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1 **Changes in population depth distribution and oxygen stratification explain the current**

2 **low condition of the Eastern Baltic Sea cod (*Gadus morhua*)**

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22   **Abstract**

23   During the past twenty years, hypoxic areas have expanded exponentially in the Baltic Sea,

24   which has become one of the largest marine "dead zones" in the world. At the same time, the

25   most important commercial fish population of the region, the Eastern Baltic cod, has

26   experienced a drastic reduction in mean body condition, but the processes relating hypoxia to

27   condition remain elusive. Here we use extensive long-term monitoring data on cod biology and

28   distribution as well as on hydrological variations, to investigate the processes that relate

29   deoxygenation and cod condition during the autumn season. Our results show that the depth

30   distribution of cod has increased during the past four decades at the same time of the expansion,

31   and shallowing, of the waters with an oxygen concentration known to be detrimental for cod

32   performance. This has resulted in a spatial overlap between the cod population and low-

33   oxygenated waters after the mid-1990s, which relates with the observed decline in cod mean

34   body condition. Complementary analyses on fish otolith microchemistry also revealed that

35   since the mid-1990s, cod individuals with low condition were indeed exposed to low-oxygen

36   waters during their life. This study helps to shed light on the processes that have led to a decline

37   of the Eastern Baltic cod body condition, which can aid the management of this population

38   currently in distress. Further studies should focus on understanding why the cod population has

39   moved to deeper waters in autumn and on analysing the overlap with low-oxygen waters in

40   other seasons to quantify the potential effects of the variations in physical properties on cod

41   biology throughout the year.

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43   **Keywords**: hypoxia, fish body condition, direct exposure, depth distribution, cod *Gadus*

44   *morhua*

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1. Introduction

The oceans and marine coastal areas are experiencing dramatic deoxygenation worldwide (Breitburg et al., 2018). Declining oxygen can have multiple direct and indirect effects on aquatic organisms and entire ecosystems (Breitburg, 2002; Rabalais et al. 2002; Wu, 2002; Diaz and Rosenberg, 2008; Levin et al., 2009). In particular, studies undertaken both in the wild and within experimental set-ups have revealed large effects of hypoxia on basic metabolism, behavior, ecology, distribution and life-history traits of fish (Pichavant et al., 2001; Eby et al., 2005; Herbert and Steffensen, 2005; Domenici et al., 2007; Stramma et al., 2012).

The Baltic Sea (Fig. 1) is one of the largest brackish areas in the world where the oxygenated, yet scarce and irregular saline water inflows from the adjacent North Sea, combined with a water residence time of about 25–30 years, make the system particularly prone to hypoxia (Carstensen et al., 2014). As a consequence, and in combination with global warming and eutrophication, the Baltic Sea has become one of the largest anthropogenic "dead zones" in the world (Breitburg et al., 2018), with well documented degradation or elimination of benthic communities and disruption of benthic food webs over vast areas (Conley et al., 2009). In particular, since the early 1990s the anoxic and hypoxic areas have increased exponentially in the southern and central Baltic Sea (Carstensen et al., 2014) (Fig. 2).

In this degraded demersal and benthic environment, the body condition (a morphometric index of fish fatness and well-being) of the dominant demersal fish population, the Eastern Baltic cod *Gadus morhua* (hereafter simply referred to as Baltic cod), has declined since the mid-1990s (Casini et al., 2016a). This decline has been related to a decrease in the main pelagic prey abundance in the main distribution area of cod (Eero et al., 2012; Casini et al., 2016a), but also to the increased extent of hypoxic and anoxic areas (Casini et al., 2016a). However, the

70   underlying mechanisms of the relationship between cod condition and hypoxia are still elusive

71   (but see Limburg and Casini, 2019). The mechanistic processes linking hypoxia and cod

72   conditions could be various and not mutually exclusive, including stress due to direct hypoxia

73   exposure, contraction in the spatial distribution of the population, and change in the

74   surrounding biota such as reduction of important benthic prey (Casini et al., 2016a). A recent

75   study pointed out the importance of the decline in the feeding level and energy intake of cod

76   after the mid-1990s, which was explained by the decline in important benthic prey in the

77   environment (Neuenfeldt et al., 2019). Lately some investigations have also put forward the

78   hypothesis that the observed changes in the distribution of demersal fish species, including cod,

79   were due to the variations in the extent of the hypoxic areas in the Baltic Sea (Orio et al., 2019),

80   although in-depth analyses were not performed to confirm this hypothesis. The low cod

81   condition in recent decades has been stressed also by the fishery that has lamented an

82   increasingly high proportion of catches of lean cod with low economic value. Low condition

83   has a negative effect on reproductive potential (Mion et al., 2018), mortality (Casini et al.,

84   2016b) and potentially also movements (Mehner and Kasprzak, 2011) with indirect effects on

85   prey and therefore food-web structure and ecosystem functioning as shown in other systems

86   (e.g. Ekau et al., 2010). Therefore, it is very important to understand the ultimate factors leading

87   to low cod condition and in particular the processes explaining the correlation between cod

88   condition and deoxygenation of the Baltic Sea water over time.

89   In this study, we further examine the mechanisms linking deoxygenation to cod condition in

90   the Baltic Sea. We specifically analyse the temporal changes in the depth distribution of cod,

91   from long-term monitoring data, in relation to the oxygen levels acknowledged in literature to

92   affect cod behavior and performance. We support these analyses investigating the relation

93   between fish exposure to hypoxia and cod condition using otolith microchemistry. Fish otoliths

94   (ear stones) composed of aragonite accrete continually throughout life and incorporate trace

95   elements, providing a direct, retrospective measure of an individual fish's environmental and

96   physiological history.

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2. Materials and methods

2.1 Biological data and estimation of cod condition

100   Biological data on Eastern Baltic cod individuals were collected during the Baltic International

101   Trawl Survey, BITS, between 1991 and 2018 (retrieved from the DATRAS database of the

102   International Council for the Exploration of the Sea, ICES; www.ices.dk) and previous

103   Swedish and Latvian bottom trawl surveys performed in 1979-1990 in the Baltic Sea (Casini

104   et al., 2016a). Cod individual body condition (Fulton's K) was estimated as $K = W/L^3 * 100$,

105   where W is the total weight (g) and L the total length (cm) of the fish. Mean condition was

106   estimated for ICES Subdivision (SD) 25 (corresponding to the main distribution area for cod

107   since the early 1990s, Orio et al., 2017) and SDs 26-28 separately. Condition was estimated for

108   small fish (represented here by the size-class 20-29 cm) and large fish (represented here by the

109   size-class 40-49 cm). We focused on the cod condition in autumn (i.e. quarter 4), corresponding

110   to the cod main growth season after spawning in spring-summer (Mion et al., 2020). Moreover,

111   for autumn long time-series of oxygen levels and extent of hypoxic areas are also available

112   (Casini et al., 2016a).

2.2 Estimation of cod depth distribution

114   Indices of cod biomass (calculated as catch-per-unit-effort, CPUE, kg/h, herein referred to as

115   biomass) and depth distribution (i.e. mean depth and interquartile range of predicted depth

116   distribution) from the BITS and historical bottom trawl surveys in SDs 25-28 from 1979 to

117   2018 were estimated for large ($\geq$ 30 cm) and small cod (15-30 cm) using a modelling procedure

118   similar to the one used in Orio et al. (2019). However, in the current study rather than including

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119   environmental variables in the models, quarter was included in interactions with latitude and

120   longitude, and with depth. To estimate the changes in cod depth distribution in SDs 26-28 that

121   account for the changes in the spatial distribution of the cod population, the SD-specific depth

122   distributions were weighted by the annual SD-specific cod CPUEs from the bottom trawl

123   surveys in quarter 4, estimated from the same model.

124   **2.3 Depth of hypoxic layers**

125   Baltic cod has been shown to avoid oxygen concentrations below 1 ml/l (approximately 1.4

126   mg/l) (Schaber et al., 2012). Therefore, time-series of the depth at which 1 ml/l oxygen

127   concentration was encountered by SD were obtained from the Swedish Meteorological and

128   Hydrological Institute (SMHI, www.smhi.se).

129   Time-series of depth at which 4 ml/l oxygen concentration was encountered by SD were also

130   obtained from SMHI. This oxygen concentration, on average, has been found to affect the

131   performance of fish (Vaquer-Sunyer and Duarte, 2008). Specifically for cod, 4 ml/l has been

132   found as threshold under which an effect on condition and growth starts to be observable

133   (Chabot and Dutil, 1999). Therefore, we expected that the occurrence of cod in areas and depths

134   with an oxygen concentration $\leq$ 4 ml/l would lead to an increase in the proportion of cod

135   individuals with very low condition and a decrease in mean condition in the population.

136   To relate the depths at which 1 ml/l and 4 ml/l oxygen concentrations were encountered to cod

137   depth of occurrence and condition in SDs 26-28, the oxygen depths by SD were weighted with

138   the annual SD-specific cod CPUEs from the bottom trawl surveys estimated from the same

139   models in quarter 4. In this way, the oxygen circumstances in the SDs where cod was more

140   abundant were weighted the most.

141   **2.4 Otolith microchemistry**

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142 Otoliths (N = 154) were selected from Baltic cod collected in the study area in the 1980s-2010s

143 from BITS and historical bottom trawl surveys in February (Limburg and Casini, 2019). These

144 were cleaned, transversely sectioned, and analysed by laser ablation inductively coupled

145 plasma spectrometry. A spot of 100-micron diameter was driven at 5 μm/sec, 10 Hz, to create

146 a transect from the otolith core to the outer dorsal edge, collecting a suite of elements (see

147 Limburg and Casini, 2018 for details). For the analysis described here, we took the ratio of

148 manganese to magnesium along this continuous transect. Manganese, although redox-sensitive

149 and thus available as dissolved Mn^{2+} and Mn^{3+} at low oxygen concentrations, is also affected

150 by the fish's growth rate (Limburg et al., 2015; suggested by Thomas et al., 2019). Dividing

151 manganese by the corresponding, growth-sensitive magnesium (from the same replicate) to

152 some extent corrects for the growth effect (Limburg and Casini 2018, 2019). Our metric for

153 hypoxia exposure is the fraction of an annual growth band wherein this Mn/Mg ratio exceeds

154 an age-based threshold (Limburg and Casini 2018, 2019). We tested this metric as a function

155 of cod condition categorized into "high" (condition ≥ 0.9) and "low" (condition < 0.9) groups,

156 and tested whether this had changed over time (before the year 2000, and from 2000 onward).

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158 **3. Results**

159 **3.1 Cod condition**

160 Cod condition increased slightly between the mid-1970s and mid-1990s, but declined abruptly

161 thereafter. This pattern was similar in SD 25 and SDs 26-28 for both small and large cod (Fig.

162 3), but after the mid-1990s condition dropped more for large cod. The percentage of large fish

163 with very low condition (< 0.8, see Eero et al., 2012) increased from the end of 1990s in both

164 SD 25 and SDs 26-28 reaching in recent years 30-40%. The percentage of small fish with low

165 condition also increased, but lagged temporally behind the large cod, and at 10-20% of

166 observations was lower than the high incidences of large cod in poor condition (Fig. 3). In

167 general, in SD 25 condition declined slightly more (and the percentage of fish with very low

168 condition increased more) than in SDs 26-28 after the mid-1990s.

169 **3.2 Cod depth distribution**

170 Large cod in SD 25 were distributed between 30 and 50 m depth (average of 40 m depth) at

171 the beginning of the time-series, but have been found in deeper waters since the late 1990s

172 (Fig. 4A). In SDs 26-28 large cod were distributed between 35 and 55 m depth (average 45 m)

173 at the beginning of the time-series, while afterwards they moved deeper and since the mid-

174 1990s they became distributed between 50 and 70 m depth (average 60 m) (Fig. 4C). Along

175 with the change in mean depth, large cod in SDs 26-28 have shown a contraction of the range

176 of depth distribution in the past 20 years. Small cod were distributed somewhat shallower than

177 the large fish, but also moved into deeper waters during the time period investigated. In SD 25,

178 these shifted distribution from between 30 and 50 m depth (average 40 m depth) to 45-60 m

179 depth (average 53 m) (Fig. 5A). In SDs 26-28 small cod moved deeper with time as well, from

180 30-50 m depth (average 40 m) to 50-63 m depth (average 55 m), and experienced a contraction

181 of the range of depth distribution similar to what occurred for the large fish in this area (Fig.

182 5C).

183 **3.3 Depth of hypoxic layers**

184 The depth at which 1 ml/l was encountered remained fairly constant at around 70 m in SD 25,

185 while in SDs 26-28 it became shallower from being deeper than 100 m before the early 1990s

186 to 70-80 m in the past twenty years (Fig. 4A,C and 5A,C). The depth at which 4 ml/l was

187 encountered diminished in SD 25 from 60-65 m at the beginning of the time period to 50-55 m

188 during the past twenty years, while in SDs 26-28 it became shallower from being 70-80 m

189 before the early-1990s to 55-60 m in the past fifteen years (Fig. 4A,C and 5A,C). The oxygen

190   depths in SDs 26-28, accounting for the SD-specific distribution of the cod, did not differ much

191   between large and small cod (compare Fig. 4C and Fig. 5C).

3.4 Depth overlap between cod and hypoxic layers

193   In SD 25, large cod depth distribution never overlapped with depth with oxygen ≤ 1 ml/l along

194   the time period analysed, while in SDs 26-28 there was an overlap in a couple toward the end

195   of the time-series (Fig. 4A,C). On the other hand, large cod distribution heavily overlapped

196   with the depth with oxygen ≤ 4 ml/l since the mid-1990s (Fig. 4A,C) and the overlap, although

197   oscillating, increased in the past twenty years reaching values above 50% in SD 25 and up to

198   100% in SDs 26-28 (Fig. 4B,D).

199   Small cod distribution never overlapped with depth with oxygen ≤ 1 ml/l along the time period

200   analysed, neither in SD 25 nor SDs 26-28 (Fig. 5A,C). On the other hand, small cod distribution

201   overlapped with the depth with oxygen ≤ 4 ml/l since mid-1990s (Fig. 5A,C) and the overlap,

202   although oscillating, increased in the past fifteen years reaching values higher than 60% both

203   in SD 25 and SDs 26-28 (Fig. 5B,D).

204   There was a strong positive correlation between the percentage of the cod population in waters

205   ≤ 4 ml/l and the percentage of cod individuals with very low condition (for large cod, r = 0.71

206   and 0.74 in SD 25 and SDs 26-28, respectively; for small cod, r = 0.58 and 0.59 in SD 25 and

207   SDs 26-28, respectively). There was also a strong negative correlation between the percentage

208   of the cod population in waters ≤ 4 ml/l and mean cod condition (for large cod, r = -0.77 and -

209   0.76 in SD 25 and SDs 26-28, respectively; for small cod, r = -0.60 and -0.54 in SD 25 and

210   SDs 26-28, respectively).

3.5 Otolith microchemistry

212   Fish exposed to hypoxia as measured by otolith chemistry showed different responses as a

213   function of their condition at time of capture and the time period (pre- or post-2000; Fig. 6).

214   Prior to 2000, the annual duration of hypoxia exposure was relatively low (35.4%); for the

215   years 2000 and onward, the percent duration rose to 51.8%. More strikingly, when divided

216   further into groups by fish condition, pre-2000 fish were not significantly different with respect

217   to hypoxia exposure regardless of condition. After 2000, fish with condition < 0.9 had been

218   exposed considerably longer to hypoxia (62.7% ± 3.6) than fish with condition ≥ 0.9 (40.9% ±

219   5.1; Fig. 6). The effect sizes of interaction of time period and condition were large and highly

220   significant ($F_{1,746} = 23.287$, $p = 2 \times 10^{-6}$).

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222   **4. Discussion**

223   In this paper, we analysed the potential mechanisms relating Baltic Sea deoxygenation with

224   changes in Eastern Baltic cod body condition during the past four decades. To this end, we

225   investigated the changes in depth distribution of the cod population and the vertical changes in

226   oxygen gradients based on long-term biological and hydrological monitoring data. Moreover,

227   we supplemented these analyses with proxies for hypoxia exposure from individual fish otolith

228   microchemistry.

229   **4.1 Cod depth of distribution and overlap with hypoxic areas**

230   Our analyses show an increase in the areas with an oxygen level below cod tolerance (i.e.

231   oxygen ≤ 1 ml/l; Schaber et al., 2012). Moreover, this oxygen threshold has also shifted with

232   time towards shallower depths, determining an overall contraction of the potentially suitable

233   habitat for cod (Casini et al., 2016a). Declines in oxygen concentrations have caused a

234   contraction of the habitat and the distribution of fish in other systems (Eby and Crowder, 2002;

235   Stramma et al., 2012; Breitburg et al., 2018) with measurable effects on, for example,

236   individual growth (e.g. Campbell and Rice, 2014). In the Baltic Sea, however, this change

237   seems not to have affected the cod depth of distribution in autumn, since the latter has been

238   always above 70-75 m, a depth only in few years reached by the waters with 1 ml/l. On the

239   other hand, it could be hypothesized that during the latest decade the cod population was unable

240   to occupy deeper habitats because of the vertical rise of this oxygen layer. This hypothesis

241   seems to be supported by the decline in the range of depth distribution (i.e. a squeeze of the

242   cod habitat occupation) shown by both large and small cod in SDs 26-28 during the past twenty

243   years. Explaining the temporal changes in the depth distribution of cod is beyond the scope of

244   this paper, but a potential reason could be that cod seek deeper layers to avoid too warm waters,

245   which could be detrimental when resources are scarce. In fact, pelagic prey have declined after

246   the mid-1990s in the southern and central Baltic Sea (Casini et al., 2016a) and therefore cod

247   might go deeper to optimize metabolism. Small cod, moreover, could seek deeper waters to

248   escape from the predation of the increased seals and aquatic birds (Orio et al., 2019).

249   The depth where dissolved oxygen falls to ≤ 4 ml/l ("sub-lethal" level, i.e. level that has been

250   shown in previous studies to affect cod performance; Chabot and Dutil, 1999; Vaquer-Sunyer

251   and Duarte, 2008) has shallowed during the past four decades, as a consequence of

252   deoxygenation. Our analysis revealed that this vertical rise, together with the deepening of the

253   cod depth distribution, has resulted in that cod has started to dwell more and more in these

254   hostile low-oxygen waters. This is consistent with observations of hypoxia exposure proxied

255   by otolith chemistry (Limburg and Casini, 2018 and 2019; this study, see below). The overlap

256   between cod depth distribution and "sub-lethal" oxygen layers occurred and reinforced only

257   after the mid-1990s, concomitant with the decline in cod condition, while in earlier years the

258   cod population was occurring above those layers. Therefore, according to our expectations and

259   hypothesis, the negative effects of hypoxia on cod condition could only arise after the mid-

260   1990s. This is also in accordance with our otolith microchemistry analysis (see below) and

261   previous investigations that suggested that in the earlier years (before the mid-1990s) cod

262   condition was regulated by other factors, such as pelagic prey biomass and density-dependence

263 (Casini et al., 2016a, Limburg and Casini, 2019). The progressively higher proportion of the

264 cod population in "sub-lethal" oxygen layers, as revealed by our study, conforms also to the

265 increasingly higher proportion of individuals in extremely low condition (< 0.8 Fulton's K),

266 which include starving fish and fish close to the condition mortality threshold (Eero et al., 2012;

267 Casini et al., 2016b).

268 **4.2 Otolith microchemistry**

269 The complementary analyses performed on fish otolith microchemistry confirmed that since

270 the mid-1990s, cod individuals with low condition were indeed exposed to low-oxygen waters

271 during their life. Duration of hypoxia exposure as measured in Baltic cod otoliths has increased

272 markedly since mid-1990s (Limburg and Casini, 2018) and was found in our study to be

273 significantly greater in fish in poor condition at time of capture. This is a remarkable finding,

274 given that condition is measured only once during life (at capture), and the observations of

275 hypoxia exposure are taken throughout life. This suggests that currently, condition may carry

276 over from chronic exposure to low oxygen, which weakens fish and produces a cascade of

277 effects, from reduced metabolic scope leading to lower activity and slower digestion (Claireaux

278 and Chabot, 2016), to greater susceptibility to disease and parasites (e.g., Sokolova et al.,

279 2018). In contrast, in fish captured prior to 2000 the overall exposure to hypoxia was lower and

280 showed no relationship with condition. Thus the otolith microchemistry analysis confirmed the

281 that, pre-2000, factors other than hypoxia played a greater role in shaping cod condition as

282 concluded also by Casini et al. (2016a).

283 Although we have shown here that direct oxygen exposure is likely a key factor shaping cod

284 condition after the mid-1990s, other factors might contribute to explain the decline in condition

285 as well (Casini et al., 2016a). The more severe decline in condition in SD 25 compared to SDs

286 26-28, for example, could be due to the higher density of cod in the southern Baltic Sea during

287   the past twenty years (Orio et al., 2017) leading to density-dependent effects, and the lower

288   abundance of sprat, the main pelagic fish prey for cod, in this area (Casini et al., 2014).

289   Moreover, deoxygenation, by deteriorating the benthic communities, has likely affected

290   negatively important benthic prey for cod and therefore influenced also indirectly cod condition

291   and growth (Neuenfeldt et al., 2019).

292   **5. Conclusions**

293   We have shown here the potential mechanisms linking deoxygenation to cod condition in the

294   Baltic Sea. A combination of increased depth of distribution of the cod population and a vertical

295   rise of the "sub-lethal" oxygen layers has led cod dwelling progressively more in hostile low-

296   oxygen waters, contributing to explain the reduction in cod condition in the past two decades.

297   Further analyses should focus on revealing the reasons of the shift of cod distribution to deeper

298   and less-oxygenated waters. We stress that our depth analyses were focused on the autumn

299   season, when cod growth is maximised for the accumulation of energy reserves to be utilized

300   for spawning the following spring-summer (Mion et al., 2020). The changes in cod depth of

301   distribution are different in other seasons, especially those before and during spawning (Orio

302   et al., 2019), when cod could have different environment requirements for reproduction.

303   Therefore, further analyses should be performed to investigate the changes in cod population

304   depth distribution in relation to oxygen stratification in other seasons to better understand the

305   biotic and abiotic spatio-temporal dynamics, and their effects on cod performance, over the

306   entire year.

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Data availability

311 Time-series used in this study are available upon request to the corresponding author.

Author contribution

314 MC designed and coordinated the study. MC, MH, AO and KL prepared the raw data. MC

315 estimated cod condition, MH performed the hydrographic modelling, AO performed the cod

316 distribution modelling, and KL prepared and analysed the cod otoliths. MC prepared the first

317 draft of the manuscript and all authors contributed to the final version.

Competing interests

319 The authors declare that they have no conflict of interest.

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466 **Figure captions**

467 Fig. 1. Bathymetric Map of the Baltic Sea divided into ICES Subdivisions (SDs). The study

468 area includes the SDs 25–28 (i.e. the Central Baltic Sea).

469 Fig. 2. Maps of the Baltic Sea with superimposed the areas with oxygen concentration $\leq$ 1 ml/l

470 (black, avoided by cod) and $\leq$ 4 ml/l (grey, sub-lethal level, producing negative effects on cod

471 performance) in 1990 (panel A) and 2018 (panel B). Time-series of the total area (km^2) with

472 oxygen concentration $\leq$ 1 ml/l and $\leq$ 4 ml/l in the SDs 25-28 (panel C). Data were from the

473 Swedish Meteorological and Hydrological Institute (SMHI, www.smhi.se) (see also Casini et

474 al., 2016a).

475 Fig. 3. Temporal developments of mean cod condition ($\pm$ 1 s.d.) in Subdivision 25 and

476 Subdivisions 26-28 for small cod (20-29 cm) and large cod (40–49 cm). Superimposed (grey

477 bars) the temporal developments of the percentage of cod with very low condition (< 0.8) for

478 the respective areas and length classes.

479 Fig. 4. Time-series of large cod ($\geq$ 30 cm) depth distribution (mean and interquartile range of

480 each predicted depth distribution; see Orio et al., 2019) as well as depths of oxygen

481 concentration 1 ml/l and 4 ml/l, for Subdivision 25 (panel A) and Subdivisions 26-28 (panel

482 C). Panels B and D, time-series of the percent of large cod in waters with oxygen concentration

483 $\leq$ 4 ml/l, in Subdivision 25 and Subdivisions 26-28.

484 Fig. 5. Time-series of small cod (15-30 cm) depth distribution (mean and interquartile range of

485 each predicted depth distribution; see Orio et al., 2019) as well as depth of oxygen

486 concentration 1 ml/l and 4 ml/l, for Subdivision 25 (panel A) and Subdivisions 26-28 (panel

487 C). Panels B and D, time-series of the percent of small cod in waters with oxygen concentration

488 $\leq$ 4 ml/l, in Subdivision 25 and Subdivisions 26-28.

489 Fig. 6. Differences in otolith chemistry as related to hypoxia and fish condition for pre-2000

490 and 2000s. Within-year hypoxia exposure duration is proxied by the fraction of each annual

491 growth band in which the otolith Mn/Mg ratio exceeds age-specific thresholds. These are

492 categorized by condition factor (high condition is 0.9 or greater) measured at time of capture

493 (see Limburg and Casini, 2019).

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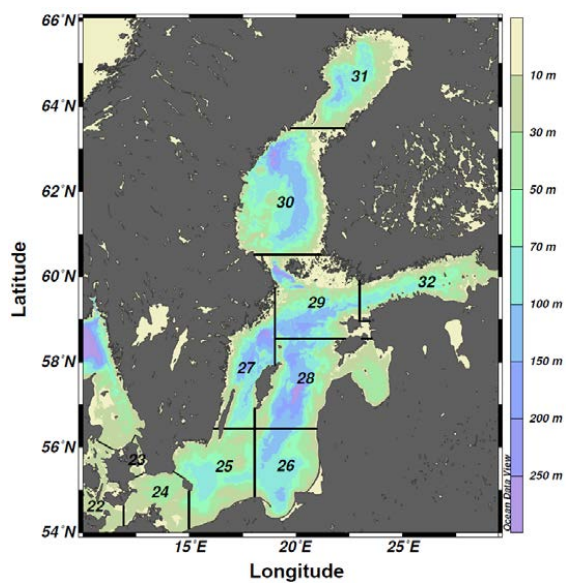
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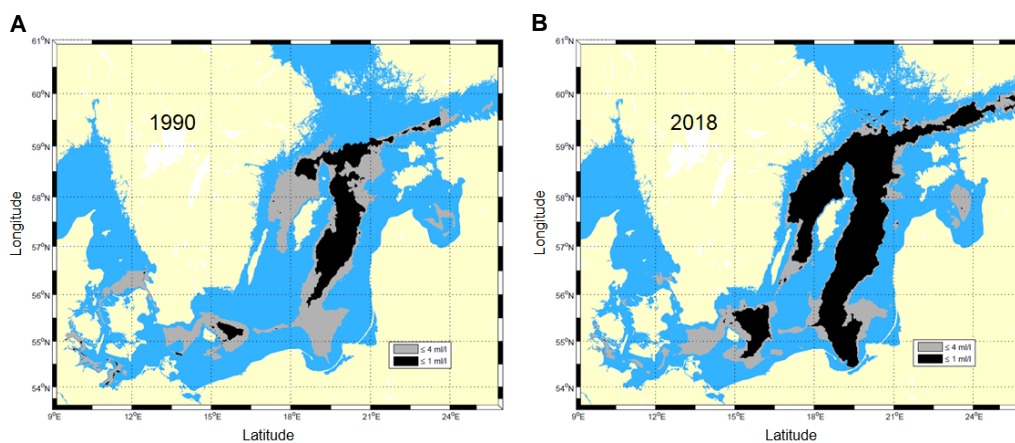
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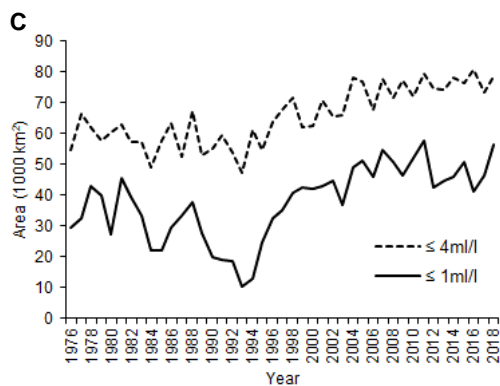
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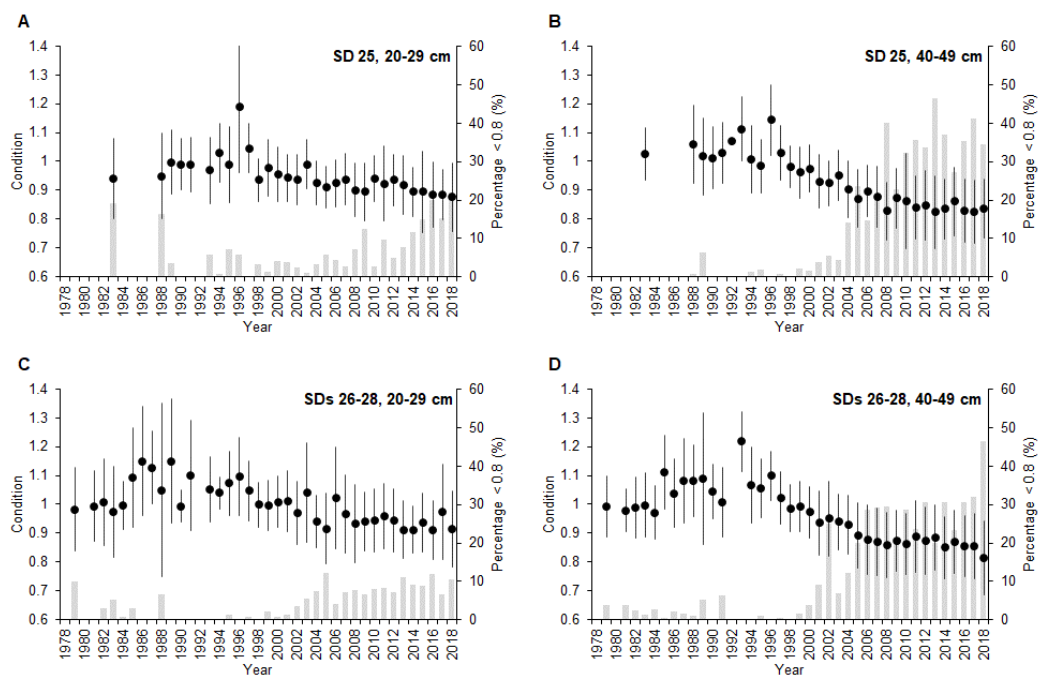533

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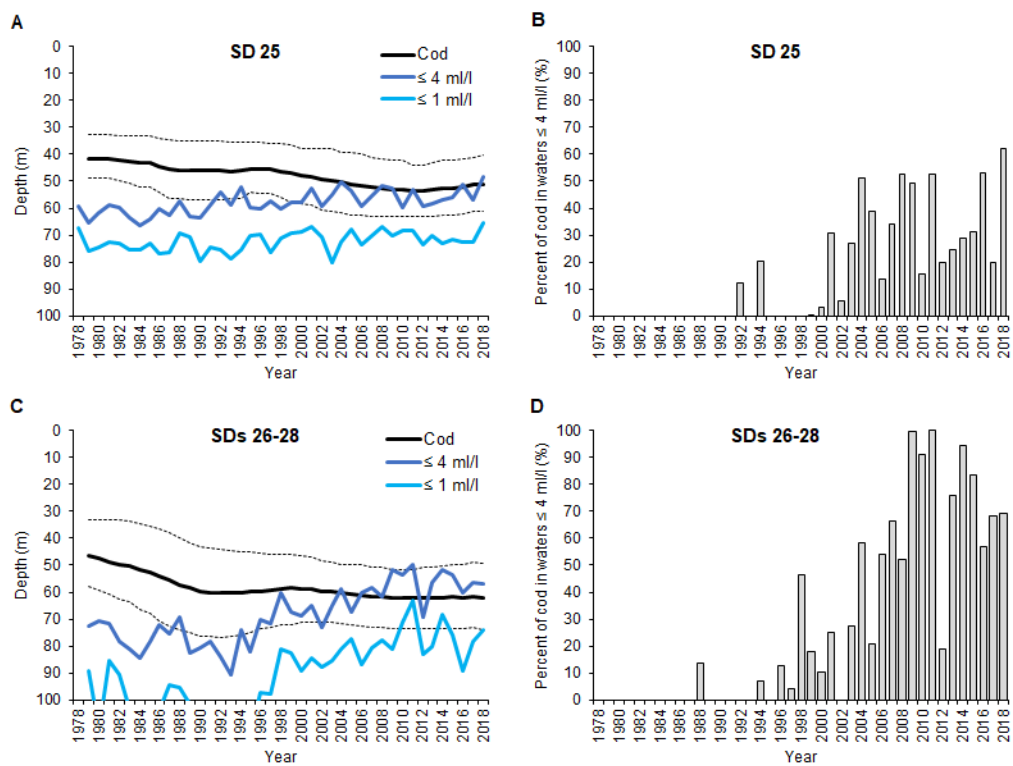542

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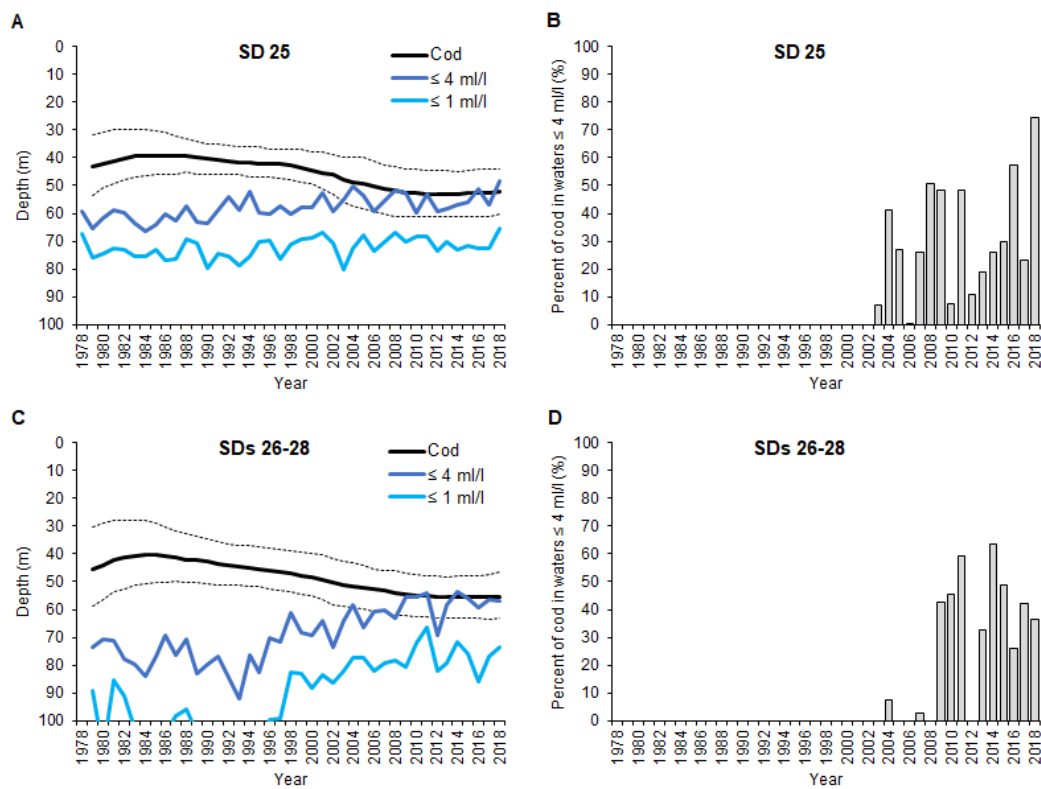551
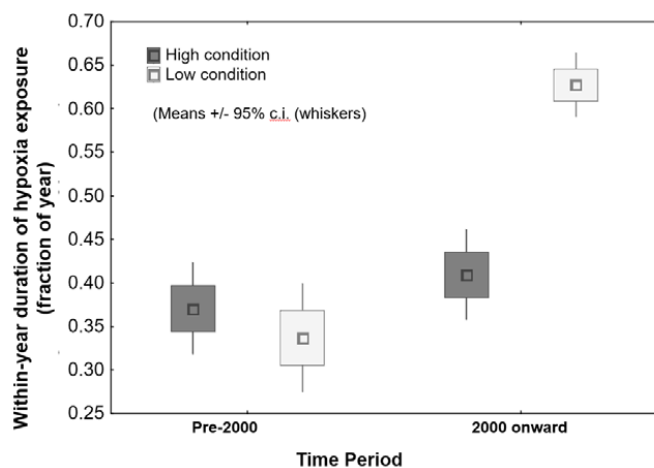
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