Title: VARIATIONS IN LENGTH AND GROWTH OF GREENLAND HALIBUT JUVENILES IN RELATION TO ENVIRONMENTAL CONDITIONS

Article Type: Research Paper

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Manuscript Region of Origin: CANADA

1   **VARIATIONS IN LENGTH AND GROWTH OF GREENLAND HALIBUT JUVENILES IN**

2   **RELATION TO ENVIRONMENTAL CONDITIONS**

3

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10

11   **Abstract**

12   Greenland Halibut (*Reinhardtius hippoglossoides*), especially juveniles, are abundant in the St.

13   Lawrence estuary, where oxygen levels are very low (18–25% saturation). Current data suggest that

14   juveniles may be sedentary in this region. We investigated the relative importance of oxygen for

15   juvenile growth in different areas occupied by juveniles in the estuary and Gulf of St. Lawrence

16   (EGSL). More specifically, we examined the mean size-at-age for 1- and 2-year-old juveniles as well

17   as the growth rate in different areas in relation to oxygen, depth, temperature, and juvenile density.

18   Overall, oxygen concentration was found to affect juvenile Greenland Halibut growth: growth rate

19   varied inversely with dissolved oxygen levels and significantly decreased when oxygen conditions

20   were below 80 μmol/L (~ 25% saturation). Temperature did not affect juvenile growth rates within the

21   range found in these areas (4.95–5.14°C). Mean lengths in 1- and 2-year-old juveniles (17 and 27 cm,

22   respectively) as well as length increment estimates from 1 to 2 years old in the EGSL were much

23   higher than those observed in other populations of Greenland Halibut. Length increment from ages 1

24   and 2 ranged between 8 and 12 cm for temperatures varying from 3.7 to 5.5°C. We found the highest

25   abundance of juveniles in bottom waters characterized by low oxygen concentrations and also found

26   that there was continuous juvenile growth over the year; these observations suggest that the negative

27   impacts of dissolved oxygen should be limited and/or largely compensated by other physical or

28   biological characteristics of the EGSL, such as food abundance, food availability, and/or predator

29   density.

30   **Keywords:** Greenland Halibut, growth, hypoxia, temperature, fish density.

31

1. Introduction

Climate change is expected to have impacts on the biology and ecology of marine organisms and ecosystems (Brierley and Kingsford, 2009). Changes in the physical (temperature, ocean current patterns) and biogeochemical (oxygen content, primary productivity, plankton community structure) conditions of different marine ecosystems are expected to lead to strong shifts in species distribution, phenology, and marine fisheries productivity (Edwards and Richardson, 2004; Richardson and Schoeman, 2004; Perry et al., 2005; Hiddink and Hofstede, 2008; Rosa and Seibel, 2008; Cheung et al., 2010, Pörtner, 2010). In particular, pronounced changes are expected in the distribution and abundance of marine fishes (Cheung et al., 2013) along with modifications in their growth, survival, and reproduction (Beaugrand et al., 2002; 2003). Development and growth, and thus organism size, are affected by temperature, oxygen level, and other factors such as resource availability (Irie and Fisher, 2009; Pauly and Kinne, 2010). Recently, Daufresne et al. (2009) and Sheridan and Bickford (2011) showed that rising temperatures associated with a reduction in oxygen availability result in reductions in body size of marine fishes. A recent model examining the integrated changes in ecophysiology and distribution of 600 species of exploited demersal marine fishes around the world demonstrated that the assemblage-averaged maximum body weight could experience a global reduction of 14 to 24% from 2000 to 2050 based on a high-emission scenario of anthropogenic greenhouse gases (Cheug et al., 2013). About half of this reduction in size is due to changes in distribution and abundance while the remainder is linked to physiological modifications.

A hypoxia trend in bottom waters (> 150 m) of the lower St. Lawrence estuary was observed between 1930 and the mid-1980s, with dissolved oxygen (DO) levels decreasing by half in the deep-water layers. This was mainly due to (1) an increase in the proportion of warm, oxygen-poor North Atlantic central water coming into the system, (2) an increase in organic matter flow into the surface layer, and (3) an 11% to 27% increase in the rate of bacterial respiration (Gilbert et al., 2007; Genovesi

56 et al., 2011). This DO decrease was accompanied by a warming of bottom waters by about 2°C (Gilbert

57 et al., 2005; Genovesi et al., 2011). Since the mid-1980s, oxygen levels in the bottom waters have

58 remained stable (Gilbert et al., 2005).

59 Ait Youcef et al. (2013) examined the potential effects of hypoxia on the spatial distribution and

60 abundance of Greenland Halibut *Reinhardtius hippoglossoides*, which has been one of the most

61 important commercial demersal flatfish species in this region over the last 20 years. Juvenile and adult

62 Greenland Halibut are concentrated in the estuarine portion of the Gulf of St. Lawrence (habitats

63 characterized by low oxygen levels, ~ 21% saturation) at both high and low levels of stock abundance.

64 These authors highlighted a strong association between high fish densities and low oxygen

65 concentrations, indicating a high tolerance of Greenland Halibut to hypoxia. Although low levels of

66 oxygen did not directly affect fish distribution, they could have marked effects on growth when

67 adequate food is available. Indeed, under laboratory conditions, Dupont-Prinet et al. (2013) showed

68 that severe hypoxia (19% saturation; levels presently encountered in the St. Lawrence estuary) reduced

69 the aerobic scope by 72% compared to normoxia and increased the duration of digestive processes in

70 Greenland Halibut juveniles. However, whether this reduction of aerobic scope would impact the

71 growth of wild fish has not been assessed.

72 A reduction in growth rate would be of major concern because 16% of the Greenland Halibut

73 biomass, including a high concentration of juveniles (1 and 2 years old), is found in the St. Lawrence

74 estuary (MPO, 2010), which is characterized by low DO levels. Indeed, the estuary has been identified

75 as the main nursery area in this system (Ait Youcef et al., 2013). Moreover, juvenile Greenland Halibut

76 that settle in the St. Lawrence estuary are sedentary for at least their first two years of life (Ait Youcef

77 et al., 2013). The aim of this study is to determine the relative importance of dissolved oxygen on the

78 growth of juvenile Greenland Halibut. To do this, we examined the environmental characteristics of

79 different areas occupied by juveniles. More specifically, growth rate and mean size at age 1 and 2 in

80   juveniles in the different areas were examined in relation to DO, depth, temperature, and juvenile

81   density. The mean size-at-age of juveniles in early spring and fall in the St. Lawrence estuary was used

82   to determine the seasonal growth pattern. Finally, the relative importance of low DO levels was

83   examined by comparing juvenile sizes-at-age observed in other populations.

84

2. Material and Methods

2.1. Data collection

Biological data for Greenland Halibut were obtained from the multidisciplinary research bottom-trawl survey conducted in the estuary and Gulf of St. Lawrence (EGSL; NAFO Division 4RST) each summer since 1990 by the Department of Fisheries and Oceans, Canada (DFO). Surveys used a stratified random sampling strategy with predetermined strata based on geographic region and depth (Gagnon, 1991). A detailed description of the survey design is provided in Ait Youcef et al. (2013). Additional data were also obtained from smaller scale bottom-trawl surveys conducted in the spring (April–May) and fall (October) from 2006 to 2010 in the St. Lawrence estuary. These surveys also used a stratified random sampling design, with tows made in depths ranging from 150 m to 350 m.

For each survey, total catch weight and individual fish length (fork length, cm) and weight (g) of Greenland Halibut were recorded for each set; sex and maturity stage were also noted. For sets with large catches, a random sample of a maximum of 175 individuals was analyzed. In the summer surveys, CTD casts were done at each trawl station to obtain temperature and salinity profiles. Starting in 2004, CTD profilers were equipped with Sea-Bird SBE43 oxygen sensors to measure dissolved oxygen levels at each trawl station. Beginning in 2006, an Aanderaa 3930 oxygen optode / temperature sensor was also attached to the trawl. Some CTD profiles were also done during the spring and fall surveys. A data logger (Vemco minilog-TD) was installed on the trawl to record trawl depth and bottom temperature for each set.

2.2. Depth, temperature, dissolved oxygen, and fish density

Average yearly depths, temperatures, and dissolved oxygen concentrations in strata from the EGSL occupied by Greenland Halibut juveniles were calculated from data collected during the DFO summer multidisciplinary surveys. The abundance of juveniles in each tow was used as the weighting

108 factor in calculations. Average depth, temperature, and dissolved oxygen concentrations were estimated

109 for each stratum each year. Depth, temperature, and juvenile density were analyzed for the 1990 to

110 2012 period while dissolved oxygen concentrations were analyzed for the 2004 to 2012 period.

111 Fish density per area, determined as the mean number of Greenland Halibut juveniles per

112 standard tow in each area $\bar{Y}_t$, was calculated as:

113 $$\bar{Y}_t = \sum_{h=1}^{K} \frac{A_h}{A_T} \bar{y}_h \qquad (1)$$

114 where A_h is the surface of stratum h, A_T the total surface of the area, K the number of strata in the area,

115 and $\bar{y}_h$ the mean number of juveniles per standard tow in stratum h. Fish with lengths smaller than or

116 equal to 30 cm were considered as juveniles, and most of these fish are considered to be of age 1 and 2

117 (DFO, 2011).

118 *2.3. Length-frequency distribution*

119 Mean lengths-at-age and growth of Greenland Halibut juveniles were estimated from length-

120 frequency distributions of the different surveys. For each survey, length-frequency distributions were

121 analyzed for three distinct areas to take into account spatial variations in environmental conditions and

122 fish densities in the EGSL (Ait Youcef et al., 2013). The three areas identified were (1) the St.

123 Lawrence estuary (SLE), (2) the area northeast of Anticosti Island (NEA), and (3) the Laurentian

124 Channel (LC) (Fig. 1). In the delineation of these areas, the homogeneity of the physical conditions for

125 the different strata included in each area was tested.

126 In the absence of age determination, an analysis of the length-frequency distribution was used to

127 determine the mean lengths at age of Greenland Halibut juveniles. This analysis was restricted to the

128 juvenile stage, since juveniles are considered to be sedentary for at least their first two years of life in

129 the EGSL (Ait Youcef et al., 2013). Length-frequency distributions were analyzed separately for each

130   area and year between 1990 and 2012. Only fish measuring less than 40 cm were considered for the

131   analysis. Mean lengths-at-age and juvenile growth obtained were related to environmental factors

132   (depth, temperature, and oxygen) and fish density.

133   Fish length-frequency distributions typically show distinct modes representing different age

134   groups (Macdonald, 1987). Mixed probability density functions (mixture models) were fit to each

135   distribution to determine the mean length for each mode (i.e., age group) (Ricker, 1975). The mixed

136   probability density function is a weighted sum of k probability density functions:

137      $$g(x|\pi, \mu, \sigma) = \pi_1 f(x|\mu_1, \sigma_1) + \cdots + \pi_k f(x|\mu_k, \sigma_k) \qquad (2)$$

138   where π represents the mixing proportion of the total population, μ the mean, and σ the standard

139   deviation of the different components present in the distributions (Everitt and Hand, 1981). All mixture

140   models were fit using normal distributions. Mixture models were fit to observed frequency distributions

141   using maximum likelihood estimation. A goodness-of-fit test based on the chi-square approximation to

142   the likelihood ratio statistic (Rao, 1965) was used for each model to determine how adequately the

143   mixture distributions g(x) fit the observed length-frequency histograms (Du, 2002). For goodness-of-fit

144   tests, we used $\alpha = 0.05$. All analyses were performed with the Mixdist package (Macdonald, 2010) in R

145   version 2.12.0 software (R, 2010).

146   *2.4. Juvenile growth*

147   Very few young-of-the-year (0^+) are caught in the summer (August) survey. Larvae that hatch in

148   the winter are caught as pelagic postlarvae, with a size between 3.0 and 7.9 cm (modal length 6.3 cm)

149   in August (Ouellet et al., 2011). Thus, the first mode of the length-frequency distributions in August

150   represents juvenile fish of age 1. In the absence of precise information on the size of postlarvae in

151   August, the mean size at age 1 estimated from the length-frequency distributions was considered to

152   represent the growth of age 1 juveniles between their hatch in winter and August of the following year

153 (i.e., 18–20 months later). The size increment between modal lengths from the length-frequency

154 distributions of successive years, corresponding to fish originating from the same cohorts, was used as

155 the measure of juvenile growth.

156   The seasonal growth of juveniles was estimated from an analysis of the length-frequency

157 distributions of Greenland Halibut in the spring and fall surveys conducted in the St. Lawrence estuary

158 from 2006 to 2010. Size increments for different cohorts were tracked from modal lengths in

159 successive length-frequency distributions between April and October (summer) and between October

160 and April (winter). Seasonal variation in growth was determined by comparing the length increment

161 per day of the cohorts during summer and winter. Length increment per day (LD) for each season was

162 estimated for age 1 and 2 fish of each cohort as:

163 $LD = (LT - Lt) / \Delta t$ (3)

164 where LT and Lt are fish lengths at the end and start of the period, respectively, and Δt the number of

165 days between measurements.

166 *2.5. Statistical analyses*

167   Differences in depth, bottom temperature, dissolved oxygen concentration, juvenile fish density,

168 and mean size at age among the different areas (SLE, NEA, and LC) were assessed using analysis of

169 variance. Normality and homogeneity of variances were verified using the Komolgorov-Smirnov

170 distribution test and the Brown-Forsythe test, respectively (Quinn and Keough, 2002). Fish density data

171 were transformed (square root) to obtain normality and homogeneity of variances. Two-way ANOVAs

172 were used to detect significant effects of area and year on depth occupied, bottom temperature,

173 dissolved oxygen concentration, and juvenile fish density. One-way ANOVAs were used to detect

174 significant effects of area and year on mean size at ages 1 and 2 as well as length increment between

175 ages 1 and 2.

176   The relative importance of depth, bottom temperature, dissolved oxygen concentration, and fish

177   density on juvenile growth was determined using generalized additive models (GAM) (Hastie and

178   Tibshirani, 1990). A log-link function and Gaussian error distribution were used for GAM as it gave

179   the best fit. A cubic B-spline smoother was used to explain the variability in juvenile growth associated

180   with the different variables. Analyses were done using the mgvc package in R version 2.12.0 software

181   (R, 2010).

182   Variability in the seasonal growth of juveniles was tested by comparing length increments of the

183   different cohorts of fish tracked in the spring and fall surveys. Length increments per day for ages 1

184   and 2 of the different cohorts during summer (April–October) and winter (October–April) were

185   compared using one-way ANOVAs. Normality and homogeneity of variances were verified using the

186   Komolgorov-Smirnov distribution test and the Brown-Forsythe test, respectively (Quinn and Keough,

187   2002).

188

3. Results

3.1. Depth, temperature, dissolved oxygen, and juvenile Greenland Halibut density

The average characteristics of zones of the SLE, LC, and NEA in which Greenland Halibut juveniles were present are reported in Table 1. Average depth, bottom temperature, dissolved oxygen concentration, and juvenile Greenland Halibut density varied among the three areas and between years (Fig. 2). Greenland Halibut juveniles were found at different depths in the three areas ($F_{2, 627} = 52.68$, P < 0.001), but the average depths within which fish were captured did not change over the years ($F_{22, 627} = 0.71$, P = 0.83), and no interaction between areas and years was observed ($F_{44, 627} = 0.4$, P = 0.99). The average depth within which juveniles were captured was significantly lower in NEA than in SLE and LC (Table 1).

The average bottom temperatures where Greenland Halibut juveniles were captured generally varied between 4.0 and 5.5°C in the 1990–2012 period. Significant differences were observed between areas ($F_{2, 581} = 10.4$, P < 0.001) and years ($F_{22, 581} = 7.6$, P < 0.001), with a significant interaction between the two factors ($F_{44, 581} = 2.97$, P < 0.001). Lower temperatures were observed at the beginning of the time series in all areas, and temperatures were lower in SLE and NEA than in LC (Table 1).

Significant variations in dissolved oxygen concentrations were observed among the three areas ($F_{2, 238} = 172.7$, P < 0.001). The lowest dissolved oxygen concentrations were in SLE and the highest in LC (Table 1). Differences were observed among years ($F_{8, 238} = 2.25$, P = 0.024), and no interaction was observed between areas and years ($F_{16, 238} = 1.51$, P = 0.1). The highest densities of juvenile Greenland Halibut were found in SLE (Fig. 2). The average number of juvenile fish per standard tow in SLE (166.41 ± 10.2) was considerably higher than in NEA (39.13 ± 4.07) or LC (18.89 ± 1.8). Juvenile density was significantly different among areas ($F_{2, 677} = 507.57$, P < 0.001) and years ($F_{22, 677} = 16.57$,

211 P < 0.0001), and there was a significant interaction between areas and years ($F_{44,\ 677}$ = 4.36, P < 0.001),

212 indicating different patterns of variations between years in the three areas.

213 *3.2. Length-frequency distributions*

214   Length-frequency distributions were generally characterized by the presence of four distinct

215 modes (Fig. 3). Mean lengths at age 1 to 4 were attributed to the four successive modal lengths in the

216 frequency distributions for the different surveys, areas, and years. Depending on the time of the survey,

217 modal lengths varied between 12 and 19 cm for age 1, between 22 and 29 cm for age 2, between 30 and

218 35 cm for age 3, and between 37 and 39 cm for age 4. The distinct gap in the length-frequency

219 distributions of age 1 and 2 fish alllowed estimations of the mean lengths-at-age for these two age

220 classes to be very precise. Reliable estimates of modal lengths at age 3 were also obtained for the April

221 and October surveys conducted in SLE. However, modal lengths at age 3 were less reliable—especially

222 in the August surveys—in NEA and LC due to the low numbers of fish with lengths greater than 30

223 cm. Modal lengths for age 4 were not considered in the analysis. Thus, 1- and 2-year-old fish were

224 considered for the analysis of juvenile growth in relation to bottom temperature, dissolved oxygen

225 levels, and juvenile fish density. Nevertheless, we tracked the different cohorts from ages 1 to 3 in the

226 April and October surveys to estimate the seasonal growth of juveniles.

227 *3.3. Mean length and growth of 1- and 2-year-old juveniles*

228   Mean lengths at age 1 and 2 varied significantly among the years ($F_{22,\ 44}$ = 7.87, P < 0.001 and

229 $F_{22,\ 36}$ = 2.46, P = 0.008 for ages 1 and 2, respectively) in the summer surveys (Fig. 4). Mean length at

230 age 1 was the same among areas ($F_{2,64}$ = 0.55, P = 0.22) while significant differences ($F_{2,\ 56}$ = 3.25,

231 P < 0.046) in mean length at age 2 were present among the different areas. However, a posteriori

232 pairwise comparisons failed to detect such differences (Table 2). Length increments between ages 1

233 and 2 in successive surveys (i.e., the same cohort) differed among areas ($F_{2,\ 54}$ = 13.16, P < 0.001) but

234   not among years ($F_{21,\,35}$ = 1.09, P = 0.399). The average length increment was higher in NEA than in

235   SLE or LC (Table 2).

236   GAM did not show any significant effects of depth, temperature, dissolved oxygen, or fish density on

237   the length of one-year-old juveniles (1990-2012 depth, temperature, and fish density: Deviance

238   explained =   27.5%, GCV score = 0.65274, Scale est. = 0.56835,   n = 67; 2004-2012, dissolved

239   oxygen: Deviance explained = 13.6%, GCV score = 0.38459, Scale est. = 0.3561, n = 27). Depth (p <

240   0.001) and juvenile fish density (p < 0.029) significantly affected the length increment of fish of the

241   same cohort between ages 1 and 2 in August for successive years (Fig. 5): 49.2% of the variability in

242   length increment between 1990 and 2012 was explained by these two covariates (Deviance explained =

243   49.2%, GCV score = 0.58378, Scale est. = 0.51859, n = 57). When restricted to the 2004–2012 period,

244   where dissolved oxygen concentration values were available, GAM indicated significant effects of

245   dissolved oxygen (p < 0.001) and temperature (p < 0.021) (Deviance explained = 96.3%, GCV score =

246   0.23547, Scale est. = 0.084743, n = 24) on length increment between ages 1 and 2 (Fig. 6).

247   Temperature and dissolved oxygen explained 96.3% of the total variance.

248   *3.4. Seasonal growth rate*

249   No variation in the seasonal growth of juvenile Greenland Halibut in the St. Lawrence estuary

250   was observed for the 2006–2010 period. Changes in mean length through time for Greenland Halibut

251   cohorts hatched between 2004 and 2008 were continuous and linear (Fig. 7). Mean length increments

252   per day observed for 1- and 2-year-old juveniles of the different cohorts were not significantly different

253   between summer (April–October) and winter (October–April) (0.027 ± 0.002 vs. 0.028 ± 0.002, p =

254   0.86, and 0.016 ± 0.002 vs. 0.022 ± 0.006, p = 0.18, for 1- and 2-year-old juveniles respectively).

255

4. Discussion

Our results suggest a significant negative effect of DO on growth of Greenland Halibut juveniles in the EGSL. However, such negative impacts are likely limited and/or largely compensated by the other physical (e.g., temperature) or biological (e.g., food abundance and availability) characteristics of the EGSL. Our results also indicate that the sizes-at-age estimated for EGSL Greenland Halibut juveniles are higher than those observed in other populations of Greenland Halibut (Table 3).

Both mean length-at-age of 2-year-old juveniles and length increments between ages 1 and 2 differed among the three EGSL areas, which were characterized by differences in oxygen, temperature, depth, and fish density conditions. However, no difference was observed for 1-year-old juveniles. It should be emphasized that the mean size at age 1 represents growth from hatching in winter to August of the following year (i.e., 18 to 20 months later). During their first 5 to 7 months of life, prior to settlement, larvae and post-larvae are pelagic and transported by water currents. At settlement (August), larvae have already reached 5 to 8 cm (Ouellet et al., 2011). However, because there is no data on average size at settlement in the three studied areas, and because of the possible integration of growth effects from environmental conditions occurring before metamorphosis, the mean length for 1-year-old fish obtained in our study may not be representative of growth effects related to post-settlement environmental conditions.

The highest length increments between ages 1 and 2 were found in the lower depths of NEA. NEA oxygen, temperature, and fish density conditions are different from the other two areas, but their effects on growth are difficult to assess. Indeed, the NEA's highest growth was achieved at lower temperatures than those in LC, and DO and juvenile density in NEA were intermediate to those found in SLE and LC.

278   GAM analysis for the 1990–2012 period indicates that change in length increment from 1 to 2

279   years old is associated with juvenile density and depth, with these two factors explaining 49.2% of the

280   variability. Juvenile density was higher in hypoxic and cold areas (SLE), and the lowest densities were

281   found in LC. Fish density has been considered to be an important factor in determining growth rate,

282   with intra-specific competition for food access affecting feeding success (Sinclair et al., 2002; Raätz

283   and Lloret, 2005; Swain et al., 2007). Lower food availability may exacerbate density-dependent

284   competition for food and even increase the incidence of cannibalism. Theoretically, growth rate should

285   decrease with increasing density (Hempel, 1957), and the results for length increment between ages 1

286   and 2 support this hypothesis. It should also be noted that several studies have found a positive

287   relationship between growth and survival of juvenile marine fish (Anderson, 1988; Houde, 1997;

288   Sogard, 1997).

289   GAM analysis also indicates that a very large proportion of the growth variability was associated

290   with DO during the 2004–2012 period, which was characterized by high juvenile density. However, it

291   should be noted that temperature also had a significant effect, even though it explained a lower portion

292   of this variability. DO estimates varied significantly among the three areas: DO levels in SLE were

293   almost half the average concentration measured in LC with intermediate levels in NEA. Length

294   increments from ages 1 to 2 varied inversely with DO level and were significantly lower at DO

295   concentrations below 80 μmol/L. Fish need oxygen to generate energy for body maintenance,

296   locomotion, and biosynthetic processes (Van Dam and Pauly, 1995). Low oxygen levels (hypoxia) can

297   affect growth and reproduction, and therefore the survival of aquatic species, by acting directly on their

298   physiology and metabolism (Fry, 1971; Brett, 1979). Two hypotheses have been proposed to explain

299   the decrease in growth when fishes are exposed to long-term hypoxia: (1) an increase in the energetic

300   cost of ventilation, which decreases the amount of energy available for growth (Kramer, 1987); and (2)

301   a decrease in food intake, which allows fish to save energy (Brett, 1979; Kramer, 1987; Jobling, 1993).

302 Dupont-Prinet et al. (2013) studied the effects of hypoxia on oxygen consumption in Greenland

303 Halibut. They found that the critical oxygen threshold for juveniles was 15% saturation, and that severe

304 hypoxia (19% saturation) reduced the aerobic scope by 72% compared to normoxia and increased the

305 duration of digestive processes. However, this tolerance threshold remains lower than the average

306 oxygen conditions found in our three areas.

307   Our results did not show a direct effect of temperature on length increment between ages 1 and 2

308 for the 1990–2012 period. Temperature is considered as a major or even decisive environmental factor

309 influencing growth since it governs the rate of metabolic reactions affecting all physiological processes

310 in ectotherms: metabolism, food intake, and nutritional efficiency (Burel et al., 1996; Imsland et al.,

311 2001). Changes in temperature could have a marked effect on feeding rate and growth efficiency, and

312 consequently on growth rate. A previous study on juvenile Greenland Halibut from Disko Bay (west

313 coast of Greenland) showed that temperature had a major impact on growth (Sünksen et al., 2010).

314 These authors found that, at depths ranging between 201 and 400 m, the mean total length of 1-year-old

315 Greenland Halibut increased from about 13 cm to 15 cm when the temperature rose from 1.5°C to 3°C

316 and that length increment by year 2 increased from 7.5 to 9.5 cm when temperature rose by 2.5–3.0°C.

317 Based on these results, the authors calculated that total length increased by 1.5 cm/°C. The EGSL

318 population of Greenland Halibut is at the southern limit of the geographical range for this species, and

319 temperature is high compared to the whole distribution range. A higher growth rate for 1-year-old

320 Greenland Halibut in the Gulf of St. Lawrence compared with that measured in other Canadian Atlantic

321 waters has been ascribed to generally higher temperatures in this region (Bowering, 1983). Even

322 though 1.5°C differences are also present among the three studied areas in the EGSL, we did not

323 observe a significant—or even a slight—effect of temperature on growth (1990–2012 period). This

324 could be due to the fact that the optimal temperature for juvenile Greenland Halibut growth may have

325 been reached. Clearly the effect of temperature on juvenile growth in the EGSL needs further

326 investigation. In addition, the abundance of food could be a factor that needs to be considered, although

327 the juvenile diet may include different prey types. In a survey covering NAFO division 4RS (Northern

328 Gulf of St. Lawrence), Savenkoff et al. (2009) reported that the most important prey items for small

329 Greenland Halibut were shrimp, large zooplankton, and capelin (96.8% of the diet). In juveniles that

330 we captured in the St. Lawrence estuary in 2009, the most important prey items found in stomachs

331 were crustaceans (26%), euphausiids (15.6 %), capelin (11.7%), and shrimp (6.9%) (n = 212; Ait

332 Youcef, unpublished data). It should also be emphasized that the mean lengths at ages 1 and 2 and

333 length increments estimated in our study were higher than those estimated in other populations of

334 Greenland Halibut (Table 4). Length increments between ages 1 and 2 ranged from 8 to 12 cm for

335 temperatures between 3.7°C and 5.5°C in the present study; these values fit well within projections

336 made by Sünksen et al. (2010) (i.e., an increase of 1.5 cm/°C) for inter-population comparisons.

337 Despite significant DO effects on growth, our results comparing growth from the EGSL

338 population to data reported for other populations led us to conclude that a negative impact of low DO is

339 not pronounced enough to result in a displacement of juvenile fish to areas with higher DO.

340 Furthermore, the highest juvenile fish density is in SLE (Ait Youcef et al., 2013), where average

341 temperature and DO are the lowest. Again, temperature, food abundance, or food availability may

342 largely compensate for DO effects on growth.

343 Our results indicate continuous growth in juveniles throughout the year (data from 2006 to 2010).

344 The presence of upwellings, which enhance productivity and promote biomass accumulation, is well

345 known in the St. Lawrence ecosystem (Lavoie et al., 2007; Lesage et al., 2007; Ouellet, 2007; Plourde

346 and McQuinn, 2010). Juveniles were mostly found at depths where the annual bottom temperature is

347 stable and food access is constant. Seasonal growth variations are not a rare event in juvenile marine

348 fishes, but only a few studies have examined winter growth in the field. For example, in Atlantic cod,

349 seasonal patterns in growth and condition resulting from cycles of energy accumulation and depletion

350   have been described (Eliassen and Vahl, 1982a; 1982b; Holdway and Beamish, 1984; Lambert and

351   Dutil, 1997a; Schwalme and Chouinard, 1999); these fluctuations result from feeding opportunities,

352   gonad maturation, reproduction, migration, or overwintering. A continuous seasonal growth rate allows

353   faster growth of young fish; this not only reduces their vulnerability to size-selective predation but also

354   enables juveniles to exploit a wider range of prey items (Gibson, 1994; Van der Veer et al., 1994).

355   Continuous growth during the juvenile stage may enhance recruitment and reduce recruitment

356   variability. Indeed, it has been shown that variability in the growth of juvenile flatfish can have an

357   impact on recruitment, either by affecting survival in the case of size-selective mortality or by affecting

358   duration of the juvenile stage (Anderson, 1988; Gibson, 1994; Van der Veer et al., 1994; Iles and

359   Beverton, 2000; Juanes, 2007; Stenberg, 2007). Both processes—size-selective mortality and size-

360   dependent onset of maturation—have been found in field studies on flatfish (Van der Veer et al., 1994).

361

5. Conclusion

Juvenile growth of Greenland Halibut in the EGSL decreases with juvenile density. Under current conditions, oxygen is positively related to growth. Negative effects related to dissolved oxygen were observed below the threshold of 80 μmol/L. The Greenland Halibut population in the EGSL is at the southern limit of the species' distribution range and is characterized by high temperatures (~ 5℃) and abundant food. This probably allows fish to have optimal growth: the mean sizes at age and length increments between ages 1 and 2 estimated during our study were larger than those observed in other populations of Greenland Halibut. This suggests that the negative effects of DO could be limited and/or compensated by food access, as demonstrated by the continuous growth of juveniles over the year. Future climate change may directly impact water temperature as well as the frequency and duration of hypoxia events (Pörtner and Knust, 2007). From the 1930s to the 1980s, the bottom waters of the St. Lawrence estuary warmed by ~ 2°C (Gilbert et al., 2005). Cheung et al. (2013) demonstrated that the effects of warming on metabolic rate extend to marine fishes. They suggested that—given their physiological responses to warming and changes in oxygen level—oxygen-limited growth in aquatic animals and species distribution shifts will translate into a reduction in individual body size. The negative effects of dissolved oxygen could then be enhanced, which could directly influence Greenland Halibut recruitment in the EGSL.

386 **References**

387 Ait Youcef, W., Lambert, Y., Audet, C., 2013. Spatial distribution of Greenland halibut
388 *Reinhardtius hippoglossoides* in relation to abundance and hypoxia in the Estuary and Gulf of St.
389 Lawrence. Fish. Oceanogr. 22, 41-60.

390 Anderson, J.T., 1988. A review of size dependent survival during pre-recruit stages of fishes in
391 relation to recruitment. J. Northwest. Atl. Fish. Sci. 8, 55-66.

392 Albert, O.T., 2003. Migration from nursery to spawning area in relation to growth and maturation of
393 Greenland halibut (*Reinhardtius hippoglossoides*) in the Northeast Arctic. J. Northwest. Atl. Fish.
394 Sci. 31, 113-125.

395 Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., 2003. Plankton effect on cod
396 recruitment in the North Sea. Nature 426, 661-664.

397 Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A. Edwards, M., 2002. Reorganisation of North
398 Atlantic marine copepod biodiversity and climate. Science. 296, 1692-1694.

399 Bowering, W.R., 1983. Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius*
400 *hippoglossoides* (Walbaum), in the Canadian Northwest Atlantic. Fish. Bull. 81, 599-611.

401 Bowering, W.R., Nedreaas, K.H., 2001. Age validation and growth of Greenland halibut
402 (*Reinhardtius hippoglossoides* (Walbaum)): A comparison of populations in the northwest and
403 northeast Atlantic. Sarsia. 86, 53-68.

404 Brett, J.R., 1979. Environmental factors and growth. In Fish Physiology, Vol. 8 (Hoar, W. S., Randall,
405 D. J. Brett, J. R. (Eds). New York, pp. 599-675.

406 Brierley, A.S., Kingsford, M.J., 2009. Impacts of climate change on marine organisms and
407 ecosystems. Curr. Biol. 19, 602-614.

408 Burel, C., Person-Le Ruyet, J., Gaumet, F., Le Roux, A., Sévère, A., Boeuf, G., 1996. Effects of
409 temperature on growth and metabolism in juvenile turbot. J. Fish. Biol. 49, 678-692.

410 Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., Pauly, D.,

411   2010. Large-scale redistribution of maximum catch potential in the global ocean under climate

412   change. Glob. Change Biol. 16, 24-35.

413 Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares, M. L.,

414   Watson, R., Pauly, D., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on

415   marine ecosystems. Nat. Clim. Change. 3, 254-258.

416 Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic

417   ecosystems. Proc. Natl. Acad. Sci. 106, 12788-12793.

418 DFO, 2011. Assessment of the Greenland halibut stock in the Gulf of St. Lawrence (4RST) in 2010.

419   DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2011/013. 13 p.

420 Du, J., 2002. Combined algorithms for fitting finite mixture distributions. Master's thesis, McMaster

421   University, Hamilton, Ontario. 124 p.

422 Dupont-Prinet, A., Vagner, M., Chabot, D., Audet, C., 2013. Impact of hypoxia on the metabolism

423   of Greenland halibut (*Reinhardtius hippoglossoides*). Can. J. Fish. Aquat. Sci.70, 461-469.

424 Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and

425   trophic mismatch. Nature. 430, 881-884.

426 Eliassen, J.-E., Vahl, O., 1982a. Seasonal variations in biochemical composition and energy content

427   of liver, gonad and muscle of mature and immature cod, *Gadus morhua* (L.) from Balsfjorden,

428   northern Norway. J. Fish. Biol. 20, 707-716.

429 Eliassen, J.-E., Vahl, O., 1982a b. Seasonal variations in the gonad size and the protein and water

430   content of cod, *Gadus morhua* (L.), muscle from Northern Norway. J. Fish. Biol. 20, 527-533.

431 Everitt, B.S., Hand, D.J., 1981. Finite mixture distributions. Chapman and Hall, London, 143 p.

432 Fry, F.E.J., 1971. The effect of environmental factors on the physiology of fish. In: Hoar, W.S.,

433   Randall, D.J. (Eds.), Environmental Relations and Behavior (VI), New York, pp. 1-98.

434 Gagnon, P. 1991. The effects of set to strata allocation adjustments. Can. Atl. Fish. Sci. Advis. Com.

435   Res. Doc. 1991/062. 8 p.

436 Genovesi, L., De Vernal, A., Thibodeau, B., Hillaire-Marcel, C., Mucci, A., Gilbert, D., 2011.

437   Recent changes in bottom water oxygenation and temperature in the Gulf of St. Lawrence:

438   Micropaleontological and geochemical evidence. Limnol. Oceanogr. 56, 1319-1329.

439 Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes.

440   Neth. J. Sea Res. 32, 191-206.

441 Gilbert, D., Chabot, D., Archambault, P., Rondeau, B., Hébert, S., 2007. Appauvrissement en

442   oxygène dans les eaux profondes du Saint-Laurent marin: causes possibles et impacts

443   écologiques. Nat. Can. 131, 67-75.

444 Gilbert, D., Sundby, B., Gobeil, C., Mucci, A., Tremblay, G.-H., 2005. A seventy-two year record of

445   diminishing deep-water oxygen in the St. Lawrence estuary: the northwest Atlantic connection.

446   Limnol. Oceanogr. 50, 1654-1666.

447 Hastie, T., Tibshirani, R., 1990. Generalized Additive Models. Chapman and Hall, London.

448 Haug, T., Gulliksen, B., 1982. Size, age, occurrence, growth, and food of Greenland halibut

449   *Reinhardtius hippoglossoides* (Walbaum) in coastal waters of western Spitzbergen. Sarsia. 68,

450   293-297.

451 Hempel G. A., 1957. Short note on the relationship between stock density and growth. Joint

452   ICES/ICNAF/FAO Scientific meeting. ICNAF Special Publications. 2, 35.

453 Hiddink, J.G., Hofstede, R., 2008. Climate induced increases in species richness of marine fishes.

454   Glob. Change Biol. 14, 453-460.

455 Holdway, D.A., Beamish. F.W.H., 1984. Specific growth rate and body composition of Atlantic cod

456   (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. 81, 147-170.

457 Houde, E.D., 1997. Patterns and consequences of selective processes in teleost early life histories.

458   In: Chambers, R.C., Trippel, E.A. (Eds.), Early life history and recruitment in fish populations.

459   Chapman and Hall, London, pp. 173-196.

460 Iles T.C., Beverton R.J., 2000. The concentration hypothesis: the statistical evidence. ICES J. Mar.

461   Sci. 57, 216-227.

462 Imsland, A.K., Foss, A., Gunnarsson, S., Berntssen, M.H., FitzGerald, R., Bonga, S. W., Ham, E.

463   V., Nævdal, G., Stefansson, S.O. 2001. The interaction of temperature and salinity on growth and

464   food conversion in juvenile turbot (*Scophthalmus maximus*). Aquaculture. 198, 353-367.

465 Irie, T., Fischer, K. 2009. Ectotherms with a calcareous exoskeleton follow the temperature-size rule

466   - evidence from field survey. Mar. Ecol. Prog. Ser. 385, 33-37.

467 Jobling, M., 1993. Bioenergetics: feed intake and energy partioning. In: J.C. Rankin and F.B.

468   Jensen. Fish ecophysiology. Chapman and Hall, London.

469 Juanes, F., 2007. Role of habitat in mediating mortality during the post-settlement transition phase

470   of temperate marine fishes. J. Fish Biol. 70, 661-677.

471 Kramer, D.L., 1987. Dissolved oxygen and fish behaviour. Env. Biol. Fish. 18, 81-92.

472 Lambert, Y., Dutil, J.-D., 1997a. Condition and energy reserves of Atlantic cod (*Gadus morhua*)

473   during the collapse of the northern Gulf of St. Lawrence stock. Can. J. Fish. Aquat. Sci. 54, 2388-

474   2400.

475 Lavoie, D., Starr, M., Zakardjian, B. Larouche, P., 2007. Identification of ecologically and

476   biologically significant areas (EBSA) in the Estuary and Gulf of St. Lawrence: primary

477   production. DFO Can. Sci. Advis. Sec. Res. Doc. 2007/079. 33 p.

478 Lesage, V., Gosselin, J.F., Lawson, J., Hammill, O., 2007. Ecologically and biologically significant

479   areas (EBSAs) in the Estuary and Gulf of St. Lawrence - a marine mammal perspective. DFO

480   Can. Sci. Advis. Sec. Res. Doc. 2007/046. 96 p.

481 Macdonald, P., Du, J., 2010. Mixdist: Finite Mixture Distribution Models. R package version 0.5-3.

482   Macdonald, P.D.M., 1987. Analysis of length-frequency distributions. *In*: Summerfelt, R.C., Hall,

483   G.E. (Eds.), Age and growth of fish. Iowa State University Press, Ames, pp. 371-384.

484   MPO, 2010. Évaluation du stock de flétan du Groenland du golfe du Saint-Laurent (4RST) en 2009.

485   Secr. can. de consult. sci. du MPO, Avis sci. 2010/028.

486   Ouellet, P., 2007. Contribution to the identification of ecologically and biologically significant areas

487   (EBSA) for the Estuary and the Gulf of St. Lawrence: the fish eggs and larvae and crustacean

488   decapods larvae layer. DFO Can. Sci. Advis. Secr. Res. Doc. 2007 ⁄ 011. 70 p.

489   Ouellet, P., Bui, A. O. V., Bernier, B., 2011. Greenland halibut (*Reinhardtius hippoglossoides*

490   Walbaum, 1792) early stage distribution in the Gulf of St. Lawrence. J. Northw, Atl. Fish. Sci.

491   43, 121-129.

492   Pauly, D., Kinne, O., 2010. Gasping fish and panting squids: oxygen, temperature and the growth of

493   water-breathing animals: *In*: Kinne, O. (Ed), Excellence in ecology. Book 22. International

494   Ecology Institute, Oldendorf/Luhe, pp. 216.

495   Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in

496   marine fishes. Science. 308, 1912-1915.

497   Plourde, S., McQuinn, I.A., 2010. Ecologically and biologically significant areas in the Gulf of St.

498   Lawrence: zooplankton and secondary production. DFO Can. Sci. Advis. Sec. Res. Doc. 2009 ⁄

499   104. 31 p.

500   Pörtner, H.O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating

501   climate-related stressor effects in marine ecosystems. J. Fish. Biol. 213, 881-893.

502   Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation

503   of thermal tolerance. Science. 315, 95-97.

504   Quinn, G. P., Keough, M. J., 2002. Experimental design and data analysis for biologists. Cambridge

505   University Press, Cambridge. 556 p.

506 R, 2010. A language and environment for statistical computing. R Foundation for Statistical
507 Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

508 Raätz, H. J., Lloret, J., 2005. Long-term variability of growth and recruitment of cod (*Gadus*
509 *morhua*) off Greenland. J. Mar. Sci. 62, 1310-1321.

510 Rao, C.R., 1965. Linear statistical inference and its applications. Wiley, New York.

511 Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast
512 Atlantic. Science. 305, 1609-1612.

513 Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations.
514 Bulletin 191 of the Fisheries Research Board of Canada. 400 p.

515 Rosa, R., Seibel, B.A., 2008. Synergistic effects of climate-related variables suggest future
516 physiological impairment in a top oceanic predator. Proc. Natl. Acad. Sci. 105, 20776-20780.

517 Savenkoff, C., Vaolois, S., Chabot, D., Hammill, M.O. 2009. Input data and parameter estimates for
518 ecosystem models of the Northern Gulf of St. Lawrence (2003-2005). Can. Tech. Rep. Fish.
519 Aquat. Sci. 2829, 117 pp.

520 Schwalme, K., Chouinard, G. A., 1999. Seasonal dynamics in feeding, organ weights, and
521 reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence.
522 ICES J. Mar. Sci. 56, 303–319.

523 Sheridan, J.A., Bickford, D., 2011. Shrinking body size as an ecological response to climate change.
524 Nat. Clim. Change. 1, 401-406.

525 Sinclair, A. F., Swain, D. P., Hanson, J.M., 2002. Disentangling the effects of size-selective
526 mortality, density, and temperature on length-at-age. Can. J. Fish. Aquat. Sci. 59, 372-382.

527 Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull.
528 Mar. Sci. 60, 1129-1157.

529   Stenberg, C., 2007. Recruitment processes in West Greenland waters: with special focus on

530   Greenland halibut (*Reinhardtius hippoglossoides*, W). Ph.D. thesis. Technical University of

531   Denmark. 44 p.

532   Sünksen, K., Stenberg, C., Grønkjær, P., 2010. Temperature effects on growth of juvenile Greenland

533   halibut (*Reinhardtius hippoglossoides* Walbaum) in West Greenland waters. J. Sea Res. 64, 125-

534   132.

535   Swain, D. P., Sinclair, A. F. Hanson, J. M., 2007. Evolutionary response to size-selective mortality

536   in an exploited fish population. Proc. R. Soc. B. 274, 1015-1022.

537   van Dam, A.A., Pauly, D., 1995. Simulation of the effects of oxygen on fish feeding and growth of

538   Nile tilapia *Oreochromis niloticus* (L.). Aquacult. Res. 26, 427-440.

539   Van der Veer, H.W., Berghahn, R. Rijnsdorp, A.D., 1994. Impact of juvenile growth on recruitment

540   in flatfish. Neth. J. Sea Res. 32, 153-173.

541   Vollen, T., Albert, O.H., Nilssen, E.M., 2004. Diet composition and feeding behaviour of juvenile

542   Greenland halibut (*Reinhardtius hippoglossoides*) in the Svalbard area. J. Sea Res. 51, 251-259.

543 **Figure captions**

544 Fig. 1: Bathymetry of the estuary and Gulf of St. Lawrence with delineations showing the different

545 areas discussed in this study: St. Lawrence estuary (SLE), Laurentian Channel (LC), and the area

546 northeast of Anticosti Island (NEA).

547

548 Fig. 2: Mean annual conditions experienced by juvenile Greenland Halibut in the St. Lawrence estuary

549 (SLE), Laurentian Channel (LC), and northeast of Anticosti Island (NEA) areas for the 1990–2012

550 period: depth (a), temperature (b), dissolved oxygen (c), and fish density (d).

551

552 Fig. 3: Examples of length-frequency analysis generated by fitting mixtures of distributions. Four

553 components corresponding to age groups are fitted to the length-frequency distributions of Greenland

554 Halibut in the St. Lawrence estuary in April (a) and August (b) 2010. Histograms represent observed

555 length frequencies, gray lines the components corresponding to age groups, and black lines the sum of

556 the different components. Triangles along the x-axis indicate mean lengths of the age groups.

557

558 Fig. 4: Mean lengths of age 1 (a) and age 2 (b) Greenland Halibut juveniles in the St. Lawrence estuary

559 (SLE), Laurentian Channel (LC), and northeast of Anticosti Island (NEA) areas in August for the

560 1990–2012 period.

561

562 Fig. 5: Results of GAM regressions for the effects of depth (a), temperature (b), and juvenile fish

563 density (c) on length increments between ages 1 and 2 for the 1990–2012 period. The gray areas

564 indicate 95% confidence intervals.

565

566   Fig. 6: Results of GAM regressions for the effects of dissolved oxygen (a) and temperature (b) on

567   length increments between ages 1 and 2 for the 2004–2012 period. The gray areas indicate 95%

568   confidence intervals.

569

570   Fig. 7: Changes in the mean length of Greenland Halibut from different cohorts hatched between

571   2004 and 2008 (C-2004 to C-2008) with standard deviation. Mean lengths for each cohort were

572   measured on fish caught in the St. Lawrence estuary in April and October from 2006 to 2010. O:

573   October; A: April.

574

Table 1
Mean annual depth (m), bottom temperature (°C), oxygen concentration (μmol/L), and Greenland Halibut juvenile density (mean number per tow) in zones of the St. Lawrence estuary (SLE), Laurentian Channel (LC), and northeast of Anticosti Island (NEA) areas where Greenland Halibut juveniles were present. Average values, standard errors (SE), minimum and maximum values, and number of observations (n) are presented.

		SLE	LC	NEA
Depth	Average	297.1	305.9	248.5
	SE	2.7	3.3	2.2
	Min–max	267.4–309.1	253.6–335.3	233.3–267.3
	n	182	355	159
Temperature	Average	4.95	5.14	4.98
	SE	0.028	0.024	0.060
	Min–max	3.65–5.21	3.97–5.47	3.94–5.51
	n	177	322	151
Oxygen	Average	73.3	112.0	99.0
	SE	1.3	1.9	2.2
	Min–max	66.7–77.4	99.0–127.2	89.6–124.1
	n	70	135	60
Fish density	Average	166.4	18.9	39.1
	SE	10.2	1.8	4.1
	Min–max	6.2–1011.24	0–229.1	0–296.1
	n	182	404	160

Table 2
Average length (cm) at ages 1 and 2 and average length increment (cm) between ages 1 and 2 in successive years for juvenile Greenland Halibut in the St. Lawrence estuary (SLE), Laurentian Channel (LC), and northeast of Anticosti Island (NEA) areas. Average values, standard deviations (SD), minimum and maximum values, and number of observations (n) are presented for each area. Different letters indicate statistically significant differences ($P < 0.05$) among areas.

		SLE	LC	NEA
Length at age 1	Average	17.2	16.9	16.8
	SD	0.7	0.9	0.9
	Min–max	15.8–18.5	15.6–18.3	15.6–18.7
	n	23	22	22
Length at age 2	Average	26.7	26.9	27.5
	SD	1.1	0.6	1.1
	Min–max	24.8–29.1	26.0–28.4	25.5–29.5
	n	23	16	20
Length increment between age 1 and 2	Average	9.4[a]	9.8[a]	10.6[b]
	SD	0.8	0.6	0.9
	Min–max	8.1–11.7	8.9–10.6	8.9–11.8
	n	22	15	20

Table 3
Mean total lengths (cm) of 1- and 2-year-old juveniles and length increment between ages 1 and 2 for different populations of Greenland Halibut from published studies.

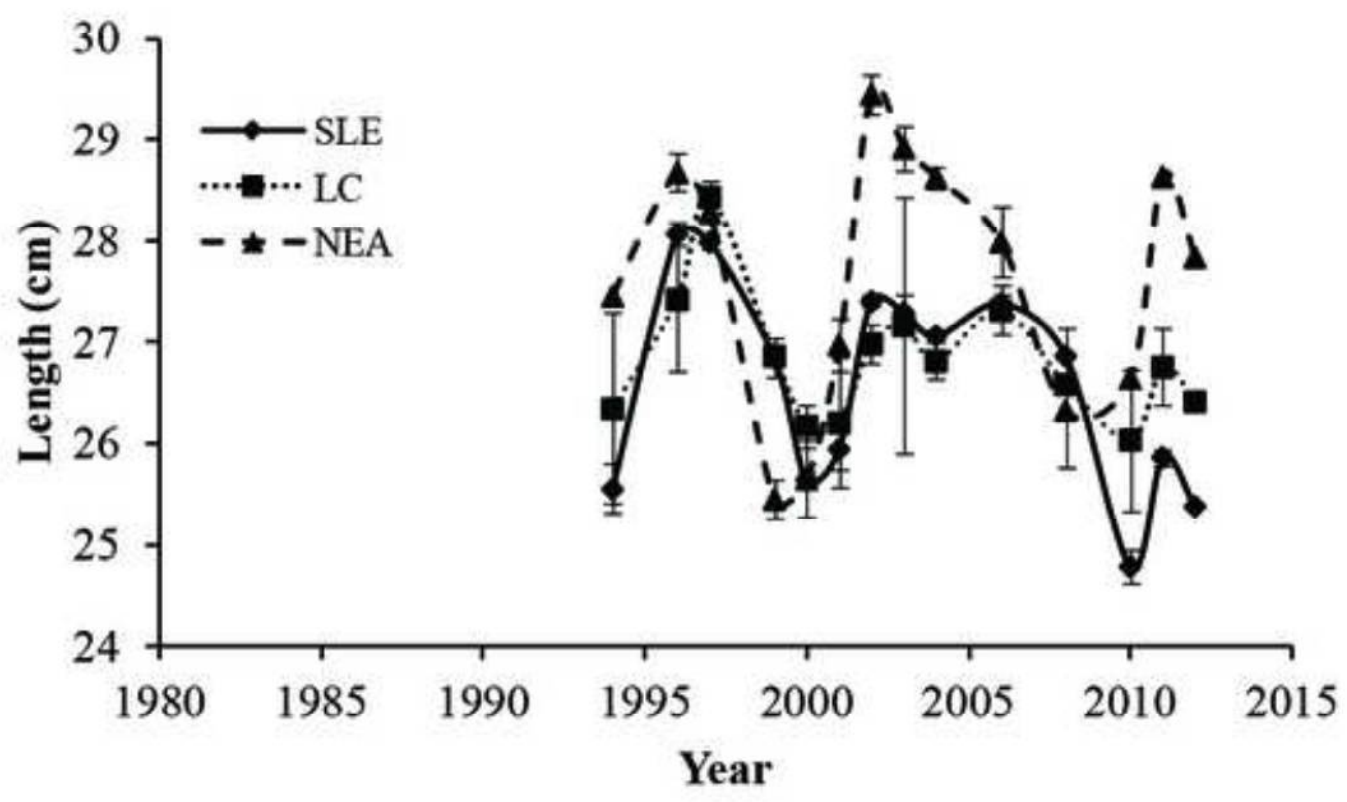| Zone, Time of year	Reference	Mean length (cm)		Length increment between age 1 and 2
		1 year old	2 years old	
Coastal waters of western Spitsbergen	Haug & Gulliksen, 1982	13.7		7.6
Southern Labrador July	Bowering & Nedreaas, 2001	10.5–12.5	16.5–18.5	6–8
Newfoundland Autumn	Bowering & Nedreaas, 2001	8.5–10.5	16.5–18.5	
Northeast Atlantic June–August	Bowering & Nedreaas, 2001	12–14	21	7–9
Northeast Arctic October–January	Albert, 2003	13–15	21–23	
Hinlopen (Svalbard archipelago) December–January)	Vollen et al., 2004	10	17	
Disko Bay July–September	Sünksen et al., 2010	13–15	20.5–25	
Estuary and Gulf of St. Lawrence August	present study	15.8–18.7	24.8–29.5	8–12
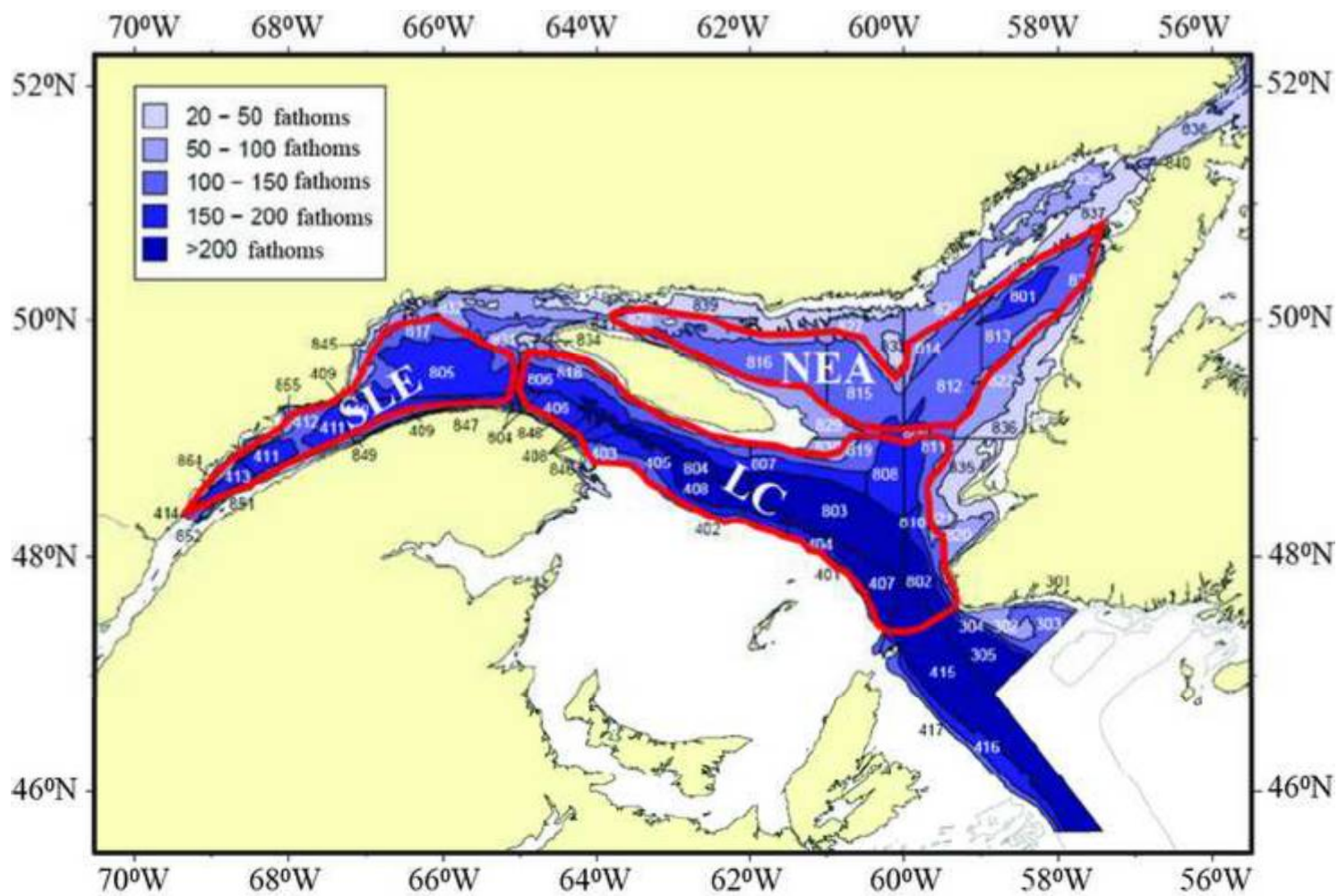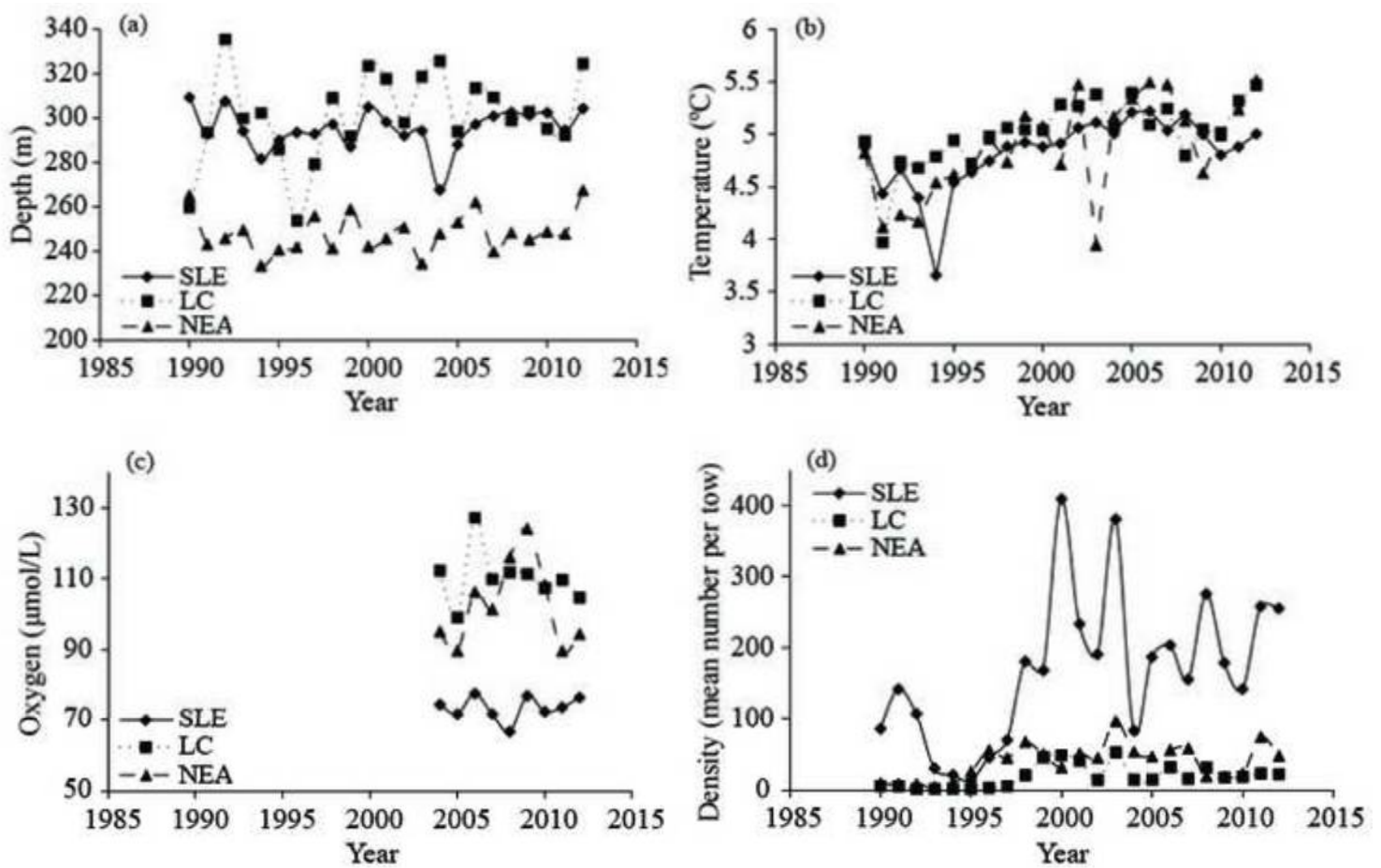
Figure 3
[Click here to download high resolution image](#)
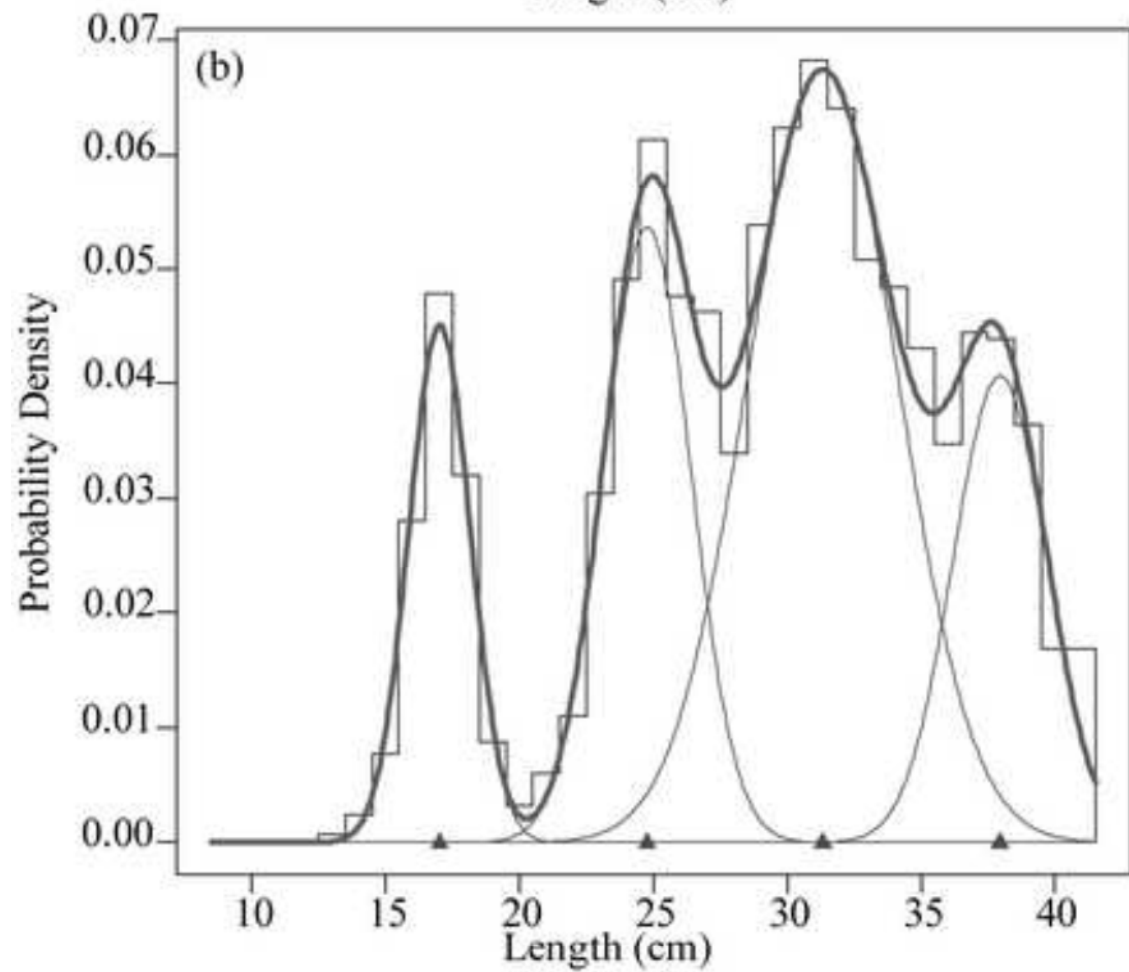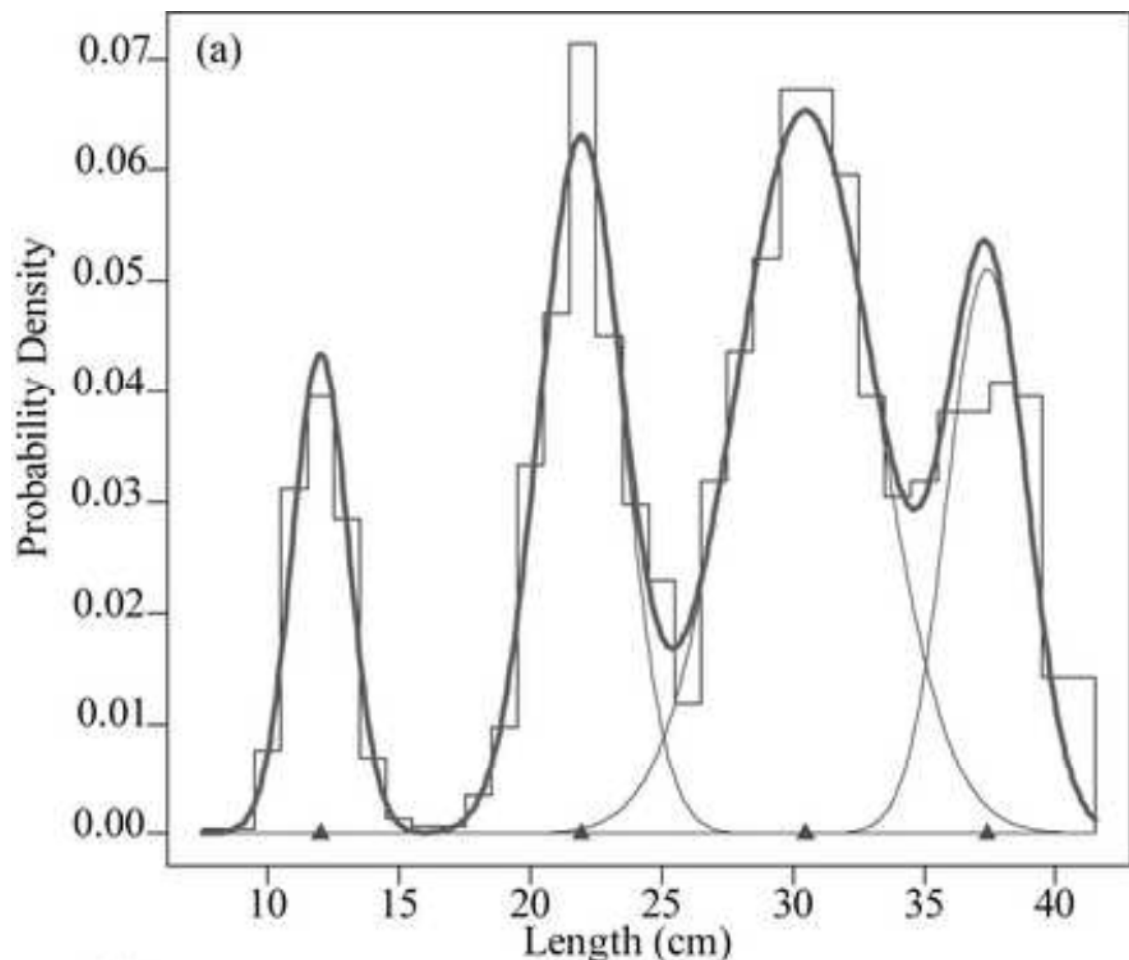
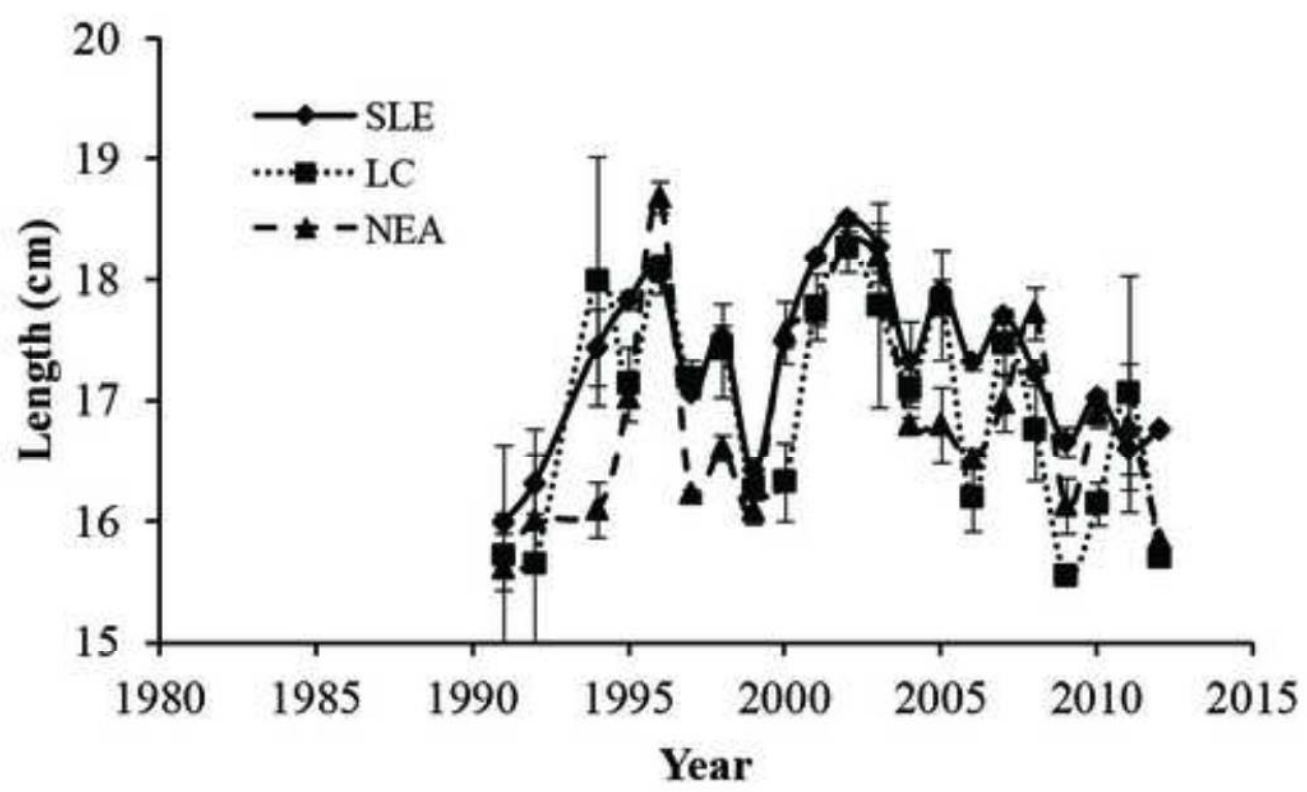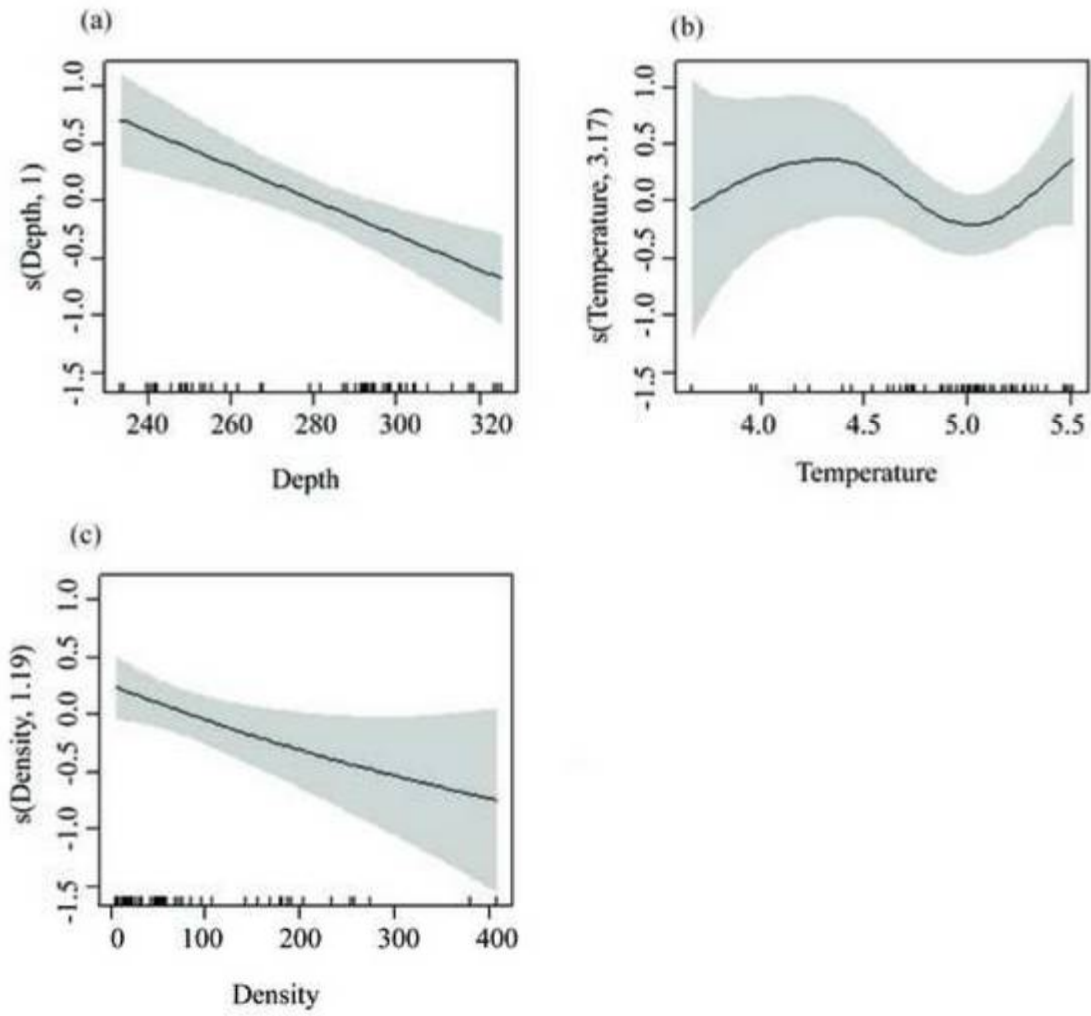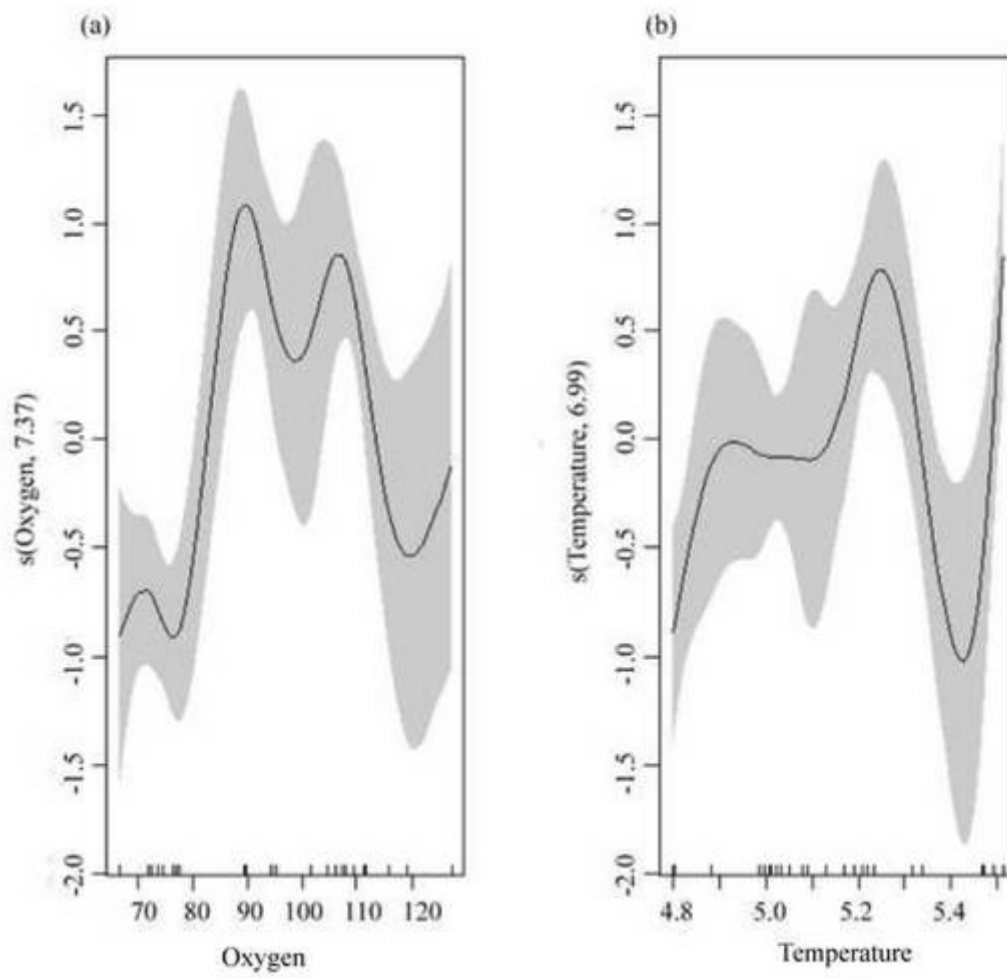**Figure 4**
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Figure 6

Figure 7