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1 Northern cod comeback

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Draft

8 Abstract: The great “northern” cod (*Gadus morhua*) stock, formerly among the world’s largest
9 and *the* icon for depletion and supposed non-recovery of marine fishes, is making a major
10 comeback after nearly two decades of attrition and fishery moratorium. Using acoustic-trawl
11 surveys of the main pre-spawning and spawning components of the stock, we show that biomass
12 has increased from tens of tonnes to >200 thousand tonnes within the last decade. The increase
13 was signalled by massive schooling behaviour in late winter first observed in 2008 in the
14 southern range of the stock (Bonavista Corridor) after an absence for 15 years, perhaps spurred
15 by immigration. Increases in size composition and fish condition and apparent declines in
16 mortality followed, leading to growth rates approaching 30% per annum. In the spring of 2015,
17 large increases in cod abundance and size composition were observed for the first time since the
18 moratorium in the more northerly spawning groups of this stock complex. The cod rebound has
19 paralleled increases in the abundance of capelin, *Mallotus villosus*, whose abundance declined
20 rapidly in the cold early 1990s but has recently increased during a period of warm ocean
21 temperatures. With continued growth in the capelin stock and frugal management (low fishing
22 mortality), this stock could rebuild, perhaps within less than a decade, to historical levels of
23 sustainable yield. More generally, if this stock can recover, the potential exists for recovery of
24 many other depleted stocks worldwide.

25

26 Keywords: Northern cod, cod spawning columns, acoustic survey, commercial extinction,
27 rebuilding marine fish

28

29 Introduction

30 Many fish stocks worldwide have been overexploited to the point of commercial extinction
31 (FAO 2012), with predictions of the decline or elimination of all major marine fisheries (Worm et
32 al. 2006, but see Worm et al. 2009). Among depleted stocks, the great “northern” Atlantic cod
33 (*Gadus morhua*) stock complex off Newfoundland and Labrador (Northwest Atlantic Fishery
34 Organization (NAFO) Divisions 2J3KL), once among the largest cod stocks in the world, is often
35 held up as *the* icon for decline and mismanagement (Rose 2007) and long-term or non-recovery
36 (Rice 2006). This stock once comprised several million tonnes and supported annually a major
37 seasonal fishery of 200,000-400,000 tonnes for hundreds of years (Rose 2007). The stock was
38 heavily depleted by overfishing in the 1960s and again in the 1980s, in the later period catalyzed
39 by reduced productivity (Rose 2004; Hilborn and Litzinger 2009; Halliday and Pinhorn 2009).
40 The largest decline occurred in the first years after 1990 during a very cold oceanographic period;
41 other species suffered a similar fate, in particular capelin, the cod’s main prey, that declined 30-
42 fold from 1990 to 1991 in both Russian and Canadian surveys (Bakanev 1992; DFO 2015a).

43 The offshore component of the northern cod stock has long been recognized to be complex
44 (Templeman 1966). The stock was hypothesized to comprise groups that conduct post-spawning
45 migrations from the offshore shelf region to coastal feeding areas along three main migration
46 highways (Rose 1993; Figure 1). The highways were posited to follow the Hawke Channel south
47 of Hamilton Bank in the north (NAFO Division 2J), the Notre Dame Channel north of Funk
48 Island Bank in the middle (NAFO Division 3K), and the Bonavista Corridor south and east of
49 Funk Island Bank in the south (NAFO Divisions 3KL). In the early 1990s overall stock decline
50 was accompanied by a major southward distribution shift (deYoung and Rose 1993). As a
51 consequence, most of what remained of the stock became concentrated during the overwintering
52 and spawning period (January to June) in the Bonavista Corridor (Rose 1993; Atkinson et al.
53 1994) (Fig. 1). The two more northerly routes were depleted with little evidence of spawning
54 aggregation or migration to the coast during the 1990s or early 2000s.

55 During the decade from 1995-2006, the offshore components of the stock were at very low
56 levels in all regions, with individual fish in poor condition and spawning at very small size,
57 especially in the north (Bratney et al. 2008; Fudge and Rose 2008). The only large aggregation of
58 over-wintering and spawning northern cod was located inshore in Smith Sound, a small fjord on
59 the western side of Trinity Bay (Knickle and Rose 2010; Rose et al. 2011). At its peak, this
60 aggregation measured about 26,000 t, and unlike the offshore fish, retained a wide length and age
61 distribution and good condition. But beginning in 2007, the Smith Sound aggregation declined
62 rapidly each year until by 2010 few fish over-wintered or spawned there. Concomitantly, the
63 numbers of cod in the adjacent offshore Bonavista Corridor began to increase, leading to
64 speculation that Smith Sound cod had ventured offshore (Rose et al. 2011). Indeed, both the fall
65 trawl survey of the Department of Fisheries and Oceans (DFO) and the winter acoustic-trawl
66 survey reported here showed an increase in cod biomass in the Bonavista Corridor that was
67 difficult to explain by local production alone. Recently, a modelling study examined that
68 disparity by including acoustic-trawl survey data from Smith Sound and an assumption that
69 maturing fish regrouped with the Bonavista Corridor cod after 2007 (Cadigan 2015). In effect,
70 doing so changed the catchability (q) of the main DFO trawl survey over time, with a model that
71 fit most existing data better and further suggested that northern cod spawning biomass may have
72 been underestimated in recent years based on the fall trawl survey alone.

73 Several predictions of northern cod rebuilding took little account of the spatial or ecological
74 complexity of the decline or how rebuilding might occur, leading to overly optimistic projections
75 of stock growth based on untenable assumptions of productivity (e.g., Roughgarden and Smith
76 1996; Myers et al. 1997). In contrast, deYoung and Rose (1993) had predicted a much slower
77 decadal rebuilding based on a changed environment and prey field and putative northward spatial
78 expansion from the collapsed core in the Bonavista Corridor. Rose et al. (2000) reinforced those
79 earlier predictions on how rebuilding of the northern cod would occur. To quote “based on the
80 present studies, we cannot forecast a timetable for rebuilding, but we can forecast steps thought to
81 be diagnostic of the stage of rebuilding. In stage 1, holding to the theory that *northern spawning*

82 *drives population abundance in the northern stock* (italics added), abiotic and biotic conditions in
83 the north must revert to favourable states for cod.... Of importance are warming conditions and
84 the return and reestablishment of capelin as a major food source. In stage 2, adult cod reverse the
85 southerly shift back to the north and in time reform large (>100,000 t) spawning aggregations....
86 In stage 3, recruitment of juveniles across the shelf will begin. We are currently at stage 1.”

87 Although several additional factors have been put forth in attempts to explain both the lack
88 of rebuilding of the northern cod, including phenotypic or genetic changes in life history
89 characteristics (Hutchings 1999; Olsen et al. 2004; Fudge and Rose 2008) and continued
90 overfishing (Shelton et al. 2006), the potential importance of a lack of food, in particular capelin,
91 has been repeatedly noted (Rose and O’Driscoll 2002; Davoren and Montevocchi 2003;
92 Obradovich et al. 2013; Mullett and Rose 2014; Buren et al. 2014).

93 In this paper, we document the rebound of the northern cod within the past decade from a
94 biomass of a few percent of its former size to several hundred thousand tonnes and growing. We
95 examine factors that may have influenced the rapid transition from unproductive to productive
96 status, improved condition, and extended age and size structure. In particular, we examine spatial
97 shifts and immigration, and the potential impacts of temperature and food supply, namely capelin
98 (*Mallotus villosus*), and the fishery.

99 Methods

100 **The Migration Corridors**

101 The Bonavista Corridor is a basin on the northeast coast of Newfoundland spanning NAFO
102 Divisions 3KL and holding warm (2-4°C) Atlantic Ocean water in its depths (Rose 1993; Figure
103 1). To the south is the northern rise of the Grand Bank, and to the northwest the Funk Island
104 Bank. To the east the boundary is the shelf break, where depths increase to over 1000 m within
105 several miles. The Bonavista Corridor forms the southern-most cross-shelf migration path of the

106 northern cod (Rose 1993). Here, the northern cod aggregated to spawn in the early 1990s as the
107 stock collapsed.

108 North of the Bonavista Corridor and the Funk Island Bank lies the Notre Dame Channel,
109 which leads to the northern northeast coast of Newfoundland and is the middle spawning area and
110 predicted migration path (Fig. 1). Off Labrador, the Hawke Channel is the northernmost
111 migration route to the coast from the outer reaches of the Belle Isle and Hamilton Banks (Fig. 1).

112 **Survey and analytical methods**

113 The northern cod within the Bonavista Corridor have been surveyed in late-winter to spring
114 with calibrated scientific echosounders beginning in 1990 (Table 1). The surveys were designed
115 to capture the time of maximum aggregation, mostly of age 4+ fish, as they overwintered near the
116 shelf break (Wroblewski et al. 1995) then dispersed somewhat as they migrated and spawned in
117 the shallower waters of the shelf and banks (Rose 1993). During this entire period, cod
118 aggregations are typically contracted laterally but expanded vertically, at times to >100 m off
119 bottom and are only rarely mixed with other species (<1% of 1 nautical mile sampling units),
120 making delineation of cod on echograms relatively simple and detection rates high. These factors
121 make northern cod at this time of year highly amenable to acoustic survey methods (see Figure 2
122 for typical echograms of cod aggregations). Survey equipment, designs and analyses have
123 evolved over these decades, but backscatter measures from calibrated echosounders are thought
124 to be comparable over time. Standard methods of acoustic integration of 38 kHz signals were
125 employed throughout (Simmonds and MacLennan 2005) as in previous reports (e.g., Rose 2003;
126 Mello and Rose 2009). A linear seafloor dead-zone correction was made based on the mean
127 backscatter in the bottom 5 m but seldom surpassed 20% of the total integrated backscatter from
128 cod (Ona and Mitson 1996). A length-based target strength model ($TS_{dB} = 20 \log_{10} \text{length} - 67.5$,
129 after Rose 2009) incorporating mean length of cod in the catch was used to convert backscatter to
130 cod densities. Biomass was calculated based on densities and mean weight of sampled fish.

131 Among years, survey areas and sampling intensity followed grid patterns that varied from year to
132 year (near standard 5 nautical mile spaced latitudinal grid since 2012), with sampling intensity
133 being lower in most years in the mid-1990s when very few fish were encountered (the surveys
134 from 1990-1994, 2007-2008, and 2012-2015 had more intensive sampling). In general, years with
135 higher density aggregations and hence higher spatial variance received more coverage. To make
136 comparisons over the two and a half decades, a simple analytical approach was used in which
137 survey data were randomly sampled with a bootstrapping procedure (1000 times) with n equal to
138 the number of survey measures (1 nautical mile [1852 m] integrated densities). Confidence
139 intervals (95%) were determined by dropping the largest and smallest estimates (2.5% each).
140 Differences in survey design and hardware-software improvements likely influenced results to
141 some extent but were thought unlikely to affect the strong trends in the survey data; various
142 analytical approaches yielded similar results (Mello and Rose 2008, 2009), and overall trends far
143 surpassed errors. Caution implies that these results be regarded as minimum estimates of cod
144 biomass in the full stock.

145 The Hawke Channel has been surveyed in winter and spring using similar acoustic-trawl
146 techniques in several years since 1994. The Notre Dame Channel area was never subjected to a
147 systematic survey but many passes over it were made since 1994 in winter and spring with only a
148 few fish located. A more complete survey of the outer portions of the northern Notre Dame
149 Channel was conducted in the spring of 2015.

150 Targeted otter trawl fishing sets to catch cod for tagging and in conjunction with the
151 acoustic surveys have been conducted in the Bonavista Corridor from 1984-2015, during which
152 over 59,000 cod have been measured. Lengths of all fish caught and tagged were recorded in 5
153 cm intervals. The earlier data (prior to 1995 from Taggart et al. 1995) used an Engels Hi-rise
154 commercial trawl with wider meshes than after 1995 when the Campelen trawl was introduced
155 and used for most subsequent fishing; hence fish < 50-55 cm in length are underrepresented in the
156 earlier sampling (McCallum and Walsh 1994). A few experimental sets were made in 2012 and

157 2013 with the larger GOV trawl (Reid et al. 2012). During the more limited surveys and tagging
158 in Hawke Channel a total of 8,216 cod were measured.

159 Fulton's condition factor (K) was estimated for Bonavista Corridor cod from these spring
160 (May-June) surveys with extensive sampling from 2000-2003 (n = 1,609) and 2012-2014 (n =
161 6,384). K was calculated as gutted weight (g) x total length (cm)⁻³ x 100.

162 Production was estimated by taking survey biomass indices (the annual estimate for the
163 acoustic surveys) and landings data, then calculating production as the sum of catch and change
164 in biomass per annum for years with <2 years between consecutive surveys. Fifty percent of the
165 reported landings (for the sentinel and stewardship fisheries the mean annual catch was 3400 t
166 between 1995 and 2014) were assumed to come from the Bonavista Corridor, although not
167 making this assumption or changing the percentage made little difference on the overall
168 productivity pattern. The recreational catch was not included as there were no data (DFO 2015b).

169 Capelin survey estimates (median with 95% CIs) indicating minimum biomass in the stock
170 range south of 50 °N latitude (near the northern extent of the Bonavista Corridor) were provided
171 by Francis Mowbray (DFO St. John's) and published in DFO (2015a). These surveys were
172 conducted on the *RV Gadus Atlantica* and *CCGS Teleost*, the same vessels used for most of the
173 present surveys (see Table 1) employing some of the same personnel using similar or the same
174 echosounders and methods.

175 Computational and statistical analyses were done in Systat (San Jose, CA, USA) and R (R
176 Core Team 2014) using standard methods. The cross-correlations in Systat estimated missing
177 values by local quadratic smoothing. All graphics were done in Grapher and Surfer (Golden
178 Software, CO, USA).

179

180 Results

181 In the Bonavista Corridor, in 1990, acoustic estimates of cod totalled over 450,000 t, but by
182 1992, the last year of major spawning and migration, one constricted group remained which
183 measured a few km in diameter and contained about 100,000 t (Fig. 3a). By 1994, the numbers of
184 fish had declined so rapidly that only a remnant of small fish (in poor condition) remained in the
185 Corridor, and few fish could be located anywhere else within the stock range. Surveys and
186 research that followed in the mid to late 1990s could locate few fish in the Bonavista Corridor or
187 anywhere else within the former range of the full stock, and most were <45 cm in length (Fig. 4).
188 By 2003, cod biomass within the Bonavista Corridor had increased only marginally to about 5000
189 t of mostly small and immature cod.

190 The next survey of the Bonavista Corridor occurred in 2007 and indicated that biomass had
191 increased to about 17,000 t. In 2008, biomass increased to approximately 75,000 t, a stock level
192 not observed since 1992 (Fig. 2). This increase was unprecedented and difficult to account for by
193 local production or survey error alone. Moreover, the 2008 survey located the first large cod
194 aggregation that had been observed in the offshore region since 1992 (Fig. 2b). The fish were
195 vertically extended forming structures up to 100 m off the seafloor – as had been observed in the
196 early 1990s (Fig. 2a) but not during the intervening period. The largest school spanned about 1.5
197 km and rose >150 m off the seafloor. Densities within this school ranged up to 1 fish·m⁻³. In all
198 surveys since 2008, large spawning aggregations, replete with pelagic columns and stacks (Rose
199 1993; Mello and Rose 2009; Knickle and Rose 2012), have been repeatedly observed (Fig. 2c,d).
200 Surveys in the springs of 2012-2014 have shown increases in biomass each year from
201 approximately 120,000 t in 2012 to 238,000 t in 2014.

202 In 2015, the most recent spawning survey, large aggregations of cod spanning a wide range
203 of sizes were found again in the Bonavista Corridor, but previously unknown aggregations were
204 surveyed to the north in the outer Notre Dame Channel and the southern Hamilton Bank and

205 Hawke Channel (Figs. 3a, 4). This was the first survey of the southern Hamilton Bank-Hawke
206 Channel region since 2008 and the first ever of the outer Notre Dame Channel. In all areas, cod
207 ranged up to >1 m in length (maximum 115 cm) and many fish were in spawning condition (Fig.
208 4; Notre Dame Channel data not shown as there is no comparable time series). The aggregations
209 were extensive covering many nautical miles and dense in each region with many pelagic
210 columns and stacks evident (e.g., Fig. 2d). Biomass estimates are not yet available from this
211 survey but are almost certain to show an increase over earlier surveys as a consequence of the
212 increased spatial coverage showing northward distribution of spawning cod.

213 An index of spawning biomass from bottom trawl surveys conducted by the DFO for the
214 full northern cod range from 1986 to 2014 corresponds well with the acoustic estimates from the
215 Bonavista Corridor during the period of overlap (Fig. 3a). Of particular note are the steep decline
216 from 1990-1994 and the increase beginning in 2006-2007. The trawl estimates are marginally
217 higher than the acoustic estimates from 1995-2001, the time of the lowest estimates in both
218 series. Prior to 1990 the trawl estimates are higher than at any time since (to >1 million tonnes)
219 but for this era there are no comparable acoustic estimates.

220 Almost in parallel with the decline and increase in cod has been changes in the biomass of
221 capelin (Fig. 3b). Capelin within most of the range of the northern cod collapsed in the early
222 1990s, according to both Canadian and Russian acoustic-trawl surveys, and remained very low
223 until about 2007. Since then, with the exception of 2010 when few capelin were located, the
224 surveys have indicated a higher abundance of capelin than has existed at any time from the crash
225 in 1991 until 2006 (DFO 2015a).

226 The cold sea temperatures that were pervasive during the early 1990s abated quickly in the
227 mid-1990s and have been warming subsequently (Fig. 3c).

228 The size of the fish is germane to recovery. During the 1980s, despite massive overfishing
229 in the 1960s, cod measuring >75 cm in length remained common in the Bonavista Corridor, and
230 fish >100 cm were also present in lesser numbers (Fig. 4). By the early 1990s, however, few fish
231 >75 cm could be found, although fish ranging from 55-75 cm were still common. Beginning in
232 the mid-1990s and as late as 2003, very few fish >50 cm could be located. By 2007 and 2008,
233 sizes began to increase, with fish ranging up to 70 cm once again commonly caught. Taking into
234 account differences in research nets between the late 1980s and 2007-2008 (the older nets had
235 reduced selectivity for smaller fish), the size structures of the two periods are relatively similar.
236 In the later survey period of 2012-2014, large fish (>75 cm) were again common in the Corridor.
237 It is not possible to directly compare the ages of these fish across the decades, as age data were
238 not available for the tagged fish. It is possible, however, based on length-age comparisons
239 (unpublished data held by G.A. Rose) to estimate approximate age composition; this indicates
240 that fish >6 years old were common in the 1980s, becoming increasingly rare by the early 1990s,
241 and mostly absent from the mid 1990s to the mid-2000s. By 2008, however, fish >6 years of age
242 comprised about 11% of the aged fish from the surveys, which is comparable to the late 1980s,
243 and by 2012-2015, comprised >30% of the surveyed catch. Hence the changes in size
244 distributions are almost certainly the result of changes in age structure and not size at age.

245 A comparison of body condition of cod caught during the surveys in May and June in the
246 Bonavista Corridor as indicated by Fulton's condition index (K) is informative (Fig. 5). The
247 decline in K of fish of lengths >40 cm (age 4 or 5) that occurred during the early 2000s (2000-
248 2003 in Fig. 5) has abated in recent years (2012-2014).

249 Biomass production in the Bonavista Corridor over the past decade has been variable (Fig.
250 6). After some years of negative production, post-1995 production remained low but positive
251 until the mid-2000s, after which there have been rapid increases (Fig. 5). An exponential model
252 fit suggested that on average growth has proceeded at approximately 30% per annum. Despite the
253 simplicity of these models, it is noteworthy that residuals for both biomass and production were

254 mostly negative prior to 2008, which supports the notion that additional factors have been
255 impacting stock growth. The low number of measures of other factors such as capelin and
256 temperature in corresponding years precluded inclusion of other variables in these models.

257 Single variable cross-correlations of cod biomass in the Bonavista Corridor with capelin
258 biomass as measured in the DFO spring acoustic survey and bottom temperature at Station 27
259 (Fig. 3) during 1995-2014 were both significant at lag 0 (Fig. 7). Capelin biomass was also
260 significant both a year in advance (lag 1) and after (lag -1) the measure of cod biomass. The
261 correlation with both variables was stronger ahead of time than after, especially so for
262 temperature. The limited harvests from the fishery were not correlated at any lag with the
263 rebuilding track of the stock.

264 Discussion

265 The northern cod is making a remarkable comeback from commercial extinction, with
266 production increasing rapidly since 2007 for the first time in nearly 2 decades. One feature of both
267 the decline and the comeback is how quickly such changes can occur. The predicted stepped
268 rebuilding over decades (Rose et al. 2000) appears to have been borne out, with step 1 being an
269 improved environment resulting in rebuilding in the south in the Bonavista Corridor with increases
270 in abundance, condition and size structure. Step 2 has followed, first observed in the spring of 2015,
271 with all three spawning-migration routes predicted by Rose (1993) populated with a wide size
272 structure of fish. Step 3 is the generation of strong recruitment from all three regions. Although the
273 acoustic surveys reported here cannot give reliable estimates of juvenile abundance, elevated
274 catches of juveniles in fishing sets conducted outside the spawning aggregations in 2015, reports
275 from DFO trawl surveys (DFO 2015b) and anecdotal evidence from fishermen all suggest that
276 stronger recruitment may already be occurring.

277 We further note that in assessing the state of fish stocks, and perhaps more importantly in
278 assessing how a stock is responding to changes in the environment or to fishing pressure,
279 observations of behavioural changes may provide signals as important as changes in measured
280 abundance. The rapid decline that occurred in the early 1990s occurred during a period of equally
281 rapid distribution shifts in cod (deYoung and Rose 1993) and its main prey capelin (Frank et al.
282 1996). Cod became hyper-aggregated in the Bonavista Corridor by 1990 in a few aggregations with
283 very high densities (Rose and Kulka 1999), signalling a major change in the ecosystem and negative
284 production for both species - by 1993 no cod aggregations could be located in the Bonavista
285 Corridor or to the north, and few capelin. The re-establishment of aggregative behaviours in cod
286 associated with spawning, first observed in 2008 after a decade and a half of seeming dispersal, was
287 likely a harbinger of positive change for production in this stock (Fig. 2b).

288 Several questions arise from these observations. One concerns the source of the rebuilding
289 fish. Has all rebuilding resulted from local increases in production or have there been spatial
290 shifts with immigration from adjacent areas? Of the three spawning groups, we know the most
291 about the development of the Bonavista Corridor group. For that group, a key question is what
292 happened around 2007 to kick-start a relatively abrupt increase in productivity? As with the
293 decline in the late 1980s and early 1990s, it seems doubtful that a single factor caused this to
294 occur. Environmental conditions were improving, no doubt, but temperatures had been warming
295 since the late 1990s with little apparent impact on productivity – mostly negative residuals from
296 both the abundance and productivity models. The abundance of capelin is likely key, with
297 availability to cod in the Bonavista Corridor increasing since 2006 after almost 2 decades of low
298 abundance. Capelin biomass has been strongly correlated with rebounding cod biomass, which
299 supports earlier notions that northern cod could not rebuild without them (Rose and O’Driscoll
300 2002), as well as recent modelling (e.g., Burin et al. 2014) and laboratory studies (Mullowney
301 and Rose 2014) using different approaches and data. It is also possible that immigration of fish
302 occurred, most likely from Smith Sound. The sudden and not easily explained increases in both
303 the DFO fall trawl survey (Cadigan 2015) and the present acoustic-trawl spring survey in 2008

304 with apparent decreases in mortality of age 4-6 year old cod occurred at the same time the Smith
305 Sound cod were dispersing (Rose et al. 2011; Cadigan 2015). Although no appropriate year-class
306 data are available from Smith Sound for the early 2000s, it is plausible that these were relatively
307 strong, because the 1990 and 1992 founder year-classes were abundant with substantial spawning
308 potential in those years (Rose 2003). Moreover, the sentinel fishery data show some of those year
309 classes to be strong inshore (Brattey et al. 2008a). In 2007, for example, the 2002 year-class
310 would have been 5 years old, the time of maturation and migration to spawn, and by 2007, the
311 onshore-offshore migration via the Bonavista Corridor was re-occurring (Brattey et al. 2008b),
312 following more or less the same pattern as had been evident in the early 1990s (Rose 1993). In
313 addition, there is little evidence of genetic differences between these adjacent groups, most likely
314 they belong to a meta-population (Smedbol and Wroblewski 2002; Rose et al. 2011). Hence,
315 although all evidence is indirect, the coincidence of the decline in Smith Sound, the likelihood of
316 strong early 2000 year-classes there which would have been at the age of joining a spawning
317 group within their meta-population by 2007, the onset of cross-shelf migration, and the better fit
318 of a population model by taking immigration into account, are all consistent with a sudden
319 increase in abundance in the Bonavista Corridor adult population being the result of emigration
320 from Smith Sound. Additional research will be required to either confirm or reject these
321 contentions.

322 The origin of the Notre Dame Channel and Hawke Channel groups is less certain. During
323 the late 1990s and early 2000s, the abundance of potential spawning fish (>40 cm) was very low
324 in all of the offshore, but particularly in the northern regions. Of note, there were fewer capelin in
325 these northern channels than in the Bonavista Corridor as a consequence of the decline and
326 southward distribution shift of capelin in the early 1990s (Frank et al. 1996). Subsequent feeding
327 by cod on capelin was almost nil in the north (Krumsick and Rose 2012). Meanwhile, the
328 Bonavista Corridor group increased to over 200,000 t, hence it is possible that some of the
329 Bonavista Corridor fish moved north to seed the groups in the Notre Dame Channel and
330 Hamilton Bank-Hawke Channel. Indeed, Bentzen et al. (1996) reported no distinguishable

331 genetic features in a microsatellite study that included fish from the eastern Funk Island Bank
332 (Bonavista Corridor), Belle Isle Bank and Hamilton Bank (NAFO 2J) from samples collected in
333 1992 and 1993, which were subsequently pooled as “North” fish. In more recent studies, small
334 genetic differences were reported among cod from Hawke Channel (NAFO 2J) and further south
335 (Beacham et al. 2002; Rose et al. 2011) but the extent of intermixing among these groups remains
336 controversial, hence the origin of the northern spawning groups is a key research question.
337 Tagging with satellite transmitting popup tags has been implemented in effort to address this
338 issue (Rose et al. 2013) although investigations of age and growth regimes, as well as otolith
339 micro-chemical and molecular genetic patterns, are warranted.

340 The rebuilding of abundance, size and age structure, and fish condition, is noteworthy.
341 Undoubtedly these factors are related. The much improved condition of older fish in May-June in
342 particular supports predictions first made in the early 1990s that environmental factors played a
343 significant role in the suppression of productivity in this stock and would delay rebuilding until
344 conditions improved (deYoung and Rose 1993), a view consistent with considerable research
345 over the past two decades (Rice 2006; Rothschild 2007; Greene and Pershing 2007; Lilly 2008;
346 Hilborn and Litzinger 2009). Late winter to spring is the time of poorest condition in cod and
347 when condition related mortality is expected to be highest (Dutil and Lambert 2000, Mullowney
348 and Rose 2014). As shown recently in a laboratory study, if cod in very poor condition are given
349 an adequate diet of rich fish, their subsequent growth, condition and reproductive performance
350 will match those that began in good condition (Mullowney and Rose 2014).

351 It is likely no coincidence that the increased production of cod coincided with an
352 improvement of the food supply in the Bonavista Corridor, particularly capelin (Fig. 3b), the
353 chief prey of the northern cod historically. Capelin virtually disappeared north of the Bonavista
354 Corridor in the early 1990s (Frank et al. 1996; DFO 2015a). In the Bonavista Corridor, capelin
355 remained in reduced numbers when the stock was at its lowest, and cod diet reflected that (e.g.,
356 Krumsick and Rose 2012). In recent years, anecdotal evidence suggests capelin have returned to

357 the north although no surveys have been done. A strong relationship between cod and capelin is
358 in keeping with bottom-up influences on this Northwest Atlantic ecosystem (Greene and Pershing
359 2007; Buren et al. 2014; Mullaney and Rose 2014; Mullaney et al. 2014). On the other hand,
360 there has been no decline in numbers of top predators, harp (*Phoca groenlandica*) and hood
361 (*Cystophora cristata*) seals (DFO 2014), and harvests have been relatively low, hence it is
362 difficult to postulate how top-down effects (downward trophic cascades) could have been
363 involved in such a rapid increase in the northern cod (e.g., Frank et al. 2005).

364 In keeping with the importance of a fish-rich diet shown in laboratory studies and here
365 statistically by cross-correlation of cod and capelin biomass, cod condition has improved
366 markedly over the past decade. The decline in condition observed in the 1990s and early 2000s
367 once fish reached approximately 40 cm in length was attributed largely to a lack of capelin in the
368 diet once cod reached a size where alternative prey would no longer satisfy metabolic
369 requirements (Sherwood et al. 2007). Our data support that result but further indicate that the
370 depression of condition has now abated. At present, condition increases more or less continuously
371 as fish grow. Improved reproductive potential is to be expected (Sherwood et al. 2007; Wright
372 and Trippel 2009).

373 We stress that neither the full “northern” cod, nor the Bonavista Corridor group, are by any
374 definition fully rebuilt or recovered at this stage. What is important in our findings is that this
375 stock is making a strong comeback after nearly 2 decades of attrition, from levels thought to be a
376 few percent of the maximum historical stock biomass (COSEWIC 2010). At present, cod
377 utilizing the Bonavista Corridor have increased to approximately 50% of the 1990 biomass of
378 450,000 t. Nevertheless, the historically large and important stock region to the north off
379 Labrador has been slower to rebuild, and predictably so (deYoung and Rose 1993), although the
380 present results indicate that rebuilding has begun. What is key at this stage is to recognize that
381 this full stock complex can and is rebuilding, despite some generally negative perspectives on its
382 state and recovery potential (e.g., Hutchings and Reynolds 2004; COSEWIC 2010). Whatever

383 environmental hurdles faced since fishing was reduced, they appear to have ameliorated, resulting
384 in the rebuilding of much of the spatial structure of spawning that underpinned productivity in
385 this once great stock (step 2 of Rose et al. 2000). Without doubt the relatively low removals from
386 this stock over the past decades has been essential to recovery. Step 3 and the production of larger
387 and more broadly distributed and recruited year-classes is predicted to follow. While timing
388 remains uncertain, continued protection from excessive fishing remains key to achieving that
389 outcome. We also point out that if this stock, arguably the most mismanaged and overfished
390 worldwide (although there are other contenders for that title), can comeback from abundances of
391 a few percent of historic norms, then with judicious management even the largest and most
392 severely impacted marine fish stocks can potentially recover.

393

394 We conclude that the northern cod is making a remarkable comeback. Since 2007, cod
395 biomass in over-wintering and spawning aggregations in the Bonavista Corridor has increased
396 from a few thousand to >200 thousand tonnes. Abundance, size structure, and condition have all
397 improved. The main factors that kick-started the increase appear to be capelin abundance and
398 perhaps immigration of at least one strong year-class, which occurred during a period of
399 favourable climate and low removals through the fishery. For the first time since the stock
400 collapse over 2 decades past, spawning aggregations were observed and assessed in May 2015 in
401 the northern ranges of the Notre Dame Channel and Hamilton Bank-Hawke Channel, which will
402 likely increase the current perception of spawning biomass considerably. As predicted earlier,
403 rebuilding is occurring in steps – we are now at the third and final step – the production of
404 widespread and strong recruitment.

405

406

407

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417 CFER) for work at sea over the past two and a half decades.

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423 Table 1. Research cruises conducted from 1990 to 2015 and echosounders and software utilized
 424 in the analysis of the acoustic data (all calibrated 38 kHz systems as per Foote et al. 1987). On the
 425 *RV Gadus Atlantica*, the transducer was in a towed body, on the *CCGS Teleost* hull mounted and
 426 on the *RV Celtic Explorer* on a drop keel.

<u>Year</u>	<u>Month</u>	<u>Vessel</u>	<u>Echosounder</u>	<u>Type</u>	<u>Software</u>
1990	May-June	<i>Gadus Atlantica</i>	BioSonics	B102	BioSonics ¹
1991	May-June	<i>Gadus Atlantica</i>	BioSonics	B102	BioSonics
1992	May-June	<i>Gadus Atlantica</i>	BioSonics	B102	BioSonics
1993	May-June	<i>Gadus Atlantica</i>	BioSonics	B102	BioSonics
1994	May-June	<i>Gadus Atlantica</i>	BioSonics	B102	BioSonics
1995	May-June	<i>Gadus Atlantica</i>	Simrad	EK500	EP500 ²
1998	May-June	<i>Teleost</i>	Simrad	EK500	Fasit ³
2000	June	<i>Teleost</i>	Simrad	EK500	Fasit
2002	June	<i>Teleost</i>	Simrad	EK500	Fasit
2003	June	<i>Teleost</i>	Simrad	EK500	Fasit
2007	March	<i>Teleost</i>	Kongsberg	EK60	Echoview ⁴
2008	March	<i>Teleost</i>	Kongsberg	EK60	Echoview
2012	May	<i>Celtic Explorer</i>	Kongsberg	EK60	Echoview
2013	May	<i>Celtic Explorer</i>	Kongsberg	EK60	Echoview
2014	May	<i>Celtic Explorer</i>	Kongsberg	EK60	Echoview
2015	May	<i>Celtic Explorer</i>	Kongsberg	EK60	Echoview

427

428 ¹ Proprietary integration software for BioSonics analog echosounders, BioSonics Inc., Seattle
 429 WA.

430 ² Editing and display software for the EK500 echosounder, Simrad Corp., Horten, Norway.

431 ³ Proprietary display, editing and integration software developed for digital acoustic data,
 432 Fisheries Conservation Chair, Memorial University of Newfoundland.

433 ⁴ Myriax, Hobart, Australia.

434

435 Figure captions

436 Figure 1. The northeast Newfoundland shelf showing predicted migration highways from
437 offshore overwintering and spawning grounds to summer inshore feeding areas (reproduced and
438 re-annotated from Rose 1993). Bonavista Corridor tagging and survey area hatched.

439 Figure 2. Echograms of cod from the acoustic surveys showing a) migrating and spawning cod in
440 the Bonavista Corridor in June 1990; b) in March 2008, the first observed aggregation in the
441 Bonavista Corridor since 1992; c) spawning aggregation in the Bonavista Corridor in May 2014;
442 and d) spawning aggregation in the Notre Dame Channel in May 2015. For each panel, seabed is
443 indicated in dark red, vertical blocks span 1 nautical mile (1852 m) and horizontal blocks 50 m.
444 In all cases, cod are distributed >100m off bottom.

445 Figure 3. a) Biomass of cod (mean with 95% CIs, closed circles) measured using scientific
446 echosounders in the overwintering to spawning period (March to June) within the Bonavista
447 Corridor from 1990 to 2014. Estimates from 1990-1992 from Rose (1993); 1995-2005 from Rose
448 et al. 2011; 2007-2008 modified from Mello and Rose 2007, 2008; also shown is spawning
449 biomass index from Department of Fisheries and Oceans fall bottom trawl surveys for all of
450 NAFO Divisions 2J3KL from 1986-2014 (mean, no CIs given, open circles, 1990-2014 from
451 DFO 2015, 1986-1989 from Brattey et al. 2010); b) median biomass of capelin from Canadian
452 surveys (circles) with 95% CIs (crosses) (courtesy of F. Mowbray, DFO St. John's) and Russian
453 surveys in early 1990s (diamonds) from Bakanev (1992); and c) mean bottom sea temperatures at
454 Station 27 off St. John's from 1985-2014 (from Colbourne et al. 2014).

455 Figure 4. Length-frequency proportions for cod caught in directed fishing sets during acoustic
456 survey and tagging research from 1984 to 2015. Total n=59,481 for the Bonavista Corridor and
457 8,216 for Hawke Channel. Note that nominal bins on each panel are lower limits of 5 cm groups
458 (e.g., 40-44 cm shows as 40, 100-104 as 100). Also, in the 1984-88 data all fish >85 cm were
459 binned at 85 cm and low proportions of fish >100 cm in length do not show at the scales shown.

460 Figure 5. Mean Fulton's condition factor (K) for cod in May-June in the Bonavista Corridor in
461 years 2000-2003 (n=1609; open circles with 95% CIs) and 2012-2014 (n=6384; closed circles).
462 Bins are decadal (10-19 cm, 20-29 cm...).

463 Figure 6. Acoustic-trawl survey estimates for the Bonavista Corridor of a) biomass of cod from
464 1995 to 2014 with exponential equation [$\ln(\text{biomass}) = 0.2975 * \text{year} - 594$; $r^2 = 0.94$]; and b)
465 productivity [$\ln(\text{biomass}) = 0.2733 * \text{year} - 546$; $r^2 = 0.80$].

466 Figure 7. Cross-correlations of cod biomass in the Bonavista Corridor and capelin biomass (1990-
467 2014) from the Department of Fisheries and Oceans Canada spring survey (DFO 2015a) (bars)
468 and bottom temperatures at Station 27 (from Colbourne et al. 2014) (points). Correlations above
469 0.5 are significant.

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470 References

- 471 Atkinson, B.A., Rose, G.A., Murphy, E., and Bishop, C.A. 1997. Distribution changes and
472 abundance of northern cod (*Gadus morhua*): 1981-1993. Can. J. Fish. Aquat. Sci. 54 (Suppl.1):
473 132-138.
- 474 Bakaney, V.S. 1992. Results from acoustic capelin surveys in Div. 3LNO and 2J+3KL in 1991.
475 NAFO SCR 92/1.
- 476 Beacham, T.D., Bratley, J., Miller, K.M., Le, K.D., and Withler, R.E. 2002. Multiple stock
477 structure of Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador determined from
478 genetic variation. ICES J. Mar. Sci. 59: 650-665.
- 479 Bentzen, P., Taggart, C.T., Ruzzante, D., and Cook, D. 1996. Microsatellite polymorphism and
480 the population structure of Atlantic cod (*Gadus morhua*) in the northwest Atlantic. Can. J. Fish.
481 Aquat. Sci. 53: 2706-2721.
- 482 Bratley, J., Cadigan, N.G., Dwyer, K., Healey, B.P., Morgan, M.J., Murphy, E.F., Maddock
483 Parsons, D., and Power, D. 2008a. Assessments of the cod (*Gadus morhua*) stock in NAFO
484 Divisions 2J3KL (April 2007 and April 2008). Can. Sci. Adv. Secr. Res. Doc. 2008/086.
- 485 Bratley, J., Healey, B.P., and Porter, D.R. 2008b. Northern cod (*Gadus morhua*) 16 years after
486 the moratorium: new information from tagging and acoustic telemetry. Can. Sci. Adv. Secr. Res.
487 Doc. 2008/047.
- 488 Bratley, J., Cadigan, N.G., Dwyer, K., Healey, B.P., Morgan, M.J., Murphy, E.F., Maddock
489 Parsons, D., and Power, D. 2010. Assessment of the cod (*Gadus morhua*) stock in NAFO
490 Divisions 2J+3KL in 2010. Can. Sci. Adv. Secr. Res. Doc. 2010/103.

- 491 Buren A.D., Koen-Alonso M., Pepin P., Mowbray F., Nakashima B., Stenson G., and Ollerhead,
492 N. 2014. Bottom-up regulation of capelin, a keystone forage species. PLoS ONE 9(2): e87589.
493 doi:10.1371/journal.pone.0087589
- 494 Cadigan, N. 2015. A state-space stock assessment model for northern cod, including under-
495 reported catches and variable natural mortality rates. Can. J. Fish. Aquat. Sci. 10.1139/cjfas-
496 2015-0047.
- 497 Colbourne, E., Holden, J., Craig, J., Senciall, D., Bailey, W., Stead, P., and Fitzpatrick, C. 2014.
498 Physical oceanographic conditions on the Newfoundland and Labrador Shelf during 2013. Can.
499 Sci. Adv. Secr. Sci. Adv. Res. Doc. 2014/094.
- 500 COSEWIC. 2010. COSEWIC assessment and status report on the Atlantic cod *Gadus morhua* in
501 Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. Xiii + 105pp.
502 (www.sararegistry.gc.ca/status.status_e.cfm).
- 503 Davoren, G.K., and Montevecchi, W.A. 2003. Signals from seabirds indicate changing biology of
504 capelin stocks. Mar. Ecol. Prog. Ser. 258: 253-261.
- 505 deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus*
506 *morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. 50: 2729-2741.
- 507 DFO. 2014. Status of northwest Atlantic harp seals, *Phagophilus groenlandicus*. Can. Sci. Adv.
508 Secr. Sci. Adv. Rep. 2014/11.
- 509 DFO. 2015a. Assessment of capelin in subarea 2 and Divisions 3KL in 2015. Can. Sci. Adv.
510 Secr. Sci. Adv. Rep. 2015/036.
- 511 DFO. 2015b. Northern (NAFO Divs. 2J3KL) cod stock update. Can. Sci. Adv. Secr. Sci.
512 Response 2015/018.

- 513 Dutil, J.-D., and Lambert, Y. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus*
514 *morhua*). Can. J. Fish. Aquat. Sci. 57: 826-836.
- 515 FAO. 2012. The state of world fisheries and aquaculture 2012. FAO, Rome.
- 516 Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., and Simmonds, E.J. 1987. ICES
517 Coop. Res. Rep. No. 144.
- 518 Frank, K.T., Carscadden, J.E., and Simon, J.E. 1996. Recent excursions of capelin (*Mallotus*
519 *villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Can. J.
520 Fish. Aquat. Sci. 53: 1473-1486.
- 521 Frank, K.T., Petrie, B., Choi, J.S., and Leggett, W.C. 2005. Trophic cascades in a formerly cod-
522 dominated ecosystem. Science 308: 1621-1623.
- 523 Fudge, S.B., and Rose, G.A. 2008. Life history co-variation in a fishery depleted Atlantic cod
524 stock. Fisheries Research 92: 107-113.
- 525 Greene, C.H., and Pershing, A.J. 2007. Climate drives sea change. Science 315: 1084-1085.
- 526 Halliday, R.G., and Pinhorn, A.T. 2009. The roles of fishing and environmental change in the
527 decline of Northwest Atlantic groundfish populations in the early 1990s. Fish. Res. 97: 163-182.
- 528 Hilborn, R., and Litzinger, E. 2009. Causes of decline and potential for recovery of Atlantic cod
529 populations. Open Fish Sci. J. 2: 32-38.
- 530 Hutchings, J.A. 1999. Influence of growth and survival costs of reproduction on Atlantic cod,
531 *Gadus morhua*, population growth rate. Can. J. Fish. Aquat. Sci. 56: 1612-1623.
- 532 Hutchings, J.A., and Reynolds, J.D. 2004. Marine fish population collapses: consequences for
533 recovery and extinction. BioSci. 54(4): 297-309.

- 534 Knickle, D.C., and Rose, G.A. 2010. Seasonal spawning and wind-regulated retention-dispersal
535 of early life stage Atlantic cod (*Gadus morhua*) in a Newfoundland fjord. Fish. Oceanogr. 19(5):
536 397-411.
- 537 Knickle, D.C., and Rose, G.A. 2012. Acoustic markers of Atlantic cod (*Gadus morhua*)
538 spawning in coastal Newfoundland. Fish. Res. 129-130: 8-16.
- 539 Krumsick, K.J., and Rose, G.A. 2012 Atlantic cod (*Gadus morhua*) feed during spawning off
540 Newfoundland and Labrador. ICES J. Mar. Sci. 69: 1701-1709.
- 541 Lilly, G.R., Wieland, K., Rothschild, B.J., Sundby, S., Drinkwater, K., Brander, K., Ottersen, G.,
542 Carscadden, J.E., Stenson, G.B., Chouinard, G.A., Swain, D.P., Daan, N., Enberg, K., Hammill,
543 M.O., Rosing-Asvid, A., Svedang, H., and Vasquez, A. 2008. Decline and recovery of Atlantic
544 cod (*Gadus morhua*) stocks throughout the North Atlantic. In Resiliency of Gadid Stocks to
545 Fishing and Climate Change, pages 39-66. Alaska Sea Grant College Program.
- 546 McCallum, B.R., and Walsh, S.J. 1994. Campelen 1800. Survey trawl reference manual. Dep. of
547 Fisheries and Oceans, Newfoundland, Canada.
- 548 Mello, L.G.S., and Rose, G.A. 2008. A trawl acoustic survey of offshore overwintering northern
549 cod, Feb.-Mar. 2007. Can. Sci. Adv. Res. Doc. 2008/048.
- 550 Mello, L.G.S., and Rose, G.A. 2009. A trawl acoustic survey of offshore overwintering northern
551 cod, Feb.-Mar. 2008. Can. Sci. Adv. Res. Doc. 2009/099.
- 552 Mullaney, D., and Rose, G.A. 2014. Is recovery of northern cod limited by poor feeding: the
553 capelin hypothesis revisited. ICES J. Mar. Sci. doi:10.1093/icesjms/fst188
- 554 Mullaney, D., Dawe, E.G., Colbourne, E.B., and Rose, G.A. 2014. A review of factors
555 contributing to the decline of Newfoundland and Labrador snow crab (*Chionocetes opilio*). Rev.
556 Fish. Biol. Fisheries 24: 639-657.

- 557 Myers, R.A., Mertz, G., and Fowlow, P.S. 1997. Maximum population growth rates and recovery
558 times for Atlantic cod, *Gadus morhua*. Fishery Bulletin
- 559 Obradovich, S., Carruthers, E., and Rose, G.A. 2014. Bottom-up limits to Newfoundland capelin
560 (*Mallotus villosus*) rebuilding: the euphausiid hypothesis. ICES J. Mar. Sci. 71 (4): 775-783.
- 561 Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., and Dieckmann, U.
562 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod.
563 Nature 428: 932-935.
- 564 Ona, E., and Mitson, R.B. 1996. Acoustic sampling and signal processing near the seabed: the
565 deadzone revisited. ICES J. Mar. Sci. 53: 677-690.
- 566 Reid, D.G., Kynock, R.J., Penny, I., Summerbell, K., Edridge, A., and O'Neill, F.G. 2012. A
567 comparison of the GOV survey trawl with a commercial whitefish trawl. Fish. Res. 121-122:
568 136-143.
- 569 R Development Core Team. 2014. R: A language and environment for statistical computing. R
570 Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- 571 Rice, J.C. 2006. Every which way but up: the sad story of Atlantic Groundfish, featuring
572 Northern cod and North Sea cod. Bull. Mar. Science: 429-465.
- 573 Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature 366:
574 458-461.
- 575 Rose, G.A., and Kulka, D.W. 1999. Hyper-aggregation of fish and fisheries: how CPUE increased
576 as the northern cod declined. Can. J. Fish. Aquat. Sci. 56(Suppl. 1): 118-127.

- 577 Rose, G.A., deYoung, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution
578 shifts and overfishing the northern cod: a view from the ocean. *Can. J. Fish. Aquat. Sci.* 57: 644-
579 664.
- 580 Rose, G.A., and O'Driscoll, R.L. 2002. Capelin are good for cod: can the northern stock rebuild
581 without them? *ICES J. Mar. Sci.* 59: 1018-1026.
- 582 Rose, G.A. 2003. Monitoring coastal Northern cod: towards an optimal survey of Smith Sound,
583 Newfoundland. *ICES J. Mar. Sci.* 60: 453-462.
- 584 Rose, G.A. 2004. Reconciling effects of overfishing and climate change on Newfoundland cod
585 over 500 years. *Can. J. Fish. Aquat. Sci.* 61: 1553-1557.
- 586 Rose, G.A. 2007. Cod: the ecological history of the north Atlantic fisheries. Breakwater books, St.
587 John's, Canada. 591pp.
- 588 Rose, G.A. 2009. Variations in the target strength of Atlantic cod during vertical migration. *ICES*
589 *J. Mar. Sci.* 66: 1205-1211.
- 590 Rose, G.A., Nelson, J., and Mello, L.G.S. 2011. Isolation or metapopulation: whence and whither
591 the Smith Sound cod. *Can. J. Fish. Aquat. Sci.* 68: 152-169.
- 592 Rose, G.A., Rowe, S., and King, G. 2013. The amazing journey of tag 17. *The Osprey.*
593 Newfoundland and Labrador Nat. Hist. Soc., St. John's, Canada.
- 594 Rothschild, B.J. 2007. Coherence of Atlantic cod stock dynamics in the northwest Atlantic
595 Ocean. *Trans. Amer. Fish. Soc.* 136: 858-874.
- 596 Roughgarden, J., and Smith, F. 1996. Why fisheries collapse and what to do about it. *Proc. Nat.*
597 *Acad. Science USA* 93: 5078-5083.

- 598 Shelton, P.A., Sinclair, A.F., Chouinard, G.A., Mohn, R., and Duplisea, D.E. 2006. Fishing under
599 low productivity is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Can. J.
600 Fish. Aquat. Sci. 63: 235-238.
- 601 Sherwood, G.D., Rideout, R., Fudge, S.B. and Rose, G.A. 2007. Influence of diet on growth,
602 condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*):
603 Insights from stable carbon isotopes. Deep-Sea Res. II 54: 2704-27 09.
- 604 Simmonds, E.J., and MacLennan, D. 2005. Fisheries acoustics: theory and practice. Blackwell
605 Science, Oxford UK.
- 606 Smedbol, R.K., and Wroblewski, J.S. 2002. Metapopulation theory and northern cod population
607 structure: interdependency of subpopulations in recovery of a groundfish population. Fish. Res.
608 55: 161-174.
- 609 Taggart, C.T., Penney, P., and George, C. 1995. The 1954-1993 Newfoundland cod-tagging
610 database: statistical summaries and spatial-temporal distributions. Can. Tech. Rep. Fish. Aquat.
611 Sci. No. 2042.
- 612 Templeman, W. 1966. Marine resources of Newfoundland. Bulletin of the Fisheries Research
613 Board of Canada 154: 1-170.
- 614 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C.,
615 Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., and Watson, R.
616 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314: 787-790.
- 617 Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S. Costello, C., Fogarty, M.J., Fulton,
618 E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R.,
619 Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., and Zeller, D.
620 2009. Rebuilding global fisheries. Science 325: 578-585.

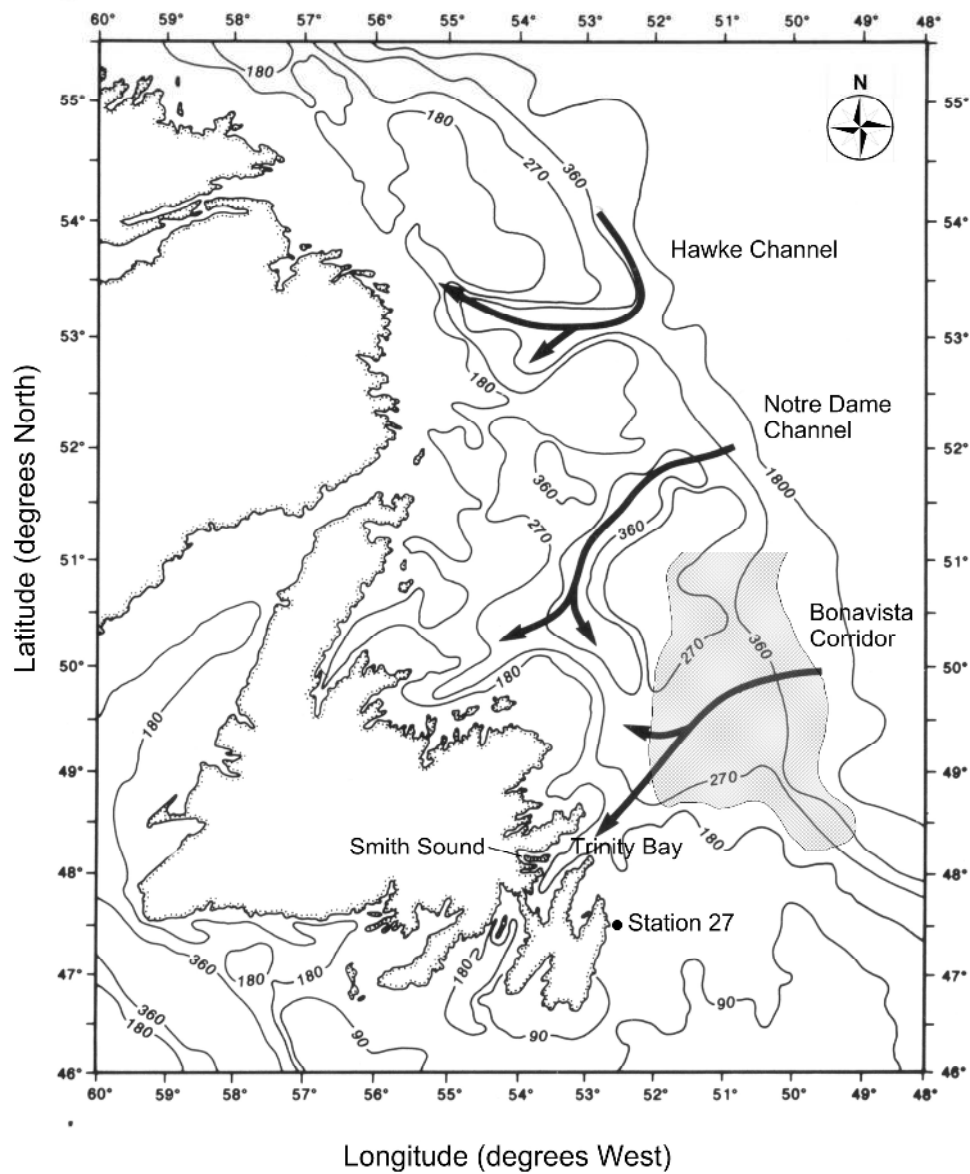
621 Wright, P.J., and Trippel, E.A. 2009. Fishery-induced demographic changes in the timing of
622 spawning: consequences for reproductive success. *Fish and Fisheries* 10 (3): 283-304.

623 Wroblewski, J.S., Kulka, D.W., Narayanan, S., Oake, A.M., Collier, A.G., and McGrath, B.D.
624 1995. Winter distribution and movements of northern Atlantic cod (*Gadus morhua*) along the
625 Newfoundland-Labrador continental shelf edge derived from observations on commercial
626 trawlers. *Fish. Oceanography* 4(2): 128-146.

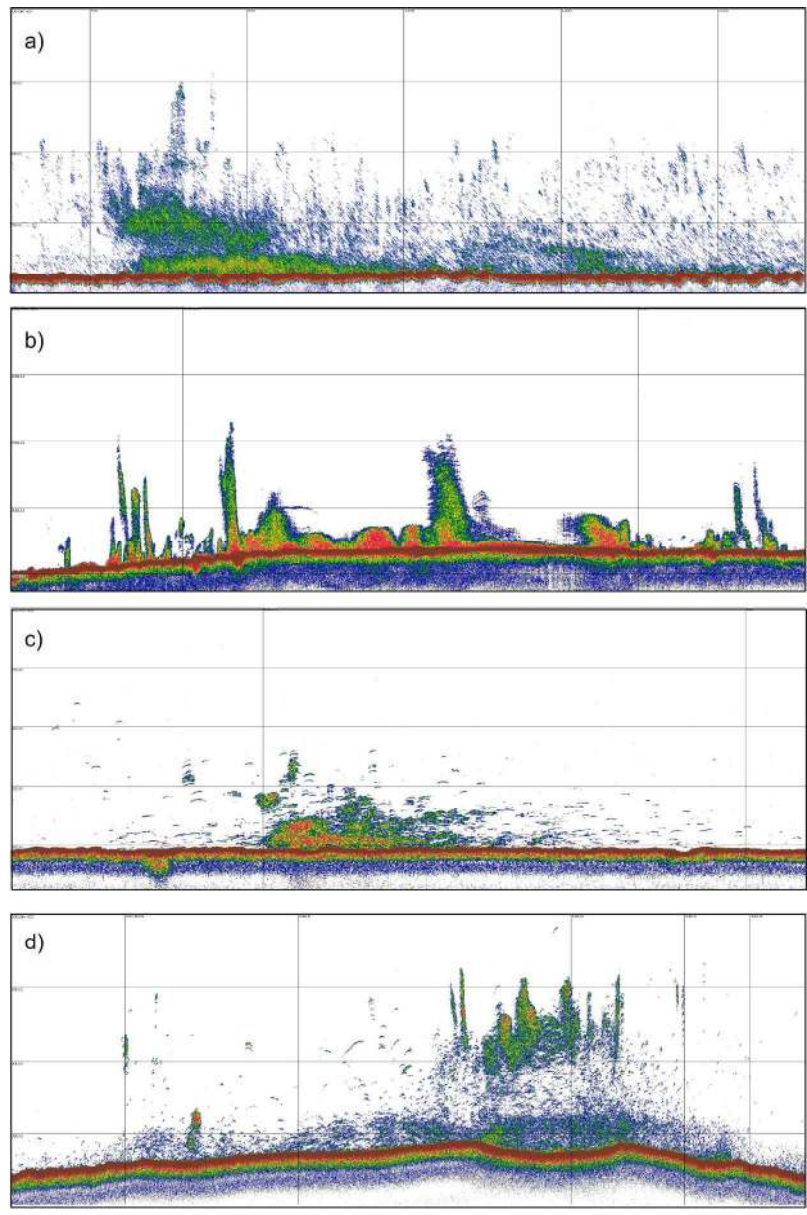
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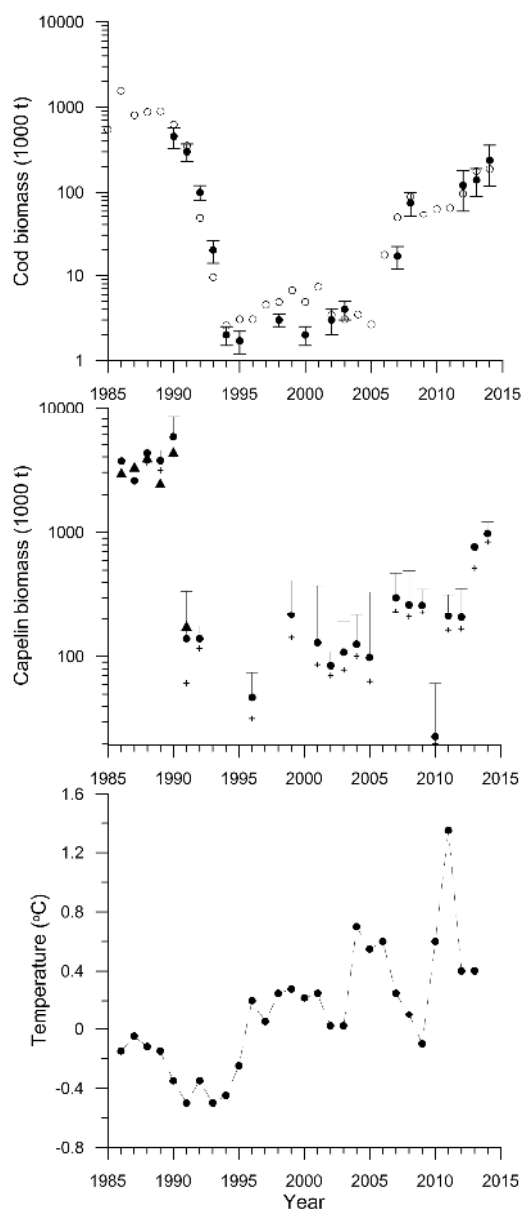
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The northeast Newfoundland shelf showing predicted migration highways from offshore overwintering and spawning grounds to summer inshore feeding areas (reproduced and re-annotated from Rose 1993).
 Bonavista Corridor tagging and survey area hatched.
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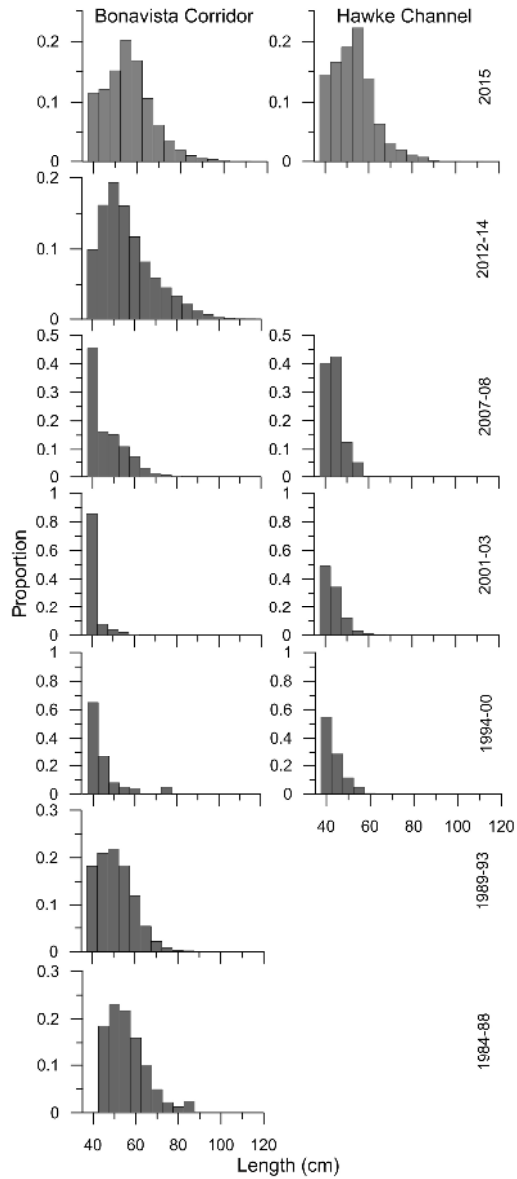


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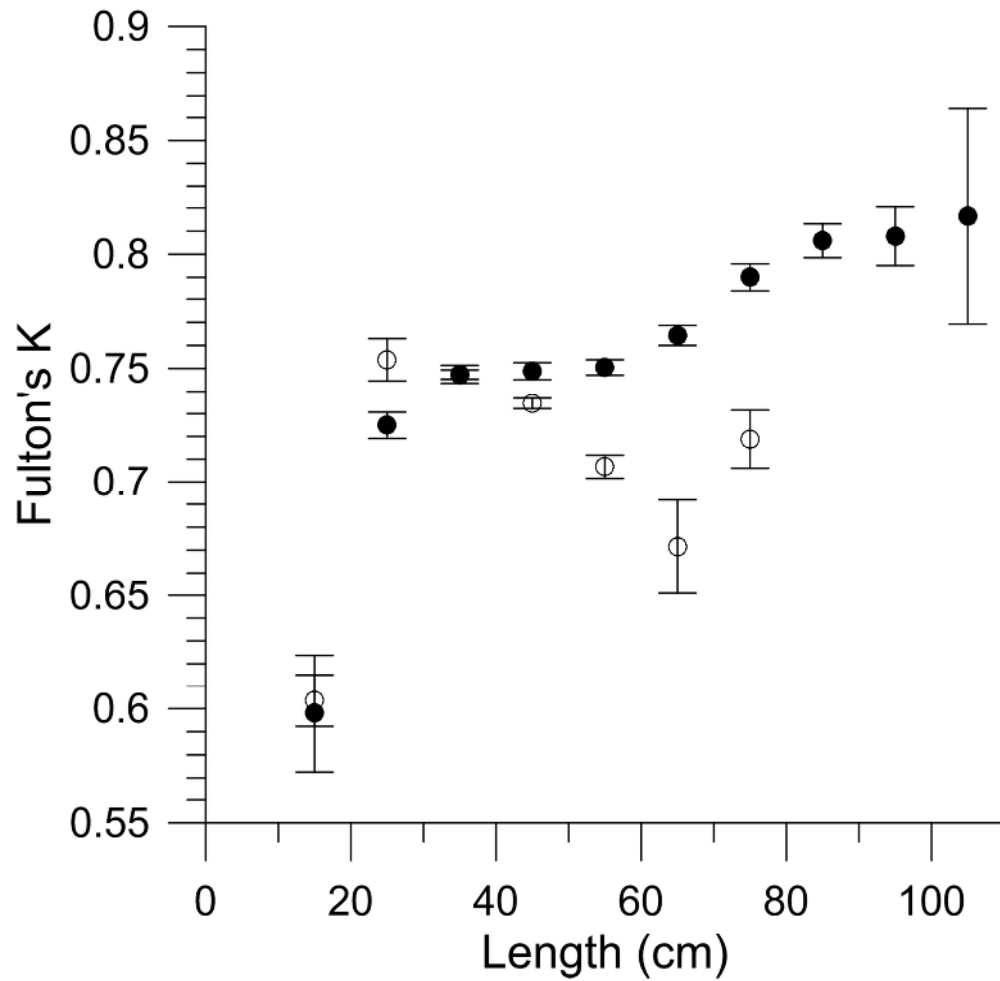


Biomass of cod (mean with 95% CIs, closed circles) measured using scientific echosounders in the overwintering to spawning period (March to June) within the Bonavista Corridor from 1990 to 2014. Estimates from 1990-1992 from Rose (1993); 1995-2005 from Rose et al. 2011; 2007-2008 modified from Mello and Rose 2007, 2008; also shown is spawning biomass index from Department of Fisheries and Oceans fall bottom trawl surveys for all of NAFO Divisions 2J3KL from 1986-2014 (mean, no CIs given, open circles, 1990-2014 from DFO 2015, 1986-1989 from Bratley et al. 2010); b) median biomass of capelin from Canadian surveys (circles) with 95% CIs (crosses) (courtesy of F. Mowbray, DFO St. John's) and Russian surveys in early 1990s (diamonds) from Bakanev (1992); and c) mean bottom sea temperatures at Station 27 off St. John's from 1985-2014 (from Colbourne et al. 2014).

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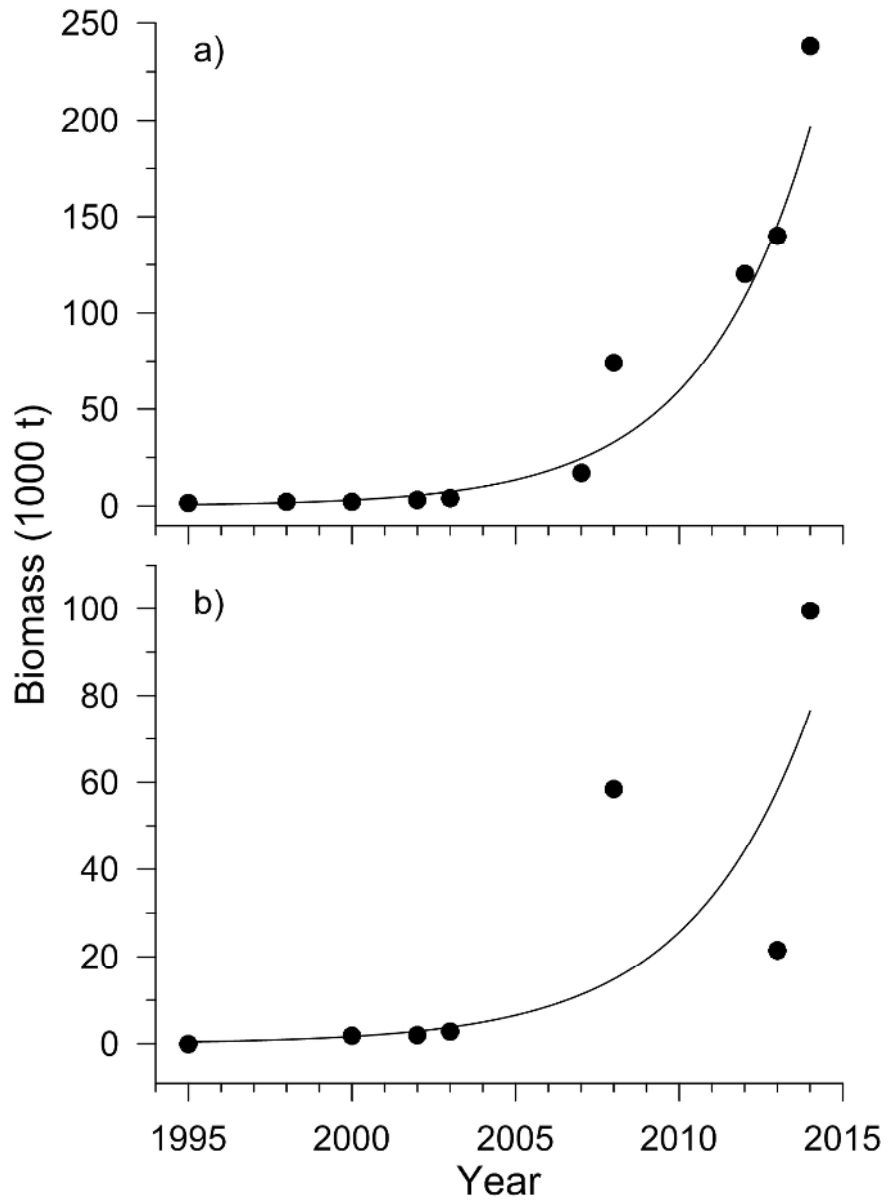


264x465mm (300 x 300 DPI)

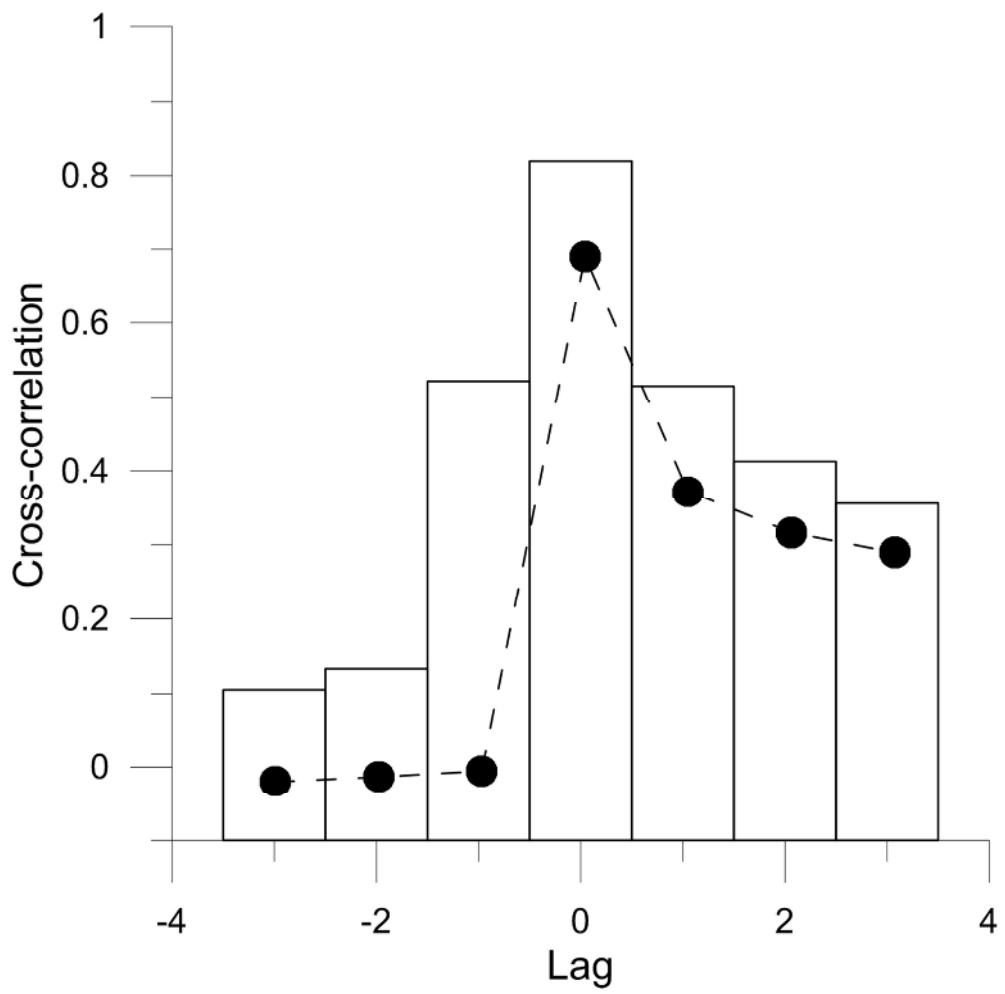


Mean Fulton's condition factor (K) for cod in May-June in the Bonavista Corridor in years 2000-2003 (n=1609; open circles with 95% CIs) and 2012-2014 (n=6384; closed circles). Bins are decadal (10-19 cm, 20-29 cm...).

133x129mm (300 x 300 DPI)



169x233mm (300 x 300 DPI)



119x117mm (300 x 300 DPI)