1   # Ontogenetic movements of cod in Arctic fjords and the Barents Sea as

2   # revealed by otolith microchemistry

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36

Abstract

44

45   The distribution of Atlantic cod (*Gadus morhua*) in northern Norwegian waters is expanding eastward

46   and northward in the Barents Sea and along western Svalbard. In the Arctic fjords of Svalbard, cod

47   has become abundant, but little is known about the biology, origin, or residence patterns of these

48   populations. To address this issue, we used Laser Ablation Inductively Coupled Plasma Mass

49   Spectrometry (LA-ICP-MS) to quantify the trace elemental composition of cod otoliths at age-0, age-3

50   and the year of spawning at five distinct locations in northern Norway and western Svalbard.

51   Chemical composition data was used to identify natal sources of cod, their broad-scale migration

52   patterns, and to determine if cod are currently resident in Arctic fjords. Our results suggest that cod

53   collected at Kongsfjord, Isfjord, outside Svalbard, Lofoten, and Porsangerfjord recruited mainly from

54   the Barents Sea, conforming to the Northeast Arctic cod ecotype. The degree of chemical overlap

55   between Porsangerfjord and Isfjord cod, however, varied with fish age, suggesting individual

56   movements consistent with the Norwegian coastal cod ecotype. Finally, the chemical composition of

57   mature fish at Isfjord, and to a lesser extent Kongsfjord, suggest that cod from the Barents Sea might

58   have recently established residency in these two Arctic fjords.

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Keywords

61   Life history, Svalbard, migration, micro elemental composition, LA-ICP-MS, Gadus *morhua*

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Introduction

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68   The current era of climatic warming is changing the distributions of marine ectotherms as they seek

69   to follow their optimal thermal tolerance limits (Sunday et al. 2012). These changes in biogeography

70   may be due to the direct effects of temperature on physiological functioning. At the same time,

71   temperature may also lead to altered trophic structure, for example by stimulating zooplankton

72   production and shifting energy flows from benthic to pelagic food webs (Carroll and Carroll 2003) or

73   changes in the ranges of competitors (Lancaster et al. 2017).

74

75   In the Barents Sea, warming trends are causing shifts in ecosystem structure and function,

76   subsequently affecting landings of commercially important species (Beaugrand et al. 2014;

77   Wiedmann et al. 2014; Fossheim et al. 2015). Indeed, during warm periods, the distribution of the

78   northeast Arctic population of Atlantic cod (*Gadus morhua*), expands farther east and north in the

79   Barents Sea and along western Svalbard (Nakken and Raknes 1987; Fossheim et al. 2015; Fall et al.

80   2018) while spawning tends to occur farther north along the Norwegian Coast (Sundby and Nakken

81   2008). Recruitment (Hjermann et al. 2007) and somatic growth rate (Michalsen et al. 1998) also tend

82   to be higher than during colder periods, with the net effect of increasing overall cod productivity

83   (Brander 2010). Recently, the Barents Sea cod biomass has achieved record high levels due to the

84   interaction between favorable climate and fisheries management, as increased temperature and

85   lower fishing mortalities have promoted higher recruitment and growth (Lilly et al. 2013; Kjesbu et al.

86   2014).

87

88   Cod populations in the northern North Atlantic are genetically distinct. There is a suite of local

89   populations along the Norwegian coast including the fjords of western Svalbard that are often

90   designated as Norwegian Coastal Cod (NCC), though cod from different fjords are often genetically

91   distinct from one another (Fevolden and Pogson 1997). Cod in the coastal complex are stationary in

92   contrast to the migratory Northeast Arctic Cod (NEAC), and ample attention has focused on genetic

93   differences between these ecotypes (e.g. Nordeide et al. 2011; Michalsen et al. 2014). The migratory

94   ecotypes of cod, and in particular the NEAC, sustain very large populations in comparison to

95   stationary populations such as those in the NCC complex. NEAC and NCC also contrast in life history

96   traits (reviewed in Yaragina et al. 2011; Ottersen et al. 2014). Briefly, the NCC spawns along the coast

97   of Norway and within fjords (Jakobsen 1987; Michalsen et al. 2014). Cod spawning in sheltered fjord

98   areas have more local recruitment dynamics than cod spawning in more open coastal areas, with

99   pelagic eggs and larvae remaining mostly in coastal environments while offspring grow close to their

100   spawning sites (Knutsen et al. 2007; Myksvoll et al. 2011; Rogers et al. 2014). Given these limited

101   movements, NCC have significantly different population genetic structures throughout its entire

102   range (Dahle et al. 2018). NEAC are typically found across the Barents Sea (Bergstad et al. 1987;

103   Michalsen et al. 2014), spawning along the Norwegian coast, but especially near the Lofoten Islands

104   and the Møre region (Bergstad et al. 1987; Sundby and Nakken 2008; Olsen et al. 2010). After

105   spawning, the pelagic eggs, larvae and pelagic juveniles are carried northeastwards by the Norwegian

106   Coastal Current and concentrate mainly in the central Barents Sea (Vikebø et al. 2005). The 0-group

107   switches from a pelagic to a demersal phase with the highest concentrations occurring in the

108   southeastern Barents Sea and along the Polar Front. A large proportion of fish that are four years or

109   more in age follow the spawning migration of capelin, thus moving from the Polar Front southward

110   to the coast in late winter, remaining there during the spring and migrating north again during the

111   summer. The mature part of the population extends this winter-feeding migration farther

112   southwards to the spawning areas during the spawning season in February and March (Yaragina et al.

113   2011; Ottersen et al. 2014).

114

115   Changing environmental conditions can lead to range expansion (or contraction) and to increasing

116   interactions between ecotypes along the northern Norwegian coast and especially in the Barents

117   Sea. The northward expansion of cod and other North Atlantic fish may have ecosystem-level

118   implications for Svalbard fjords (Renaud et al. 2012; Berge et al. 2015; Brand and Fischer 2016),

119   which have been traditionally inhabited by local cod (NCC). During the warm years of 1873-1882, cod

120   were abundant in Svalbard fjords as well as in coastal waters on the west and northwest Spitzbergen.

121   By 1879, the hand-held line fishery operating in shallow waters yielded 595 000 individuals. The

122   subsequent cooling period yielded catches in 1883 of only three individuals (Iversen 1934). Since

123   about 1913 however, warming of waters around Svalbard and its Spitsbergen fjords have favored

124   increased abundances of boreal species which have been expanding their distribution in the Arctic

125   (Blacker 1957, 1965; Drinkwater 2006; Pavlov et al. 2013; Fossheim et al. 2015; Falk-Petersen et al.

126   2015; Misund et al. 2016; Leopold et al. 2019). It remains uncertain however, if cod in Svalbard fjords

127   have settled permanently, resembling the NCC stocks, or are only transient residents and undertake

128   seasonal migrations much as NEAC.

129

130   Because of the focus on distinguishing migratory and non-migratory (NEAC vs NCC) cod (Nordeide et

131   al. 2011), most of the genetic and morphological markers have only recently been developed with

132   resolution to detect fine-scale changes in origin or distribution. This level of resolution is required to

133   determine connectivity patterns and interactions of cod from different areas. Otolith trace element

134   analysis can aid in addressing questions of origin and distribution in fish as the chemical composition

135   of the calcium carbonate-based material can provide insight into the overall physiological condition

136   of the organism, its relationship to the environment, and be used to infer the environmental

137   conditions fish experience over their lifespan, and/or movements and migration patterns (Campana

138   and Thorrold 2001; Chang and Geffen 2013; Morales-Nin and Geffen 2015; Tanner et al. 2016).

139   Incorporated trace elements from sequential sampling along the growth axis of otoliths have

140   provided high-resolution records of seawater chemistry for interpreting spatial and temporal

141   patterns in temperature, salinity, hydrography, food supply, as well as behavioral aspects such as

142   migrations (Vander Puten et al. 2000; Gillikin and Bouillon 2007; Chang and Geffen 2013; Morales-

143   Nin and Geffen 2015; Reis-Santos et al. 2018). For cod, otolith microchemistry has successfully been

144   applied to identify drift and mixing of cod from different geographic origins (e.g. Campana et al.

145   1994; Jónsdóttir et al. 2006; Thorisson et al. 2011; Wright et al. 2018).

146

147   In this study, we analyzed the chemical composition of cod otoliths collected from five distinct

148   locations in Northern Norway and western Svalbard to identify possible natal sources of cod in these

149   areas, broad-scale migration patterns, and to determine if cod are resident in Arctic fjords. Special

150   emphasis was placed on otoliths collected in the Svalbard fjords, where abundance of cod has

151   increased markedly in parallel with warming temperatures. In particular, the years 2006-2013, for

152   which otoliths were selected, corresponds to a period of increased water temperatures and reduced

153   winter ice formation in the Svalbard fjords, which might have enabled NEAC to move into the

154   Svalbard fjords. We thus aim to understand whether cod sampled in Svalbard represent a range

155   extension by migratory NEAC or NCC fish that have adapted to the Svalbard environment.

156

Materials and Methods

157

Sample selection and study sites

158

159   Cod otoliths were selected from a collection at the Norwegian Institute of Marine Research (IMR).

160   We focused on five distinct locations: the Lofoten area (Nordland), the fjords Porsangerfjord

161   (Finnmark), Kongsfjord (Spitsbergen) and Isfjord (Spitbergen), and outside the Svalbard archipelago

162   (Figure 1). Otoliths from 2006-2013 had been classified by stock (NCC and NEAC) by age readers using

163   standard morphological features (Sundby and Nakken 2008; Nordeide et al. 2011). Samples were

164   selected for this study based on the following criteria: 1. Place of collection (Isfjord, Kongsfjord,

165   Porsangerfjord, Lofoten or outside Svalbard), 2. Fish age (0, 3 and presence of at least one spawning

166   zone (Rollefsen 1935)), and 3. Readability (i.e. ease of age interpretation) (Table 1). Fish in

167   Kongsfjord, Isfjord and outside Svalbard were collected in the months of August and September.

168   Porsanger samples were collected in October and November and finally, Lofoten samples were

169   collected in April.

170

171   The rationale behind choosing otoliths with a spawning zone from such sites and ages is based on the

172   life history traits and movement patterns of cod, e.g. migrations from the Barents Sea to major

173   spawning sites in the Lofoten area (NEAC). NCC from the fjords of the northern coast and Svalbard

174   probably spawn locally. As such, the following assumptions were made:

175

176   i)   Fishes from a common natal source are expected to show a similar otolith chemical

177   composition at age-0, irrespective of location of collection;

178   ii)   Differences in chemical composition with age denotes fish movement across

179   different environments while similarities suggest residency in the same environment.

180

181   Environmental conditions at collection sites

182   Marine environmental conditions vary considerably among sites and differences in otolith chemistry

183   were expected. Specifically, Kongsfjord (231 km^2; length 27 km; width 4-10 km) and Isfjord (area

184   3084 km^2; length 98 km; width 24 km) in Svalbard are strongly influenced by the south-to-north

185   flowing West Spitsbergen Current, though colder and fresher water masses are often located in the

186   nearshore from glacial and river inputs. Mean yearly freshwater input into Kongsfjord and Isfjord has

187   been estimated at 7 X 10^6 m^3 and 3400 X 10^6 m^3 respectively (for more hydrographical information,

188   see Svendsen et al. 2002; Nilsen et al. 2008). Due to recent changes in large-scale atmospheric

189   circulation patterns, warm Atlantic water is brought into the fjords more frequently, which halts ice

190   formation and also facilitates the introduction of more southerly species (Pavlov et al. 2013;

191   Gluchowska et al. 2016; Muckenhuber et al. 2016; Nilsen et al. 2016; Wiencke and Hop 2016). Prior

192   to 2007, these and other fjords of Svalbard were regularly covered by sea ice during winter, but

193   regular winter ice cover has become rare (Cottier et al. 2007; Nilsen et al. 2008; Nilsen et al. 2016;

194   Wiencke and Hop 2016). All Kongsfjorden otoliths (n = 6) and most Isfjorden otoliths (7 out of 9)

195   were collected after 2006 coinciding with this period of low ice coverage in the fjords and

196   temperatures similar to those experienced by cod in the Barents Sea.

197

198   Porsangerfjord (1877 km^2) in northern Norway is an open fjord with relatively little fresh water input,

199   though there is a gradient along the fjord from warmer Atlantic waters near the ocean to colder,

200   fresher waters inland. There is ice formation between January and May (Eilertsen and Skarðhamar

201   2006; Myksvoll et al. 2012; Fuhrmann et al. 2015; Cieszyńska and Stramska 2018). Spawning of

202   coastal cod occurs in Porsangerfjord from the end of February to the middle of April (Otterå et al.

203   2006) with potential for high egg retention (Jakobsen 1987; Myksvoll et al. 2012). Farther south, the

204   Lofoten archipelago is considered the main spawning ground for both NEAC and NCC. Here, the

205   Norwegian Coastal Current splits into two branches, the smaller branch entering Vestfjord, while the

206   major branch passes the islands to the west and mixes with the warmer Norwegian Atlantic Current

207   (Mitchelson-Jacob and Sundby 2001; Höffle et al. 2014).

208

209   Trace element analysis

210   The selected otoliths were embedded in epoxy and then sectioned using a low speed saw at the

211   Institute of Marine Research otolith lab facilities (Bergen, Norway). Thin sections were cut to

212   approximately 0.6 mm thick and mounted on microscope slides. Trace element analysis was

213   conducted at the Woods Hole Oceanographic Institute Plasma Mass Spectrometry Facility (Woods

214   Hole, Massachusetts, USA) by Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-

215   MS) using a Thermo Finnigan Element 2 sector field ICP-MS coupled with a New Wave Research UP

216   193nm excimer laser. LA-ICP-MS setup was similar to that of Günther and Heinrich (1999) as

217   modified by Thorrold et al. (2001). Laser sampling was set to 150um spots with 100% output power

218   and a 10Hz repetition rate. The isotopes ^{7}Li, ^{25}Mg, ^{48}Ca, ^{55}Mn, ^{138}Ba, ^{88}Sr, and ^{208}Pb were measured.

219   The Microanalytical Carbonate Standard (MACS-3, U.S. Geological Survey) was ablated and used as a

220   standard to relate measurements to elemental concentration A blank and the MAC-3 standard were

221   run after every twelfth sample. ^{48}Ca was used as an internal standard by normalizing the

222   concentrations of all other elements to the calcium concentration, as a ratio of elemental

223   concentration to calcium concentration by molecular weight. Samples were ablated at the end of the

224   growth year at age-0, age-3, and the year after the first spawning zone (age-S). For most individuals,

225   the age at first spawning was 6 years (average 6.7 years, ±1.24 SD), as determined by the visual

226   change in otolith growth referred to as a spawning zone (Rollefsen 1935). For individuals that

227   spawned for the first time in the year of capture, samples were taken at the edge of the otolith.

228

229   Statistical analysis

230   Two statistical approaches were used to assess whether the composition of otoliths differed with

231   respect to fish age, site of sampling, or year of capture. First, non-metric multidimensional scaling

232   (NMDS) was performed on Euclidean distance dissimilarity matrices calculated on three dimensions

233   from the natural logarithm (ln(x)) transformed element data using the computer program Canoco 5

234   ver. 5.12© (1997-2019 Biometris, Wageningen Research Foundation, Wageningen University and

235   Research, the Netherlands and Peter Šmilauer, Czech Republic). The data were ln-transformed to

236   reduce the effect of extreme values. The NMDS plots indicated the level of similarity between

237   microelement data of each fish with respect to age (0, 3, mature) and calendar year of the sample.

238 For example, a 6-year-old fish caught in 2006 that spawned first at age-5, yielded measurements for

239 the years 2000 (age 0), 2003 (age 3), and 2005 (age-5). To test whether chemical composition was

240 statistically different between the three age groups at each site, ANOSIM analyses were performed

241 using the computer program Primer 7 ver. 7.0.13 © PRIMER-E (Quest Research Limited). In order to

242 explore whether residency was similar among mature fish, an NMDS was performed on mature fish

243 (age-S) data only. The NMDS scores for each site were then compared using ANOVA.

244

245 The second approach was to calculate a likelihood score for each fish at each site of collection (LS).

246 Here we assumed that the elemental signal of each collection site is represented by the mature fish

247 signal of individuals collected at that site. We subsequently tested how similar the elemental values

248 of each age-0 and age-3 fish were compared to mature fish signature of each site. The score was

249 calculated for each element as:

250
$$LS = \frac{Ev - \bar{x}\,(Evs)}{\sigma\,(Evs)}$$

251 Where

252 Ev = Otolith element concentration (ln-transformed)

253 Evs = Otolith element concentration at maturity (ln-transformed)

254 σ = standard deviation

255 $\bar{x}$ = mean

256

257 The likelihood score for each site and fish is the sum of the otolith chemical elements. The site with

258 the lowest score is the most likely site (given our data availability) that an individual fish resided at

259 each age. Initial exploratory data analyses indicated a lack of differences between the sites when the

260 elemental values of Mg and Sr were included in the analyses due to their high concentrations and

261   consistency in values. Therefore; all subsequent analyses concerned only the elements Li, Mn, Ba and

262   Pb.

263

264   For some of the sites, only a small number of otoliths were collected in the same year (Table 1). To

265   test whether our results could be affected by temporal variability in elemental values (i.e. a year

266   effect), four mixed effect models were run on the scores from an exploratory NMDS analysis

267   performed on all otolith data (Morrongiello and Thresher 2015):

268

269   •   Model 1. A random intercept model for fish ID.

270   •   Model 2. A random intercept for fish ID, with the factor age as fixed effect.

271   •   Model 3. A random intercept for Fish ID with the factor year as fixed effect.

272   •   Model 4. A random intercept for fish ID, with the factors age and year as fixed effects.

273

274   Where "fish ID" refers to the different fish individuals (taking the repeated measurement structure of

275   the data into account), "age" refers to the age (0, 3 or S) of the fish, and "year" refers to the calendar

276   year of the sample. The best model was selected based on the Akaike information criterion (AIC).

277   Note that in these analyses we are not trying to explain clustering patterns. Our aim here was to test

278   if some of the variance in NMDS scores is better explained by fish age and/or by calendar year. Of

279   course, additional variance is likely explained by residence location, but collection site was not

280   included as a factor in these analyses, because fish residence is unknown for fishes at age-0 and age-

281   3.

282

283   Results

284   Trace element trends

285   All trace element concentrations from samples were greater than the limit of detection outlined in

286   Jochum et al. (2012). Trace elemental analyses revealed differences in the element concentrations of

287   otoliths from different sites (Online Resource 1). The highest trace element values were in general

288   found in Age-0 fishes (Figure 2). For mature fish (Age-S), the molecular weight ratios values of Li

289   ranged from 3.12E-06 mmol mol^{-2} in Porsangerfjord to 6.48E-05 mmol mol^{-2} in Isfjord. On average,

290   the highest Li values were found in otoliths from Lofoten and the lowest from Porsangerfjord. The

291   values of Mn ranged from 1.23E-07 in Kongsfjord to 3.38E-05 outside Svalbard. Mn values were on

292   average highest in Lofoten and lowest in Kongsfjord. Ba values varied from 1.37E-06 in Isfjord to

293   1.21E-05 outside Svalbard. Ba was lowest in the Lofoten otoliths, on average, and highest in

294   Porsangerfjord otoliths. Pb varied from 1.10E-09 in Isfjord otoliths to 3.27E-07 in Kongsfjord otoliths.

295   Otoliths sampled outside Svalbard had the lowest Pb average values and Kongsfjord otoliths the

296   highest.

297

298   Non-metric multidimensional scaling analyses

299   The NMDS plots show the level of similarity among the otolith elemental composition at age for each

300   of the sites (Figure 3). The combined variation explained between axis 1 and 2 varied from 79.4%

301   (Svalbard outside) to 86.6% (Kongsfjord). At all sites, clustering of elemental values occurred around

302   each age group (0, 3, mature), rather than at each individual otolith. The greatest distances between

303   clusters of age groups occurred between age-0 and maturity suggesting different occupancy at age.

304   This was especially the case for samples from outside Svalbard and Lofoten, where overlapping in

305   chemical concentrations occurred to a higher degree between age-3 and maturity. Interestingly at

306   these two sites, the age-0 formed a more compact cluster than at any of the other sites/age groups.

307   Kongsfjord showed almost no overlapping, with three very distinct age groups. In contrast, the

308   chemical composition in samples from the fjords Porsangerfjord and Isfjord overlapped for all age

309   classes, especially between age-0 and age-3. The ANOSIM test revealed significant differences in

310   otolith chemical composition between most of the age groups at each location (Table 2) except

311   Lofoten (age 3, matured) and Kongsfjorden (age 0, 3 and age 3, matured). The R statistic values,

312   which when close to unity are indicative of complete group separation (Clarke and Warwick 2001),

313   were in the high range ($R > 0.7$) only for the pair wise comparisons between ages 0 and 3 in Lofoten

314   ($R = 0.71$) and between ages 0 and mature in Lofoten, Isfjorden, Kongsfjorden and Svalbard ($R >$

315   0.78). At Isfjorden, R values between age 0 and mature were somewhat high ($R = 0.51$).

316

317   For mature cod, the non-parametric ANOVA performed on the NMDS scores on mature fish data

318   revealed that "site" had a significant effect on the scores (Figure 4). We assume here that the

319   chemical composition measured in the year after first spawning is representative of the chemical

320   signature of their collection site. A pairwise t-test showed that the Svalbard fjords of Isfjord, and to a

321   lesser extent Kongsfjord, are different from the rest of the sample sites (p-value = 0.0052; corrected

322   Bonferroni p-value = 0.052). At these two sites, the year of capture coincided with year of spawning

323   in five out of eight samples from Kongsfjord and four out of six fish from Isfjorden), which increases

324   the confidence in using the Age-S composition as a local marker.

325

326   Among the four mixed effect models used to test for a potential "year effect", "age" explained most

327   of the variance, with the lowest AIC. Inclusion of the factor "year" (model 3) did not improve the AIC

328   score suggesting that more of the clustering is explained by fish age than by calendar year (Online

329   resource 2).

330

331   Likelihood scores

332   The likelihood scores revealed possible overlapping distributions among fish at age 0, 3 and mature

333   fish across collection sites (Figure 5A). Again, the central assumption in this analysis is that the

334   chemical composition of the increment after reaching maturity adequately represents the chemical

335   signature of their collection site. Most age-0 and age-3 fishes collected in the Svalbard Fjords (Isfjord

336   and Kongsfjord) and Lofoten have a chemical composition most similar to the mature individuals

337   collected outside Svalbard. For Porsangerfjord the results are more variable. However, none of the

338   collection sites showed evidence of resident populations.

339   As the chemical signature of otoliths from mature individuals did not significantly differ among

340   Porsangerfjord, Lofoten, and outside Svalbard , and between mature individuals from Isfjord and

341   Kongsfjord, these sampling sites were merged (Figure 5B). The likelihood scores when then

342   recalculated using only the two categories Isfjord/Kongsfjord and Porsangerfjord /Lofoten/Svalbard-

343   outside. These analyses indicated that fish at age-0 and age-3 generally have a chemical composition

344   most similar to mature fish from areas outside Svalbard. Some age-3 fish, however, were classified

345   as having a similar chemical composition of matured fish collected in Isfjord/Kongsfjord, suggesting

346   some individuals may migrate into these fjords well before spawning.

347

Discussion

349   Otoliths have been shown to record the chemical environment experienced by an individual fish

350   throughout its lifetime and as such can be employed as a natural marker to identify fish that inhabit

351   different environments (Campana and Thorrold 2001; Kerr and Campana 2014; Tanner et al. 2016;

352   Reis-Santos et al. 2018). We analyzed the composition of cod otoliths collected at five sites across

353   Arctic Norway to identify possible natal sources and large-scale migration patterns. We also sought

354   to determine if cod populations are resident or visitors in Artic fjords, where sea temperatures have

355   been increasing, thus providing more suitable environments for the establishment of temperate

356   species. Our general expectation was that a high degree of overlap between microelement

357   composition of fish in different age groups would denote residency (NCC), and little overlap between

358   age groups would suggest large seasonal migrations (NEAC). Our results suggest that cod collected at

359   Kongsfjord, Isfjord, outside Svalbard, Lofoten, and Porsangerfjord recruited mainly from the Barents

360   Sea, conforming to the Northeast Arctic cod ecotype. The degree of chemical overlap between

361   Porsangerfjord and Isfjord cod, however, varied with fish age, suggesting individual movements

362   consistent with the Norwegian coastal cod ecotype. Finally, the chemical composition of mature fish

363   at Isfjord, and to a lesser extent Kongsfjord, suggest that cod from the Barents Sea might have

364   recently established residency in these two Arctic fjords.

365

366   Lofoten, open waters of Svalbard and Kongsfjord samples

367   At Lofoten, open waters outside Svalbard, and Kongsfjord, all otoliths were classified as NEAC based

368   on morphology. The NMDS analysis and the *R* pairwise values in the ANOSIM test revealed little

369   overlap with respect to chemical composition at age, with the age-0 group clustering separately from

370   age-3 and mature groups, which indicated pronounced movement patterns. The likelihood scores

371   suggested that the chemical composition of individual otoliths collected at Lofoten and Kongsfjord is

372   closest to those of mature fish collected outside Svalbard, suggesting that these fish may share a

373   common origin. These results match the current understanding of NEAC stock distribution and life

374   history, which is widely spread along the Norwegian coast and the Barents Sea, especially between

375   the continental slope and the Polar Front.

376

377   Consistent with these findings, the adult portion of NEAC performs large-scale migrations (up to 1000

378   km) from the Barents Sea to feed and spawn along the Norwegian coast, with spawning usually

379   occurring from early March to the end of April (Bergstad et al. 1987; Yaragina et al. 2011; Färber et

380   al. 2018). The exact location of the spawning sites varies with temperature, but the main spawning

381   sites are located near Lofoten (Sundby and Nakken 2008; Yaragina et al. 2011; Langangen et al.

382   2019). After spawning, eggs and larvae drift north from the spawning grounds and east into the

383   Barents Sea. The highest concentrations occur in the central Barents Sea, near the Polar Front during

384   August-September when the age 0-group fish settle to the demersal phase (Yaragina et al. 2011). Age

385   groups 1-3 concentrated mostly in the southeastern Barents Sea and along the Polar Front, and their

386   migrations tend to follow the seasonal shifts in the front. Cod shift from planktivory to piscivory, and

387   by age 4, a large proportion follow and feed on spawning capelin during their migrations to the coast

388   (Yaragina et al. 2011). During the NEAC feeding and especially the spawning migrations, an overlap in

389   distribution occurs with NCC (Jakobsen 1987; Yaragina et al. 2011; Michalsen et al. 2014). A higher

390   overlap between the age-3 and mature groups at Lofoten and outside Svalbard as shown in our

391   results might be a result of these purported migrations into the coast.

392

393   Porsangerfjord and Isfjord samples

394   Porsangerfjord and Isfjord samples differed chemically from the other sites, with an apparent

395   discrepancy between the NMDS and likelihood analyses. First, the NMDS analysis showed some

396   overlap among all age groups within each fjord, indicating a common residency among fishes at

397   different ages. At these two locations, most of the R values obtained from the ANOSIM test were

398   close to zero (0.11-0.34), except for Isfjorden (r = 0.51 at ages 0 and mature) indicating little

399   segregation among groups (Clarke and Warwick 2001). Porsangerfjord, where all otoliths were

400   classified as coastal cod based on morphological properties, previous tagging studies have shown

401   high recapture rates of marked cod within the fjord (93%) (Jackobsen 1987) providing evidence

402   residency. In addition, numerical models suggest a high retention rate for cod eggs in Porsangerfjord

403   (Myksvoll et al. 2011; Myksvoll et al. 2012). The high retention of eggs and residency rates suggest

404   that Porsangerfjord cod could complete its life cycle within the fjord. Little is known about cod life

405   history in Isfjord, but a similar life strategy to that of Porsangerfjord cod is plausible (see section 4.3).

406   In general, our Porsangerfjord and Isfjord NMDS results show agreement with expectations regarding

407   NCC, which tend to be resident in fjords and have short spawning migrations (Jakobsen 1987;

408   Michalsen et al. 2014). The likelihood analysis showed, however, that most of the age-0 and age-3

409   samples at Isfjord and Porsanger were chemically more similar to the mature samples from Svalbard

410   and Lofoten, indicating that fishes generally recruit in offshore waters before moving into the fjords.

411   Again, for mature cod, the ANOVA analysis showed that Porsangerfjord cod had a more similar

412   chemical otolith composition to mature fishes collected at Lofoten and outside Svalbard. A possible

413   explanation of this apparent discrepancy between our analyses could be due to the overlap in

414   distribution of the NEAC and NCC cod that can occur during spawning and feeding migrations (Olsen

415   et al. 2010), or when fjord-spawning cod leave the fjords after spawning to inhabit coastal areas

416   (Jacobsen et al. 1987). At these times, both stocks will experience similar environmental conditions

417   which likely will be reflected in the otolith chemical composition. The variety of reproductive life

418   history traits displayed by coastal cod described above (limited movement, migration to coastal

419   areas, outside/inside fjord spawning, local retention of eggs, etc.) is likely the cause a higher chemical

420   overlap between fish of different ages (age-0, 3 and matured) at Porsangerfjord, as well as the higher

421   variability of NMDS scores of mature fish.

422

423   Kongsfjord and Isfjord settlement and spawning movements

424   Otoliths from mature fish from Isfjord showed a different chemical composition than those from the

425   other localities, except Kongsfjord, suggesting that some of the mature fishes in these Svalbard fjords

426   remain in the fjords instead of joining spawning migrations to the south. Moreover, about 65% of the

427   Kongsfjord and Isfjord otoliths were collected on the same year as the formation of the first

428   spawning zone, suggesting that these fish might have spawned within or in areas near the fjord. The

429   age-0 likelihood results, however, indicated offshore recruitment into both fjords. Together, these

430   results might indicate a new settlement of Barents Sea cod into the fjords, presumably related to the

431   more favorable conditions for cod due to climate warming. Most of our Svalbard fjord samples were

432   collected after 2006, coinciding with the period of increased temperatures that have facilitated the

433   establishment of boreal species in the Arctic, including Svalbard fjords (Berge et al. 2015; Fossheim et

434   al. 2015; Bergstad et al. 2017; Leopold et al. 2019). The hypothesis of new settlement finds further

435   support in the 2-category likelihood analyses, showing that some of age-3 fish have similar chemical

436   composition to mature Isfjord/Kongsfjord otoliths. It is conceivable that these fish recruited into the

437   fjords before age-3 and then remained there for the rest of their life, thus presumably reflecting the

438   environmental chemical composition there. A similar case has occurred with the mussels *Mytilus*

439   spp., which have resettled in Svalbard after a 1000-year absence, triggered by warming oceans

440   (Berge et al. 2005). The likely vectors for the reestablishment of these mussels, that are now

441   reproducing locally, are larval advection by ocean currents and introductions by ship traffic (Leoplold

442   et al. 2019).

443

444   In this paper we assume otolith chemistry composition variation to occur due to the differences in

445   environmental factors experienced by fishes at different ages and/or sites. Otolith chemistry,

446   however, is influenced not only by environmental factors but also by physiological and genetic

447   factors (Chang and Geffen 2013; Grønkjær 2016; Izzo et al. 2018). Yet regardless of the intrinsic

448   processes regulating the incorporation of the trace elements in the otolith, environmental factors are

449   considered the main drivers of variation for certain elements (Reis-Santos et al. 2018). Thus,

450   exposure to site-specific environmental conditions can provide otolith trace elements signatures

451   (Brown et al. 2019). For cod, multielement otolith chemistry analyses have proven effective

452   identifying regional differences over large geographic areas (Chang and Geffen 2013), lending

453   support to a microchemical approach. We acknowledge that we based our analyses on relatively few

454   individuals, which may introduce greater uncertainty than with higher replication. Yet, given the

455   strong overlap between the sites for most micro-elements (for age-S fishes) it is questionable if a

456   larger sample size would have increased precision and changed the main findings of our study. Some

457   uncertainty is caused by our assumption that the chemical composition of age-S fishes reflects the

458   chemical composition of the collection sites, as well as due to variation in the year of sampling.

459   Nevertheless, our results from the Barents Sea and Porsanger tend to corroborate what is known

460   about movement patterns of NEAC and NCC. For Kongsfjord and Isfjord, where cod life history is less

461   investigated, most otoltihs were collected on the same year as spawning occurred, thus presumably

462   reflecting the environmental chemical composition there.

463

464   If the cod in Svalbard fjords are indeed newly settled, then they might establish local populations

465   leading to eventual local life history adaptations, as the species can be highly sedentary (Knutsen et

466   al. 2011; Rogers et al. 2014; Michalsen et al. 2014; Dahle et al. 2018). Our results so far indicate a life

467   history more similar to that of Porsanger cod. Tagging and tracking experiments with *a posteriori*

468   otolith chemical analysis might elucidate whether fishes from the Svalbard fjords are in fact,

469   establishing resident populations in the fjords, as will be expected as global warming progresses.

470

471   ## Compliance with Ethical Standards

472   The authors do not have any conflict of interest. No live fish were directly involved in the present

473   study.

474

475

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707   ## Table 1

708   Table 1. Location, year of collection and age of cod (*Gadus* morhua) otoliths employed for
709   microelement analyses. NEAC = Northeast Arctic Cod; NCC = Norwegian Coastal Cod

Place of collection, morphological type/year	Age at capture							
	6	7	8	9	10	11	12	Total
Isfjord (All NEAC)	**2**	**3**	**2**	**2**				**9**
2006	1							1
2008			1	1				2
2009	1	3	1					5
2013				1				1
Kongsfjord (All NEAC)		**3**	**1**	**2**				**6**
2007		3	1					4
2013				2				2
Lofoten (All NEAC)		**3**	**5**	**1**	**1**	**1**		**11**
2006		1	1	1				3
2008		1	2					3
2011			1			1		2
2013		1	1		1			3
Porsanger (All NCC)		**4**	**4**	**2**	**1**	**1**		**12**
2008		1						1
2011		1	2					3
2013		2	2	2	1	1		8
Svalbard_outside (All NEAC)		**3**	**3**	**6**	**2**		**1**	**15**
2009		1						1
2012				2	1		1	4
2013		2	3	4	1			1
Grand Total	**2**	**16**	**15**	**13**	**4**	**2**	**1**	**53**

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720   ## Table 2

721   Table 2. Analysis of similarity (ANOSIM) of cod (*Gadus morhua*) otolith chemical composition with
722   age as a factor at each sampling site.

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Area	Sample statistic (R)	Significance level	R Statistic		
			Age 0, 3	Age 0, S	Age 3, Matured
Lofoten	0,57	0,10 %	0,708*	0,903*	0,051
Porsangerfjorden	0,194	0,10 %	0,132*	0,342*	0,111*
Isfjorden	0,296	0,10 %	0,312*	0,506*	0,179*
Kongsfjorden	0,367	0,30 %	0,091	0,783*	0,207
Svalbard outside	0,476	0,10 %	0,522*	0,794*	0,126*

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742 Figure 1
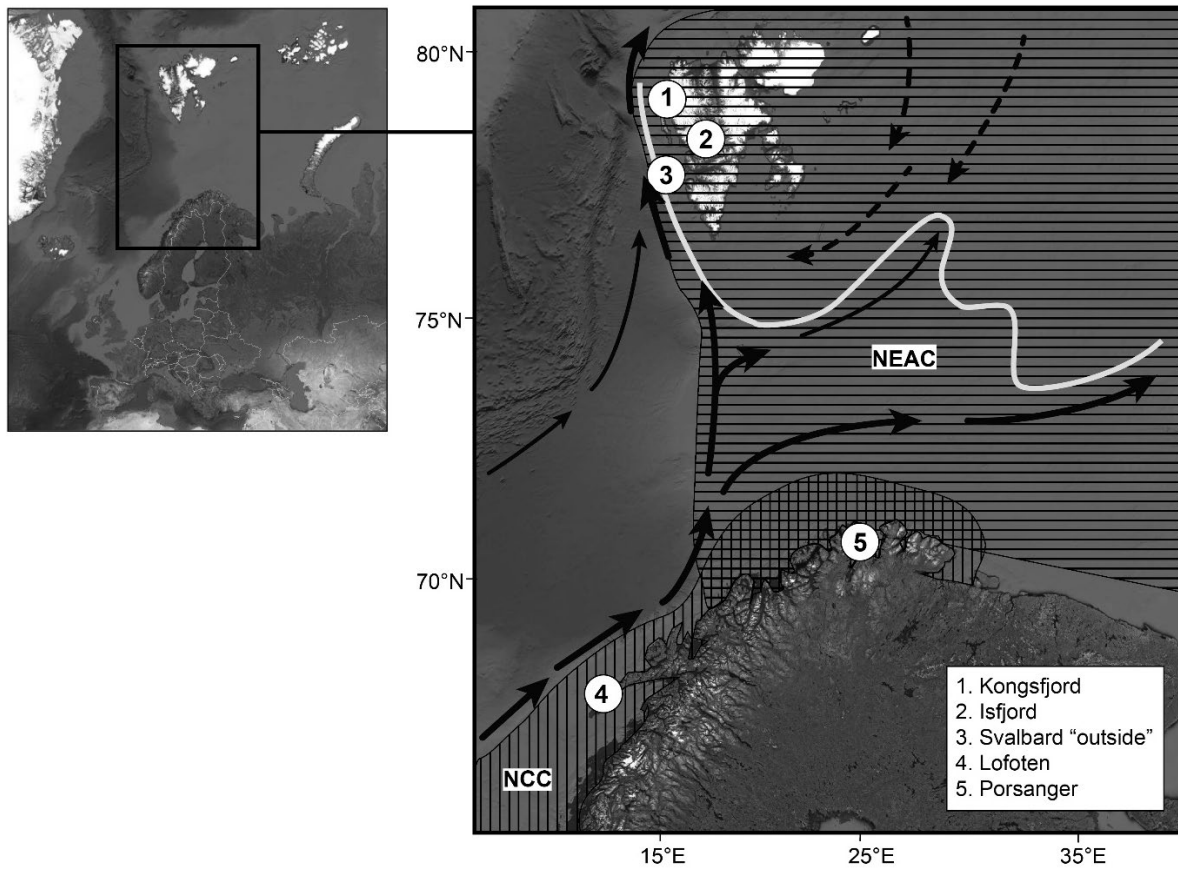
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744 Figure 1. Map of collection stations for cod (*Gadus morhua*) as well as the distributions of the

745 Northeast Arctic cod (NEAC) and the Norwegian coastal cod (NCC) stocks. Thick arrows depict warm

746 Atlantic currents while thin arrows depict cold Arctic currents. The white line depicts the average

747 position of the Polar Front. Background map from, Google Earth Pro (US Dept of State Geographer,

748 Image IBCAO copyright 2019 Google, Image Landsat Copernicus) and ocean currents and polar front

749 from BarentsWatch (www.barentswatch.no).

750   Figure 2
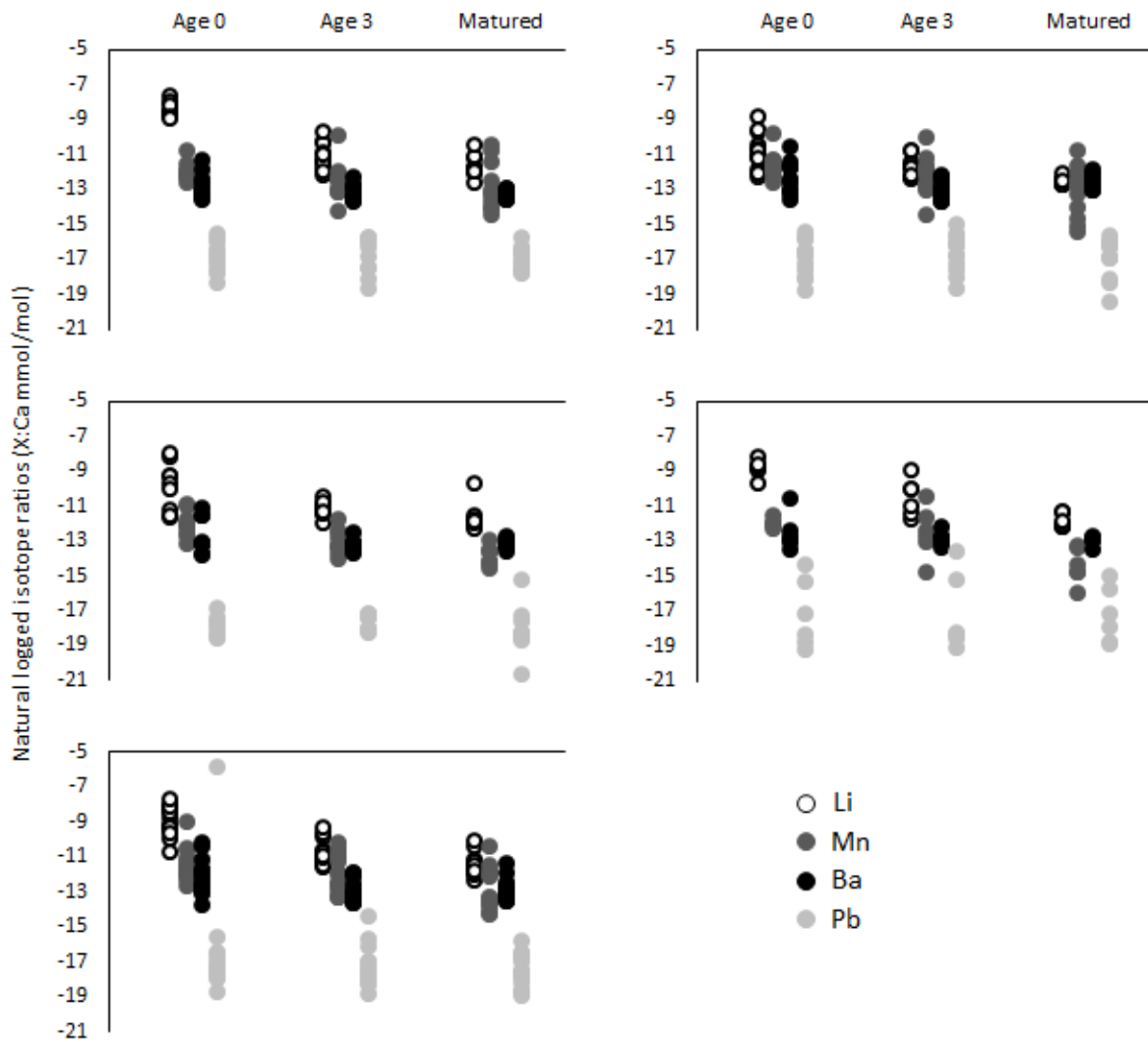
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752   Figure 2. Microelement concentration of cod (*Gadus morhua*) otoliths collected at five sampling sites.
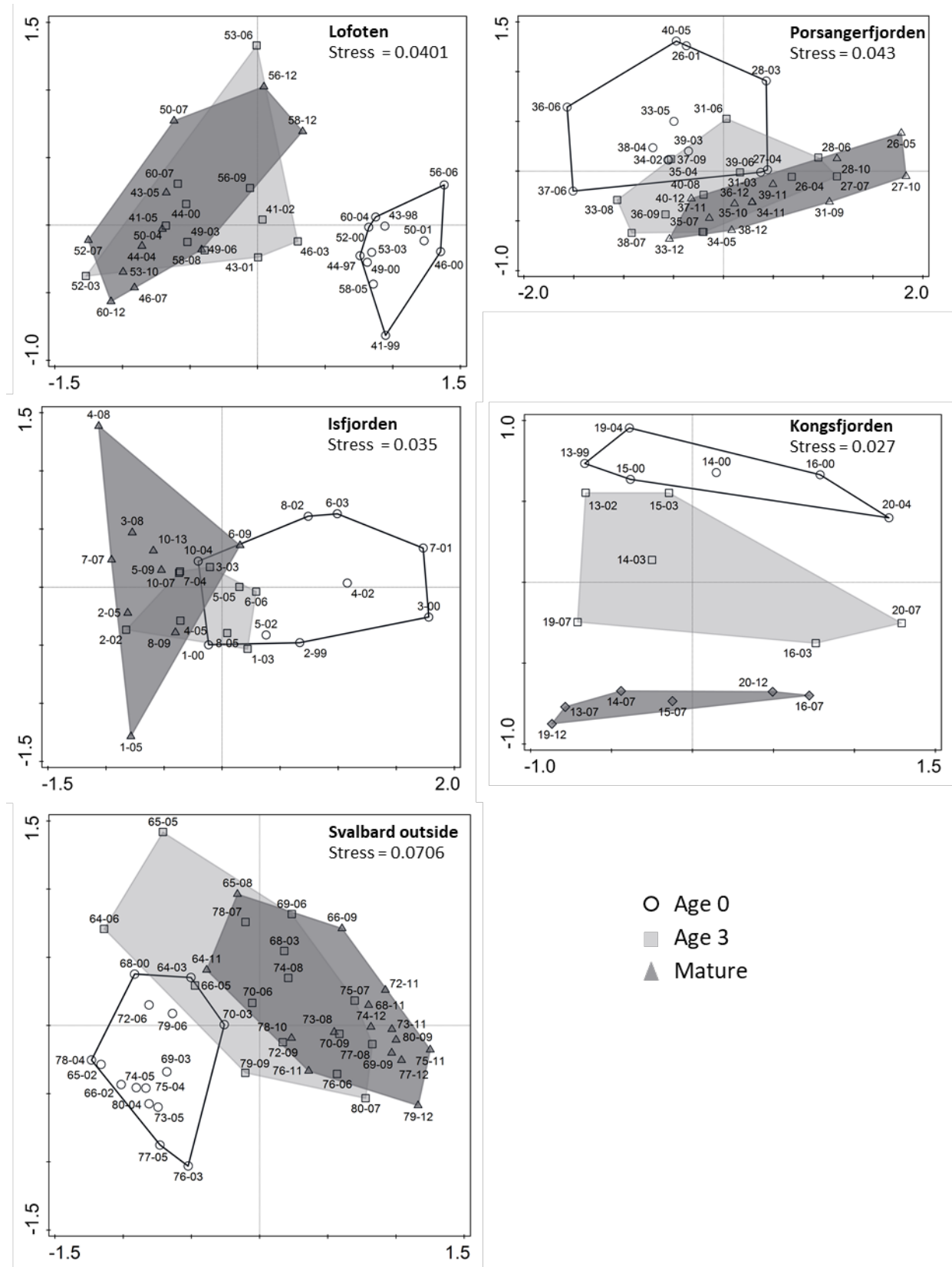
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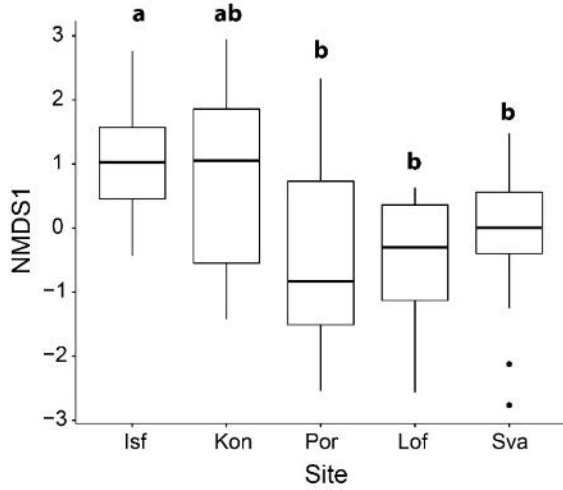
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763   Figure 3

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765   Figure 3. NMDS analyses of cod (*Gadus* morhua) otolith chemical composition for different ages at
766   five sampling sites. Data labels indicate samples at age-0, age-3 and maturity.

767   Figure 4

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770   Figure 4. Box plot of site differences in NMDS scores (for first dimension) in cod (*Gadus morhua*)
771   otoliths of mature fishes, using four elements (Li, Mn, Ba, Pb). Letters indicate significant differences
772   at a *p*-value < 0.05 with a Bonferroni correction. Outliers are denoted by dots either below or above
773   the whisker lines which extend from the quartiles.

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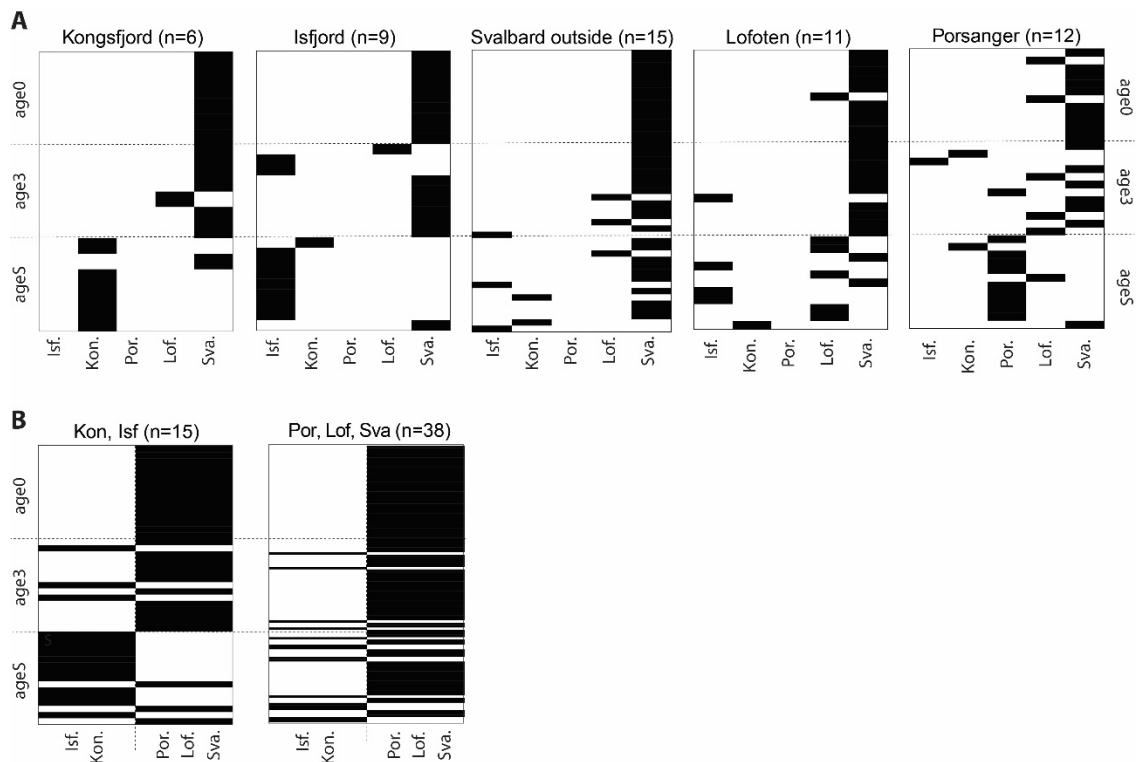
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Figure 5

Figure 5. Visualization of likelihood scores among the five sites, the black box indicating the lowest score likelihood. (A) Possible residence of cod (*Gadus morhua*) at different ages for each sampling site. (B) Re-calculated likelihood scores using only two categories: Isfjord/Kongsfjord and Porsangerfjord /Lofoten/Svalbard-outside following a merger of sampling sites based on similarities in chemical signature of mature individuals (see text for details). All otoliths collected in Kongsfjord, Isfjord, Svalbard outside and Lofoten were classified as Northeast Arctic Cod based on morphological features. Porsangerfjord otoliths were classified as Norwegian Coastal Cod.