



Spatial distribution of Greenland halibut *Reinhardtius hippoglossoides* in relation to abundance and hypoxia in the Estuary and Gulf of St. Lawrence

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3 **1 Spatial distribution of Greenland halibut *Reinhardtius hippoglossoides* in**
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6 **2 relation to abundance and hypoxia in the Estuary and Gulf of St.**
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11 **ABSTRACT**

12 Annual bottom-trawl surveys (1990–2010) were used to examine associations between
13 environmental conditions, spatial distribution, and size-specific abundance of Greenland
14 halibut *Reinhardtius hippoglossoides* in the estuary and Gulf of St. Lawrence (EGSL), and
15 to test the influence of hypoxic conditions on habitat selection. Size classes representing
16 juvenile, immature and adult fish were used for the analyses. The highest concentrations of
17 fish were found in the St. Lawrence estuary at both high and low levels of stock abundance.
18 The areas occupied by 50%, 75%, and 95% of juvenile fish expanded with higher
19 population abundance. However, contrary to our predictions, densities in marginal habitats
20 did not increase at a higher rate than in optimal habitats. Fish longer than 32 cm were
21 distributed over a broader area than juvenile fish. Their abundance explained a limited
22 proportion of the variability in spatial distribution. The spatial dynamics of Greenland
23 halibut in the EGSL is best described by a proportional density model where the rate of
24 increase in local density is associated with population abundance. Habitats selected by
25 Greenland halibut were characterized by low dissolved oxygen (DO) levels. The strong
26 association between high fish densities and low DO concentrations indicates a high
27 tolerance of Greenland halibut to hypoxia. It also indicates that negative effects, if present,
28 could be compensated by other factors like food availability and/or refuge from predation.
29 The results of this study also clearly define the St. Lawrence estuary as the major nursery
30 area for the EGSL population.

31 **Key words:** hypoxia, density dependent, habitat selection, spatial distribution, Greenland

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For Peer Review

34 INTRODUCTION

35 Understanding patterns in the spatial distribution of marine fish populations in relation to
36 habitat availability is an important consideration in the management of exploited resources
37 (Kruse *et al.*, 2001). The distribution and abundance of marine species in relation to
38 environmental variables have been the subjects of many ecological studies; it has been
39 suggested that the relationship between geographic distribution and population abundance
40 is the result of density-dependent habitat selection (MacCall, 1990). Based on the ideal free
41 distribution (IFD) theory, if individuals have a perfect knowledge of their environment and
42 are free to move among available habitats, they will select habitats maximizing their fitness
43 (Fretwell and Lucas, 1970): during periods of low abundance, only the best habitats should
44 be occupied, while individuals would occupy less optimal habitats as abundance increases.
45 In conditions of high abundance, the best habitats based on abiotic factors would be less
46 attractive and profitable due to increased intraspecific competition for food and space.

47 Density-dependent spatial distributions have been described for a variety of pelagic
48 species such as California sardine *Sardinops sagax caerulea* (MacCall, 1976), northern
49 anchovy *Engraulis mordax* (Radovich, 1976), Peruvian anchovy *Engraulis ringens* (Csirke,
50 1980), Atlantic menhaden *Brevoortia tyrannus* (Schaaf, 1980), Atlantic herring *Clupea*
51 *harengus* (Winters and Wheeler, 1985), and longfin squid *Loligos pealei* (Lange, 1991).
52 For demersal species, evidence for density-dependent spatial distributions is less conclusive
53 (Craig *et al.*, 2005). Positive correlations between abundance and occupied area have been
54 reported for Atlantic cod *Gadus morhua* (Rose and Leggett, 1991; Swain and Wade, 1993;
55 Swain and Sinclair, 1994; Atkinson *et al.*, 1997), and haddock *Melanogrammus aeglefinus*
56 (Crecco and Overholtz, 1990; Marshall and Frank, 1995). However, other studies on

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3 57 various populations of silver hake, *Merluccius bilinearis*, haddock, *Melanogrammus*
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5 58 *aeglefinus*, pollock, *Pollachius virens*, red hake, *Urophycis chuss*, yellowtail flounder,
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8 59 *Limanda ferruginea*, winter flounder, *Pseudopleuronectes americanus*, American plaice
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10 60 *Hippoglossoides platessoides*, Atlantic cod and a Clupeoidea, *Sardinella* sp. did not
11
12 61 provide support for density-dependent habitat selection (Murawski and Finn, 1988, Swain
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14 62 and Morin, 1996, Schneider *et al.*, 1997, Petitgas, 1998).

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17 63 Habitat selection by marine fishes depends on a variety of biotic factors, such as
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19 64 prey and predator abundances, and on abiotic factors (Swain *et al.*, 1998, Swain and Benoît,
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21 65 2006). Depth, water temperature, salinity, and dissolved oxygen (DO) are among the
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23 66 common physical factors that have been related to the distribution of demersal fish
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25 67 (D'Amours, 1993, Castonguay *et al.*, 1999, Mueter and Norcross, 1999, Neuenfeldt and
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27 68 Beyer, 2003, Cote *et al.*, 2004, Craig *et al.*, 2005, Swain and Benoît, 2006).

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29
30 69 Greenland halibut (*Reinhardtius hippoglossoides*) is widely distributed in the
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32 70 estuary and Gulf of St. Lawrence (EGSL). It constitutes a significant component of the
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34 71 groundfish fishery resource in this region (Bowering, 1982), with a mean annual catch (~
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36 72 3500 t) representing about 52% of the total biomass of fish catches in recent years (2005 –
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38 73 2010). Greenland halibut is generally found in the channels of the EGSL at depths ranging
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40 74 between 130 and 500 m. These bottom waters are characterized by relatively stable water
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42 75 temperature (4 to 6°C) and salinity (~ 34) conditions and low concentrations of DO.
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44 76 Between 1930 and the mid-1980's, oxygen concentrations in the bottom waters of the lower
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46 77 St. Lawrence estuary decreased by 48%, i.e., from 125 $\mu\text{mol L}^{-1}$ (37.7% saturation) to an
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48 78 average of 65 $\mu\text{mol L}^{-1}$ (20.7% saturation) (Gilbert *et al.*, 2005). The current DO
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50 79 concentrations in the estuary are close to levels that have caused either significant
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3 80 mortalities or changes in migration patterns, trophic relationships, community structure,
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5 81 productivity, or biodiversity in other ecosystems (Diaz and Rosenberg, 1995; Wu, 2002).
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8 82 Despite the importance of this phenomenon in the St. Lawrence ecosystem, its effect has
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10 83 only been studied on one fish species, Atlantic cod, which was shown to be sensitive to
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12 84 hypoxia (D'Amours, 1993; Chabot, 2004). Greenland halibut appears to be more tolerant to
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14 85 hypoxia than cod given its presence and its high abundance in deep waters reported to have
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16 86 low DO levels. However, the impact of hypoxia on habitat selection by Greenland halibut
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18 87 has never been assessed. Furthermore, no detailed analysis of the distribution of this species
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20 88 in relation to fish density, development stage and/or environmental conditions has been
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22 89 conducted in our area of interest (i.e. the EGSL).
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27 90 The aims of the present study were 1) to describe associations among fish
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29 91 distribution, fish density, and physical characteristics considered to be important in the
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31 92 EGSL (spatial location, depth, temperature, and DO) in relation to fish size; 2) to assess
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33 93 the importance of DO in habitat selection by Greenland halibut; 3) to determine whether
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35 94 Greenland halibut distribution in this area follows ideal free distribution (IFD) theory.
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37 95 Generalized Additive Model (GAM) techniques were used to study the effects of
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39 96 environmental variables on fish distribution. To assess whether the IFD theory may apply
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41 97 to Greenland halibut distribution, we examined relationships between abundance and
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43 98 spatial distribution of both juvenile and adult fish in periods of low and high abundance.
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100 MATERIALS AND METHODS

101 *Data collection*

102 Data used in the present study were obtained from the summer multidisciplinary bottom-
103 trawl surveys conducted annually from 1990-2010 by Fisheries and Oceans, Canada (DFO)
104 and yearly sentinel fishery surveys conducted in collaboration with the industry from 1995
105 to 2010. These surveys use a stratified random sampling strategy with predetermined strata
106 based on geographic region and depth. The number of stations sampled per stratum is
107 proportional to the surface area, with a minimum of three stations per stratum for the
108 smaller strata (Bourdages *et al.*, 2008, 2010). Between 163 and 238 fishing stations were
109 sampled each year over 32 strata in the DFO survey. From 1990 to 2003, the DFO surveys
110 were conducted on board the RV “*Alfred Needler*” using a URI bottom trawl with a 19 mm
111 liner in the codend (24 min tows). Since 2004, surveys have been conducted on the RV
112 “*Teleost*”, which is equipped with a Campelen 1800 trawl with 13 mm liner (15 min tows).
113 The URI trawl data was converted to Campelen trawl data based on comparative fishing
114 experiments held in 2004 and 2005 (Bourdages *et al.*, 2007). Between 261 and 311 fishing
115 stations were sampled each year in the sentinel fishery survey. This survey, conducted by
116 nine otter trawlers does not cover the St. Lawrence estuary (i.e. 4 strata).

117 During the DFO surveys, conductivity, temperature, and depth (CTD) profiles were
118 obtained at each trawl station, allowing measurements of temperature, salinity, and water
119 density. Since 2004, CTD profilers have been equipped with Sea-Bird SBE43 oxygen
120 sensors to measure DO levels at each sampling station. An Aanderaa 3930 oxygen optode /
121 temperature sensor was also attached to the trawl from 2006 to 2010. Only temperature data
122 were collected for each trawl station in the sentinel fishery surveys.

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3 123 Greenland halibut caught in each tow were measured until a maximal sample of 175
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5 124 fish per tow was analyzed. Sex and sexual maturity of each fish were noted.
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8 125 *Analyses*
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10 126 To determine whether the distribution of Greenland halibut was heterogeneous according to
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12 127 fish size, we examined variations in abundance and spatial distribution and relationships
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14 128 with abiotic factors for juveniles and adults, males and females, grouped in different size
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16 129 classes. Four size classes were used for the analyses: 13–22 cm, 23–31 cm, 32–43 cm, and
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18 130 ≥ 44 cm. The first two size classes are largely represented by juvenile fish classified as one-
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20 131 and two-years-old, respectively, with no distinction between sexes, and are grouped as one
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22 132 size class, 15-31 cm, for the analyses. In the absence of age determination, peaks in size
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24 133 frequency distributions and distinct hiatus in the frequencies were used to determine the
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26 134 size ranges and to classify fish as age 1 or 2 (Morin and Bernier 2003, DFO, 2011). The
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28 135 32–43 cm size class was largely represented by mature males while most females in the
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30 136 same size class were immature. The largest size class included a high proportion of mature
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32 137 females; few males reached lengths ≥ 44 cm (DFO, 2006, 2010, 2011).
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39 138 *Abundance*
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41 139 Stratified mean catch per standard tow \bar{Y}_t in both surveys was used as an index of
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43 140 Greenland halibut abundance (Smith, 1990):
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$$\bar{Y}_t = \sum_{h=1}^K \frac{A_h}{A_T} \bar{y}_{ht} \quad (1)$$

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52 142 where A_h is the area of stratum h , A_T is the total area surveyed, K is the number of strata,
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54 143 and \bar{y}_{ht} is the mean catch rate of Greenland halibut of a particular size class in stratum h
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3 144 and year t . The spatial distribution of Greenland halibut abundance was mapped using the
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5 145 ACON data visualization software (<http://www.mar.dfo-mpo.gc.ca/science/acon>; last
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7 146 accessed 13 November 2007). Interpolation between data points to draw contours was done
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9 147 using Delaunay triangles. The logarithm of catch numbers per standard tow from the DFO
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11 148 surveys were used to represent changes in spatial distribution for each size class. Spatial
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13 149 distribution was mapped for periods of low and high abundance of Greenland halibut that
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15 150 were determined using blocks of successive years represented by distinct levels of
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17 151 population abundance.
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22 *Geographic range*

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24 153 Density-dependent spatial distributions of Greenland halibut were examined using methods
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26 154 presented in Swain and Sinclair (1994), Marshall and Frank (1995), Swain and Morin
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28 155 (1996), and Craig et al. (2005).
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31 156 The geographic range was estimated as the minimum area over which a specified
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33 157 percentage of Greenland halibut was distributed. The minimum area over which 95% of
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35 158 Greenland halibut were distributed was used as the measure of geographic range and an
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37 159 index of distribution, which was calculated for the four size classes. This index depends
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39 160 only on spatial spread, which is independent of the estimate of abundance (Swain and
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41 161 Sinclair, 1994). Cumulative distribution functions weighted by catch $F(c)$ of Greenland
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43 162 halibut were calculated as:
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$$48 \quad F(c) = 100 \frac{\sum_{h=1}^K \sum_{i=1}^{n_h} \frac{A_h}{A_T} X_{hi} I}{\sum_{h=1}^K \sum_{i=1}^{n_h} \frac{A_h}{A_T} X_{hi}} \quad \text{Where } I = \begin{cases} 1 & \text{if } X_{hi} \leq c \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

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3 164 where n_h is the number of trawl tows in stratum h , X_{hi} is the number of Greenland halibut
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5 165 caught in tow i in stratum h , and c is a level of Greenland halibut density (i.e., number per
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7 166 standard tow); the other symbols are as described for equation (1). $F(c)$ provides an
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9 167 estimate of the percentage of Greenland halibut (for a given sex and size class in a given
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11 168 year) occurring at a local density of c or less. The cumulative area $G(c)$ in relation to
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13 169 Greenland halibut catch was calculated as:

$$G(c) = 100 \sum_{h=1}^K \sum_{i=1}^{n_h} \frac{A_h}{A_T} I \quad \text{Where } I = \begin{cases} 1 & \text{if } X_{hi} \leq c \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

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171 F was evaluated at intervals of 0.1, and the density c_{05} corresponding to $F=5$ was
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173 calculated. $G(c_{05})$ is the estimated area containing the most sparsely distributed 5% of the
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175 catch (including areas where no fish were caught). Thus, the minimum area containing 95%
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177 of Greenland halibut (D_{95}) is given by:

$$D_{95} = A_T - G(c_{05}) \quad (4)$$

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176 The minimum areas over which 75% (area 75) and 50% (area 50) of Greenland halibut
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178 were spread were also estimated. Relationships between indices of distribution area of a
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180 size class and indices of abundance of that size class were examined in order to take into
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182 account the difference in spatial distribution between size groups. The distribution area of
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184 each size class was also examined in relation to the index of total population abundance.
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186 Mean distributional areas occupied by the different size classes of Greenland halibut for
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188 periods of low and high abundance levels were also compared. In the absence of
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190 homogeneity in variances, non-parametric Friedman test was used to compare occupied
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192 areas in relation to size class and abundance level (i.e. low and high).

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3 185 *Regional variation in distribution and rates of local density change*

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5 186 Relationship between local density and relative abundance was used to examine density-
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8 187 dependent spatial distributions at the regional scale (Marshall and Frank, 1995; Swain and
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10 188 Morin, 1996; Craig *et al.* 2005). According to Myers and Stokes (1989), the relationship
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12 189 between local density y_{hit} and total population abundance N_t is described by a power
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15 190 function:

$$16 \quad y_{hit} = \alpha_h N_t^{\beta_h} \quad (5)$$

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20 191 where y_{hit} represents Greenland halibut catch (for a particular size class) in tow i of stratum
21 192 h in year t and N_t is the measure of total population abundance in year t . β_h describes how
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23 193 regional catch rate varies with relative abundance. β_h was estimated using the following
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25 194 generalized linear model:
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$$28 \quad E[y_{hit}] = \mu_{ht} = \exp(a_h + \beta_h \ln N_t) \quad (6)$$

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33 196 where a_h is the log of α_h in the previous equation.
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36 198 In a density-dependent situation with the population expanding into marginal
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38 199 habitats as abundance increases, β_h is expected to be < 1 in optimal habitats and > 1 in
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40 200 marginal habitats (Marshall and Frank, 1995). Based on this assumption, a negative
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42 201 relationship should be observed between β_h for each stratum and some index of habitat
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44 202 quality. In the same way as was done by Swain and Morin (1995), mean catch rate per
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46 203 stratum for the years of lowest abundance was used as an index of habitat quality for each
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48 204 stratum to test this assumption.
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53 205 *Generalized additive models (GAM)*

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55 206 Generalized Additive Models (GAM) (Hastie and Tibshirani, 1990) were used to examine
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3 207 the influence of ambient environmental conditions (spatial location, depth, temperature, and
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5 208 DO) and annual population abundance on the number of fish caught per tow at the different
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8 209 stations in the EGSL. GAMs are non-parametric generalizations of multiple linear
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10 210 regressions that are not restricted to specific functional relationships (i.e., linearity) or
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12 211 underlying statistical distributions (i.e., normality) of the data (Hastie and Tibshirani, 1990,
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15 212 Swartzman *et al.*, 1992). Thus, GAMs can be advantageous for examining environmental
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17 213 and stock relationships that are unlikely to be monotonic, linear, or parametric (Maravelias
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19 214 and Reid, 1997). The dependent variable (i.e., number of fish per tow) was modeled as the
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21 215 additive sum of the predictor variables, whereby scatterplot smoothings replace the least-
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23 216 squares estimates used in multiple linear regressions (Hastie and Tibshirani, 1990). The
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25 217 general form of a GAM assumes that the mean response (μ) is related to the predictor
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27 218 variables (X_1, \dots, X_p) by the following relationship:

$$g(\mu) = \alpha + \sum_{j=1}^p f_j (X_j) \quad (7)$$

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220 where $g(\mu)$ = link function, defines the relationship between the response and the additive
221 predictor, α = intercept term, and f_j is the unspecified smoothing function. The observed
222 response is assumed to obey some type of underlying exponential statistical distribution
223 (e.g., Gaussian, Poisson, binomial, or Gamma distribution) with the specified mean, μ
224 (Hastie and Tibshirani, 1990). Appropriate link functions and error distributions were
225 chosen on the basis of residual plots (Hastie and Tibshirani, 1986; Swartzman *et al.*, 1992;
226 Borchers *et al.*, 1997). A GAM with a log-link function and Gaussian error distribution was
227 found to be adequate for the data modeled here. The GAM used cubic B-spline smoother

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3 228 for mean annual abundance, latitude, longitude, depth, temperature and oxygen to explain
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5 229 the variability in the number of fish catch per tow. GAMs explaining the largest total
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8 230 deviance were selected as final models.
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10 231 Separate GAMs for each size class were used to determine the importance of
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12 232 population abundance of each size class and environmental factors on the catches of that
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15 233 size-class. The first analyses applied over the entire time series (1990-2010) did not include
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17 234 DO as a dependent variable. Separate GAMs for the 2004-2010 period were used to
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20 235 determine the importance of DO on the Greenland halibut catches. In all models, a
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22 236 backfitting method was used to determine the relative contribution of the different
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25 237 variables. The relative contribution of the variables to the model was determined by the
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27 238 change in the total deviance explained by the full model and the model with the different
28
29 239 selected variables dropped.
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31 240 Finally, the spatial distribution of DO concentrations in the EGSL was examined
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34 241 using a GAM linking DO to longitude, latitude, depth and temperature. Annual variations
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36 242 between 2004 and 2010 were also examined by including a year effect in the model. All
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38 243 statistical analyses were performed using the R version 2.12.0 software.
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3 245 **RESULTS**
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5 246 Between 1990 and 2010, there were periods of low and high abundance for both Greenland
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7 247 halibut juveniles and adults in the estuary and Gulf of St. Lawrence (Fig. 1). The variations
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9
10 248 in abundance for the different size classes were well correlated between both the DFO and
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12 249 sentinel fishery surveys (r^2 between 0.49 and 0.58). However, the analysis of the
13
14 250 relationships between spatial distribution and abundance indices was restricted to DFO
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16
17 251 surveys, the time series for these surveys being more extended in terms of time and spatial
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19 252 coverage; the sentinel fishery did not cover 4 strata in the St. Lawrence estuary.
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22 253 Low juvenile (fish between 15 and 31 cm) abundance was observed up to 1997, but
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24 254 their abundance was high from 1998 to 2010 (Fig. 1a). The 32–43 cm size class was
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26 255 represented by mature males and immature females. To take into account this size-specific
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28 256 difference in maturity, abundance was first analyzed according to the sex of individuals.
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30 257 Based on the similar results obtained for both sexes male and female data were
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32 258 subsequently pooled for all analysis (Fig. 1b). Two distinct periods of abundance were
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34 259 observed for this size class: a low abundance period between 1990 and 1999 and a high
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36 260 abundance period between 2000 and 2010 with a maximum abundance level reached in
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38 261 2003. The abundance of fish longer than 44 cm, largely represented by mature females
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40 262 (68% of females and 30% of males), was low between 1990 and 2002. From 2003 onward,
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42 263 the abundance remained at a high level (Fig. 1c).
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48 264 The mean catch rate of juveniles was 16 ± 8 fish per standard tow during the period
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50 265 of low abundance, whereas it was 53 ± 18 fish per standard tow in the period of high
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52 266 abundance. A five-fold increase in the mean catch rate for the 32–43 cm size class was
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55 267 observed between the period of low and high abundance; mean catch increasing from 8 ± 3
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3 268 to 41 ± 11 fish per standard tow. The abundance of larger Greenland halibut (≥ 44 cm)
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5 269 varied from 3 ± 1 to 8 ± 1 fish per standard tow during periods of low and high abundance,
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8 270 respectively.

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10 271 *Geographic distribution*

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12 272 During periods of low abundance, juvenile fish and fish in the 32–43 cm size class mainly
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14 273 occupied the eastern part of the estuary and north of Anticosti Island (Fig. 2a, c). The area
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17 274 occupied by these two size classes increased with higher catch rate; during periods of high
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20 275 abundance, they occupied the whole St. Lawrence Estuary and extended their distribution
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22 276 to beyond the estuary (Fig. 2). Juveniles were virtually absent in southeast part of the EGSL
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24 277 (i.e. $\sim 48^\circ\text{N}$ and -60°W) during periods of both low and high abundance. Fish longer than
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27 278 44 cm showed a more homogeneous distribution throughout the St. Lawrence system (Fig.
28
29 279 2) compared to the two other size classes.

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31 280 *Abundance in relation to distribution*

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34 281 Significant correlations were observed between the indices of distributional area (D_{95} , D_{75} ,
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36 282 and D_{50}) of a size class and the relative abundance of that size class ($Y_{s,t}$) (Table 1). Areas
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38 283 including 95% and 75% of Greenland halibut were significantly density-dependent and
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40 284 increased as abundance increased for juveniles and adult fish longer than 44 cm (Fig. 3).

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43 285 The relationship between the area including 50% of the fish and relative abundance
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45 286 was only significant for juveniles (Table 1). No relationship ($p > 0.05$) was found between
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48 287 distributional area (D_{95} , D_{75} and D_{50}) and relative abundance for Greenland halibut in the
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50 288 32–43 cm size range. Relationships between distributional area of the different size classes
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53 289 with the index of total population abundance (Y_t) are with a few exceptions similar to those
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55 290 obtained using size-specific abundance index ($Y_{s,t}$) (Table 1). Changes in the significance

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3 291 levels for D_{95} and D_{75} for the 32-43 cm size class and D_{75} for fish ≥ 44 cm nevertheless
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5 292 correspond to similar and low coefficients of determination.
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8 293 Distributional areas occupied by 95%, 75%, and 50 % of the juvenile fish were
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10 294 smaller than for fish longer than 32 cm (Table 2). Friedman non-parametric tests indicated
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12 295 significant effects of both size class ($p < 0.004$) and abundance level (i.e. low vs high)
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14 296 ($p < 0.02$) on distributional areas with no significant interaction between the two factors
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16 297 ($p > 0.13$). At low abundance, the areas occupied by juvenile fish (15- 31 cm) for all
17
18 298 percentages of fish represented 53% to 73% of the areas occupied by the two other size
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20 299 classes. At high abundance, areas occupied by the juveniles represented 80% to 89% of the
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22 300 areas occupied by fish longer than 32 cm.
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26 301 *Regional variation in distribution and rates of local density change*

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28 302 Significant changes in local density in relation to abundance were observed in most strata
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30 303 for the three size classes (i.e. slope β significantly different than 0). The regressions
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32 304 between rate of local density change (β) and the index of habitat quality (i.e. mean catch
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34 305 rate in a stratum during low abundance) were not significantly ($p > 0.15$) different than 0 for
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36 306 each size class (Fig. 4). Thus, there was no evidence that the rate of increase in marginal
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38 307 habitat (i.e. low index of habitat quality) was higher than in optimal habitat when the
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40 308 abundance increased. Instead, a proportional increase in abundance is observed for the three
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42 309 size classes in both optimal and marginal habitats (Fig. 4).
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46 310 *Abundance in relation to abiotic factors*

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48 311 The following GAM formulation explained the largest deviance in the catches of Greenland
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50 312 halibut for the three different size classes during the 1990 to 2010 period:
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$$\text{Log}_e(Y_{s,t} + 1) = s(\bar{Y}_{s,t}) + s(\text{longitude} : \text{latitude}) + s(\text{depth}) + s(\text{temperature}) \quad (8)$$

For the 2004-2010 period that includes DO as an additional variable the model explaining the largest deviance was:

$$\text{Log}_e(Y_{s,t} + 1) = \bar{Y}_{s,t} + s(\text{longitude} : \text{latitude}) + s(\text{depth}) + s(\text{temperature}) + s(\text{oxygen}) \quad (9)$$

GAM regressions indicated significant non-linear relationships for the different covariates on the catches (i.e. number of fish per standard tow) of the three Greenland halibut size classes (Tables 3 and 4). Final models for the entire time period explained between 59% and 77% of the variations in the catches (Table 3). For the 2004-2010 period, the GAM including DO as an additional dependent variable explained 73% to 86% of the variations in the GH catches (Table 4).

The highest juvenile concentrations (i.e. 15-31 cm) in both low and high population abundance periods were observed towards the western part of the estuary and Gulf of St. Lawrence (west of 66°W) and in a smaller area north of Anticosti Island centered at ~ 49.5°N 62°W (Fig. 5). In both areas, largest concentrations were found at depths greater than 200 m and temperatures between 5 and 6°C. The number of fish per tow was also positively related to the mean annual abundance of the juveniles (Fig. 5). Concentrations of fish in the 32–43 cm size class followed a very similar pattern. The highest concentrations were observed in the same areas, depths and temperatures with number of fish per tow increasing with higher mean annual abundance of the 32-43 cm fish (Fig. 6). Larger Greenland halibut (≥ 44 cm) as well were found in higher concentrations in the same depth and temperature ranges but had a different spatial distribution (Fig. 7). High concentrations were centered in three distinct areas; the St. Lawrence estuary (~ 48.7°N 68°W), the

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3 335 Gaspésie peninsula (~ 49.5°N 65°W), and the northeast part of the Gulf (~ 50.2°N 58.5°W).

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5 336 The number of fish per tow was also positively related to the mean annual abundance of
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8 337 that size class of fish.

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10 338 For all size classes, the relative contribution of the mean annual abundance of the fish
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12 339 in explaining the variability in the catches was less important than spatial location and
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14 340 environmental factors (Table 5). The decrease in total deviance explained when mean
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16 341 annual abundance was dropped from the final models indicates a relative contribution
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18 342 between 7 and 9.2% of annual abundance indices in explaining variability in the catches.
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20 343 The spatial location had the highest relative contribution to the variations in the catches of
21
22 344 the juveniles and fish in the 32-43 cm fish, the total deviance explained by the models
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24 345 decreasing by 31 and 25%, respectively, when longitude and latitude were dropped from
25
26 346 the final models. The relative contribution of depth and temperature is lower than spatial
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28 347 location (14.3 and 17.6% change in deviance, respectively) but more important than the
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30 348 mean annual abundance of the fish (Table 5). In large fish (≥ 44 cm), spatial location and
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32 349 environmental factors (i.e. depth and temperature) had equal relative contributions to the
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34 350 variations in the catches.

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36 351 DO included as an additional environmental variable had a significant influence on
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38 352 the variations in the catches of all size classes for the period between 2004 and 2010 (Table
39
40 353 4). Fish of all sizes were largely found in waters characterized by low DO levels (< 130
41
42 354 $\mu\text{mol/L}$). Highest concentrations of fish were observed in waters with the lowest DO levels
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44 355 (Figs 8, 9 and 10). Sixty-seven percent of the sets in the survey with the highest catch rates
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46 356 were located in areas with DO levels lower than $70 \mu\text{mol/L}$.

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48 357 As observed in the first series of analysis, all covariates for the models covering the
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3 358 2004-2010 period had significant non-linear effects on the catches with very similar shape
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5 359 of the smooth functions (Figs 8, 9 and 10). The only exception was for larger fish where, in
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8 360 the final GAM, temperature had no significant effect on catches. Variations in the mean
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10 361 annual abundance of fish had a significant but minor relative contribution (% change in
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12 362 deviance between 0.3 and 0.6) to the variability in catches (Table 6). The relative
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14 363 contribution of individual covariates indicated a higher contribution of spatial location on
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16 364 the variability of juvenile catches (8.3% change in deviance) and significant but lower
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18 365 relative contribution of DO and depth (3.5 and 2.9 % change in deviance). For Greenland
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20 366 halibut of the two other size classes, spatial location and depth had comparable relative
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22 367 contributions in explaining the variability in the catches (Table 6). For all size classes, the
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24 368 combined contribution of all covariates is lower than the total deviance explained by the
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26 369 final models indicating some correlation between covariates. The increased relative
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28 370 contribution of spatial position and depth and temperature when these covariates are
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30 371 combined with DO indicate the strong association between DO and Greenland halibut
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32 372 catches (Table 6).

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38 373 Ninety-five percent of the variability in DO concentrations in the EGSL between
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40 374 2004 and 2010 is explained by a GAM including longitude, latitude, depth and temperature.
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42 375 Year effect although significant has a very minor relative contribution to the model (i.e.
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44 376 0.2% change in total deviance when dropped from the full model). Smooth functions for the
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46 377 covariates indicate that low DO concentrations are largely associated with depths between
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48 378 200 and 350 m and temperatures between 4 and 6°C (Fig. 11). Moreover, DO
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50 379 concentrations decrease in a westward direction with lowest values in the St. Lawrence
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52 380 estuary (68°W).

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3 382 **DISCUSSION**
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5 383 The spatial distribution of Greenland halibut in the estuary and the Gulf of St. Lawrence
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7 384 (EGSL) is dependent on fish size, population abundance, and physical characteristics of the
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10 385 environment. Variations in local fish density indicate that the major area of occupancy for
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12 386 juvenile fish (< 31 cm) is the western part of the EGSL ecosystem. The highest juvenile
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15 387 concentrations are found in the St. Lawrence estuary (west of longitude 67° W) regardless
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17 388 of stock abundance. The areas containing 50%, 75%, and 95% of juvenile fish are density-
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19 389 dependent, with the area of occupancy expanding as population abundance increases.
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21 390 Although significant, the stock abundance of juveniles explains a limited proportion (27 to
22
23 391 32%) of the variability in their spatial distribution. Abundance indices and spatial
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25 392 distributions that are calculated from the same survey data (i.e. DFO surveys) cannot be
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27 393 considered as independent. However, the good correspondence between abundance indices
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29 394 from DFO and sentinel fishery surveys indicates a low potential for spurious correlations
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31 395 from unmeasured factors related to or influencing the DFO surveys. Due to the shorter time
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33 396 series and lower spatial coverage of the sentinel fishery survey, it was thus considered
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35 397 acceptable and preferable to only use DFO survey data for the analysis.
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40 398 The area of occupancy for juveniles is smaller than for larger-sized groups (i.e., >
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42 399 32 cm). The area occupied by the different percentages of juvenile fish (i.e., D_{50} , D_{75} , and
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44 400 D_{95}) represented 54 to 73% of the area occupied by larger fish during periods of low stock
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46 401 abundance and between 81 and 88% for periods of higher stock abundance. Based on
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48 402 variations in local fish density and restricted areas of occupancy, the St. Lawrence estuary
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50 403 can be considered the primary nursery area for the EGSL Greenland halibut stock. The very
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52 404 low abundance of juvenile fish in summer and winter surveys conducted at the end of the
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3 405 1970s in the Gulf of St. Lawrence (eastern part) also supports this assumption (Bowering,
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5 406 1982). At the time of these surveys which did not cover the St. Lawrence estuary, it was
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7 407 even hypothesized that recruitment may come from outside the Gulf of St. Lawrence
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9 408 (Bowering, 1982). Size frequency distributions of juvenile Greenland halibut indicate that
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11 409 fish smaller than 31 cm consist of one- and two-year-old fish (Morin and Bernier 2003,
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13 410 DFO, 2011). Thus, juvenile Greenland halibut that settle in the St. Lawrence estuary appear
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15 411 to be sedentary for at least their first two years of life.
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20 412 GAM analyses indicate that the abundance of juvenile fish is associated with
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22 413 geographic location, environmental factors and mean annual abundance (i.e. population
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24 414 density). Longitude, latitude, depth, temperature and annual abundance explained 76.6% of
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26 415 the variability in juvenile catches (i.e. number of fish per standard tow) during the whole
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28 416 period (1990–2010). Spatial location (longitude and latitude) alone accounted for most of
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30 417 this variation. The relative contribution of environmental variables (i.e., depth and
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32 418 temperature) in explaining the variability in juvenile catches was lower than spatial location
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34 419 but more important than the variations in the mean annual abundance of the juveniles.
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36 420 During the period of high stock abundance (2004–2010), 82.9% of the variability in
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38 421 juvenile catches was explained by all the covariates studied with spatial location (longitude
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40 422 and latitude) explaining the largest variability when considering individual effects of each
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42 423 single covariate (8.3% change in total deviance compared to 0.6 to 3.5 % for other
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44 424 covariates). Cross correlations between DO, spatial location, temperature and depth result
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46 425 in a high association between catches and low DO concentrations. Combination of spatial
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48 426 location and DO explained 37.1% of the variability in the juvenile catches while
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50 427 combination of depth, temperature and DO explained 21.9% of the variability in the
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3 428 catches.
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5 429 When systematic measurements of dissolved oxygen were done (2004–2010), areas
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7 430 with the lowest DO concentrations (hypoxic areas) were located in the western part of the
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9 431 EGSL ecosystem (i.e., St. Lawrence estuary; 49°N and west of 64°W) at depths ranging
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11 432 between 200–300 m. At both low and high abundances, the highest juvenile concentrations
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13 433 were observed in areas characterized by these low DO levels. DO concentrations in the
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15 434 bottom waters of the lower St. Lawrence estuary were stable, with a mean value of 65 μmol
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17 435 L^{-1} from the mid-1980s to 2003 (Gilbert *et al.*, 2005). Measurements made in the same area
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19 436 between 2004 and 2010 in the present study indicate identical and stable concentrations
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21 437 (mean 64.5 $\mu\text{mol L}^{-1}$). Based on this information, we can conclude that the highest
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23 438 concentrations of juvenile fish during the period of low stock abundance were in the
24
25 439 hypoxic areas. Thus, during periods of both low and high abundance juvenile fish
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27 440 preferentially selected habitats characterized by the lowest dissolved oxygen levels. DO
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29 441 levels in these areas ($\sim 20\%$ saturation) are not severe enough to result in an active
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31 442 displacement of juvenile fish out of the St. Lawrence estuary.
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36 443 Under the theory of density-dependent habitat selection (Fretwell and Lucas, 1970;
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38 444 MacCall, 1990), spatial variations in local density reflect gradients in resource availability,
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40 445 with local density being highest where resources are abundant (optimal habitat) and lowest
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42 446 where resources are scarce (marginal habitat). At low abundance levels, individuals should
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44 447 occupy the optimal habitats; as abundance increases, density will increase in these preferred
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46 448 habitats and individuals will also begin to occupy marginal habitats. During the period
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48 449 covered by the present study, juvenile Greenland halibut appear to follow this expected
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50 450 pattern of expansion in habitat. Density-dependent habitat selection provides a possible
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3 451 explanation for the change in juvenile distributional area between periods of low and high
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5 452 abundance in the EGSL. However, correlations between abundance and occupied area do
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7
8 453 not necessarily demonstrate a causal relationship or prove the presence of density-
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10 454 dependent habitat selection (Shepherd and Litvak, 2004). Further work showing changes in
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12 455 fish condition and growth in optimal habitats, for instance, would be necessary to clearly
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14 456 demonstrate the presence of density-dependent habitat selection.

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17 457 Contrary to predictions in changes in local density in optimal versus marginal habitats
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19 458 (Marshall and Frank, 1995), the rate of increase in local density in the marginal habitats
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21 459 was not higher than in the optimal habitats. Based on this result and the fact that variations
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23 460 in the mean annual abundance of the juveniles (i.e. density) explains a limited proportion of
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25 461 the variability in the spatial distribution of the juveniles, the spatial dynamics are probably
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27 462 better defined by a proportional density model (Hilborn and Walters, 1992). In this model,
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29 463 the area occupied by the fish does not vary and an increase in population abundance is
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31 464 associated with an increase in fish density at all points, fish density remaining a constant
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33 465 proportion of population abundance. These results for juvenile Greenland halibut are
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35 466 similar to those reported by Swain and Morin (1996) for American plaice in the southern
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37 467 Gulf of St. Lawrence and for Atlantic cod in the northern Gulf of St. Lawrence (NAFO
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39 468 Division 4R) (Tamdrari *et al.*, 2010). No tendency was observed for percent changes in
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41 469 plaice or cod density to be greater in marginal habitats than in optimal habitat as population
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43 470 size changed.

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46 471 No apparent density-dependent effect on area of occupancy was observed for the 32–
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48 472 43 cm size class. For the largest size-class (≥ 44 cm), a significant density-dependent effect
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50 473 was observed for the areas containing 95% and 75% of the fish. However, the maximum
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3 474 area of occupancy was rapidly reached. At low population abundances, the areas containing
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5 475 95% and 75% of the fish were approximately 43000 and 24000 km², respectively. For
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8 476 higher population abundances, the mean areas of occupancy were more or less stable at ~
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10 477 53000 and 27000 km², respectively, even with a two to three-fold increase in population
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12 478 size. The area containing 50% of the fish did not change within the observed range in
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15 479 population abundance. These observations imply that the most suitable habitats occupied by
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17 480 larger Greenland halibut (i.e., > 32 cm) are not saturated and that local density may
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19 481 increase without leading to intra-specific competition. The absence of relationships between
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21 482 the rate of change in local fish density and the indices of habitat quality suggests that the
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23 483 spatial dynamics of larger Greenland halibut are similar to that observed for the juveniles.
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26 484 Local density increased with population abundance but fish density remained a constant
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28 485 proportion of population abundance.

31 486 The spatial distribution and local density of juvenile fish is different from that of
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33 487 larger Greenland halibut. Juveniles are highly concentrated in the St. Lawrence estuary
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35 488 (identified as the major nursery area) while adults are more widely distributed in the Gulf.
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37 489 Similar differences in spatial distribution have been observed in other Greenland halibut
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39 490 populations, with clear separations between juvenile and adult spatial distributions being
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41 491 noted in the Barents Sea and in west Greenland waters (Jørgensen, 1997a; Albert, 2003).

45 492 The highest concentrations of juvenile Greenland halibut observed in the hypoxic
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47 493 areas of the St. Lawrence ecosystem indicate that the current levels of dissolved oxygen (~
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49 494 20% saturation) are not at threshold levels that will influence the spatial distribution of this
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51 495 species. Moreover, the high index of recruitment observed in several years since 1990 (i.e.,
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53 496 1997, 1999, 2002, and 2004) also suggests that these hypoxic waters are not causing

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3 497 recruitment failures for Greenland halibut (DFO, 2011). The high catches of fish in waters
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5 498 with low DO concentrations may indicate an enhanced catchability of Greenland halibut
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8 499 due to impaired gear trawl avoidance. However, studies on Atlantic cod and Greenland
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10 500 halibut demonstrated that both species could hardly keep up with the towing speed of the
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12 501 trawls (100-180 cm/sec; 2.2-3.9 body length/sec) for a prolonged period of time, even in
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14 502 normoxia (Dutil *et al.*, 2007, Albert *et al.*, 2003). Trawl avoidance in Greenland halibut was
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16 503 related to detection time, take-off and direction of swimming (Albert *et al.* 2003). Given the
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18 504 limited capacity for sustained swimming (i.e. cruising speed related to aerobic metabolic
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20 505 processes), burst swimming, an anaerobic metabolic process independent of ambient DO,
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22 506 may be more important for escapement. It was also observed that escapement beneath the
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24 507 ground-gear which is independent of ambient DO, was higher in smaller fish. Acclimation
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26 508 to hypoxia may also increase subsequent hypoxia tolerance and swimming performance (Fu
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28 509 *et al.*, 2011). In goldfish (*Carratius auratus*) an increase of 18% in Ucrit (sustained
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30 510 swimming for 48h at 70% of critical swimming speed) was observed following acclimation
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32 511 to hypoxia (Fu *et al.*, 2011). Although increase catchability at low DO cannot be
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34 512 completely rejected we conclude that the low DO concentrations and the range in DO
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36 513 concentrations where Greenland halibut are mostly found (~ 20 to 60% saturation levels)
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38 514 do not result in different catchability between areas in the EGSL.
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46 515 Habitat selection by juvenile fish may result from the high tolerance of the fish to
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48 516 low DO levels and interactions between the effects of density-dependent resources (i.e.,
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50 517 spatial variation in food availability) and density-independent factors (i.e., depth,
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52 518 temperature). It has been shown that under laboratory conditions, juvenile Greenland
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54 519 halibut could tolerate DO levels as low as 14.89 ± 0.92 % saturation (Dupont-Prinet, pers.
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3 520 comm.). Small Greenland halibut are also known to feed mainly on shrimp *Pandalus*
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5 521 *borealis*, capelin *Mallotus villosus*, and large zooplankton species such as euphausiids,
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7 522 mysids and hyperiid amphipods in the EGSL (Fréchet, 1987; Savenkoff *et al.*, 2009). These
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9 523 species are all abundant in the St. Lawrence estuary (Plourde *et al.*, 2001; 2002; 2003;
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11 524 2010).

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14 525 Many studies have demonstrated that this area, characterized by up-welling, is very
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16 526 productive and favours biomass accumulation (Lavoie *et al.*, 2007; Lesage *et al.*, 2007;
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18 527 Ouellet, 2007; Plourde and McQuinn, 2010). However, hypoxic conditions may limit the
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20 528 growth of juvenile fish even if food resources are abundant. For example, the lower
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22 529 tolerance limit in oxygen concentration for Atlantic cod is $88 \mu\text{mol L}^{-1}$ (i.e. 28 %
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24 530 saturation) (Plante *et al.*, 1998) but oxygen saturation levels up to 70% can limit growth
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26 531 capacity by affecting the metabolic scope, which reduces food intake of fish (Chabot and
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28 532 Dutil, 1999). Further work on the growth of juvenile Greenland halibut is necessary to
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30 533 examine this possibility.

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33 534 Hypoxic areas in the EGSL could represent a refuge from predators for juvenile
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35 535 Greenland halibut. Based on diet composition, very low predation has been observed on
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37 536 juveniles (Savenkoff *et al.*, 2009). Cannibalism has been observed in other stocks
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39 537 (Rodriguez-Marin *et al.*, 1995; Jørgensen, 1997b; Woll and Gundersen, 2004; Dwyer *et al.*,
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41 538 2010). However, cannibalistic behaviour should be of minor importance for Greenland
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43 539 halibut in the EGSL based on spatial distribution and range in fish sizes. As mentioned, the
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45 540 different spatial distributions of juveniles and adults at higher abundance levels should limit
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47 541 interactions between fish of different sizes. Moreover, Greenland halibut caught in the
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49 542 EGSL rarely exceeds 56 cm in length (DFO, 2006) while cannibalism usually occurs in fish

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3 543 larger than 69 cm (Dwyer *et al.*, 2010). Based on the high tolerance level of sprat (*Sprattus*
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5 544 *sprattus*) to low oxygen saturation level (i.e. 7% O₂) it has been hypothesized that
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8 545 overwintering sprat could exploit hypoxic waters as a predator refuge (Kaartvedt *et al.*
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10 546 2009).

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12 547 The spatial distribution of juvenile Greenland halibut would indicate that the current
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15 548 DO levels in the St. Lawrence estuary have no direct effect on fish distribution and that
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17 549 possible negative effects associated with these hypoxic areas (i.e., survival and growth)
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20 550 may be counterbalanced by possible advantages associated with higher food availability
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22 551 and/or refuge against from predators.

23 24 552 **CONCLUSION**

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27 553 Our results suggest that the spatial dynamics of Greenland halibut in the EGSL follow a
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29 554 proportional density model where the rate of increase in local density is associated with
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31 555 population abundance. Spatial location, depth and temperature explain a large proportion of
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33
34 556 the variability in the catches. Juvenile distribution clearly indicates the St. Lawrence
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36 557 estuary is the major nursery area for the EGSL population. Habitats selected by Greenland
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38 558 halibut are characterized by low DO levels and the strong association between higher fish
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41 559 densities and the low DO concentrations indicates a high tolerance of Greenland halibut to
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43 560 hypoxia. It also suggests that negative effects, if present, could be compensated by other
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46 561 factors like food availability and/or refuge from predation. Further work on the influence of
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48 562 hypoxia on fish condition and growth performance of Greenland halibut is necessary to
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50 563 explore these possibilities.

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4

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Table 1. Correlation coefficients and significance values of the relationships between indices of distributional area (D_{95} , D_{75} , and D_{50}) of the three size classes and abundance indices. Correlations are estimated using the log transformed abundance index for the same size classes ($\ln(Y_{s,t})$) and that of all Greenland halibut ($\ln(Y_t)$) in the Estuary and the Gulf of St. Lawrence.

		D_{95}		D_{75}		D_{50}	
		$Y_{s,t}$	Y_t	$Y_{s,t}$	Y_t	$Y_{s,t}$	Y_t
15–31 cm	r^2	0.302	0.359	0.304	0.389	0.320	0.380
	p	0.010	0.004	0.010	0.003	0.007	0.003
32–43 cm	r^2	0.181	0.254	0.094	0.217	0.050	0.185
	p	0.054	0.020	0.177	0.033	0.331	0.052
≥ 44 cm	r^2	0.622	0.372	0.262	0.154	0.012	0.017
	p	< 0.0001	0.003	0.018	0.079	0.643	0.568

Table 2. Distributional area (km²) occupied by 95% (D95), 75% (D75), and 50% (D50) of the Greenland halibut from the three size classes during periods of low and high abundance. Mean values with standard deviations are presented.

Abundance	Area	15-31 cm	32-43 cm	≥ 44 cm
Low	D95	31836 ± 9220	44384 ± 11342	42908 ± 9401
	D75	14441 ± 5527	24570 ± 5223	24380 ± 4541
	D50	6567 ± 2409	12402 ± 5114	12057 ± 2645
High	D95	44383 ± 11342	51510 ± 4372	53377 ± 1708
	D75	21382 ± 3466	26291 ± 2283	27245 ± 1893
	D50	10741 ± 2438	13486 ± 3737	12111 ± 2645

Table 3. Results from the generalized additive models (GAM) for the three size classes of Greenland halibut during the 1990-2010 period. The total deviance (%) explained by the final model for each size class, the estimated degrees of freedom (EDF), F value, and probability level of significance (p) are given for each variable or interaction term.

	EDF	F	p	Deviance (%)
15-31 cm				76.6
s(longitude, latitude)	28.44	148.44	<0.00001	
s(depth)	8.64	51.83	<0.00001	
s(temperature)	7.81	5.40	<0.00001	
$s(Y_{s,t} - \text{mean annual catch tow}^{-1})$	7.88	113.9	<0.00001	
32-43 cm				73.8
s(longitude, latitude)	28.47	108.17	<0.00001	
s(depth)	8.00	72.22	<0.00001	
s(temperature)	8.63	7.11	<0.00001	
$s(Y_{s,t} - \text{mean annual catch tow}^{-1})$	7.70	134.90	<0.00001	
≥ 44 cm				58.6
s(longitude, latitude)	27.79	40.25	<0.00001	
s(depth)	8.20	42.92	<0.00001	
s(temperature)	8.30	3.64	<0.0002	
$s(Y_{s,t} - \text{mean annual catch tow}^{-1})$	2.89	176.97	<0.00001	

Table 4. Results from the generalized additive models (GAM) for the three size classes of Greenland halibut during the 2004-2010 period with DO concentration included as an additional environmental variable. The total deviance (%) explained by the final model for each size class, the estimated degrees of freedom (EDF), F value, and probability level of significance (p) are given for each variable or interaction term.

	EDF	F	P	Deviance (%)
15-31 cm				82.9
s(longitude, latitude)	23.26	13.62	<0.00001	
s(depth)	8.65	13.84	<0.00001	
s(temperature)	5.83	4.05	0.0002	
s(oxygen)	6.66	23.31	<0.00001	
$\bar{Y}_{s,t}$			<0.00001	
32-43 cm				85.8
s(longitude, latitude)	20.07	11.93	<0.00001	
s(depth)	6.39	50.85	<0.00001	
s(temperature)	6.25	2.94	0.0039	
s(oxygen)	6.99	15.38	<0.00001	
$\bar{Y}_{s,t}$			<0.00001	
≥ 44 cm				72.5
s(longitude, latitude)	25.79	6.87	<0.00001	
s(depth)	7.09	25.55	<0.00001	
s(temperature)	1.00	0.46	0.499	
s(oxygen)	5.88	9.10	<0.00001	
$\bar{Y}_{s,t}$			0.0019	

Table 5. Relative contribution of the different variables to the total deviance (%) explained by the final model for each size class of Greenland halibut during the 1990-2010 period. The relative contribution made by the identified variables or variable interaction is determined by the change in total deviance explained by the full model and the model with the different variables dropped.

Size class	Variable	Deviance explained by the model (%)	% change in deviance from full model
15 – 31 cm	Longitude, latitude	45.9	30.7
	Depth	73.2	3.4
	Temperature	74.6	2.0
	Depth and temperature	62.3	14.3
	Abundance ($\bar{Y}_{s,t}$)	69.6	7.0
32 – 43 cm	Longitude, latitude	48.5	25.3
	Depth	68.6	5.2
	Temperature	73.5	0.3
	Depth and temperature	56.2	17.6
	Abundance ($\bar{Y}_{s,t}$)	64.6	9.2
≥ 44 cm	Longitude, latitude	43.8	14.8
	Depth	53.7	4.9
	Temperature	58.3	0.3
	Depth and temperature	42.4	16.2
	Abundance ($\bar{Y}_{s,t}$)	50.9	7.7

Table 6. Relative contribution of the different variables to the total deviance (%) explained by the final model for each size class of Greenland halibut during the 2004-2010 period with DO concentration included as an additional environmental variable. The relative contribution made by the identified variables or variable interaction is determined by the change in total deviance explained by the full model and the model with the different variables dropped.

Size class	Variable	Deviance explained (%) by the model	% change in deviance from full model
15 – 31 cm	Longitude, latitude	74.6	8.3
	Oxygen	79.4	3.5
	Depth	80.0	2.9
	Temperature	81.7	1.2
	Abundance ($\bar{Y}_{s,t}$)	82.3	0.6
	Longitude, latitude and oxygen	45.8	37.1
	Oxygen and depth and temperature	61.0	21.9
32 – 43 cm	Longitude, latitude	79.7	6.1
	Oxygen	84.1	1.7
	Depth	79.1	6.7
	Temperature	85.3	0.5
	Abundance ($\bar{Y}_{s,t}$)	85.3	0.5
	Longitude, latitude and oxygen	58.8	27.0
	Oxygen and depth and temperature	55.1	30.7
≥ 44 cm	Longitude, latitude	65.8	6.9
	Oxygen	70.0	2.7
	Depth	65.7	7.0
	Abundance ($\bar{Y}_{s,t}$)	72.4	0.3
	Longitude, latitude and oxygen	55.5	17.2
	Oxygen and depth	42.4	30.3

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3 **1 List of figures**
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7 **Fig 1.** Annual variations in the abundance (mean catches in numbers per standard tow) of
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9 Greenland halibut (*Reinhardtius hippoglossoides*) in the Estuary and Gulf of St. Lawrence
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11 over the DFO and sentinel fishery surveys time series (1990-2010). Abundance indices for
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13 juveniles of both sexes (15–31 cm) (a), immature sub adult females and adult males (32–43
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15 cm) (b) and large adults of both sexes (≥ 44 cm) (c) are presented.
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20 **Fig 2.** Variations in spatial distribution of Greenland halibut in the Estuary and Gulf of St.
21
22 Lawrence during periods of low (a, c, e) and high (b, d, f) abundance for fish sizes of 15–31
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24 cm (a, b), 32–43 cm (c, d), and ≥ 44 cm (e, f). Abundance is expressed as the log of catch
25
26 numbers per standard tow for the following intervals: ■: 0.4–0.8, ■: 0.8–1.2, ■: 1.2–1.6, ■:
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28 1.6–2.0, ■: > 2.0.
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33 **Fig 3.** Relationships between indices of distributional area occupied by 95%, 75%, and
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35 50% of the fish and relative abundance (Y_t ; mean number of fish per tow) for the different
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37 size classes of Greenland halibut for the period between 1990 and 2010.
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41 **Fig 4.** Relationship between index of habitat quality and rate of local density change (β) for
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43 juveniles (a), immature sub adult females and adult males (b) and large adults (≥ 44 cm) (c).
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45 Index of habitat quality is determined by the mean catch rate during periods of low
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47 abundance and rate of local density change from eq. 6 in the text.
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51 **Fig 5.** Results of GAM regressions of the effects of spatial location (latitude and longitude),
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53 environmental variables (depth and temperature) and mean annual abundance of Greenland
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3 21 halibut on the catches (number of fish per standard tow) of juvenile fish (15-31 cm) in the
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5 22 Estuary and Gulf of St. Lawrence for the 1990-2010 period. Contour lines for
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7 23 longitude:latitude interaction indicate different levels of catches (fitted values adjusted to
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9 24 an average of 0). Solid line indicates the fitted relationships for single covariates and the
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11 25 dotted lines the 95% confidence intervals. The y-axis for individual covariates is scaled to
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13 26 an average of 0 and the rugplots on the x-axis indicate the number of observations.
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19 27 **Fig 6.** Results of GAM regressions of the effects of spatial location (latitude and longitude),
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21 28 environmental variables (depth and temperature) and mean annual abundance of Greenland
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23 29 halibut on the catches (number of fish per standard tow) of fish in the 32-43 cm size range
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25 30 in the Estuary and Gulf of St. Lawrence for the 1990-2010 period. Contour lines for
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27 31 longitude:latitude interaction indicate different levels of catches (fitted values adjusted to
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29 32 an average of 0). Solid line indicates the fitted relationships for single covariates and the
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31 33 dotted lines the 95% confidence intervals. The y-axis for individual covariates is scaled to
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33 34 an average of 0 and the rugplots on the x-axis indicate the number of observations.
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39 35 **Fig 7.** Results of GAM regressions of the effects of spatial location (latitude and longitude),
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41 36 environmental variables (depth and temperature) and mean annual abundance of Greenland
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43 37 halibut on the catches (number of fish per standard tow) of large fish (≥ 44 cm) in the
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45 38 Estuary and Gulf of St. Lawrence for the 1990-2010 period. Contour lines for
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47 39 longitude:latitude interaction indicate different levels of catches (fitted values adjusted to
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49 40 an average of 0). Solid line indicates the fitted relationships for single covariates and the
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51 41 dotted lines the 95% confidence intervals. The y-axis for individual covariates is scaled to
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3 42 an average of 0 and the rugplots on the x-axis indicate the number of observations.
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7 **Fig 8.** Results of GAM regressions of the effects of geographic location (latitude and
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9 44 longitude) and environmental variables (depth, temperature and dissolved oxygen) on the
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11 45 catches of juvenile Greenland halibut (15–31 cm) in the Estuary and Gulf of St. Lawrence
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13 46 during the 2004-2010 period. Contour lines for longitude:latitude interaction indicate
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15 47 different levels of catches (fitted values adjusted to an average of 0). Solid line indicates the
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17 48 fitted relationships for single covariates and the dotted lines the 95% confidence intervals.
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19 49 The y-axis for individual covariates is scaled to an average of 0 and the rugplots on the x-
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21 50 axis indicate the number of observations.
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27 **Fig 9.** Results of GAM regressions of the effects of geographic location (latitude and
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29 52 longitude) and environmental variables (depth, temperature and dissolved oxygen) on the
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31 53 catches of fish in the 32-43 cm Greenland halibut in the Estuary and Gulf of St. Lawrence
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33 54 during the 2004-2010 period. Contour lines for longitude:latitude interaction indicate
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35 55 different levels of catches (fitted values adjusted to an average of 0). Solid line indicates the
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37 56 fitted relationships for single covariates and the dotted lines the 95% confidence intervals.
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39 57 The y-axis for individual covariates is scaled to an average of 0 and the rugplots on the x-
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41 58 axis indicate the number of observations.
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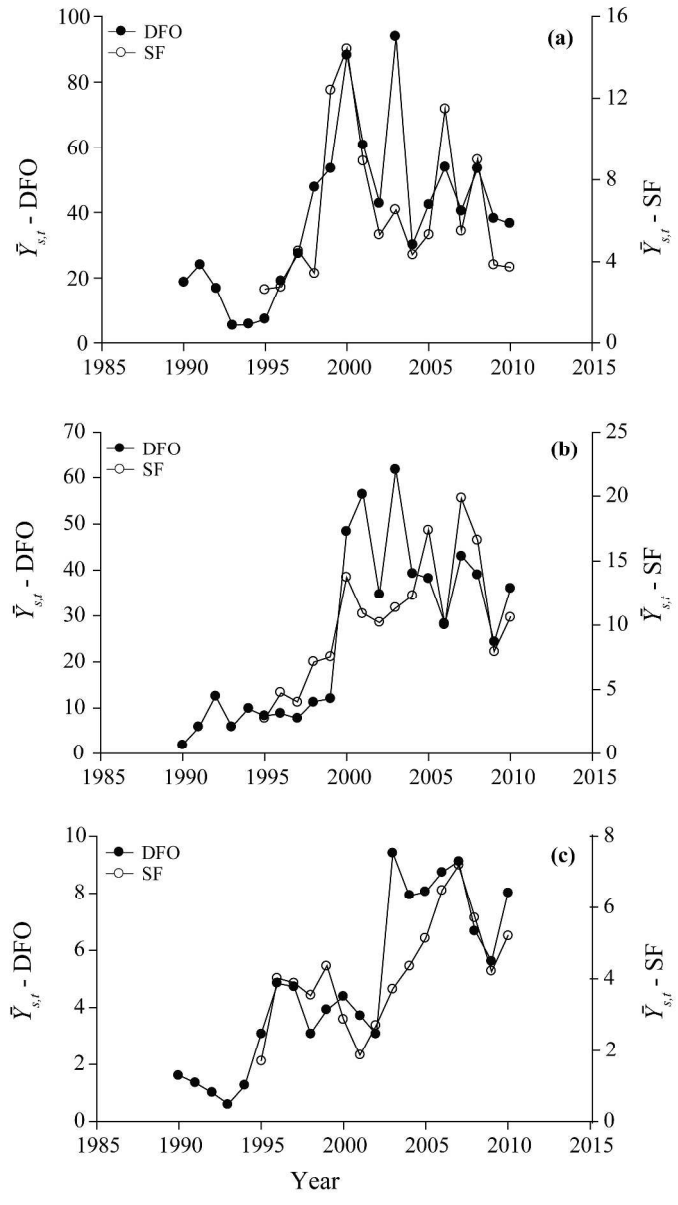
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47 **Fig 10.** Results of GAM regressions of the effects of geographic location (latitude and
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49 60 longitude) and environmental variables (depth, temperature and dissolved oxygen) on the
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51 61 catches of large Greenland halibut (≥ 44 cm) in the Estuary and Gulf of St. Lawrence
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53 62 during the 2004-2010 period. Contour lines for longitude:latitude interaction indicate
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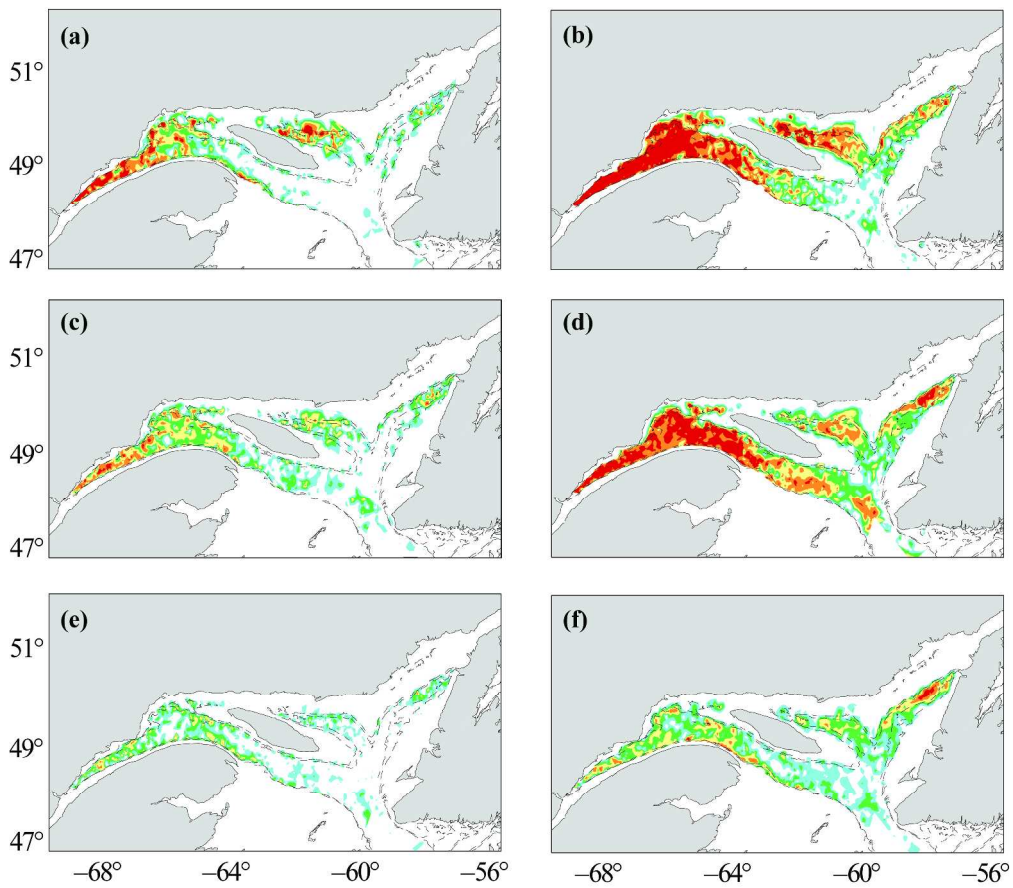
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14 67 **Fig 11.** Contour plot of GAM predictions of dissolved oxygen levels ($\mu\text{mol/L}$) from 2004
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16 68 to 2010 in the Estuary and Gulf of St. Lawrence in relation to longitude and depth.

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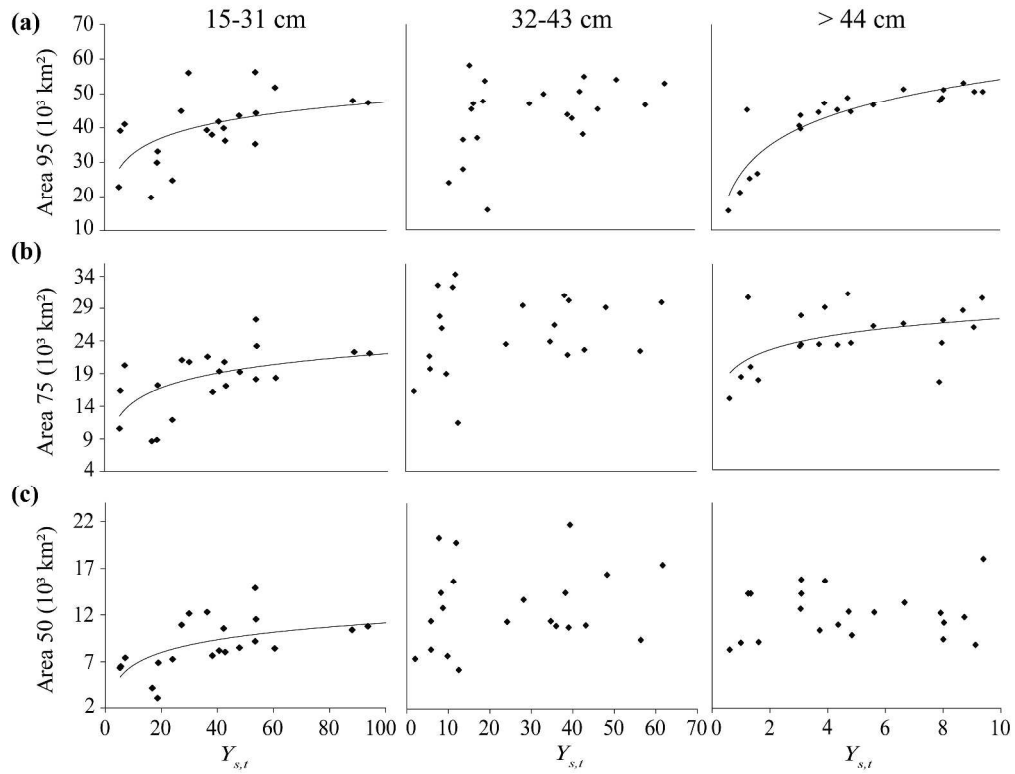
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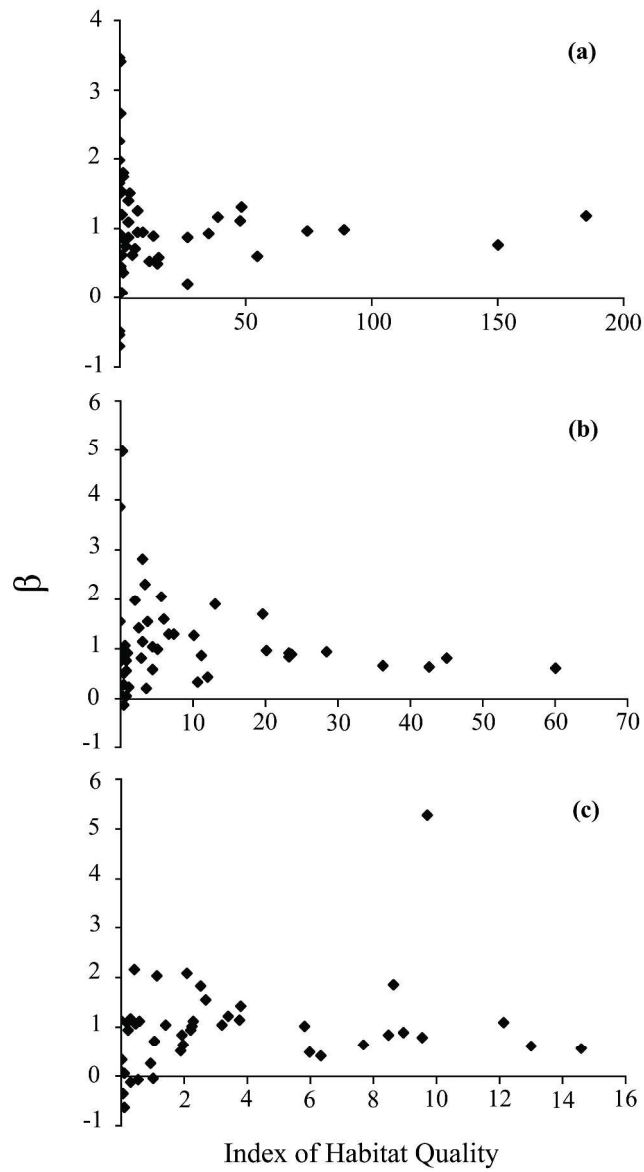


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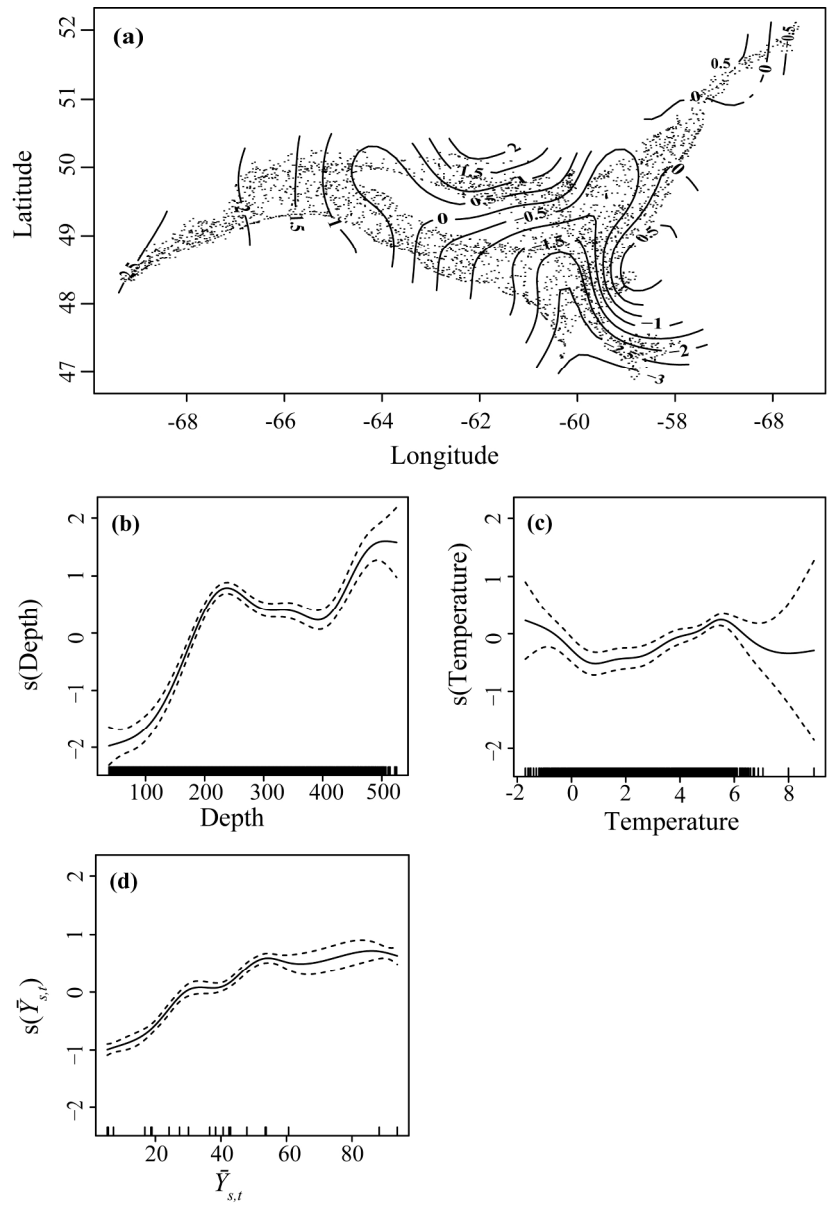
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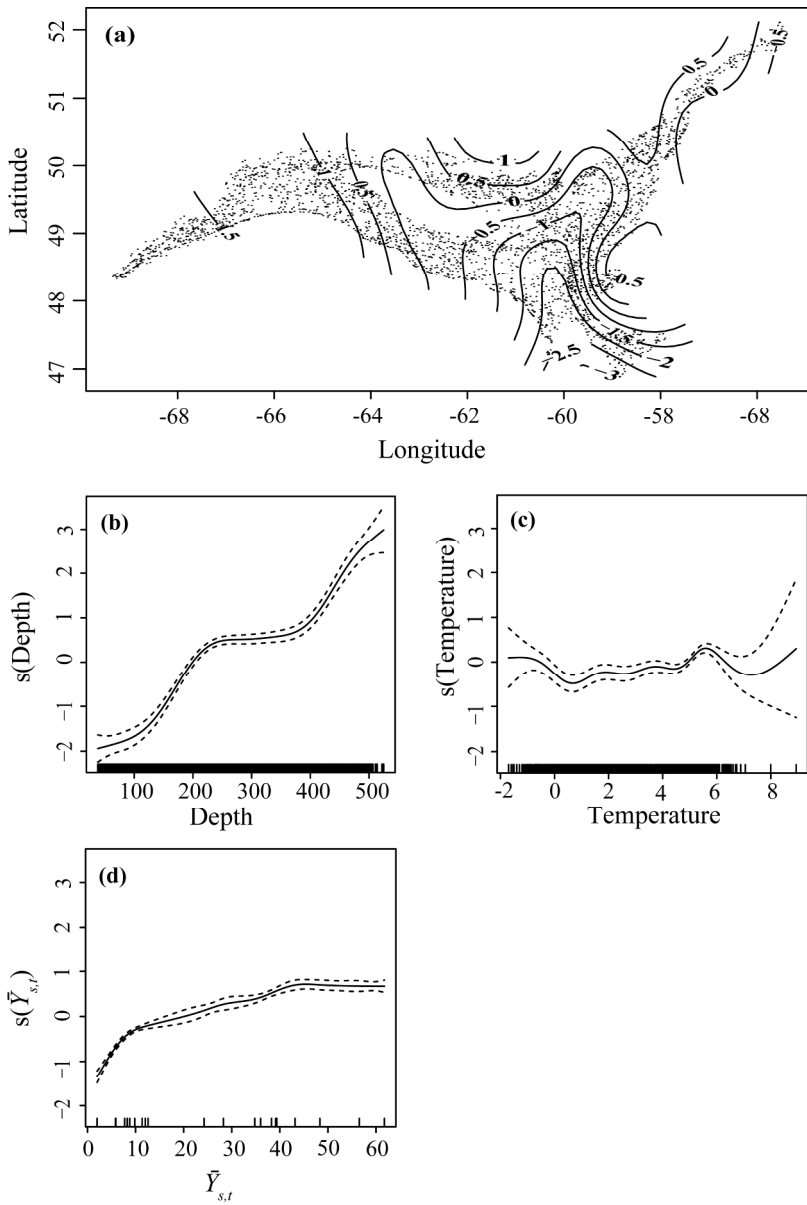


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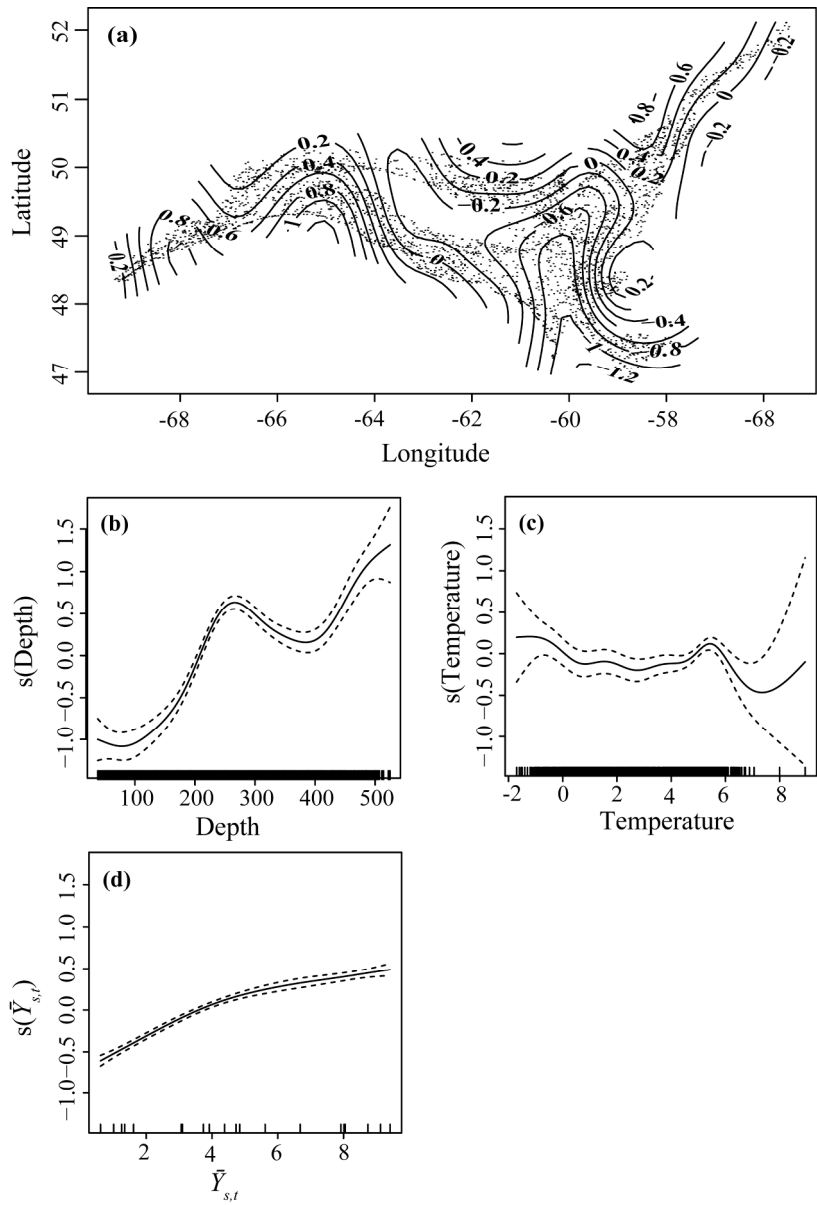
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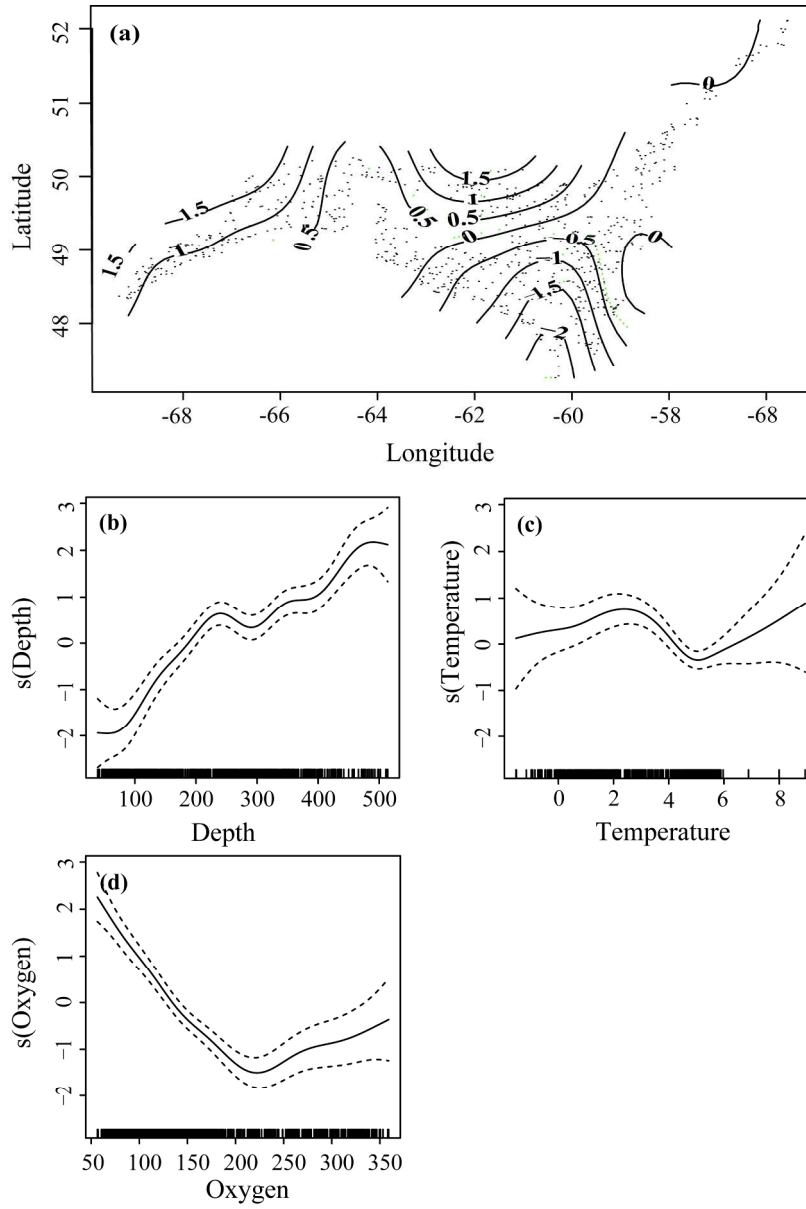
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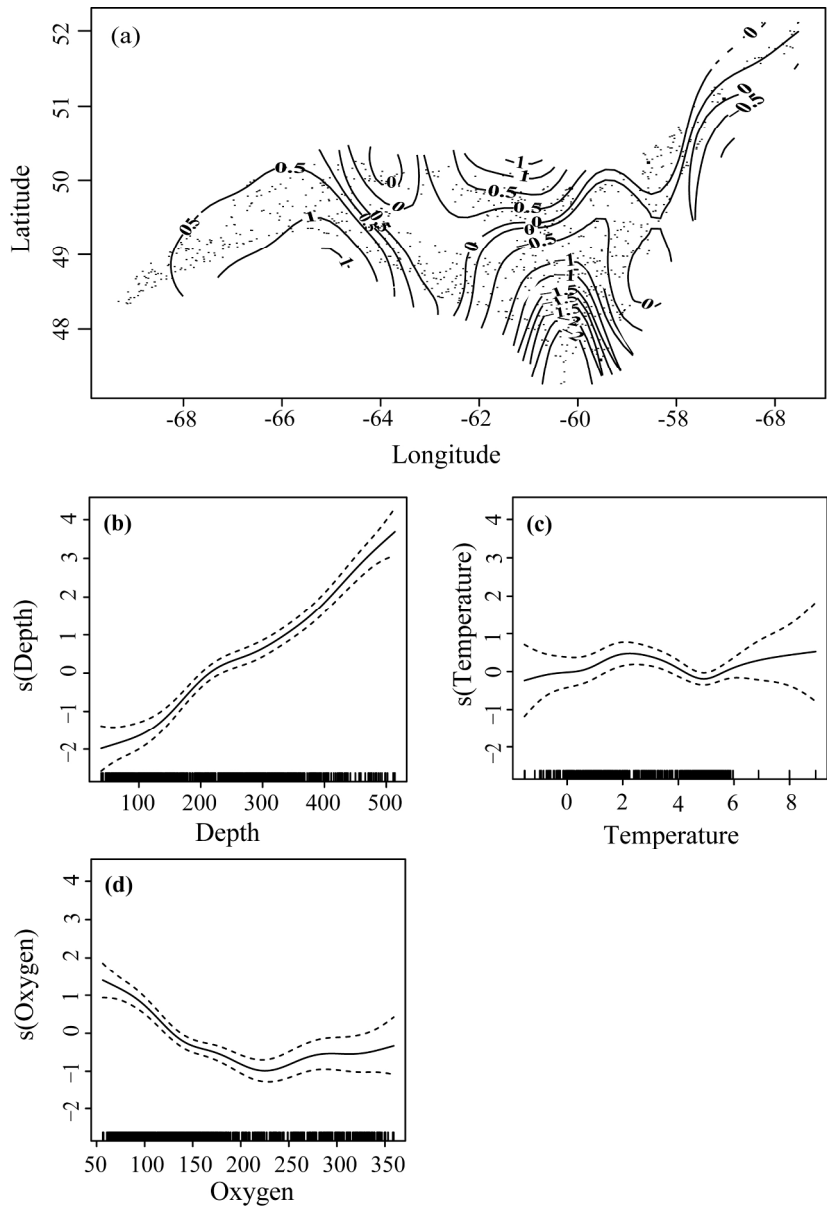
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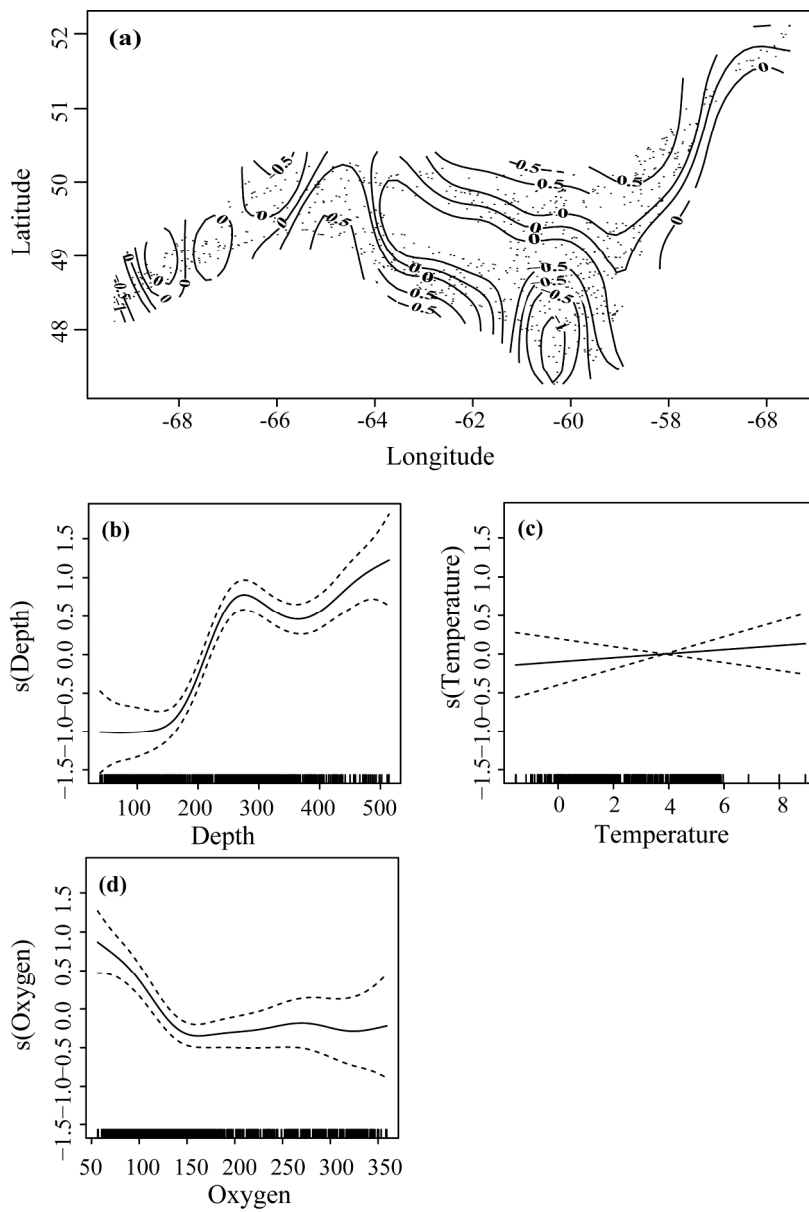
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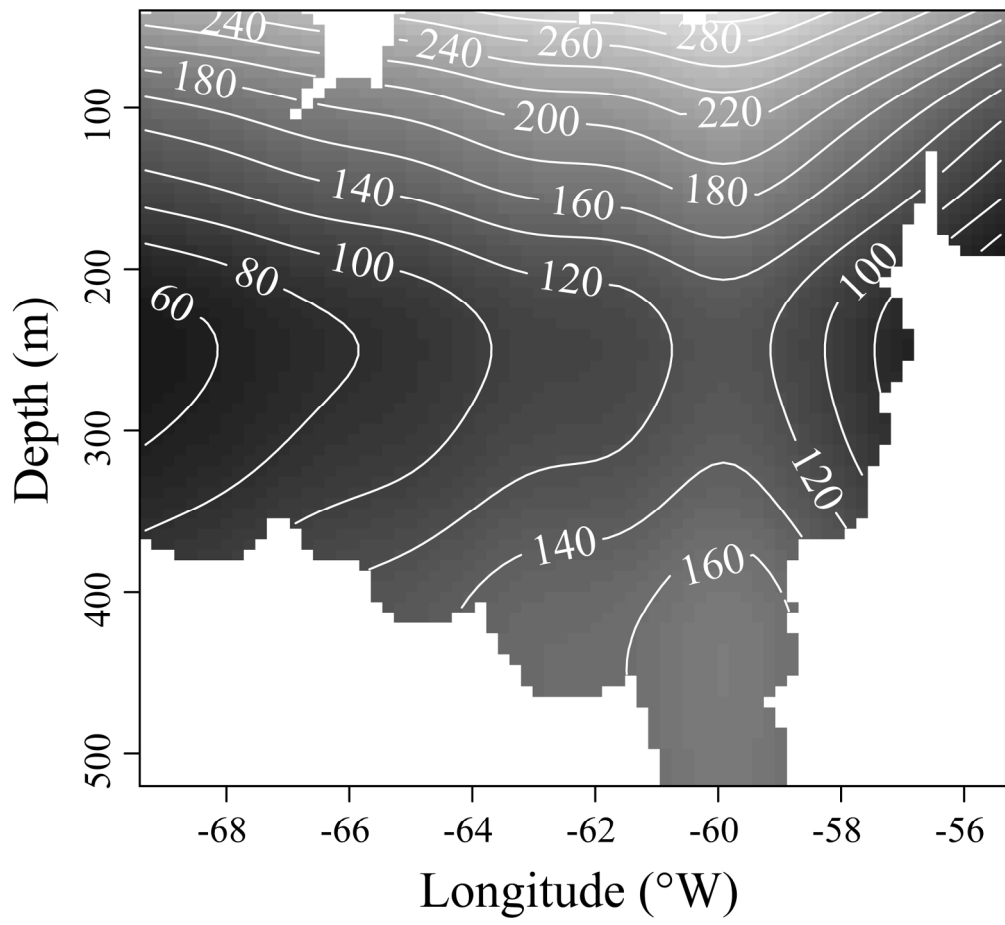
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