC	128.5 (117.4–139.6)a	0.114 (0.084–0.115)a	0.108 (-0.082–0.299)a	674
2015 NDC	102.4 (93.7–111.2)ab	0.136 (0.111–0.162)ab	0.089 (-0.082–0.260)a	370

Note: Different letters indicate overlapping confidence intervals (95%).

Bonavista Corridor biomass estimate that occurred between 2014 and 2015.

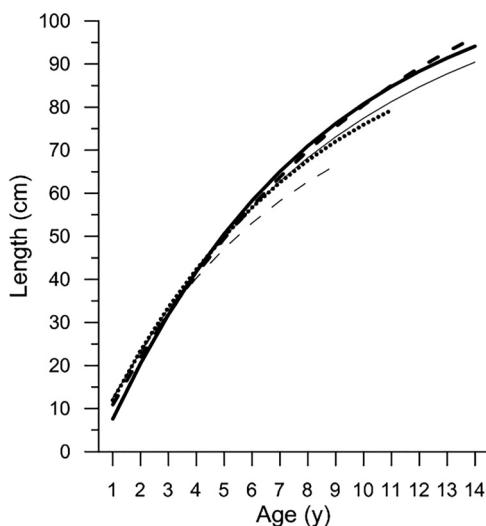
Evidence from growth rates also supports the redistribution hypothesis. The lower growth in cod from the northern regions that was evident historically (e.g., Ruivo 1957; Fleming 1960; Templeman 1966) and persisted from 1996 to 2003 (Sherwood et al. 2007) and as recently as 2014 (Cadigan and Konrad 2016; Morgan et al. 2017; this paper), was not evident in the spring of 2015. As far as we know, this is the first time that such equivalence in latitudinal growth rates has been reported within the Northern cod. Of further interest, the von Bertalanffy parameters measured in the Bonavista Corridor are comparable to those reported by Misra (1980) for Newfoundland cod captured in 1940 and 1968, which had similar values ( $L_{\text{inf}} = 112.5$  and  $K = 0.124$ ) and resultant lengths at age (e.g., approximately 70 cm at age 8). Although Misra (1980) does not report the location of his samples other than they were provided by the Newfoundland Biological Station, they almost certainly did

not come from the northern region, as little research was undertaken there in those years.

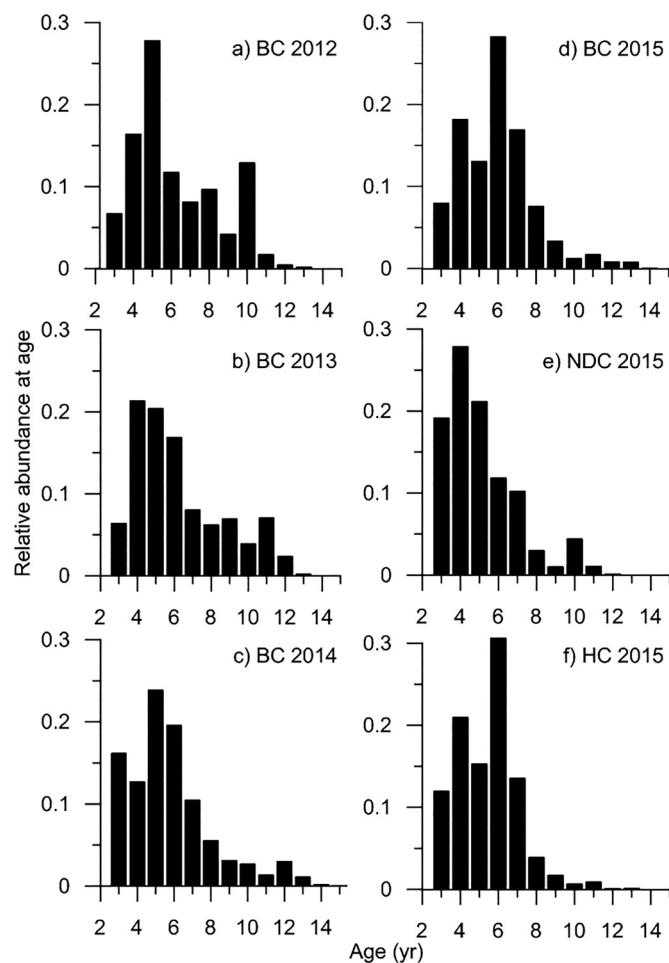
We submit that none of the present results on their own would provide conclusive evidence of redistribution, although all support that hypothesis. Nonetheless, the weight of the evidence suggests that the relatively large aggregations present in the Notre Dame Channel and in the Hawke Channel – Hamilton Bank and Belle Isle Bank region were not simply a product of local population growth but included large numbers of fish redistributed from the southern part of the stock range in the Bonavista Corridor.

Redistribution had taken place by 2015, but a more precise determination of timing remains difficult to achieve. Some speculation may be warranted until further data on distribution and coming recruitment is available. It is pertinent that some areas around the Hawke Channel that were highly populated with large cod in 2015 were surveyed in 2013 (and 2008) and showed only low densities of mostly small and immature fish mixed with relatively

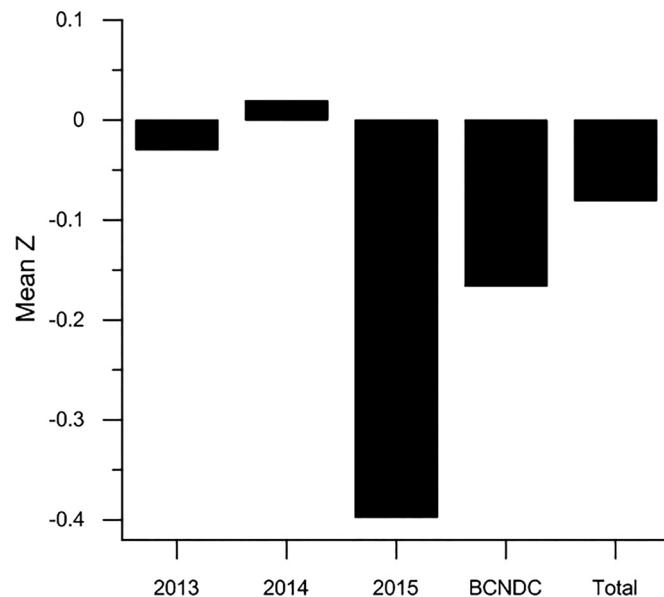
**Fig. 7.** Length at age of Northern cod from von Bertalanffy models: Bonavista Corridor 1998–2014 and 2015 (heavy solid lines), Hawke Channel – Hamilton Bank region 1996–2008 and 2015 (dashed lines), and Notre Dame Channel 2015 (dotted line). Lighter lines are from the earlier periods, darker lines from 2015.



**Fig. 8.** Relative abundance at age from acoustic-trawl surveys in the Bonavista Corridor (BC) from 2012 to 2015 and in the Notre Dame Channel (NDC) and Hawke Channel – Hamilton Bank and Belle Isle Bank region (HC) in 2015.



**Fig. 9.** Mean instantaneous mortality rates ( $Z$ ) of cod aged 5–12 in the Bonavista Corridor from 2012 to 2015 (e.g., 2013 indicates  $Z$  from 2012 to 2013). BCND (Bonavista Corridor and Notre Dame Channel) and Total are for 2015.



few adults (Mello and Rose 2009; Rose and Rowe 2015). Data from the DFO fall trawl survey are generally consistent with this interpretation, but suggest some increase in juveniles by 2012–2013, based on very low ratios of biomass to abundance (data in DFO 2016, 2017). These modest increases in juveniles could have resulted from spawning of local fish. During and after the collapse of the Northern cod in the early 1990s, with the stock at its lowest abundance, a small remnant group of spawning fish, peaking at approximately 12 000 t, remained in the Hawke Channel in the mid-1990s (Anderson and Rose 2001). Although adult abundance from then until 2015 is unknown, data from the DFO fall survey suggest it was low during this period (Brattey et al. 2010; DFO 2016), which is consistent with the 2008 and 2013 spring results. Nonetheless, it is not impossible that a low spawning biomass could have produced the modest increases in recruitment evident until 2014. The substantial increases of small fish beginning in the fall of 2014 are more difficult to reconcile with local production (DFO 2016, 2017). It seems more likely, although speculative, that this increase represented recruits from a vanguard of redistribution during 2012–2013, leading to a major shift occurring between 2014 and 2015.

Another question related to timing concerns the underlying cause of the redistribution. What triggered it? One explanation invokes a density-dependent argument, that the Bonavista Corridor density exceeded some threshold that led to expansion to relatively unoccupied former ranges to the north. Nonetheless, in 1990, the Bonavista Corridor held double the biomass assessed in 2014 (Rose 1993), but the early 1990s were very cold years and the cod were hyperaggregated there (Rose and Kukla 1999), so the comparison may be suspect. Another argument is that warming ocean conditions made northward movement more likely, as has occurred in the Barents Sea (e.g., Renaud et al. 2012). A third is that increases in feeding, especially of capelin (*Mallotus villosus*), led fish northward. We cannot distinguish among these hypotheses with present data, and it is likely that all may be involved.

How and when, if not why, a fish stock may rebuild is critical to modelling stock abundance trends and especially important for a “stock complex” or metapopulation (e.g., Cadigan 2016). The Bonavista Corridor became the core offshore area for the Northern cod during the collapse in the early 1990s and remained so for over a decade (e.g., Rose 1993; Rose and Rowe 2015; DFO 2016).

Nonetheless, from 1995 until 2008, the major extant overwintering and spawning group was located not offshore, but inshore in Smith Sound, adjacent to the Bonavista Corridor, peaking at 26 000 t during the early 2000s (Rose 2003). There is little indication from history that such a distribution of Northern cod had occurred previously (Rose 2007; Rose et al. 2011). After 2006, the Smith Sound aggregation dispersed and no longer overwintered there in large numbers, while at the same time, the cod in the Bonavista Corridor increased (Rose et al. 2011). Stock models for the offshore improved markedly under an assumption that the Smith Sound cod had dispersed to join the offshore stock (Cadigan 2016). Although confirmation through tagging that migration from the Bonavista Corridor to the inshore did not occur until 2008 (Brattey 2013), recent work using otolith microchemistry has indicated that during the 1990s the Smith Sound and Bonavista Corridor groups were essentially the same fish (Neville et al., in press). It seems evident that after 2007 and until 2014, growth in the offshore abundance occurred primarily within the Bonavista Corridor, with the formerly abundant northern groups remaining depauperate (this paper; DFO 2016). By 2014, however, an increasing number of small cod, presumably composed of ages 1 and 2 juveniles, were reported as far north as the Hamilton Bank by the DFO fall trawl survey (data in DFO 2017). In the spring of 2015, major aggregations of adult fish were located in the Notre Dame Channel and Hawke Channel – Hamilton Bank and Belle Isle Bank region (this paper; Rose and Rowe 2015; Kincaid and Rose 2017). Our hypothesis to explain this evidence is redistribution within a metapopulation, first from the southern inshore to the adjacent offshore, and then to the northern regions — basically a reversal of what occurred in the early 1990s.

Recognition of the Northern cod stock “complex” was made decades ago (e.g., Templeman 1966; Lear 1984; Taggart et al. 1994), but the independence and relative importance of its components has remained controversial. Northern components likely sustained the stock historically (May 1966; Rose 2007), but the southern components, both inshore and offshore, have maintained the stock since the decline in the early 1990s, despite evidence of some juveniles from northern spawning in the late 1990s (Anderson and Rose 2001). It is doubtful, however, if the southern components could ever produce the stock productivity once evident (Rose et al. 2000). deYoung and Rose (1993) predicted that the southern spawning observed in the early 1990s, even from 450 000 t of spawners (Rose 1993), would result in poor recruitment as a consequence of unfavourable drift of eggs and larvae (Davidson and deYoung 1995; Pepin and Helbig 1997) — this has been borne out (data in DFO 2017). As late as 2012, with the dramatic increase in spawning biomass in the Bonavista Corridor but little evidence of adults farther north, recruitment has been low. Restoration of production in this stock will almost certainly depend on the rebuilding of northern spawning components.

If the approximate timing of the range expansion and latent northern spawning increase is correct, in that major increases occurred between 2014 and 2015, then an expectation is that recruitment from 2015 could potentially be higher than in the years since the northern distribution collapsed in the early 1990s. The increase in abundance in NAFO Division 2J in the DFO fall survey in 2016 (the highest since the decline in the early 1990s), combined with the low mass reported for these fish, tends to support this contention (data in DFO 2017). The potential for greater recruitment with spawning biomass rebuilding in the north awaits verification from further data.

We believe that the present findings have application not only to the Northern cod but to other depleted stocks of cod and other species. Examples are the cod stocks off the south coast of Newfoundland (NAFO 3Ps; Lawson and Rose 2000), the Nova Scotia Banks (McKenzie and Smith 1955), and the Gulf of Maine (Ames 2004), all of which have multiple potential if not realized spawning areas. Although the Northeast Arctic cod is thought to have

two main spawning areas (Sundby and Nakken 2008), the map of spawning sites in Hjort (1914) suggests that historically there were many such areas. Some sites might have been exclusively occupied by the coastal stock, although at Lofoten, the main spawning area, both the Northeast Arctic and coastal stocks spawn, and perhaps historically that was the case elsewhere (e.g., Nordeide 1998). Pelagic species also may depend on multiple spawning sites. The Norwegian spring spawning herring (*Clupea harengus*) rebuilt from near decimation and spawning concentration in a limited coastal area of Norway to a widespread and multiple spawning site stock as it had been historically (Dragesund et al. 2008). Presumably this occurred by redistribution. Within the Northern cod ecosystem, the key forage species is capelin, whose distribution collapsed markedly and suddenly in the early 1990s (Frank et al. 1996) and in so doing almost certainly lost many of its vast number of coastal spawning sites. The lack of rebuilding in this stock may be related to a depauperate spawning distribution, especially in the north. Recent increases, albeit modest (DFO 2015), could be related to repopulation of abandoned spawning sites. If this is true, a sequential feedback mechanism is likely involved, in which core groups increase, enabling range expansion, which increases spawning potential and recruitment, which enables further range expansion. Unfortunately, there are no data that we know of available to test this notion. No matter the mechanism, increases in capelin were correlated with increased biomass and condition in the Northern cod from 2008 to 2014 (Rose and Rowe 2015), and the potential for post-2015 declines in this key prey is likely to stall productivity, which should be reflected in management of this rebuilding cod stock (Rowe and Rose 2017).

Our conclusion that the rebuilding mechanism of Northern cod is range expansion to repopulate former spawning sites, that it is not limited to local rebuilding, is critical to the management of this cod stock and likely to others that may form metapopulations such as in the North Sea (e.g., Wright et al. 2006). It is essential that the unity of Northern cod over its entire range be recognized, both inshore and offshore. Recognition includes the importance of the genetic and behavioral diversity that exists among spawning components, no matter their location or relative size (Wroblewski et al. 2005), and the likelihood of temporal discontinuities in their production (e.g., Schindler et al. 2010). Past notions that these areas may be functionally separate (e.g., Hutchings 1996; Lilly et al. 2005), and hence might be managed and harvested independently, are not supported. Furthermore, apart from small and isolated coastal groups such as in Gilbert Bay, Labrador (Hu and Wroblewski 2009), the inshore regions of the Northern cod should be included under a unified management plan. This recognizes the dominance of the diverse offshore spawning groups in supporting the fishery and the long-known early summer migration of cod to the inshore (e.g., Fleming 1960). The Northern cod stock apparently can exhibit rapid and unexpected geographical shifts as abundance and environmental conditions change. It is noteworthy that during the rapid decline in the early 1990s, cod distributions shifted south from NAFO Division 2J to 3K and 3L (Atkinson et al. 1997; Rose et al. 2000; Ruzzante et al. 2001), where they hyperaggregated (Rose and Kulka 1999). As a consequence, large numbers were caught and catch rates remained high both offshore and inshore prior to and during the total stock collapse (Rose and Kulka 1999).

Finally, and notwithstanding the importance of all spawning groups within the Northern cod metapopulation, special consideration should be given to the northern spawning areas that formerly supported the largest fisheries and are believed to be essential to full productivity in this stock. Repopulation of these spawning areas is essential to any chance of returning to historical levels of productivity, and protecting them once re-established is essential to sustaining that production. Since the spawning distribution of the Northern cod became apparent in the 1950s and 1960s (e.g., Fleming 1960; May 1966), northern spawning has

invariably coincided with relatively strong productivity, even after the major stock decline that occurred in the early 1970s, but with southern distributions, as in the 1990s, productivity has been invariably poor (DFO 2017). As stated by Rose et al. (2011), spawning in the northern region of the stock, anchored by the Hamilton Bank, is the “engine that drives the Northern cod”.

In conclusion, the present findings support the hypothesis that the recent range expansion of Northern cod has been the result of redistribution and not solely based on local production. This finding supports the hypothesis that the Northern cod comprises a metapopulation (Smedbol and Wroblewski 2002) and has critical implications for management. Movement and migration within the range of the Northern cod has been known for a long time. Over 50 years ago, May (1966) pointed out that the historically large inshore and offshore fisheries were essentially fishing the same fish. The same likely applies to fisheries prosecuted along the continental shelf from the Hamilton Bank, and historically even farther north into NAFO Division 2H, to the northern Grand Bank (Wroblewski et al. 1995; C. Bannister, former trawler captain, personal communication). The present work takes this a step further in that offshore redistribution may occur among the main spawning regions, at present to the north, the opposite of what occurred in the early 1990s (e.g., Atkinson et al. 1997). For management, we stress that far from meaning that it does not matter where the fishery is prosecuted, it perhaps matters more, as sustaining interconnected spawning components could be vital to future production. It follows that a stock assessment model that can deal with this dynamic spatial structure will be needed to fully account for the productivity and management of this stock. Further elucidation of the spatial dynamics, redistributions, and migrations within the Northern cod stock awaits additional data from ongoing studies utilizing otolith microchemistry, genetics, and data storage tagging.

## Acknowledgements

We thank the Science Branch of DFO in Newfoundland and Labrador, the Newfoundland and Labrador Department of Fisheries and Aquaculture, and the Newfoundland and Labrador Research and Development Corporation for funding ship time and personnel for the research reported here. We thank Steve Walsh for providing data on the selectivity of the Campelen research trawl and Karen Dwyer for discussions on their use by DFO. This work could not have been done without the support of the ship and scientific crews of the CCGS *Teleost* and RV *Celtic Explorer*. We regret the termination of these surveys in 2016.

## References

- Ames, T. 2004. Atlantic cod stock structure in the Gulf of Maine. *Fisheries*, **29**: 10–28. doi:[10.1577/1548-8446\(2004\)29\[10:ACSSIT\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2004)29[10:ACSSIT]2.0.CO;2).
- 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. doi:[10.1139/f01-068](https://doi.org/10.1139/f01-068).
- 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. doi:[10.1139/f96-158](https://doi.org/10.1139/f96-158).
- Baum, C.F. 2008. Modeling proportions. *Stata J.* **8**(2): 299–303. [ageconsearch.umn.edu/bitstream/122595/2/sjart\\_st0147.pdf](http://ageconsearch.umn.edu/bitstream/122595/2/sjart_st0147.pdf).
- Beacham, T.D., Brattey, J., Le, K.D., Miller, K.M., and Withler, R.E. 2002. Multiple stock structure of Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador determined from genetic variation. *ICES J. Mar. Sci.* **59**: 650–665. doi:[10.1006/jmsc.2002.1253](https://doi.org/10.1006/jmsc.2002.1253).
- Brander, K.M. 1994. The location and timing of cod spawning around the British Isles. *ICES J. Mar. Sci.* **51**: 71–89. doi:[10.1006/jmsc.1994.1007](https://doi.org/10.1006/jmsc.1994.1007).
- Brattey, J. 2013. Harvest rates and movements of cod (*Gadus morhua*) in NAFO Divs. 3KL from tagging and acoustic telemetry. *Can. Sci. Adv. Secr. Res. Doc.* **2013/104**.
- Brattey, 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. *Can. Sci. Adv. Secr. Res. Doc.* **2010/103**.
- Cadigan, N.G. 2016. A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. *Can. J. Fish. Aquat. Sci.* **73**(2): 296–308. doi:[10.1139/cjfas-2015-0047](https://doi.org/10.1139/cjfas-2015-0047).
- Cadigan, N.G., and Konrad, C. 2016. A cohort time-series Von Bertalanffy growth model for Northern cod (*Gadus morhua*) and estimation of the age of tagged cod. *Can. Sci. Adv. Secr. Res. Doc.* **2016/017**.
- Davidson, F.J.M., and deYoung, B. 1995. Modelling advection of cod eggs and larvae on the Newfoundland Shelf. *Fish. Oceanogr.* **4**: 33–51. doi:[10.1111/j.1365-2419.1995.tb00059.x](https://doi.org/10.1111/j.1365-2419.1995.tb00059.x).
- deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. *Can. J. Fish. Aquat. Sci.* **50**(1): 2729–2741. doi:[10.1139/f93-298](https://doi.org/10.1139/f93-298).
- DFO. 2015. Assessment of capelin in subarea 2 and Divisions 3KL in 2015. *Can. Sci. Adv. Secr. Adv. Rep.* **2015/036**.
- DFO. 2016. Stock assessment of Northern cod (NAFO Divs. 2J3KL) in 2016. *DFO Can. Sci. Advis. Sec. Rep.* **2016/026**.
- DFO. 2017. Northern (NAFO Divs. 2J3KL) cod stock update. *Can. Sci. Adv. Secr. Sci. Response* **2017/034**.
- Dragesund, O., Ostvedt, O.-J., and Toresen, R. 2008. Norwegian spring-spawning herring: history of fisheries, biology and stock assessment. In *Norwegian spring-spawning herring and Northeast Arctic Cod, 100 years of research and management*. Edited by O. Nakken. Tapir Academic Press, Trondheim, Norway. pp. 41–82.
- Ermolchev, V.A. 2009. Methods and results of in situ target-strength measurements of Atlantic cod (*Gadus morhua*) during combined trawl-acoustic surveys. *ICES J. Mar. Sci.* **66**: 1225–1232. doi:[10.1093/icesjms/fsp024](https://doi.org/10.1093/icesjms/fsp024).
- Fleming, A.M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947–1950. *Fish. Res. Board Can.* **17**(6): 775–809. doi:[10.1139/f60-065](https://doi.org/10.1139/f60-065).
- Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., and Simmonds, E.J. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. *ICES Coop. Res. Doc.* No. 144.
- Fox, C.J., Taylor, M., Dickey-Collas, M., Fossum, P., Kraus, G., Rohlfs, N., Munk, P., van Damme, J.G., Bolle, I.J., Maxwell, D.L., and Wright, P.J. 2008. Mapping the spawning grounds of North Sea cod (*Gadus morhua*) by direct and indirect means. *Proc. R. Soc. B Biol. Sci.* **275**: 1543–1546. doi:[10.1098/rspb.2008.0201](https://doi.org/10.1098/rspb.2008.0201).
- Frank, K.T., Carscadden, J.E., and Simon, J.E. 1996. Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. *Can. J. Fish. Aquat. Sci.* **53**(7): 1473–1486. doi:[10.1139/f96-078](https://doi.org/10.1139/f96-078).
- Gauthier, S., and Rose, G.A. 2001. Target strength of encaged Atlantic redfish (*Sebastes* spp.). *ICES J. Mar. Sci.* **58**: 562–568. doi:[10.1006/jmsc.2001.1066](https://doi.org/10.1006/jmsc.2001.1066).
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. *Conseil Permanent International pour L'Exploration de la Mer Rapports et Proces-Verbaux*. Vol. XX.
- Hu, L., and Wroblewski, J. 2009. Conserving a subpopulation of the northern Atlantic cod metapopulation with a marine protected area. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **19**(2): 178–193. doi:[10.1002/aqc.994](https://doi.org/10.1002/aqc.994).
- Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Can. J. Fish. Aquat. Sci.* **53**(5): 943–962. doi:[10.1139/f96-097](https://doi.org/10.1139/f96-097).
- Kincaid, K., and Rose, G.A. 2017. Effects of closing bottom trawling on fisheries, biodiversity, and fishing communities in a boreal marine ecosystem: the Hawk Bank off Labrador, Canada. *Can. J. Fish. Aquat. Sci.* **74**(9): 1490–1502. doi:[10.1139/cjfas-2016-0343](https://doi.org/10.1139/cjfas-2016-0343).
- Kulka, D.W., Wroblewski, J.S., and Narayanan, S. 1995. Recent changes in the winter distribution and movements of northern Atlantic cod (*Gadus morhua*) on the Newfoundland–Labrador Shelf. *ICES J. Mar. Sci.* **52**(6): 889–902. doi:[10.1006/jmsc.1995.0086](https://doi.org/10.1006/jmsc.1995.0086).
- Lawson, G.L., and Rose, G.A. 2000. Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Can. J. Fish. Aquat. Sci.* **57**(5): 1011–1024. doi:[10.1139/f00-026](https://doi.org/10.1139/f00-026).
- Lear, H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. *J. Northw. Atl. Fish. Sci.* **5**(2): 143–159. doi:[10.2960/J.v5.a19](https://doi.org/10.2960/J.v5.a19).
- Lilly, G., Brattey, J., Cadigan, N.G., Healey, B.P., and Murphy, E.F. 2005. Assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J3KL in March 2005. *Can. Sci. Adv. Secr. Res. Doc.* **2005/018**.
- MacCall, A.D. 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program, USA.
- May, A.W. 1966. Effect of offshore fishing on the inshore Labrador cod fishery. *International Commission for the Northwest Atlantic Fisheries Res. Doc.* **66-23**.
- McKenzie, R.A., and Smith, G.F.M. 1955. Atlantic cod populations along the southern Canadian mainland as shown by vertebral count studies. *J. Fish. Res. Board Can.* **12**(5): 698–705. doi:[10.1139/f55-037](https://doi.org/10.1139/f55-037).
- Mello, L.G., and Rose, G.A. 2008. An acoustic-trawl survey of offshore overwintering northern cod, February–March 2007. *Can. Sci. Adv. Secr. Res. Doc.* **2008/048**.
- Mello, L.G., and Rose, G.A. 2009. An acoustic-trawl survey of offshore overwintering northern cod, February–March 2008. *Can. Sci. Adv. Secr. Res. Doc.* **2009/099**.

- Misra, R.K. 1980. Statistical comparisons of several growth curves of the von Bertalanffy type. *Can. J. Fish. Aquat. Sci.* **37**(6): 920–926. doi:[10.1139/f80-121](https://doi.org/10.1139/f80-121).
- Mitson, R. 1995. Underwater noise of research vessels. *ICES Res. Rep.* **209**.
- Morgan, M.J., Koen-Alonso, M., Rideout, R.M., Buren, A.D., and Maddock Parsons, D. 2017. Growth and condition in relation to the lack of recovery of northern cod. *ICES J. Mar. Sci.* doi:[10.1093/icesjms/fsx166](https://doi.org/10.1093/icesjms/fsx166).
- Neville, V., Rose, G.A., Rowe, S., Jamieson, R., and Piercy, G. Otolith chemistry and redistributions of northern cod: evidence of Smith Sound–Bonavista Corridor connectivity. *Can. J. Fish. Aquat. Sci.* [In press.] doi:[10.1139/cjfas-2017-0357](https://doi.org/10.1139/cjfas-2017-0357).
- Nordeide, J.T. 1998. Coastal cod and North-East Arctic cod — do they mingle at the spawning grounds in Lofoten? *Sarsia*, **83**: 373–379. doi:[10.1080/00364827.1998.10413696](https://doi.org/10.1080/00364827.1998.10413696).
- Ona, E., and Mitson, R.B. 1996. Acoustic sampling and signal processing near the seabed: The deadzone revisited. *ICES J. Mar. Sci.* **53**: 677–690. doi:[10.1006/jmsc.1996.0087](https://doi.org/10.1006/jmsc.1996.0087).
- Opdal, A.F. 2010. Fisheries change spawning ground distribution of northeast Arctic cod. *R. Soc. Biol. Lett.* **6**: 261–264. doi:[10.1098/rsbl.2009.0789](https://doi.org/10.1098/rsbl.2009.0789).
- Pepin, P., and Helbig, J.A. 1997. Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland Shelf. *Can. J. Fish. Aquat. Sci.* **54**(3): 670–685. doi:[10.1139/f96-317](https://doi.org/10.1139/f96-317).
- R Core Team. 2014. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>.
- Reid, D.G., Kynoch, R.J., Penny, I., Summerbell, K., Edridge, A., and O'Neill, F. 2012. A comparison of the GOV survey trawl with a commercial whitefish trawl. *Fish. Res.* **121**: 136–143. doi:[10.1016/j.fishres.2012.01.021](https://doi.org/10.1016/j.fishres.2012.01.021).
- Renaud, P.E., Berge, J., Varpe, O., Jonne, O.J., Nahrung, J., Ottesen, C., and Hallanger, I. 2012. Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? *Polar Biol.* **35**: 401–412. doi:[10.1007/s00300-011-1085-z](https://doi.org/10.1007/s00300-011-1085-z).
- Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. *Nature*, **366**: 458–461. doi:[10.1038/366458a0](https://doi.org/10.1038/366458a0).
- Rose, G.A. 2003. Monitoring coastal northern cod: towards an optimal survey of Smith Sound, Newfoundland. *ICES J. Mar. Sci.* **60**: 453–462. doi:[10.1016/S1054-3139\(03\)00044-4](https://doi.org/10.1016/S1054-3139(03)00044-4).
- Rose, G.A. 2007. Cod: the ecological history of the North Atlantic fisheries. Breakwater Books, St. John's.
- Rose, G.A. 2009. Variations in the target strength of Atlantic cod during vertical migration. *ICES J. Mar. Sci.* **66**: 1205–1211. doi:[10.1093/icesjms/fsp085](https://doi.org/10.1093/icesjms/fsp085).
- 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. *Can. J. Fish. Aquat. Sci.* **56**(S1): 118–127. doi:[10.1139/f99-207](https://doi.org/10.1139/f99-207).
- Rose, G.A., and Porter, D.R. 1996. Target-strength studies on Atlantic cod (*Gadus morhua*) in Newfoundland waters. *ICES J. Mar. Sci.* **53**: 259–265. doi:[10.1006/jmsc.1996.0032](https://doi.org/10.1006/jmsc.1996.0032).
- Rose, G.A., and Rowe, S. 2015. Northern cod comeback. *Can. J. Fish. Aquat. Sci.* **72**(12): 1789–1798. doi:[10.1139/cjfas-2015-0346](https://doi.org/10.1139/cjfas-2015-0346).
- 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. *Can. J. Fish. Aquat. Sci.* **57**(3): 644–663. doi:[10.1139/f00-004](https://doi.org/10.1139/f00-004).
- Rose, G.A., Nelson, R.J., and Mello, L.G.S. 2011. Isolation or metapopulation: whence and whither the Smith Sound cod? *Can. J. Fish. Aquat. Sci.* **68**(1): 152–169. doi:[10.1139/F10-135](https://doi.org/10.1139/F10-135).
- Rowe, S., and Rose, G.A. 2017. Cod stocks: Don't derail cod's comeback in Canada. *Nature*, **545**: 412. doi:[10.1038/545412b](https://doi.org/10.1038/545412b). PMID:[28541331](#).
- Ruivo, M. 1957. Portuguese research report, 1956. *Int. Comm. NW Atl. Fish. Ann. Proc.* **7**: 48–57.
- Ruzzante, D.E., Taggart, C.T., Cook, D., and Goddard, S. 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. *Can. J. Fish. Aquat. Sci.* **53**(3): 634–645. doi:[10.1139/f95-228](https://doi.org/10.1139/f95-228).
- 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. doi:[10.1023/A:1012247213644](https://doi.org/10.1023/A:1012247213644).
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, **465**: 609–612. doi:[10.1038/nature09060](https://doi.org/10.1038/nature09060). PMID:[20520713](#).
- Sherwood, G.D., Rideout, R.M., Fudge, S.B., and Rose, G.A. 2007. Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): insights from stable carbon isotopes ( $\delta^{13}\text{C}$ ). *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **54**(23–26): 2794–2809. doi:[10.1016/j.dsr2.2007.08.007](https://doi.org/10.1016/j.dsr2.2007.08.007).
- Simmonds, J., and MacLennan, D.N. 2006. Fisheries acoustics: theory and practice. 2nd ed. Wiley.
- Smedbol, R.K., and Wroblewski, J.S. 2002. Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fish. Res.* **55**: 161–174. doi:[10.1016/S0165-7836\(01\)00289-2](https://doi.org/10.1016/S0165-7836(01)00289-2).
- Smedbol, R.K., McPherson, A., Hansen, M.M., and Kenchington, E. 2002. Myths and moderation in marine ‘metapopulations’. *Fish Fish.* **3**: 20–35. doi:[10.1046/j.1467-2979.2002.00062.x](https://doi.org/10.1046/j.1467-2979.2002.00062.x).
- Sundby, S., and Nakken, O. 2008. Spatial shifts in spawning habitats of Arctic-Norwegian cod related to multidecadal oscillations and climate change. *ICES J. Mar. Sci.* **65**: 953–962. doi:[10.1093/icesjms/fsn085](https://doi.org/10.1093/icesjms/fsn085).
- Taggart, C.T., Penney, P., Barrowman, N., and George, C. 1994. The 1954–1993 Newfoundland cod-tagging database: statistical summaries and spatial-temporal distributions. *Can. Tech. Rep. Fish. Aquat. Sci.* **2042**.
- Templeman, W.T. 1966. Marine Resources of Newfoundland. *Bull. Fish. Res. Bd. Can.* No. 154.
- Walsh, S.J. 1992. Size-dependent selection at the footgear of a groundfish survey trawl. *N. Am. J. Fish. Manage.* **12**: 625–633. doi:[10.1577/1548-8675\(1992\)012<625:SDSATF>2.3.CO;2](https://doi.org/10.1577/1548-8675(1992)012<625:SDSATF>2.3.CO;2).
- Wright, P.J., Neat, F.C., Gibb, F.M., Gibb, I.M., and Thordarson, H. 2006. Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J. Fish. Biol.* **69**(Suppl. C): 181–199. doi:[10.1111/j.1095-8649.2006.01262.x](https://doi.org/10.1111/j.1095-8649.2006.01262.x).
- Wroblewski, J., Kulka, D.W., Narayanan, S., Oake, A.M., Collier, A.G., and McGrath, G.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. *Fish. Oceanogr.* **4**(2): 128–146. doi:[10.1111/j.1365-2419.1995.tb00067.x](https://doi.org/10.1111/j.1365-2419.1995.tb00067.x).
- Wroblewski, J., Neis, B., and Gosse, K. 2005. Inshore stocks of Atlantic cod are important for rebuilding the East Coast fishery. *Coast. Manage.* **33**(4): 411–432. doi:[10.1080/08920750500217930](https://doi.org/10.1080/08920750500217930).