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

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Manuscripts

1   **Does redistribution or local growth underpin rebuilding of**
2   **Canada's Northern cod?**
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17   **Abstract**
18
19   The stock structure of Canada's Northern cod, the largest of many depleted groundfish

20   stocks having multiple spawning areas, is rebuilding by redistribution and not solely by

21   local population growth. In 2007-2008, late winter acoustic surveys suggested initial

22   rebuilding in the southern-most part of the offshore range (Bonavista Corridor, NAFO

23   Divisions 3KL), likely including fish dispersing from the inshore. Thereafter,

24   acoustically-determined biomass increases averaged 30% per annum (to near 240 000 t in

25   2014). In contrast, formerly dominant stock areas farther north retained few fish, mostly

26   juveniles. In 2015, however, biomass in the northern stock range (NAFO Division 2J)

27   reached 65 000 t and mid-north Notre Dame Channel (3K) reached 101 000 t, with

28   Bonavista Corridor declining to 136 000 t. Biomass pooled over all surveyed regions

29   totaled 302 000 t, consistent with sustained 30% growth. Latitudinal gradients in cod size,

30   age distributions and individual growth existed both historically and recently, but not in

31   2015. The evidence suggests that the rapid increases of depopulated northern groups

32   resulted from redistribution from the south within a metapopulation.

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38 **Introduction**

39 It has long been known that many fish stocks have multiple spawning and aggregation

40 areas (Hjort 1914; McKenzie and Smith 1955; Templeman 1966; Brander 1994).

41 Spawning area occupation may change as a result of environmental changes or the

42 impacts of harvesting (Sundby and Nakken 2008; Dragesund et al. 2008; Opdal 2010). In

43 species that aggregate, changes in abundance typically do not occur uniformly over the

44 stock area as a result of density-dependent range expansion (e.g., MacCall 1990), but

45 perhaps of key importance, depleted stocks often become concentrated in fewer areas

46 (Atkinson et al. 1997; Ames 2004; Fox et al. 2008; Dragesund et al. 2008). Restoring

47 productivity in these depleted stocks may require repopulation of diminished spawning

48 sites and capacity, hence management is predicated on how rebuilding might occur, or

49 indeed if it is possible.

50

51 The Northern cod (*Gadus morhua*) off the northeast coast of Newfoundland and Labrador

52 (Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL) was historically

53 the largest of many depleted cod stocks having multiple spawning areas (e.g., Ames 2004;

54 Rose 2007; Fox et al. 2008). After almost two decades of depletion, recent increases in

55 the Northern cod have been evident, offering the opportunity to study how rebuilding

56 might occur (Rose and Rowe 2015). It was evident that increases were first evident in the

57 southern region, termed the Bonavista Corridor (overlaps NAFO Divisions 3KL

58 boundary), first in 2007 and then more substantially in 2008 (Mello and Rose 2008,

59 2009). This was the same area that held the last large concentrations of fish in the early

60 1990s (Rose 1993). By 2015, increases in biomass and age structure were also evident in

61   the northern reaches of the stock in the Hawke Channel and outer portions of the Belle

62   Isle and Hamilton Banks (NAFO 2J) (Rose and Rowe 2015; DFO 2016; Kincaid and

63   Rose 2017). A key question posed by Rose and Rowe (2015) concerned the origin and

64   ontogeny of the fish that formed these increasing aggregations and their latent spawning

65   capacity, in particular those in the banks to the north (Templeman 1966). In essence were

66   these increases solely a result of local population growth or were redistributions

67   occurring?

68

69   How the Northern cod might rebuild, or indeed if it would, has been debated since its

70   collapse. It was argued early on that expansion and recolonization was possible within a

71   putative metapopulation in which subgroups had been depleted (Smedbol and

72   Wroblewski 2002; Smedbol et al. 2002). If the Northern cod comprised a metapopulation,

73   fostering growth in extant groups, particularly but not exclusively the Smith Sound group,

74   was of paramount importance (Anderson and Rose 2001; Rose 2003; Rose et al. 2011).

75   On the other hand, some genetic studies suggested that redistribution from the inshore

76   was unlikely, and that offshore rebuilding, if it occurred at all, was more likely to result

77   from local production of what were thought to be functionally distinct if near extirpated

78   groups (Ruzzante et al. 1996; Beacham et al. 2002; Lilly et al. 2005). Such reasoning

79   influenced management decisions to reopen inshore fisheries in the 1990s. More recently,

80   new evidence has suggested that redistribution from the inshore to offshore has taken

81   place. The Smith Sound cod comprised the largest known extant spawning biomass of the

82   Northern cod complex during 1995-2006 (Rose 2003), but dispersed thereafter

83   concurrent with a sudden and unexpected increase in the offshore biomass in the adjacent

84   Bonavista Corridor (Rose et al. 2011; Rose and Rowe 2015; Cadigan 2016). Nonetheless,

85   it remained uncertain whether or not larger scale redistribution within the offshore could

86   occur, particularly to the north in the region around the Hawke Channel and surrounding

87   banks where formerly large components of the Northern cod overwintered and spawned

88   (May 1966; Templeman 1966; Lear 1984; Rose 2007). We hypothesized that the

89   observed abundance of adult fish in the northern regions (Rose and Rowe 2015) resulted

90   at least in part not from local stock growth but from redistribution within a putative

91   metapopulation (Smedbol and Wroblewski 2002; Rose et al. 2011). According to this

92   hypothesis, increases in the north resulted from redistribution of the increasing numbers

93   of cod present in the southern range of the stock since 2007 (Mello and Rose 2009; Rose

94   and Rowe 2015; DFO 2016, 2017).

95

96   Regaining a broad northern range distribution is key to recovery of this once great stock

97   and hence to management. The importance of northern spawning to production and

98   recruitment has been postulated for many years, as a consequence of the strong southerly

99   flows of the Labrador Current over the continental shelf (Templeman 1966; deYoung and

100   Rose 1993; Davidson and deYoung 1995). An oceanographic drifter study showed that

101   northern spawning would enable transport of reproductive products southward and

102   shoreward to the shelf and northeast coast of Newfoundland (Pepin and Helbig 1997).

103   Empirical evidence that followed demonstrated the link between northern spawning in

104   and around the Hawke Channel and juvenile cod distribution and abundance to the south

105   across a wide region of the northeast Newfoundland Shelf and coastal areas (Anderson

106   and Rose 2001).

107

108   The objectives of this paper are to test several demographic and life history expectations

109   of the redistribution hypothesis. Of key diagnostic importance, after a decade of stock

110   growth at a rate approaching 30% (Rose and Rowe 2015, DFO 2016), biomass in the

111   Bonavista Corridor should have declined, or at least slowed if redistribution had occurred.

112   In addition, the strong year classes known to be present in the Bonavista Corridor should

113   be prominent in the north. Also, the historically consistent differences in size at age and

114   individual growth rates between the southern and northern regions (Ruivo 1957; Fleming

115   1960; Templeman 1966; Sherwood et al. 2007; Morgan et al. 2017) should not be evident.

116   These traits were thought to be diagnostic of residency history and thus provide means to

117   either advance or reject the redistribution hypothesis.

118

119   **Methods**

120   Acoustic surveys of the Northern cod were conducted in March of 2007 and 2008 and

121   May of 2012 to 2015, using trawling to confirm biological characteristics of acoustic

122   backscatter, based on methods developed in spring surveys since 1990 (e.g., Rose 1993;

123   Rose and Rowe 2015). These surveys were designed to coincide with the time of

124   maximum cod aggregation, as cod (mostly age 4+ years) overwintered near the shelf

125   break (Kulka et al. 1995) then spawned in shallower waters on the shelf (Rose 1993).

126   Aggregations during this period are typically contracted laterally but expanded vertically,

127   at times to >100 m off bottom, and only rarely mixed with other species, making

128   delineation of cod on echograms relatively simple and detection rates high. These factors

129   make Northern cod highly amenable to acoustic-trawl survey methods at this time of year

130   (Fig. 1 shows echograms of aggregations in 2008 – the first such large aggregations

131   encountered since 1992 and a sign that the potential for rebuilding was latent).

132

133   In March of 2007 and 2008, acoustic-trawl surveys were run along the outer part of the

134   northeast Newfoundland and Labrador Shelves from the North Cape of the Grand Bank

135   to the Hawke Channel and southern edge of the Hamilton Bank on the research vessel

136   CCGS *Teleost* (Mello and Rose 2008, 2009; Fig. 2a shows 2008, 2007 distributions were

137   similar but densities much lower). Coverage was based on research suggesting that in

138   winter cod would most likely be concentrated near the shelf break (Wroblewski et al.

139   1995, G.A. Rose unpublished data).

140

141   Based on these surveys and the notion of latent rebuilding after more than a decade of

142   little growth, more extensive acoustic-trawl systematic surveys were conducted in May of

143   2012-2015 from the RV *Celtic Explorer*, a research vessel that for acoustic surveys meets

144   internationally accepted noise standards of the International Council for the Exploration

145   of the Sea (Mitson 1995). These surveys attempted to span the continental shelf each 5 or

146   10 nautical miles from the shelf break at 500m depth to 200m on the banks, at 8-10 knots.

147   Cod were known to aggregate there prior to and during spawning and the onset of

148   onshore migration (e.g., Rose 1993, Wroblewski et al. 1995), nominally from 49° N to

149   54° N in NAFO Divisions 2J3KL. The presence of sea ice and limited ship-time restricted

150   shoreward and northward coverage to the Bonavista Corridor in 2012 and 2014 (Rose

151   and Rowe 2015), but more complete latitudinal coverage was achieved in 2013 and 2015

152   (Fig. 2 b,c). Survey coverage was thought adequate to interpolate densities (kg.m^{-2}) to

153   biomass (t) in the southern region each year (coverage was similar in 2012 and 2014 as in

154   2013 and 2015 in the Bonavista Corridor at latitudes < 51°N), but in the northern regions

155   coverage was adequate to assess biomass only in 2015. All biomass estimates should be

156   regarded as minimal for the full stock.

157

158   Vessels were equipped with an EK60 echosounder (Kongsberg Simrad, Horton, Norway).

159   Surveys from the CCGS *Teleost* used only 38 kHz, whereas on the RV *Celtic Explorer*,

160   several frequencies were employed simultaneously (18, 38, and 120 kHz). In all cases,

161   calibrations were conducted prior to each survey with standard spheres (Foote et al. 1987).

162   The 38 kHz signal was used in these analyses as it has high signal to noise ratios at all

163   depth ranges surveyed and the acoustic properties and target strength of cod at this

164   frequency are well known (e.g. Rose and Porter 1996; Ermolchev 2009; Rose 2009).

165

166

167   Standard methods of acoustic integration of 38 kHz signals were employed (Simmonds

168   and MacLennan 2006) as in previous reports (e.g., Mello and Rose 2009; Rose and Rowe

169   2015). Initially, all data were edited for any extraneous noise and bottom removal, then

170   identified cod signal was integrated in 1 nautical mile bins employing Echoview V6

171   (Myriax, Hobart, Australia). All cod signal had been verified and sampled with fishing

172   sets (see below). The procedure is straightforward – to confirm the biological

173   characteristics of the acoustic backscatter (only cod is reported here) at the various

174   densities identified on the echograms at sea, the backscatter is "targeted", with the sets

175   considered as random samples of that signal, and the catch considered to represent the

176   assigned integrated echogram backscatter. Sets targeted at cod during these surveys near-

177   invariably caught almost 100% cod, as a consequence of their aggregative behaviour at

178   this time of year (e.g., Fig. 3). Only in 2008 did catch of other species approach 10%, in

179   the other years <5%, and of these, only redfish (*Sebastes* spp.) has a target strength

180   comparable to cod (Gauthier and Rose 2001). Overall, the contributions of other species

181   to the total cod-identified backscatter was thought to be minor, and a small correction

182   was made only in 2008. A linear seafloor dead-zone correction was made based on the

183   mean backscatter in the bottom 5 m (Ona and Mitson 1996) but seldom surpassed 15% of

184   the total integrated backscatter from cod from the RV *Celtic Explorer* and only slightly

185   higher from the CCGS *Teleost*. A length-based target strength model ($TS_{dB} = 20 \log_{10}$

186   length – 67.5, after Rose 2009), based on mean length of cod in the catch, was used to

187   convert backscatter to cod densities. Mean densities were determined by a bootstrapping

188   procedure (1000 times) with n equal to the number of non-overlapping survey measures

189   (1 nautical mile [1852 m] integrated densities). Confidence intervals (95%) were

190   determined by dropping the largest and smallest estimates (2.5% each). Biomass was

191   calculated based on densities, mean weight of sampled fish and the area surveyed. We

192   note that geostatistical measures based on an equivalent area block design were also

193   computed and gave similar but more precise results, but were not used in this work to

194   enable direct comparisons with earlier surveys in which these methods were not feasible.

195

196   The fishing sets used to support the acoustic surveys were of short duration (5 to 15

197   minutes) using a Campelen 1800 research trawl. Experimentation with this trawl using

198   methods developed by Walsh (1992) has shown a near-constant selectivity by length for

199   cod > 30 cm (Steve Walsh, Department of Fisheries and Oceans, unpublished data). Two

200   sets made in 2012 used the larger GOV trawl whose length selectivity for cod is not

201   known but has been shown to be similar to that of commercial nets (Reid et al. 2012).

202   Any bias introduced by using GOV data is thought to small relative to the range of our

203   results. All sets reported here targeted cod at various densities and were standardized to

204   15-minute duration (Fig. 3). All fish caught were measured for total length and a sample

205   was selected for collection of otoliths and determinations of sex, maturity status, weights

206   and other measures. Age was estimated by microscopic examination of annuli of cracked

207   otoliths using standard procedures employed by experienced cod agers approved by the

208   Canadian Department of Fisheries and Oceans (DFO). Comparisons of the proportions of

209   length and age compositions were made using Wilcoxon paired rank sum tests on logit

210   transformations (Baum 2008). Von Bertalanffy models and parameters were estimated

211   using individual measures of age and length for fish from each region during 2015 and

212   also for fish sampled from the same regions from 1996 to 2014. Computational and

213   statistical analyses of both acoustic and catch data employed Systat (San Jose, USA), and

214   R (R Core Team 2014). All graphics were done in Grapher and Surfer software (Golden

215   Software, Colorado, USA).

216

217   **Results**

218   **Distribution**

219   In March of 2008, for the first time since 1992, dense concentrations of cod were located

220   in the northern part of the Bonavista Corridor around 50°N and 50°W near the shelf edge

221   (Figs. 1, 2a and 4a). This distribution was similar to that encountered in March of 2007

222   (not shown) but densities (kg.m^{-2}) were much higher in 2008. Much lower densities were

223   found farther north along the shelf edge in both years. Although coverage was highly

224   restricted during these years, few cod were located anywhere else or in the comings and

225   goings of the survey vessel from the surveyed area.

226

227   By May 2013, the distribution and relative densities of cod had increased substantially in

228   the Bonavista Corridor and also, but to a lesser extent, farther north in the Notre Dame

229   and Hawke Channels (Figs. 2b and 4b). Fish were located primarily on the edges of the

230   major banks that extend to the deeper waters of the channels.

231

232   In May 2015, distributions and relative densities had increased substantially in the Notre

233   Dame Channel and in the Hawke Channel-Hamilton Bank and Belle Isle Bank region, but

234   had declined in the Bonavista Corridor (Figs. 2c and 4c).

235

236   **Biomass**

237   The estimated biomass in the Bonavista Corridor grew from < 20 000 t in 2007 to near

238   240 000 t in 2014 at a rate of approximately 30% per year (Fig. 5). If stock growth had

239   continued at the same rate without emigration then the biomass would have reached

240   approximately 310 000 t in 2015, but biomass declined sharply from 2014 to 2015 to 136

241   000 t (95% CI 93 000-193 000 t) (Fig. 5). In the northern areas in 2015, biomass was

242   approximately 101 000 t (69 000-139 000 t) in the Notre Dame Channel and 65 000 t (31

243   000-106 000 t) in the Hawke Channel-Hamilton Bank and Belle Isle Bank region, which

244   far exceeded expectations based on the observations made in 2008 and 2013 (no

245 comparable biomass estimates can be made for those years as a result of diminished

246 coverage). Of key importance, the total surveyed biomass over the range of the stock in

247 2015 was approximately 302 000 t (193 000-438 000 t), similar to that expected if growth

248 rates in the Bonavista Corridor had been sustained.

249

250 **Size and Growth**

251 In 2008, larger cod (> 60 cm) were much more common in the Bonavista Corridor than

252 they were farther north (Fig. 6 a,b,c). Nonetheless, length distributions did not differ

253 among groups (Wilcoxon paired rank sum tests, Ps > 0.05), although the Bonavista

254 Corridor and Hawke Channel-Hamilton Bank and Belle Isle Bank groups differed at the

255 10% level (P=0.09). By 2013 there had been a slight shift towards larger fish farther

256 north but the larger fish remained concentrated around 50°N in the Bonavista Corridor

257 (Fig. 6 d,e,f). Length distributions in 2013 differed between the Bonavista Corridor and

258 Hawke Channel-Hamilton and Belle Isle Banks regions (P < 0.05), but not between

259 Bonavista Corridor and the Notre Dame Channel. In 2015, however, larger cod were

260 numerous in all regions and the size distributions among these groups did not differ (Ps >

261 0.05; Fig. 6 g,h,i).

262

263 In the years between the late 1990s and 2014, the von Bertalanffy growth parameters

264 (Table 1) indicate larger size at age of cod in the Bonavista Corridor, especially after age

265 5, compared to those from Hawke Channel-Hamilton Bank and Belle Isle Bank regions

266 (Fig. 7). As a result, cod aged 9 years, the oldest located in the northern region during

267 those years, were approximately 7 cm shorter than those in the Bonavista Corridor (Fig.

268   7). In the Bonavista Corridor, parameters from cod sampled in 2015 did not differ from

269   those sampled in the earlier years (Table 1, P>0.05). For the Hawke Channel-Hamilton

270   Bank and Belle Isle Bank region, however, both parameters differed significantly from

271   those measured in the earlier years (P<0.05) and became similar to those in the Bonavista

272   Corridor (P>0.05, Table 1). In 2015, cod of all ages were indistinguishable by size at age

273   in the north and south of the stock range (Fig. 7). The Notre Dame Channel size at age

274   data in 2015 were not significantly different from those from the other regions or years

275   (Table 1), and were in the middle of the Von Bertalanffy curves (Fig. 7), but there is

276   greater uncertainty about that model fit as the sample size was relatively low, with fewer

277   larger fish, compared to the other groups. No data from the earlier period for this region

278   were available for comparison.

279

280   **Age classes**

281   The progression of the relative abundance of age classes present in the Bonavista

282   Corridor was roughly consistent during 2012-2015, with the 2004 and 2002 year-classes,

283   8 and 10 years old in 2012, relatively strong (Fig. 8 a,b,c,d). In 2014 and 2015, the 2011,

284   2009 and 2008 year-classes, ages 3, 5 and 6 years respectively in 2014, were relatively

285   strong in the Bonavista Corridor (Fig. 8 c,d), and also in the Hawke Channel-Hamilton

286   Bank and Belle Isle Bank region in 2015 (Fig. 8 f). In 2015, the 2011 and 2009 year-

287   classes in the Notre Dame Channel were also well represented, and, overall, the age

288   structures did not differ among the three regions (Wilcoxon paired rank sum tests, Ps >

289   0.05). It is noteworthy that the age structures in the Bonavista Corridor and Hawke

290   Channel-Hamilton Bank and Belle Isle Bank regions were particularly well aligned (Figs.

291   8 d and f).

292

293   Instantaneous mortality rates (Z) estimated for cod of ages 5-12 years in the Bonavista

294   Corridor were low from 2012 to 2013 and 2013 to 2014 (Fig. 9). From 2014 to 2015,

295   however, the Z became extremely high relative to those in the earlier years. If fish in the

296   Notre Dame Channel were pooled with those in the Bonavista Corridor the Z was lower,

297   and if fish from all surveyed regions were pooled, the Z approached those measured in

298   the Bonavista Corridor in the earlier years (Fig. 9).

299

300   **Discussion**

301   Several lines of evidence support the hypothesis that the aggregations of cod located in

302   the Hawke Channel-Hamilton Bank and Belle Isle Bank region and Notre Dame Channel

303   in the spring of 2015 were an outcome of a northward redistribution from the Bonavista

304   Corridor, the region of initial rebuilding (Rose and Rowe 2015), and were not solely a

305   product of local production.

306

307   A compelling line of evidence comes from data on biomass distribution. After nearly a

308   decade of rapid annual growth at a rate approaching 30% (Rose and Rowe 2015; DFO

309   2016, 2017), biomass declined in the Bonavista Corridor in 2015, with concomitant

310   increases in both the Notre Dame Channel and Hawke Channel-Hamilton Bank and Belle

311   Isle Bank region. Moreover, a sum of the biomass in all three regions is consistent with a

312   continuance of the growth rates evident from 2007 to 2014 in the Bonavista Corridor. In

313   addition, the increases in size and age of fish comprising the biomass in the north are

314   difficult to explain solely by local population growth. The older year-classes present in

315   relatively large numbers in 2015 were concentrated in the Bonavista Corridor in previous

316   years, and with particular reference to the Bonavista Corridor and Hawke Channel-

317   Hamilton Bank and Belle Isle Bank regions, the relative size and year-class distributions

318   were similar in 2015 after being disparate both historically and recently. Finally, low Zs

319   assessed from 2007 to 2014 in the Bonavista Corridor are consistent with those from the

320   DFO fall survey data (DFO 2016), but the highly negative Z between 2014 and 2015

321   suggests emigration and not mortality. The fishery likely had little influence on this high

322   Z as reported landings in 2014 and 2015 were less than 5 000 t excluding the recreational

323   fishery. Even if these reported landings are underestimates the fishery is highly unlikely

324   to have been responsible for the >100 000 t decline in the Bonavista Corridor biomass

325   estimate that occurred between 2014 and 2015.

326

327   Evidence from growth rates also supports the redistribution hypothesis. The lower growth

328   in cod from the northern regions that was evident historically (e.g., Ruivo 1957; Fleming

329   1960; Templeman 1966) and persisted from 1996-2003 (Sherwood et al. 2007) and as

330   recently as 2014 (Cadigan and Konrad 2016; Morgan et al. 2017; this paper), was not

331   evident in the spring of 2015. As far as we know this is the first time that such

332   equivalence in latitudinal growth rates has been reported within the Northern cod. Of

333   further interest, the von Bertalanffy parameters measured in the Bonavista Corridor are

334   comparable to those reported by Misra (1980) for Newfoundland cod captured in 1940

335   and 1968 which had similar values ($L_{inf} = 112.5$ and $K=0.124$) and resultant lengths at

336   age (e.g., approximately 70 cm at age 8). Although Misra (1980) does not report the

337   location of his samples other than they were provided by the Newfoundland Biological

338   Station, they almost certainly did not come from the northern region as little research was

339   undertaken there in those years.

340

341   We submit that none of the present results on their own would provide conclusive

342   evidence of redistribution, although all support that hypothesis. Nonetheless, the weight

343   of the evidence suggests that the relatively large aggregations present in the Notre Dame

344   Channel and in the Hawke Channel-Hamilton Bank and Belle Isle Bank region were not

345   simply a product of local population growth but included large numbers of fish

346   redistributed from the southern part of the stock range in the Bonavista Corridor.

347

348   Redistribution had taken place by 2015, but a more precise determination of timing

349   remains difficult to achieve. Some speculation may be warranted until further data on

350   distribution and coming recruitment is available. It is pertinent that some areas around the

351   Hawke Channel that were highly populated with large cod in 2015 were surveyed in 2013

352   (and 2008), and showed only low densities of mostly small and immature fish mixed with

353   relatively few adults (Mello and Rose 2009; Rose and Rowe 2015). Data from the DFO

354   fall trawl survey are generally consistent with this interpretation, but suggest some

355   increase in juveniles by 2012-2013, based on very low ratios of biomass to abundance

356   (data in DFO 2016, 2017). These modest increases in juveniles could have resulted from

357   spawning of local fish. During and after the collapse of the Northern cod in the early

358   1990s, with the stock at its lowest abundance, a small remnant group of spawning fish,

359 　peaking at approximately 12 000 t, remained in the Hawke Channel in the mid-1990s

360 　(Anderson and Rose 2001). Although adult abundance from then until 2015 is unknown,

361 　data from the DFO fall survey suggests it was low during this period (Brattey et al. 2010;

362 　DFO 2016), which is consistent with the 2008 and 2013 spring results. Nonetheless, it is

363 　not impossible that a low spawning biomass could have produced the modest increases in

364 　recruitment evident until 2014. The substantial increases of small fish beginning in the

365 　fall of 2014 are more difficult to reconcile with local production (DFO 2016, 2017). It

366 　seems more likely, although speculative, that this increase represented recruits from a

367 　vanguard of redistribution during 2012-2013 leading to a major shift occurring between

368 　2014 and 2015.

369

370 　Another question related to timing concerns the underlying cause of the redistribution.

371 　What triggered it? One explanation invokes a density-dependent argument, that the

372 　Bonavista Corridor density exceeded some threshold that led to expansion to relatively

373 　unoccupied former ranges to the north. Nonetheless, in 1990, the Bonavista Corridor held

374 　double the biomass assessed in 2014 (Rose 1993), but the early 1990s were very cold

375 　years and the cod were hyperaggregated there (Rose and Kulka 1999), so the comparison

376 　may be suspect. Another argument is that warming ocean conditions made northward

377 　movement more likely, as has occurred in the Barents Sea (e.g., Renaud et al. 2012). A

378 　third is that increases in feeding, especially of capelin (*Mallotus villosus*) led fish

379 　northward. We cannot distinguish among these hypotheses with present data, and it is

380 　likely that all may be involved.

381

382   How and when, if not why a fish stock may rebuild is critical to modelling stock

383   abundance trends and especially important for a "stock complex" or metapopulation (e.g.,

384   Cadigan 2016). The Bonavista Corridor became the core offshore area for the Northern

385   cod during the collapse in the early 1990s and remained so for over a decade (e.g., Rose

386   1993; Rose and Rowe 2015; DFO 2016). Nonetheless, from 1995 until 2008, the major

387   extant over-wintering and spawning group was located not offshore, but inshore in Smith

388   Sound, adjacent to the Bonavista Corridor, peaking at 26 000 t during the early 2000s

389   (Rose 2003). There is little indication from history that such a distribution of Northern

390   cod had occurred previously (Rose 2007; Rose et al. 2011). After 2006, the Smith Sound

391   aggregation dispersed and no longer overwintered there in large numbers, while at the

392   same time, the cod in the Bonavista Corridor increased (Rose et al. 2011). Stock models

393   for the offshore improved markedly under an assumption that the Smith Sound cod had

394   dispersed to join the offshore stock (Cadigan 2016). Although confirmation through

395   tagging that migration from the Bonavista Corridor to the inshore did not occur until

396   2008 (Brattey 2013), recent work using otolith microchemistry has indicated that during

397   the 1990s the Smith Sound and Bonavista Corridor groups were essentially the same fish

398   (Neville et al. *in press*). It seems evident that after 2007 and until 2014 growth in the

399   offshore abundance occurred primarily within the Bonavista Corridor, with the formerly

400   abundant northern groups remaining depauperate (this paper; DFO 2016). By 2014,

401   however, an increasing number of small cod, presumably comprised of age 1 and 2

402   juveniles, were reported as far north as the Hamilton Bank by the DFO fall trawl survey

403   (data in DFO 2017). In the spring of 2015, major aggregations of adult fish were located

404   in the Notre Dame Channel and Hawke Channel-Hamilton Bank and Belle Isle Bank

405   regions (this paper; Rose and Rowe 2015; Kincaid and Rose 2017). Our hypothesis to

406   explain this evidence is redistribution within a metapopulation, first from the southern

407   inshore to the adjacent offshore, and then to the northern regions – basically a reversal of

408   what occurred in the early 1990s.

409

410   Recognition of the Northern cod stock "complex" was made decades ago (e.g.,

411   Templeman 1966; Lear 1984; Taggart et al. 1994), but the independence and relative

412   importance of its components has remained controversial. Northern components likely

413   sustained the stock historically (May 1966; Rose 2007), but the southern components,

414   both inshore and offshore, have maintained the stock since the decline in the early 1990s,

415   despite evidence of some juveniles from northern spawning in the late 1990s (Anderson

416   and Rose 2001). It is doubtful, however, if the southern components could ever produce

417   the stock productivity once evident (Rose et al. 2000). deYoung and Rose (1993)

418   predicted that the southern spawning observed in the early 1990s, even from 450 000 t of

419   spawners (Rose 1993), would result in poor recruitment as a consequence of

420   unfavourable drift of eggs and larvae (Davidson and deYoung 1995; Pepin and Helbig

421   1997) - this has been borne out (data in DFO 2017). As late as 2012, with the dramatic

422   increase in spawning biomass in the Bonavista Corridor but little evidence of adults

423   farther north, recruitment has been low. Restoration of production in this stock will

424   almost certainly depend on the rebuilding of northern spawning components.

425

426   If the approximate timing of the range expansion and latent northern spawning increase is

427   correct, in that major increases occurred between 2014 and 2015, then an expectation is

428 that recruitment from 2015 could potentially be higher than in the years since the

429 northern distribution collapsed in the early 1990s. The increase in abundance in NAFO

430 Division 2J in the DFO fall survey in 2016 (the highest since the decline in the early

431 1990s) combined with the low mass reported for these fish, tends to support this

432 contention (data in DFO 2017). The potential for greater recruitment with spawning

433 biomass rebuilding in the north awaits verification from further data.

434

435 We believe that the present findings have application not only to the Northern cod but to

436 other depleted stocks of cod and other species. Examples are the cod stocks off the south

437 coast of Newfoundland (NAFO 3Ps; Lawson and Rose 2000), the Nova Scotia Banks

438 (McKenzie and Smith 1955) and the Gulf of Maine (Ames 2004), all of which have

439 multiple potential if not realized spawning areas. Although the Northeast Arctic cod is

440 thought to have two main spawning areas (Sundby and Nakken 2008), the map of

441 spawning sites in Hjort (1914) suggests that historically there were many such areas.

442 Some sites might have been exclusively occupied by the coastal stock, although at

443 Lofoten, the main spawning area, both the Northeast Arctic and coastal stock spawn, and

444 perhaps historically that was the case elsewhere (e.g., Nordeide 1998). Pelagic species

445 also may depend on multiple spawning sites. The Norwegian spring spawning herring

446 rebuilt from near decimation and spawning concentration in a limited coastal area of

447 Norway to a widespread and multiple spawning site stock as it had been historically

448 (Dragesund et al. 2008). Presumably this occurred by redistribution. Within the Northern

449 cod ecosystem, the key forage species is capelin, whose distribution collapsed markedly

450 and suddenly in the early 1990s (Frank et al. 1996), and in so doing almost certainly lost

451 many of its vast number of coastal spawning sites. The lack of rebuilding in this stock

452 may be related to a depauperate spawning distribution, especially in the north. Recent

453 increases, albeit modest (DFO 2015), could be related to repopulation of abandoned

454 spawning sites. If this is true, a sequential feedback mechanism is likely involved, in

455 which core groups increase, enabling range expansion, which increases spawning

456 potential and recruitment, which enables further range expansion. Unfortunately, there

457 are no data that we know of available to test this notion. No matter the mechanism,

458 increases in capelin were correlated with increased biomass and condition in the Northern

459 cod from 2008-2014 (Rose and Rowe 2015), and the potential for post-2015 declines in

460 this key prey is likely to stall productivity, which should be reflected in management of

461 this rebuilding cod stock (Rowe and Rose 2017).

462

463 Our conclusion that the rebuilding mechanism of Northern cod is range expansion to

464 repopulate former spawning sites, that it is not limited to local rebuilding, is critical to the

465 management of this cod stock, and likely to others that may form metapopulations such

466 as in the North Sea (e.g., Wright et al. 2006). It is essential that the unity of Northern cod

467 over its entire range be recognized, both inshore and offshore. Recognition includes the

468 importance of the genetic and behavioral diversity that exists among spawning

469 components, no matter their location or relative size (Wroblewski et al. 2005), and the

470 likelihood of temporal discontinuities in their production (e.g., Schindler et al. 2010).

471 Past notions that these areas may be functionally separate (e.g., Hutchings 1996; Lilly et

472 al. 2005) and hence might be managed and harvested independently, are not supported.

473 Furthermore, apart from small and isolated coastal groups such as in Gilbert Bay

474   Labrador (Hu and Wroblewski 2009), the inshore regions of the Northern cod should be

475   included under a unified management plan. This recognizes the dominance of the diverse

476   offshore spawning groups in supporting the fishery and the long-known early summer

477   migration of cod to the inshore (e.g., Fleming 1960). The Northern cod stock apparently

478   can exhibit rapid and unexpected geographical shifts as abundance and environmental

479   conditions change. It is noteworthy that during the rapid decline in the early 1990s, cod

480   distributions shifted south from NAFO Division 2J to 3K and 3L (Atkinson et al. 1997;

481   Rose et al. 2000; Ruzzante et al. 2001) where they hyper-aggregated (Rose and Kulka

482   1999). As a consequence, large numbers were caught and catch rates remained high both

483   offshore and inshore prior to and during the total stock collapse (Rose and Kulka 1999).

484

485   Finally, and notwithstanding the importance of all spawning groups within the Northern

486   cod metapopulation, special consideration should be given to the northern spawning areas

487   that formerly supported the largest fisheries and are believed to be essential to full

488   productivity in this stock. Repopulation of these spawning areas is essential to any chance

489   of returning to historical levels of productivity, and protecting them once re-established is

490   essential to sustaining that production. Since the spawning distribution of the Northern

491   cod became apparent in the 1950s and 1960s (e.g., Fleming 1960; May 1966), northern

492   spawning has invariably coincided with relatively strong productivity, even after the

493   major stock decline that occurred in the early 1970s, but with southern distributions, as in

494   the 1990s, productivity has been invariably poor (DFO 2017). As stated by Rose et al.

495   (2011), spawning in the northern region of the stock, anchored by the Hamilton Bank, is

496   the "engine that drives the Northern cod".

497

498   In conclusion, the present findings support the hypothesis that the recent range expansion

499   of Northern cod has been the result of redistribution and not solely based on local

500   production. This finding supports the hypothesis that the Northern cod comprises a

501   metapopulation (Smedbol and Wroblewski 2002) and has critical implications for

502   management. Movement and migration within the range of the Northern cod has been

503   known for a long time. Over 50 years ago, May (1966) pointed out that the historically

504   large inshore and offshore fisheries were essentially fishing the same fish. The same

505   likely applies to fisheries prosecuted along the continental shelf from the Hamilton Bank,

506   and historically even farther north into NAFO Division 2H, to the northern Grand Bank

507   (Wroblewski et al. 1995; Cecil Bannister, former trawler captain, personal

508   communication). The present work takes this a step further in that offshore redistribution

509   may occur among the main spawning regions, at present to the north, the opposite of

510   what occurred in the early 1990s (e.g., Atkinson et al. 1997). For management, we stress

511   that far from meaning that it does not matter where the fishery is prosecuted, it perhaps

512   matters more, as sustaining inter-connected spawning components could be vital to future

513   production. It follows that a stock assessment model that can deal with this dynamic

514   spatial structure will be needed to fully account for the productivity and management of

515   this stock. Further elucidation of the spatial dynamics, redistributions and migrations

516   within the Northern cod stock awaits additional data from ongoing studies utilizing

517   otolith microchemistry, genetics and data storage tagging.

518

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529

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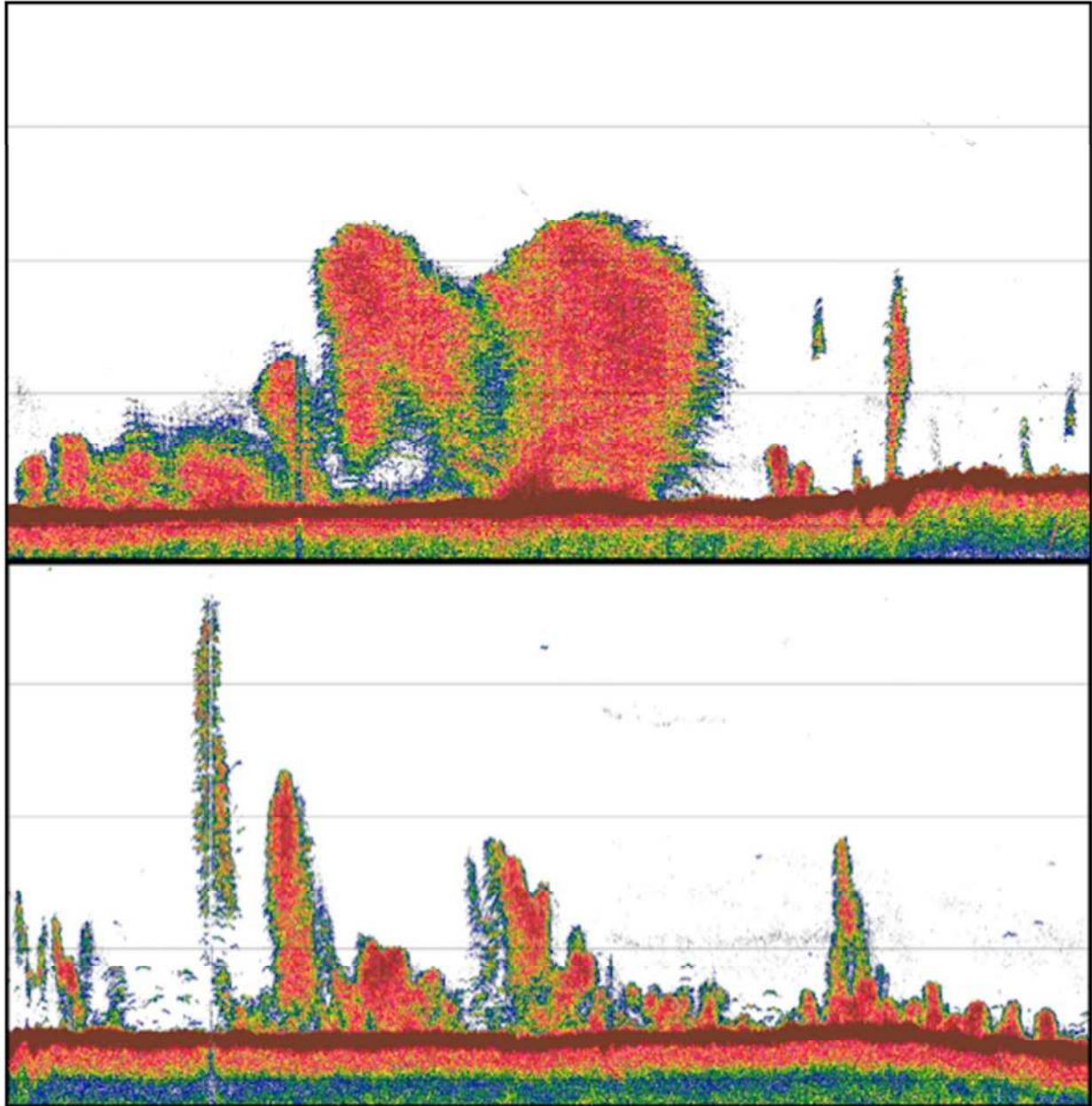796   important for rebuilding the East Coast fishery. Coast. Manage. 33 (4): 411-432.

Fig. 1. Echograms of cod in March 2008 in the Bonavista Corridor, northeast Newfoundland Shelf (EK60, 38 kHz, threshold -75 dB) from CGGS 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^3 and areal biomass of 5 kg.m^2. Catch was virtually 100% cod.
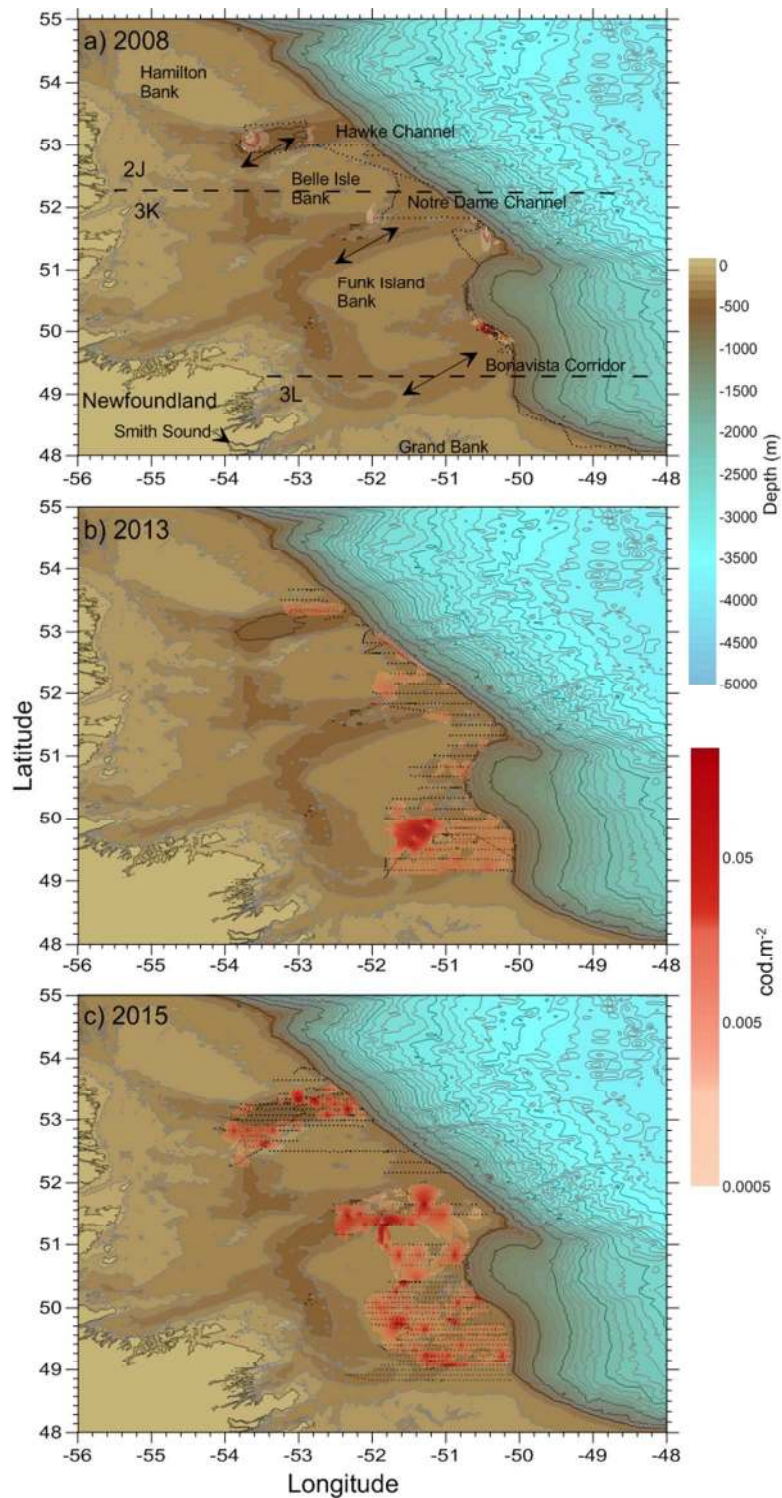
Fig. 2. Cod density (kg.m^{-2}) in a) March of 2008 and May of b) 2013 and c) 2105 and bathymetry of the northeast Newfoundland and Labrador Shelf and Banks, based on kriging of densities. Black dots represent sampling transects.
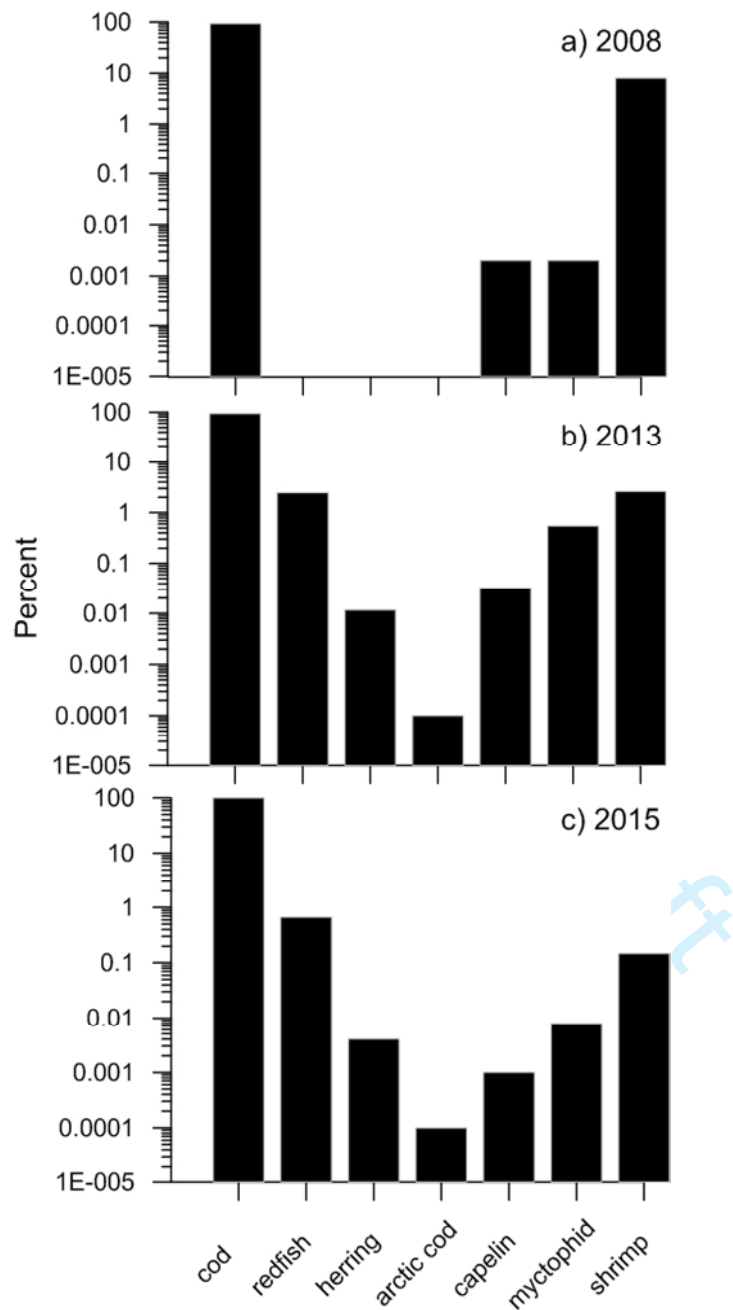
Fig. 3. Catch mass of species caught in trawl sets targeted at cod in March 2008 (a) and May 2013 (b) and 2015 (c). Log10 scale used to show minor components of catch. Species are Atlantic cod (*Gadus morhua*), redfish (*Sebastes* spp.), Atlantic herring (*Clupea harengus*), Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*), Myctophids, and shrimp (primarily *Pandalus borealis*).
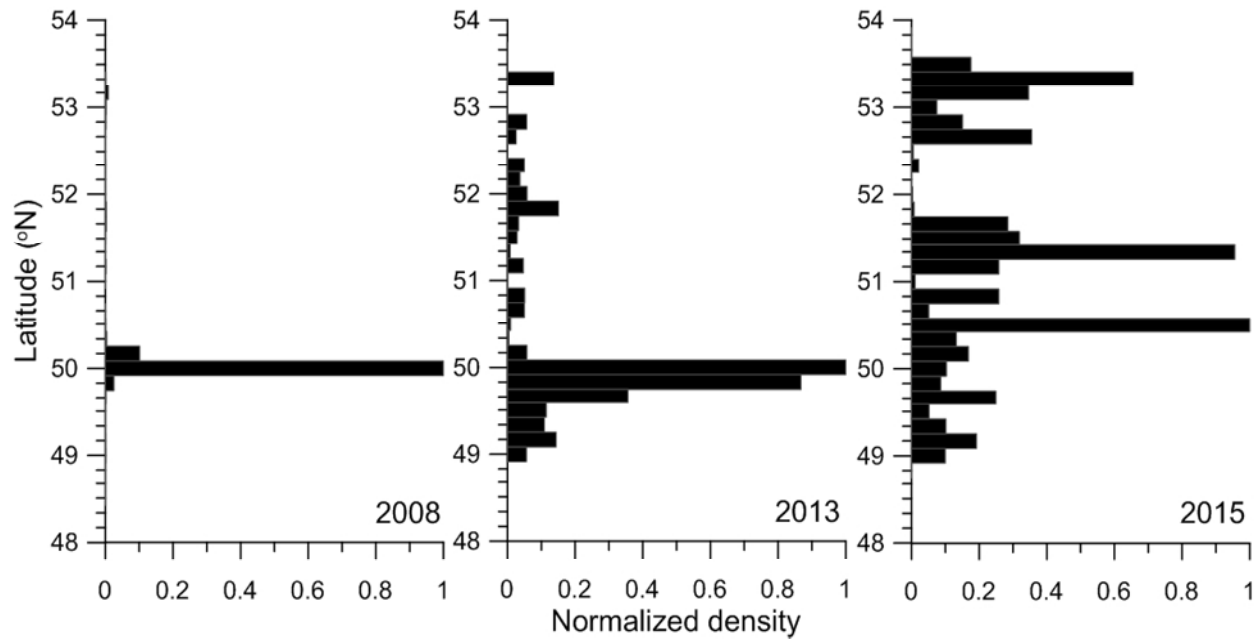
Fig. 4. Relative latitudinal distributions of northern cod during late winter early spring in 2008, 2013 and 2015. Data normalized to counter bias from inter-annual variation in sampling intensity.
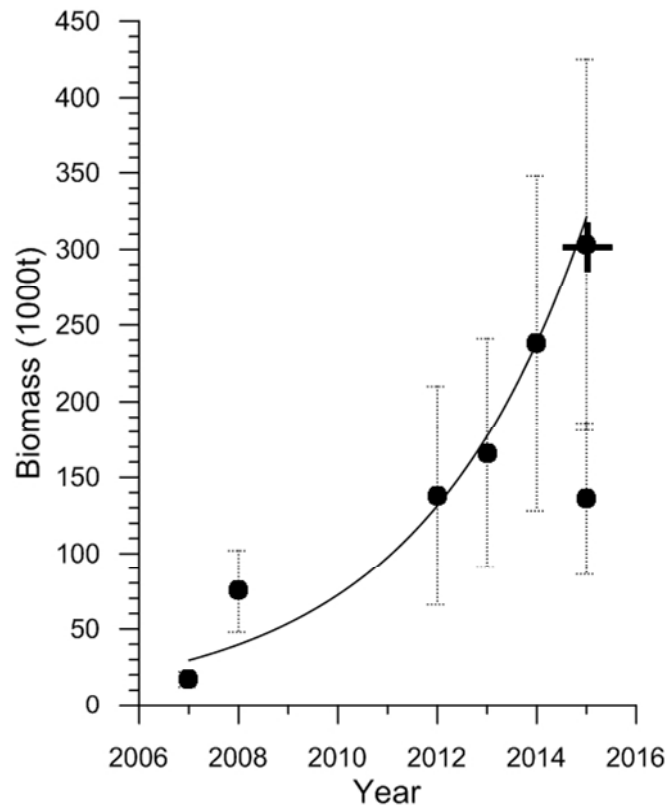
Fig. 5. Biomass of cod in the Bonavista Corridor from 2007 to 2015 with 95% CIs (solid circles).

Power curve represents best fit from 2007-2014, projected to 2015. The total biomass measured
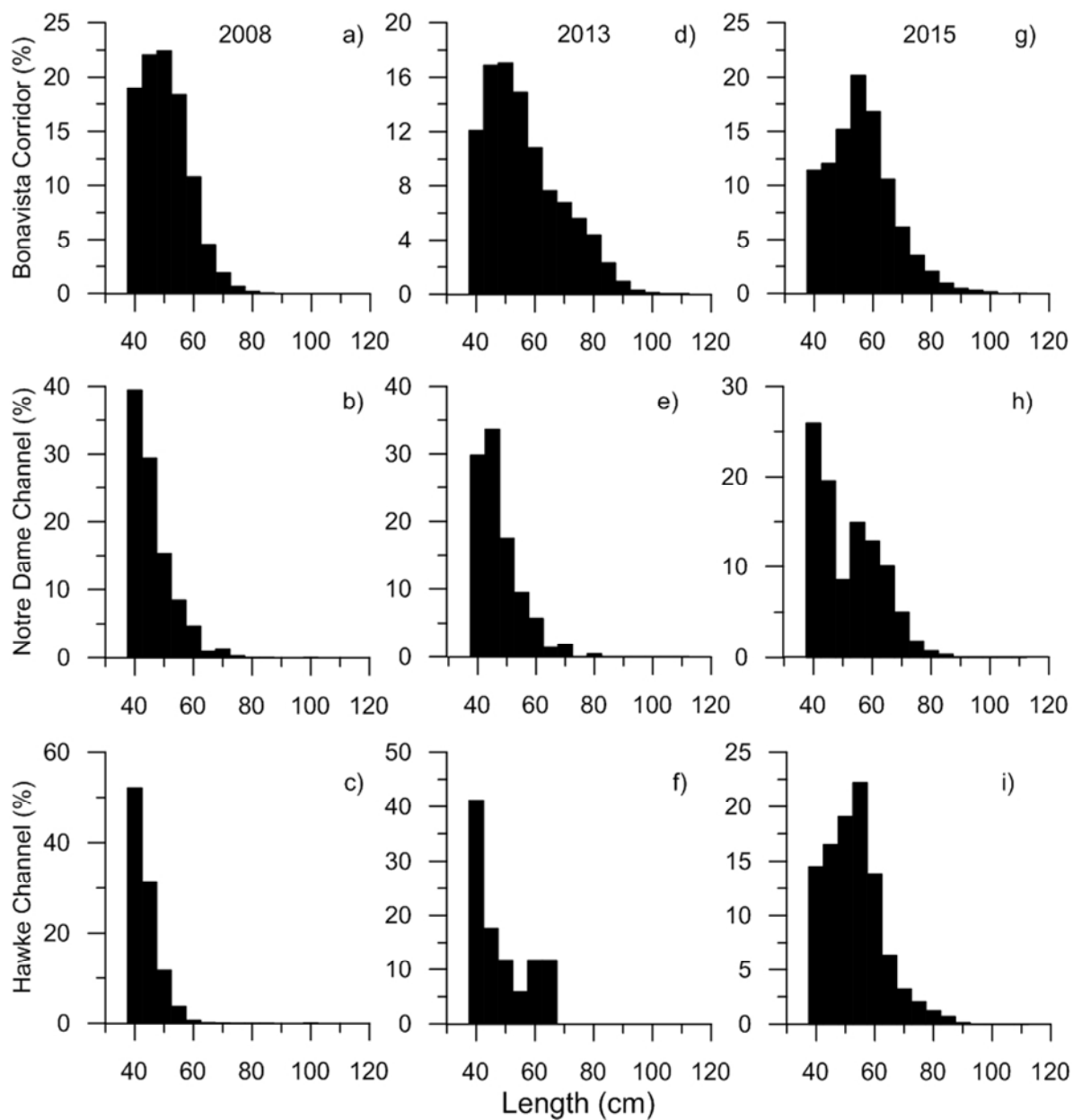
in 2015 is shown with a crossed circle.

Fig. 6. Length frequency percentages from catches of cod in 2008, 2013, and 2015 in the

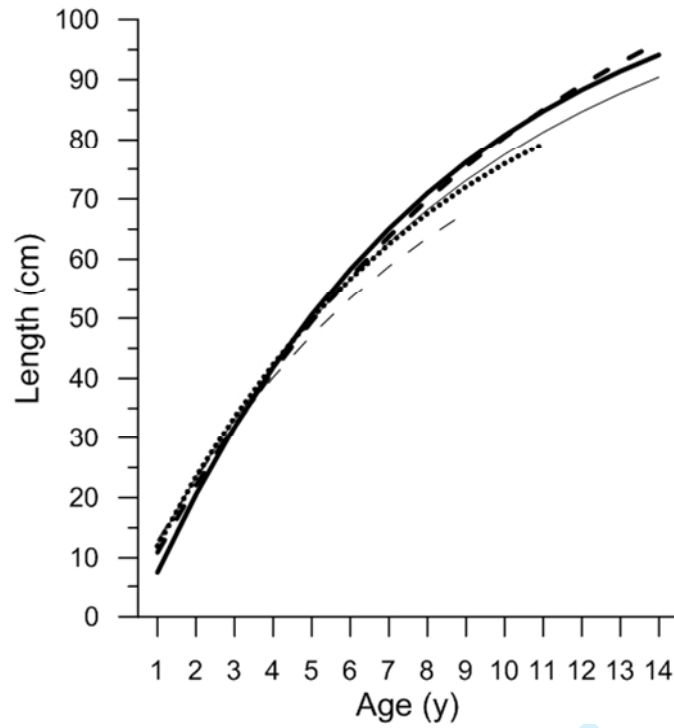Bonavista Corridor, Notre Dame and Hawke Channel-Hamilton and Belle Isle Bank regions.

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.
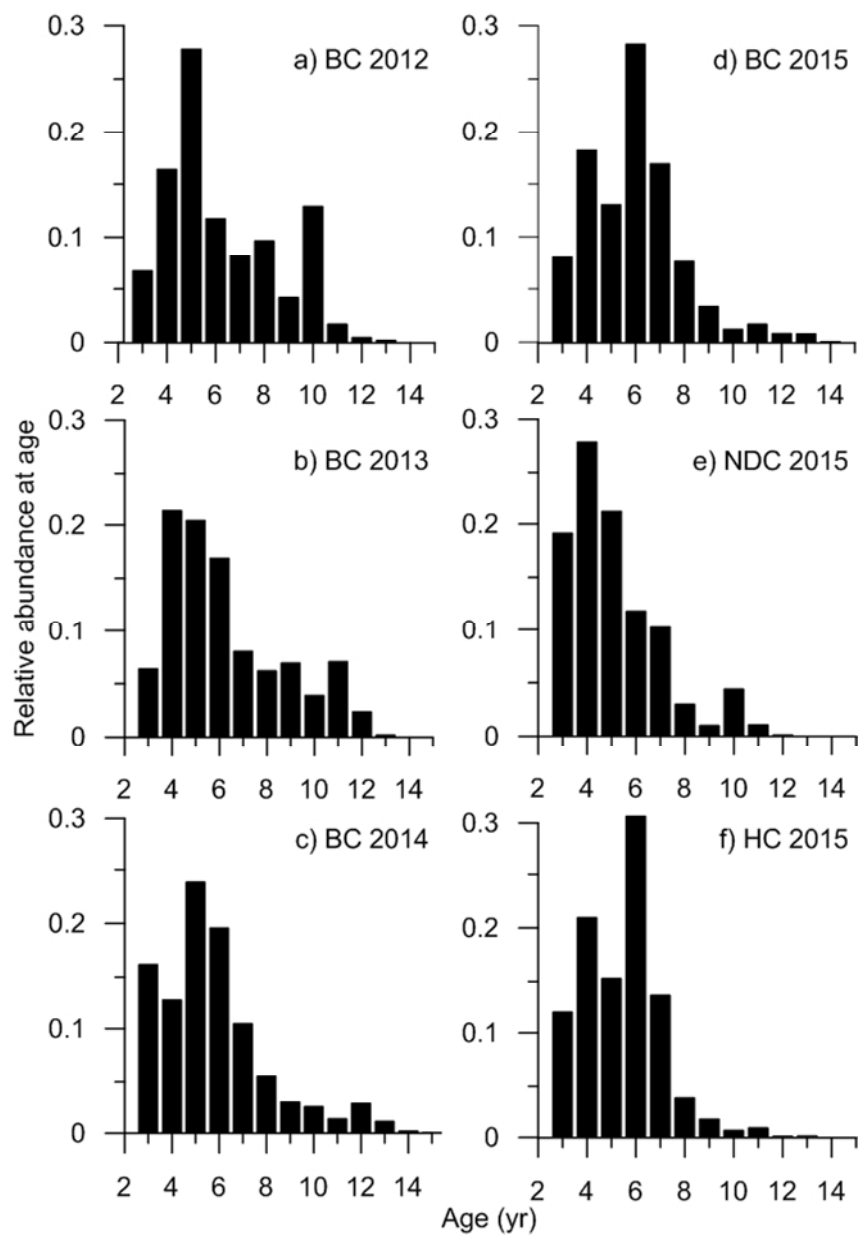
Fig. 8. Relative abundance at age from acoustic-trawl surveys in the Bonavista Corridor (BC) from 2012 to 2015 and in the Notre Dame Channel (NDC) and Hawke Channel-Hamilton and Belle Isle Bank regions (HC) in 2015.
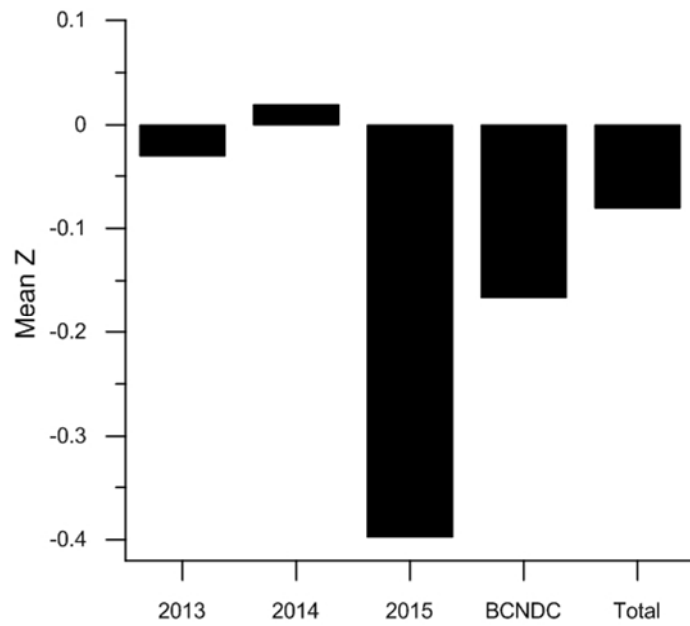
Fig. 9. Mean instantaneous mortality rates (Z) of cod aged 5-12 in the Bonavista Corridor from

2012 to 2015 (eg. 2013 indicates Z from 2012 to 2013). BCNDC and Total are for 2015.

1   Table 1. Von Bertalanffy parameters estimated from individual length and age data for

2   cod from 1998-2014 and in 2015 from the Bonavista Corridor (BC) and 1996-2013 and

3   2015 from the Hawke Channel-Hamilton and Belle Isle Bank regions (HC) and for the

4   Notre Dame Channel in 2015. Superscripts indicate overlapping CIs (95%).

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YEAR-REGION	L_{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]	10398
2015 BC	113.8 (109.7--117.9)[a]	0.130 (0.120--0.140)[a,b]	0.468(0.348--0.587)	1284
1996-2013 HC	98.5 (88.5--108.6)[b]	0.128 (0.107--0.149)[b]	-0.098 (-0.230--0.034)[a]	5369
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)[a,b]	0.136(0.111--0.162)[a,b]	0.089(-0.082--0.260)[a]	370

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