1   **Ontogenetic spatial constraints of sub-arctic marine fish species**

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28 **Abstract**

29 Marine species may respond and adapt to climate change through shifting spatial distributions,

30 but options may be limited by the occupancy of essential habitats which are anchored in space.

31 Limited knowledge of when spatial constraints are most likely to occur in marine fish life cycles

32 has impeded the development of realistic distribution forecasts. In this study, we develop and

33 implement analytical techniques to identify spatial constraints, defined by both the *consistency*

34 through which a particular geographic area is used year after year, and by the *extent* of such area

35 with respect to the entire population range. This approach is applied to simulated data and to ten

36 case studies including six groundfish species from three subarctic marine systems. Our analyses

37 illustrate that the early phase of the species' life cycle is more spatially constrained than older life

38 stages. We detected significant species-specific variability in both the degree to which species are

39 anchored in space throughout their life cycle, and the ontogenetic changes of the geographic

40 association. There is an indication that this variability can be explained by the species life history

41 strategy, highlighting the need to extend similar analyses to other species and regions. The

42 presence of ontogenetic spatial constraints, particularly during early life stages, indicates

43 restrictions exist to changes of spatial distribution and questions the assertion that global

44 warming will uniformly result in an increase in abundance and harvest at higher latitudes and

45 decreases at lower latitudes. Our study develops ecological and analytical insights that are critical

46 for accurate projections of species distributions under different climate change scenarios.

47 Key words: Adaptation, climate change, marine subarctic, spatial distribution, spatial ecology,

48 spawning

49

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Introduction

A focal point in the study of fisheries oceanography is to understand and predict how fish populations respond to climate change, and to regional and local scale oceanographic variability (Bograd et al., 2014; Cury et al., 2008; Kendall & Duker, 1998) Within this framework, one of the remaining great challenges is to quantitatively characterize the adaptive potential of marine organisms (Merilä & Hendry, 2014). Climate change is affecting ecological processes and biogeochemical cycles of many marine environments. Species may respond and adapt to these changes through both phenotypic plasticity and microevolutionary adaptations (Crozier & Hutchings, 2014; Donelson et al., 2019). For example, one way in which adult marine fish quickly adapt to climate change is by shifting their spatial distribution (Poloczanska et al., 2013). Commercial exploitation has also shown to result in spatial shifts, in particular a deepening among older age groups (Frank et al., 2018). Retrospective analyses of long-term monitoring programs have documented several shifts of marine fish spatial distribution across both latitudinal and bathymetric gradients (Nye et al., 2009; Perry, 2005; Pinsky et al., 2013, 2020). These trends are particularly evident in sub-arctic and temperate environments (Kleisner et al., 2017), where the effects of global warming appear to be the primary driver (Saba et al., 2016). Range shifts of marine fish are now impacting coastal communities that are dependent on commercial fisheries (Rogers et al., 2019; Selden et al., 2020).

There are limits to how far individuals in a population can adapt to a changing climate. Marine fish species have complex life cycles composed of multiple life history stages. Each life stage frequently has unique spatial distributions and habitat requirements (Barbeaux & Hollowed, 2018; Bartolino et al., 2011). During some life stages individuals are spatially constrained due to the presence of critical habitats and oceanographic conditions, such as bathymetry, sediment characteristics, or topographically induced currents and tides, which are also fixed in space and

85   time (Ciannelli et al., 2010; Lough et al., 2006; Stuart-Smith et al., 2021). Imprinted behavior

86   (Cury, 2019) and social facilitations (Corten, 2002) also contribute to the presence of persistent

87   spatial aggregations of individuals in geographically fixed habitats. Examples of spatially

88   constrained habitats include spawning sites (Ciannelli et al., 2014), nursery areas (Beck et al.,

89   2001), and dispersal pathways between them (Petitgas et al., 2013). During other life stages the

90   same individuals are able to change their distribution and track climate velocities (e.g., Alvarez-

91   Berastegui et al., 2014).

92   The effects of climate variability on species distributions are often assessed by examining

93   a single or few life stages utilizing readily available survey data (e.g., Kleisner et al., 2017;

94   Thorson et al., 2016; Wisz et al., 2015). However, parameterizing species distribution models in

95   this manner may produce results that over-estimate the degree of spatial re-distribution in

96   response to climate change, and result in the misinterpretation of the processes involved in

97   driving such spatial responses (Asch & Erisman, 2018). Recognizing where and when in the

98   species' life cycle spatial constraints occur is important to produce realistic distributional

99   forecasts. Spatially constrained stages may act as a bottleneck to adaptation which can have

100   fitness repercussions (Caddy, 2014). Therefore, identifying these constraints has important

101   implications for monitoring and managing marine fish species in a changing climate. To date,

102   there is no systematic knowledge of when in marine fish life cycles such spatial constraints are

103   most likely to occur.

104   Our study has two objectives: i) develop analytical techniques to identify spatial

105   constraints during a species' life cycle, ii) implement these new analytical techniques to compare

106   patterns of life history spatial constraints across species with contrasting life histories. We chose

107   to evaluate data rich species/populations from sub-arctic systems in both the North Atlantic

108   (Scotian Shelf and Barents Sea) and the North Pacific (Bering Sea) (Fig. 1). The selection of

109   species in this study balances the need to include contrasting life history strategies and highly

110   resolved life cycle data. Here we define the degree of spatial constraint by both the *consistency* at

111   which a particular geographic area is used year after year, and by the *extent* of such an area

112   relative to the entire population range. Consequently, life history stages that occupy the same

113   areas over time, and are concentrated in an area less than the population range, are deemed highly

114   constrained. In discussing our results, relevance is given to global climate change and the ways in

115   which species can adapt in the presence of strong spatial constraints. With these study goals and

116   methodologies in mind, we anticipate defining the possible existence of bottlenecks to species

117   adaptability through changes of spatial distribution, to generate hypotheses linking a species' life

118   history and the processes affecting the selection of habitat through the life cycle, and to develop

119   spatial distribution models that consider multiple life history stages and that can be used to

120   project species distributions in relation to future climate change scenarios.

121

122   **Methods**

123   The methods are organized in two sections. We first describe the quantitative metrics for

124   assessing habitat constraints, and then describe the application of these metrics to a simulated set

125   of data and ten sub-arctic fish populations that are representative of contrasting life history

126   strategies and habitat requirements.

127

128   *Metrics for assessing habitat constraint*

129   We defined the habitat constraint (HC) for a species (s) at a target age or size (a), as the product

130   of the geographic *consistency C,* dimensionless, ranging from 0 (not consistently occupied) to 1

131   (consistently occupied) at which a specific geographic location is occupied, and the geographic

132   *extent E,* dimensionless, ranging from 0 (small extent) to 1 (large extent) of that geographic

133   location:

134

135     $(HC)_a = C_a(1 - E_a)$ (1)

136

137   As such, the habitat constraint metric ranges from 0 to 1. It approaches 1 when, over the studied

138   period, fish at a target age or size consistently occupy a very small fraction of the area where the

139   population is known to occur. Conversely, the constraint metric will be close to zero when target

140   age or size distribution is highly variable from year to year and widely spread over the population

141   range. Note that the habitat constraint changes for each species, however in equation (1) the sub

142   index for species has been omitted.

143   We used Generalized Additive Models (GAMs) to determine C_a. GAMs allow for

144   nonlinearities between covariates and response, and therefore are well suited to capture unique

145   patterns of spatial dependency (Wood, 2017). Let $X_{a,lat,lon,y}$ be the natural log of the local

146   abundance of the studied species at the target age or size *a,* collected over multiple years *y*, at

147   locations defined by geographic coordinates (*lat, lon*). We quantify the consistency of habitat use

148   (C_a) as the difference of the residual error between the *base* model (2), which only includes

149   yearly variable intercepts ($\beta_{a,y}$) and the day of the year effect (i.e., phenology *d*),

150

151     $X_{a,lat,lon,y} = \beta_{a,y} + s_a(d) + \varepsilon\_b_{a,lat,lon,y}$ (2)

152

153   and the *habitat* model (3), which includes also the effect of geographic coordinates (*lat, lon*)

154

155     $X_{a,lat,lon,y} = \beta_{a,y} + s_a(d) + g_a(lat,lon) + \varepsilon\_h_{a,lat,lon,y}$ (3)

156

157   The parameter $\beta_{a,y}$ is a stage and year specific intercept, included as a fixed effect to account for

158   interannual changes in abundance. Consideration of including year as a fixed effect is most

159   important when population abundance varies from year to year but distribution does not. In such

160   circumstances a model that only includes year can explain a large portion of the data variance (R^2

161   is high) even though there is no spatial variability in the data. The function g is a two-

162   dimensional smoother that varies by stage, s is a one-dimensional smoother that also varies by

163   stage, and ε is a random error assumed to be normally distributed (on the log scale) with mean

164   equal to zero and variance equal to the residual variance of the model. We run models with a

165   Tweedie distribution and soap film smoother which yielded very similar results to the models

166   with lognormal distribution and thin plate regression splines. Models 2 and 3 are fitted separately

167   for each age or size-group of a population.

168   Given the base and habitat models in 2 and 3, the consistency metric is derived as

169   follows:

170

171     $C_a = \frac{\sum(\varepsilon\_b_{a,lat,lon,y})^2 - \sum(\varepsilon\_h_{a,lat,lon,y})^2}{\sum(\varepsilon\_b_{a,lat,lon,y})^2}$ (4)

172

173   If a target age or size group consistently uses the same habitat each year, then the error of the

174   habitat model ($\varepsilon\_h_{a,lat,lon}$) will be small, the ensuing C_a metric will be high, and approach 1. For

175   a habitat used very inconsistently from one year to the next, C_a will approach 0. Note that when

176   using field data, it is improbable for the consistency and constraint metrics to reach the

177   theoretical maximum of 1, because of uncertainty in the data.

178   The determination of C_a from models (2) and (3) is executed on presence only data (i.e.,

179   positive, non-zero catches). However, corresponding logistic regression models are also

180   implemented using the presence-absence data to estimate the probability of occurrence of the

181   target stage. The presence-absence and the presence only models are used together to predict

182   density over a regularly spaced array of stations for the calculation of habitat extent, as discussed

183   in the next paragraph.

184   Given an age or size group a, its geographical *extent* (E_a), is determined by the smallest

185   fractions of the total occupied habitat that contains a pre-specified fraction (e.g., $f=0.75$) of the

186   predicted total abundance at the raw scale, of the species at the targeted age or size. Namely,

187

188    $$E_a = \frac{A_{f,a}}{A_t} \Big/ f \qquad\qquad (5)$$

189

190   where $A_{f,a}$ is the smallest area containing a fraction f of the species total abundance at the targeted

191   age/size, and A_t is the total area occupied by the population. Because the surveys we evaluate

192   cover areas where the targeted species has never occurred and because observations are collected

193   on irregular or inconsistently sampled grids, A_t is here defined by a regular array of equally

194   spaced grid points that are less than 30 km from a location with a positive occurrence of the

195   targeted species. $A_{f,a}$ is equal to the areal sum of all the grid cells (H), each with area (h), and

196   whose cumulative fraction of predicted abundance is less than or equal to f:

197

198    $$A_{f,a} = \sum_{i=1}^{H} h_i$$

199

200   We choose the fraction f equal to 75% of the predicted abundance within the area A_t, and for

201   three of the ten case studies examined, we assessed the sensitivity of f to the habitat extent and

202   habitat constraint metrics (Appendix S1, Figs. S1-S3). To predict the density of the targeted

203   species and stage at each location in the array ($\hat{d}_{h_i,a}$), we use the delta method (Porter &

204   Ciannelli, 2018). This was achieved by taking the product of the probability of occurrence (u) and

205   the abundance (x) of the target stage and species predicted from a presence-absence and presence

206   only habitat model (3), respectively:

207

208     $$\hat{d}_{h_i,a} = \hat{u}_{hi,a}\hat{x}_{hi,a}.$$

209

210   To predict $A_{f,a}$, the array units (h) are first sorted in decreasing order of the respective

211   predicted density, such that $\hat{d}_{h\_i} \geq \hat{d}_{h_1+1}$, and their respective areas are summed until the

212   fractional abundance threshold f is reached. When so derived, the extent metrics (E_a) ranges from

213   0 to 1. It approaches 0 when the target stage is spatially clustered within the species distribution

214   range, and 1, when the target stage is uniformly distributed across the species distribution range.

215

216   *Applying constraint metrics to simulated data and species with contrasting life histories*

217   We implemented the habitat constraint models to a simulated data set and to ten case

218   studies, including six groundfish species from the Eastern Bering Sea, three from the Scotian

219   Shelf, and one from the Barents Sea (Table 1). For the simulated data set we formulated four

220   spatial distribution scenarios (Table S1), each varying in the degree of spatial autocorrelation and

221   conditional effects on position: 1. *High constraint,* with yearly stable conditional distribution on

222   the coordinate system, indicative of highly spatially correlated distribution with high spatial

223 gradients that do not change over time (Figure S4); 2. *Moderate constraint*, with yearly stable

224 conditional distribution on the coordinate system, indicative of moderately spatially correlated

225 distribution with moderate spatial gradients that do not change over time, but have greater spatio-

226 temporal variability compared to the previous scenario (Figure S5); 3. *Environmental constraint*,

227 with high and yearly variable conditional distribution on position, indicative of a highly spatially

228 correlated distribution with a latent environmental variable (e.g., water temperature), which also

229 affects distribution (Figure S6); 4. *Unconstrained*, characterized by unconditional distribution,

230 indicative of interannually variable distribution and limited spatial autocorrelation (Figure S7).

231 All scenarios were formulated using the function gstat in R (version 2.0-7), which produces

232 Gaussian random fields given variogram models and the linear coefficients specified in the

233 Appendix S2, Table (S1). For all scenarios we reproduced 20 random fields, each representative

234 of a yearly distribution, and in the Appendix S2 we show the first 10 of these fields. Results did

235 not change by increasing the number of random fields beyond 20.

236   We expect the geographic consistency metric (C) to be highest for the high constraint

237 scenario, and progressively smaller for the moderate, environmental constraint, and

238 unconstrained scenarios. We expect the habitat extent metric (E) to be low for the high constraint

239 scenario, and progressively higher for the moderate and environmental constraint scenarios, and

240 highest for the unconstrained scenario. Consequently, we anticipate the habitat constraint metric

241 (HC) to be highest for the high constraint scenario due to high geographic consistency and low

242 habitat extent, and progressively smaller for the moderate, environmental and unconstrained

243 scenarios, due to low consistency and high habitat extent.

244   Fish distribution data used in the ten case studies were collected as part of long-term

245 survey programs conducted by the agencies that oversee fisheries management and assessment in

246 their regions, including the National Oceanic and Atmospheric Administration (NOAA) for the

247   USA (Lauth et al., 2019), the Canadian Department of Fisheries and Oceans for Canada (DFO;

248   Frank et al., 2018), the Institute of Marine Research (IMR) for Norway (Fall et al., 2018), and the

249   Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) for

250   Russia (Stige et al., 2019). We only included stages of species for which the available survey

251   coverage clearly reflected the core distribution of the targeted age or size, and for years with

252   more than 40 stations sampled. In general, the timing of the juvenile and adult survey is summer,

253   while that of eggs and larval stages changes depending on the spawning phenology of the species.

254   Additional information about each survey, including years and months covered, is provided in the

255   Appendix S3.

256   To compare patterns of habitat constraint across the ten case studies we first derived an

257   index of ontogenetic development ($O_{s,a}$) as the ratio between the size or age of the examined life

258   history stage and the maximum size or age of the species (Mindel et al., 2016). If the ontogenetic

259   categories were age based, we assigned an age of 0.05 year of age to eggs and 0.15 year to larvae.

260   If the categories were size based, we assigned 1 mm to eggs and 1.5 mm to larvae. For older or

261   larger categories, we assigned the age or size measured from the survey. We are aware that

262   ontogeny does not linearly scale with either age or size. Therefore, we also considered alternative

263   ways of calculating the ontogenetic index, e.g., as the log of the age or size over the log of

264   maximum age or size. Because the results were not sensitive to the way in which the ontogenetic

265   index was calculated, we opted for the simpler linear formulation. We then fit a GAM to the

266   habitat constraint versus ontogenetic index metrics. In these analyses, the inter-species variability

267   was first included as a random term, which allowed us to estimate an average relationship across

268   the ten combinations of species and populations, and the variance components associated with the

269   fixed and random terms:

270

271     $HC_{s,a} = \beta + g(O_a) + \delta_s + \varepsilon_a$ (6)

272

273   where β is a model intercept equal to the average habitat constraint across all species and stages,

274   g is a smooth non-parametric function, δ_s is a random effect varying by combinations of species

275   and population (10 estimates) assumed to be normally distributed, and ε_a is the residual variation,

276   also normally distributed.

277   In a second GAM formulation, the inter-population variability was modeled as a fixed

278   effect, which allowed us to estimate a specific smooth term and average constraint for each

279   examined population:

280

281     $HC_{s,a} = \beta_s + g_s(O_{s,a}) + \varepsilon_a$ (7)

282

283   In GAM formulations (6) and (7), the maximum degrees of freedom for the one-dimensional

284   smooth terms were limited to three, to avoid overfitting. Significance level for the fixed effects of

285   g_s were set at 0.1.

286   Where possible, the above analyses were applied to multiple life stages, including eggs,

287   larvae, and eight or nine progressively larger or older juvenile and adult stages. Some case studies

288   did not include the egg and larval stages due to lack of taxonomic resolution (arrowtooth

289   flounder, *Atheresthes stomias*, Pleuronectidae) or because of unique life history characteristics

290   (Pacific cod, *Gadus macrocephalus*, Gadidae, possess demersal eggs); all the Scotian Shelf case

291   studies did not include the egg stage. For the Bering Sea case studies, juvenile and adult stages

292   were partitioned into eight size groups, with size thresholds chosen to create uniform sample

293   sizes. For the Scotian Shelf and Barents Sea case studies, juvenile and adult stages were

294   partitioned into nine age groups, (age-0 to age-8 and older). For each species, we only included

295   data from sampled stations that are less than 30 km away from a sampled location that had at

296   least one positive occurrence of the targeted species at any age or size. Thus, we eliminated

297   surveyed stations where the targeted species had never occurred.

298   For a given species, with the exception of the Barents Sea case study, we limited the

299   analyses to overlapping years of data availability across the stages examined. So, for the Scotian

300   Shelf case studies, we restricted the analyses from 1978 to 1982, corresponding to the years when

301   ichthyoplankton surveys were conducted. Given the limited number of ichthyoplankton years

302   available for the Scotian Shelf cases, we repeated the analyses including the full extent of the

303   adult and juvenile stages, based on annual surveys conducted during 1970-2015, and for these

304   stages we found no differences with the results obtained by only including the 1978-1982 time

305   interval. For the Bering Sea, data were available from 1982 to 2018 for adults and juveniles, and

306   from 1988 to 2018 for eggs and larvae, however, the exact years changed among the species

307   examined due to the necessity of including no less than 40 sampled stations within each year. For

308   the Barents Sea, temporal coverage differed between stages. Egg and larval data were only

309   available from 1981 to 1993, while the autumn juvenile and adult surveys were only available

310   from 2003 onward. So, in this case we could not restrict the analysis to overlapping years.

311   Further information about the years and months included in the analyses is provided in the

312   Appendix S3.

313   To estimate the relationship between habitat constraint and the ontogenetic index (Eqs. 6

314   and 7), we included species and stages that had greater than 400 stations with positive catches

315   through all years – a number of stations that correspond to less than the 10% quantile of available

316   sample sizes across all examined species and stages. A minimum of 400 stations was deemed

317   necessary to simultaneously fit one- and two-dimensional smooth functions of phenology and

318   distribution in the model (3). This caused the removal of yellowfin sole (*Limanda aspera,*

319   Pleuronectidae) eggs (n = 33), Alaska plaice (*Pleuronectes quadrituberculatus,* Pleuronectidae)

320   larvae (n = 253), Scotian Shelf haddock (*Melanogrammus aeglefinus,* Gadidae, n = 160) and cod

321   (*Gadus morhua,* Gadidae, n = 262) larvae, Scotian Shelf cod age-0 (n = 262) and age-1 (n = 333),

322   Scotian Shelf hake (*Merluccius bilinearis,* Gadidae) age-0 (n = 372), and Scotian Shelf haddock

323   age-0 (n = 283) and age-1 (n = 342). To reduce model uncertainties, the size or age specific data

324   should ideally capture the distribution range and have similar sample size across size or age

325   groups. In our applications, we removed yellowfin sole larvae because their distribution was

326   clearly truncated at the northern end of the sampled area, in spite of this stage including 603

327   stations. The majority of arrowtooth flounder abundance in the Bering Sea is within the surveyed

328   area (Ciannelli et al., 2012), thus they were still retained in the analyses. For the remaining cases,

329   the area monitored include clusters of high numerical density, and covers bathymetric and

330   oceanographic features that are representative of the habitat variability experienced throughout

331   the population range. Thus, we are confident that the data analyzed effectively captures the

332   degree to which different size or age groups distribute over space. To determine whether our data

333   inclusion criteria affected the results, we also implemented the analyses in Eqs. 6 and 7 on the

334   unrestricted set of available data. All analyses were conducted in R (version 3.6.2) and GAM

335   models were fitted with the mgcv library (1.8-33). With the exception of data from the Barents

336   Sea case study, all other data and R code are deposited in:

337   https://github.com/lciannel/lifehistoryconstraint.

338

339   **Results**

340   *Implementing habitat constraints analyses to simulated and field data*

341   *Simulated data*

342　The results of the constraint analyses on simulated data corroborate our expectations. The habitat

343　constraint metric was lowest in the unconditional (HC = 0.001) and environmental (HC = 0.01)

344　constraint scenarios and progressively higher for the moderate (HC = 0.360) and high constraint

345　scenarios (HC = 0.759, Appendix 2, Fig. S8). The high constraint scenario had highest

346　consistency (C = 0.841) and lowest habitat extent (E = 0.10) metrics, and the unconditional

347　scenario had the opposite pattern (C = 0.002, E = 0.550). The environmental constraint had high

348　explained variance (R^2) but low geographic consistency metrics, due to the interannually variable

349　abundance and spatial gradients of this scenario (Appendix 2, Fig. S6).

350　*Field data*

351　We show results for two species, walleye pollock (*Gadus chalgogrammus*, Gadidae) in the

352　Bering Sea and haddock on the Scotian Shelf. These two species are chosen because they are

353　considered representative of the other species examined. Results for the other eight case studies

354　are provided in the Appendix S4.

355　*Bering Sea walleye pollock*

356　　　The distribution of walleye pollock in the Eastern Bering Sea changes for different

357　ontogenetic stages and size groups (Fig. 2). At the egg and larval stages, the majority of the

358　estimated abundance is confined to the Alaska Peninsula and to the Pribilof Islands regions,

359　which are known spawning locations. The slight difference in distribution between egg and larval

360　stages is attributable to passive transport by currents from spawning to juvenile habitats. An

361　isolated cluster of larval abundance was identified in the Bering Sea basin region, as a result of

362　isolated high larval catches in the early year of the available time series. As individuals grow and

363　develop, they occupy larger areas of the outer (depth 100-200 m) and middle (depth 50-100 m)

364　shelf regions, illustrated by a progressive increase of the habitat extent for these stages (Fig. 2).

365　Estimates of habitat constraint decline with ontogeny, ranging from 0.22 at the egg stage to 0.06

366   at an intermediate adult stage. This is due to both a higher interannual spatio-temporal variance

367   associated with larger sized individuals, and a progressive increase of habitat extent (Fig. 3). The

368   consistency at which a stage occupies a specific geographic area decreases notably for individuals

369   in the middle of size ranges, between 383 mm and 444 mm in length, denoting large interannual

370   variability of spatial distribution at corresponding size ranges (Fig. 3).

371   *Scotian Shelf Haddock*

372   The spatial distribution of haddock on the Scotian Shelf does not change through different

373   life stages, which is unlike the pollock case study where distribution changes occurred across life

374   stages. There are, however, differences in the consistency and extent of habitat use across their

375   life history. High concentrations of haddock larvae are located at the southern and western

376   portion of the Scotian Shelf, corresponding to Browns and Emerald Banks, which are known

377   spawning grounds. Consequently, the majority of the estimated larval abundance is confined to

378   these two locations (Fig. 4). Habitat expansion and increased dispersion is observed during the

379   age-0 stage, (due to greater mobility of these juveniles), while distribution becomes concentrated

380   and patchier at older and reproductively mature life stages (age-1+) (Fig. 4).

381   Haddock's metrics of habitat constraints are higher than those of pollock, and are highest

382   between age-2 (0.26) and age-4 (0.27) and then decline for the older life stages, at age-8 (0.17)

383   and age-9+ (0.18). During the larval and age-0 stages, haddock metrics of constraint are also low,

384   but the sample size for these stages is small compared to that of other stages, and may have

385   contributed to the high interannual variability and low consistency of spatial distribution (Fig. 5).

386

387   *Inter-species comparisons*

388   By including population as a random term (Eq. 6), we found a significant and linear effect

389   of the ontogenetic index on habitat constraint across the ten case studies examined (Fig. 6). This

390   outcome implies that younger stages and size groups, on average, tend to be more highly

391   constrained in space than older stages and larger size groups. However, the variance component

392   of the random term (population) is three orders of magnitude greater than the variance explained

393   by the ontogeny effect, underscoring high inter-population (or species) variability in this

394   relationship (Table 2). Results did not change when we included species and stages that did not

395   meet our criteria for retention in the inter-specific comparisons.

396   The variability in the shape and elevation of the smoothed ontogenetic index is evident

397   from the results of the fixed effect model (Eq. 7). Three of the populations exhibit habitat

398   constraints that persist into the juvenile or even adult stages, including Alaska plaice, yellowfin

399   sole, and flathead sole (*Hippoglossoides elassodon,* Pleuronectidae) and for two of these species

400   the relationship between the ontogenetic index and habitat constraint is nonlinear (e.g., flathead

401   sole and yellowfin sole) (Fig. 7). Five populations have a gradual linear decline of habitat

402   constraint with ontogeny (Barents Sea cod, Bering Sea pollock and cod, and Scotian Shelf

403   haddock and cod), while the remaining two populations have no significant relationship between

404   habitat constraint and ontogeny (arrowtooth flounder, silver hake). In addition to variability in the

405   shape of the ontogenetic effect we also found significant variability in the elevation associated

406   with each population (Table 2). Yellowfin sole, Alaska plaice and flathead sole have the highest

407   intercept estimates, indicating a stronger overall affinity of these populations to location or

408   substrate, compared to other cases. The relationships between the metrics of habitat constraint

409   and extent with the ontogenetic index did not change with changes of the parameter f (fraction of

410   abundance for the habitat extent metric) (Appendix S1).

411

412   **Discussion**

413   *Drivers of life history spatial constraints*

414   Our analyses clearly illustrate a tendency for the early phase of the life cycle to be more

415   constrained in space than other life stages for the various marine fish species evaluated. The

416   existence of life history spatial constraints is common and well documented in terrestrial

417   vertebrates and invertebrate species, and have practical implications for conservation. For

418   example, stopover sites of long-distance migratory birds, such as the bar-tailed godwits (*Limosa*

419   *lapponica)* in the eastern Atlantic flyway (Scheiffarth et al., 2002), are critical to the completion

420   of the species' annual migration. Likewise, migrating and overwintering generations of the

421   eastern monarch butterflies *Danaus plexippus* are known to concentrate from a 4.5 million km^2

422   breeding ground during spring and summer, down to an approximately 1 km^2 area in winter

423   (Reppert & de Roode, 2018). In contrast to these examples of strong spatial affinity and site

424   fidelity for terrestrial species, the current paradigm for distribution models of marine fish species

425   (especially pelagic species; Cheung et al., 2015), is that of a loose association with discrete

426   geographic locations. This is in part because of their presumed high dispersing life history

427   strategy, and in part because of the spatially dynamic nature of pelagic seascapes. This is the

428   basic premise behind the postulate that fish species can adapt to global warming by shifting their

429   spatial distribution, leading to a redistribution of global catches, with loss of abundance at the

430   tropics and gains at higher latitudes (Cheung et al., 2010; Bindoff et al., 2019). While there is

431   mounting evidence that many marine fish species are currently redistributing, here we show that

432   some species from sub-arctic seas consistently occupy restricted geographic locations during the

433   early phases of their life cycle. The existence of these spatial constraints will limit the degree to

434   which these species can adapt to climate change through shifting distributions to higher latitudes.

435   We did not address the drivers of these spatial constraints, but it is reasonable to expect

436   that natal homing (Cury, 2019) and a life history strategy tuned to the presence and persistence of

437   topographic, sediment, and bathymetric characteristics are the primary reasons. In the Bering Sea

438   for example, organic content and sediment characteristics are correlated with higher trophic level

439   community composition and abundance in benthic habitats (Grebmeier et al., 1989). Flatfish

440   abundance has strong associations with sediment characteristics, and it is hypothesized that these

441   associations are the result of diet preferences and benthic prey availability (McConnaughey &

442   Smith, 2000). Similarly, on the Scotian Shelf there are strong habitat associations of the three

443   gadids studied here (cod, silver hake and haddock) and sediment types (Scott, 1982b; Waiwood

444   & Buzeta, 1989), and in the nearby Georges Bank newly settled juvenile cod and haddock are

445   associated with pebble-gravel deposits on the northeast side of the bank (Lough et al., 1989).

446   Bathymetric-driven circulation features, important for the dispersal and retention of fish eggs and

447   larvae, are also potential drivers of spatial constraint during early life stages (Iles & Sinclair,

448   1982). In the Bering Sea, canyons along the continental slope drive topographically steered

449   circulation (Ladd, 2014) and affect the transport pathways of slope spawned flatfish eggs and

450   larvae (Sohn et al., 2016). On the shelf, circulation features (e.g., gyres) can also aggregate and

451   retain eggs and larvae in spatially restricted areas around banks (Lough et al., 2006; O'Boyle et

452   al., 1984; Shackell et al., 1999; Smith & Morse, 1985). In our analyses of the Scotian Shelf,

453   haddock and cod larvae generally occupied Browns and Emerald banks, and silver hake was

454   found in the vicinity of Western Bank. These are known gadid spawning locations in the Scotian

455   Shelf region (Brickman, 2003; Hurley & Campana, 1989), and previous studies have underscored

456   the importance of larval retention around these banks (O'Boyle et al., 1984). While in principle

457   during spatially constrained phases of a fish life cycle, water temperature may not be an

458   important driver of spatial distribution, temperature may still act as an important covariate during

459   other life history stages. For example, the spawning habitats of walleye pollock, in both the

460   Eastern Bering Sea and western Gulf of Alaska, do not geographically change in relation to

461 variability in water temperature (Bacheler et al., 2010, 2012), while adult stages of walleye

462 pollock outside of the spawning season shift northward during warm years (Thorson et al., 2020).

463   Exploitation and predator-prey interactions may also contribute to changes of habitat

464 constraints through ontogeny. Sub-arctic systems are characterized by relatively few species,

465 some of which are commercially harvested, with strong trophic interactions (Frank et al., 2006;

466 Livingston, 2000). Strong exploitation erodes spatial structure and exploitation status is another

467 important driver of spatial constraint (Ciannelli et al., 2013). On the Scotian Shelf, Frank et al.,

468 (2018) found that exploitation drives ontogenetic-like deepening of Atlantic cod. Thus, one

469 recommendation for future analyses would be compare patterns of range shifts in relation to

470 exploitation status of the stock. Trophic interactions may shape the degree of patchiness,

471 especially in pelagic fish species. For example, (Frank et al., 1993) found that capelin larvae on

472 the Southeast Shoal of the Grand Banks were patchy during early stages, followed by increased

473 dispersion, and then, with the onset of schooling behavior, distributions became patchier and

474 were closely associated with their primary food sources. Some species, such as adult Atlantic cod

475 and walleye pollock, are prone to eating smaller and younger conspecific individuals. So, their

476 movement and distribution are linked to that of their prey (Ciannelli et al., 2007; Fall et al.,

477 2018).

478

479 *Expanding these analyses to other case studies*

480 The assessment of ontogenetic spatial constraints requires spatial data collected over multiple age

481 or size groups of a species' life cycle, ideally during oceanographically contrasting years, and

482 throughout the distributional range of the population. When data are available over different

483 seasons, it is best to separate the analyses accordingly, as species can undergo seasonal

484 contraction and expansions in their distribution. This is evident in the Barents Sea cod, with

485 winter distribution range limited by low temperature under sea ice, and therefore more

486 constrained compared to summer (Appendix S4, Figs. S23 and S25). When using field data, it is

487 impossible for the consistency and constraint metrics to reach the theoretical maximum of 1,

488 because of uncertainty in the data. The results from the simulated data are instrumental to

489 appreciate the influence of spatial and interannual variability, because they show that even for

490 scenarios in which the population distribution is highly conditional on position, the habitat

491 constraint metrics is less than 0.8. In the moderate constraint scenario, the metric is about 0.4,

492 and in the environmental and random scenarios the metrics are close to zero.

493   Not surprisingly, the availability of data for ontogenetic habitat constraint analyses is

494 often limited. Even for well-monitored systems examined here there were data gaps for specific

495 life stages, especially during the egg and larval phases. In the Scotian Shelf, for example, we only

496 had five overlapping years among larval, juvenile and adult collections, and for the Bering Sea

497 there were no overlapping years among ichthyoplankton, juvenile and adult surveys. For all three

498 species examined in the Scotian Shelf, results obtained on the full set of years in which juvenile

499 and adult data were available (1970-2015), were similar to those obtained when only the five

500 overlapping years (1978-1982) were analyzed, suggesting that a minimum of five years is

501 necessary to obtain a spatial representation of geographic consistency and extent.

502   Ontogenetic spatial constraints inferred from data rich cases could provide insights for

503 data poor species. In the cases we examined, three patterns of spatial constraint across life

504 histories were evident (Fig. 7). The first pattern is characterized by a gradual and monotonic

505 decline of spatial constraint, resulting in spawning individuals and eggs being most spatially

506 constrained, and the non-spawning adult individuals being more spatially dispersed. Gadids,

507 including walleye pollock, Scotian Shelf cod and haddock, Pacific cod and Barents Sea cod

508 follow this pattern in so far as their populations have the simultaneous presence of spatially

509   constrained and highly mobile individuals. These species have strong site fidelity at spawning

510   (Hurley & Campana, 1989; Neidetcher et al., 2014; Rose, 1993) and highly mobile adults during

511   the nonbreeding seasons. Tagging studies of adult stages of Pacific cod (> 50 cm length) indicate

512   widespread movement and occupancy during summer, and directional movement to slope

513   spawning areas during winter (Shimada & Kimura, 1984). Similarly, mature Barents Sea cod

514   undertake extensive southwards countercurrent migrations during winter toward spawning

515   grounds along the Norwegian coast and migrate northwards to vast feeding grounds in the

516   summer (Ottersen et al., 2014).

517   The second pattern is characterized by a delayed (flathead sole) or protracted (Alaska

518   plaice, yellowfin sole) period of high spatial constraint, persisting into juvenile and sub-adult

519   stages, before declining at later stages. Previous work has pointed to strong associations of

520   yellowfin sole abundance in sandy substrate, flathead sole in mixed sand and mud, and Alaska

521   plaice in mixed gravel and sand (McConnaughey & Smith, 2000). In the Bering Sea shelf,

522   bathymetry is inversely correlated with sediment size and, not surprisingly, all three species have

523   a strong affinity with specific depth ranges (Swartzman et al., 1992). Adult yellowfin sole

524   performs annual spring and fall migrations to and from spawning areas (Wilderbuer et al., 1992).

525   The timing of these migrations is influenced by water temperature and sea ice extent on the

526   Bering Sea shelf, and in turn influences availability to the survey (Nichol et al., 2019). Therefore,

527   it is possible that the rapid decline of habitat constraint of adult yellowfin sole may be driven by

528   the changes in timing of their migration and availability to the summer survey, rather than

529   interannual distribution changes.

530   The third pattern includes cases with a relatively constant level of spatial constraint

531   through the species life cycle, indicating either a loose (e.g., arrowtooth flounder) or high (e.g.,

532   silver hake) lifetime spatial associations. Species that conform to this pattern are at the

533   northernmost extreme of their range, and their spatial distribution and annual abundance may be

534   particularly sensitive to water temperature changes. For example, arrowtooth flounder in the

535   Bering Sea avoids water less than 2°C, which is typically observed in the middle shelf during

536   summer on the Bering Sea (Ciannelli et al., 2012). Similarly, silver hake on the Scotian Shelf

537   tends to occupy warmer water of the central and southwest portion of the shelf while avoiding the

538   colder northeast shelf (Scott, 1982a), and bottom water temperature on the shelf is an important

539   driver of their abundance (Reed et al., 2018).

540   We note that our cross-section of species only includes those residing in sub-arctic

541   systems, and with either benthic or demersal strategies during the adult phase. Thus, augmenting

542   these analyses with more species, including those from temperate and tropical reef species, as

543   well as species with pelagic life history strategies during the adult phase (Muhling et al., 2013),

544   would be instrumental to validate the trends of habitat constraint across the life cycle, and to

545   establish the link with life history strategies. Ultimately, this broader level of investigation would

546   further enable inference about habitat use and adaptability to climate change for data poor

547   species, for which life history trait information is known but spatial data for multiple life stages is

548   limiting.

549

550   *Implications for species distribution models*

551   Assessment of habitat constraints through the species life cycle have important implications for

552   accurate predictions of species distribution in relation to climate change. The presence of strong

553   spatial dependency for some stages indicates that within the range of examined values, water

554   temperature may not be a primary driver of spatial distribution (Stuart-Smith et al., 2021), and

555   calls into question projections of species or catch distributions based solely on water temperature.

556   Additionally, species distribution models are often parameterized using data from stages that are

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557   highly variable, such as the adult stages during the summer feeding months, which is when most

558   groundfish surveys occur in sub-arctic areas. Our analyses indicate that adult stages are more

559   likely to follow temperature or climate velocities because they are less constrained in space.

560   Consistently, stage-specific models have different prediction outcomes compared to those

561   parameterized on only one life stage (Asch & Erisman, 2018). Life history stages with high

562   habitat constraint will limit future distribution shifts and can be used as a "mask" increasing

563   accuracy of current species distribution model predictions.

564

565   *To what degree can range shift offset climate change?*

566   Populations that have both a spatially constrained and a spatially unconstrained life stages can

567   experience a further separation among their stage-specific habitats and therefore be challenged to

568   close their life cycle. This appears to be the case for both Pacific cod and walleye pollock in the

569   Bering Sea, where in recent years the juvenile and adult summer distributions have been shifting

570   progressively northward (Stevenson & Lauth, 2019), while spawning habitats are fixed in space

571   at the southern edge of their distribution range (Bacheler et al., 2012; Neidetcher et al., 2014).

572   Spawning habitats can indeed change, as shown for some of the species included in this study

573   (e.g., Barents Sea cod), however, it is difficult to determine the underlying causes (Langangen et

574   al., 2019; Opdal, 2010; Sundby & Nakken, 2008).

575   When species are constrained in space during a certain life stage they will either adapt to

576   new habitat conditions in order to change their distribution or eventually fail to survive. Adaptive

577   changes are required when the distribution of the most limiting stage is 1) geographically

578   controlled, and/or 2) the physiological tolerance limits (e.g., temperature-dependent

579   development) of the most limiting stage have been reached. In 1), for species to shift distribution,

580   adaptation must occur by linking the new geographic cues (e.g., deeper waters) to the

581   environmental conditions associated with suitable habitat (e.g., Bonamour et al., 2019). In 2), if

582   physiological tolerance limits have been reached, adaptation in the physiological response to the

583   environment would be needed before further shifts could occur. In the Gulf of Alaska for

584   example, water temperature is significantly warmer than the Bering Sea, and laboratory and

585   modeling analyses indicate that Pacific cod eggs may be experiencing thermal stress at their

586   traditional spawning sites, which may further limit recruitment (Laurel & Rogers, 2020). To

587   adapt to these changes Pacific cod may evolve new cues and spawn in cooler habitats within the

588   Gulf of Alaska, and/or shift the thermal tolerance of embryos, or perish. Models that account for

589   life history constraints as outlined here, that are extended to also include physiologically based

590   relationships (Kearney & Porter, 2009) of environmental covariates in addition to a fixed spatial

591   term, can be used to simulate plastic and adaptive responses of fish to climate change.

592   Furthermore, modelling the dispersion of free-drifting life stages and energy budget modelling of

593   migratory adults might be needed to assess whether different spatial constraints across life stages

594   will necessitate evolutionary adaptations in order for the species to close its life cycle in a future

595   climate.

596   There is unfortunately a chasm in the marine sciences literature with fisheries

597   oceanographers being more keenly aware of plastic responses of fish to climate change and life-

598   history biologists focused more on evolutionary adaptations (Hutchings, 2011). Bridging this gap

599   between plasticity and adaptations (Anderson et al., 2012; Schoener, 2011) to understand and

600   model how marine species respond to climate change and variability (Donelson et al., 2019), as

601   well as other anthropogenic stressors, will be an important advancement in marine ecology.

602

603   **Acknowledgements**

612

613   **Data availability**

614   With the exception of data from the Barents Sea case study, all other data and R code are

615   deposited in: https://github.com/lciannel/lifehistoryconstraint

616

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900   Table 1. List of case studies examined. NOAA: National Oceanic and Atmospheric

901   Administration; DFO: Department of Fisheries and Ocean; IMR: Institute of Marine Research,

902   VNIRO: Russian Federal Institute of Fisheries and Oceanography. For additional information

903   about sample sizes, years, and months included in each case study, see Appendix S3 (Table S1).

904   Ich= Ichthyoplankton survey, BT = bottom trawl survey, MT = midwater trawl.

Common and scientific names	Area	Max size or age	Survey type	Stages available	Source
Walleye pollock (*Gadus chalcogrammus*, Gadidae)	Eastern Bering Sea	910 mm	Ich, BT	Eggs, larvae, juveniles, adults	NOAA
Flathead sole (FH, *Hippoglossoides elassodon*, Pleuronectidae)	Eastern Bering Sea	650 mm	Ich, BT	Eggs, larvae, juveniles, adults	NOAA
Arrowtooth flounder (ATF, *Atheresthes stomias,* Pleuronectidae)	Eastern Bering Sea	980 mm	BT	Juveniles, adults	NOAA
Pacific cod (*Gadus macrocephalus*, Gadidae)	Eastern Bering Sea	1170 mm	BT	Juveniles, adults	NOAA

Alaska plaice (AP, *Pleuronectes quadrituberculatus*, Pleuronectidae)	Eastern Bering Sea	720 mm	BT	Eggs, larvae†, juveniles, adults	NOAA
Yellowfin sole (YFS, *Limanda aspera*, Pleuronectidae)	Eastern Bering Sea	700 mm	BT	Eggs†, larvae, juveniles, adults	NOAA
Atlantic cod (*Gadus morhua*, Gadidae)	Barents Sea	15 years	Ich, MT, BT	Eggs, larvae, juveniles, adults	IMR, VNIRO
Atlantic cod (*Gadus morhua*, Gadidae)	Scotian Shelf	15 years	Ich, BT	Larvae†, juveniles†, adults	DFO
Silver hake (*Merluccius bilinearis*, Gadidae)	Scotian Shelf	15 years	Ich, BT	Larvae, juveniles†, adults	DFO
Haddock (*Melanogrammus aeglefinus*, Gadidae)	Scotian Shelf	15 years	Ich, BT	Larvae†, juveniles†, adults	DFO

(†) Indicates stages that were not included in the analyses of habitat constraints vs ontogenetic index (Equations 6 and 7) due to a small sample size.

908   Table 2. Results of the GAM models for the analyses of habitat constraints versus ontogenetic

909   index. Model results are shown for two different formulations, including the first in which

910   population is a random term (δ, Eq. 6), and the second with population as a fixed effect (Eq. 7).

911   The values reported for the intercept terms (β) indicate their estimated mean, and the values

912   reported for the smooth terms ($g(O)$) indicate the estimated degrees of freedom. I is in indicator

913   variable (0,1) specifying the species/population considered (s). For the fixed effect model, species

914   are sorted in decreasing order of their p-value for the smooth term. Signif. codes: '***' <0.001,

915   '**' < 0.01, '*' < 0.05, '.' < 0.1. YFS: Yellowfin sole. ATF: Arrowtooth flounder

Mixed effect model	$HC_a = \beta + g(O_a) + \delta_s + \varepsilon_a$		
	Adjusted R^2 = 0.673, Dev = 71.0%, n = 86		
	β	$g(O_a)$	δ_s
Estimate	0.201 ***	1.000 ***	
Variance component		4.05 x 10^{-5}	8.12 x 10^{-2}
Fixed effect model	$HC_{s,a} = \beta * I_s + g(O_{s,a}) * I_s + \varepsilon_a$		
	R^2 = 0.831, Dev = 97.7%, n = 86		
	$\beta * I_s$		$g(O_{s,a}) * I_s$
ATF	0.217 ***		1.691
Silver hake	0.249 ***		1.289
Pacific cod	0.065 ***		1.299
Scotian cod	0.153 ***		1.831 .
Barents cod	0.129 ***		1.000 *
Haddock	0.244 ***		1.000 *

Pollock	0.111 ***	1.710 *
Alaska plaice	0.279 ***	1.591 ***
Flathead sole	0.281 ***	1.970 ***
YFS	0.370 ***	1.983 ***

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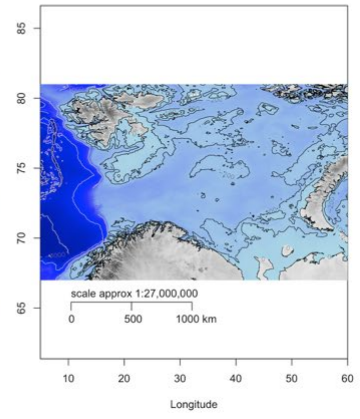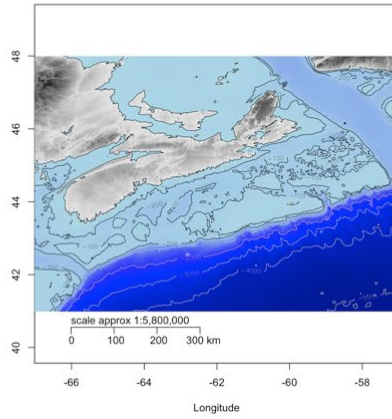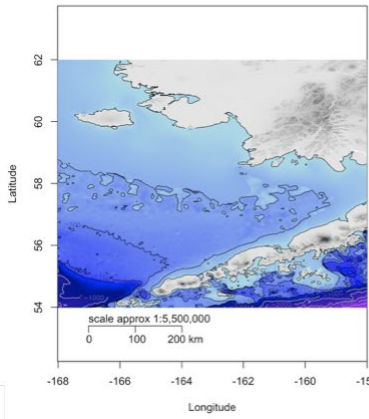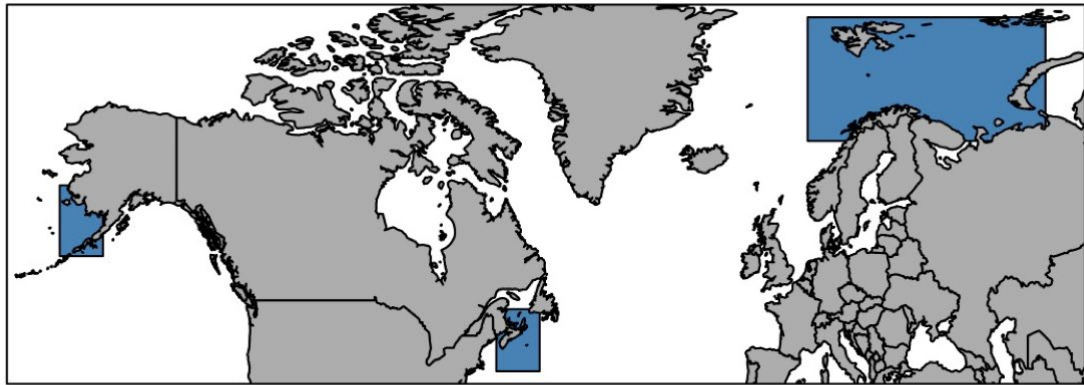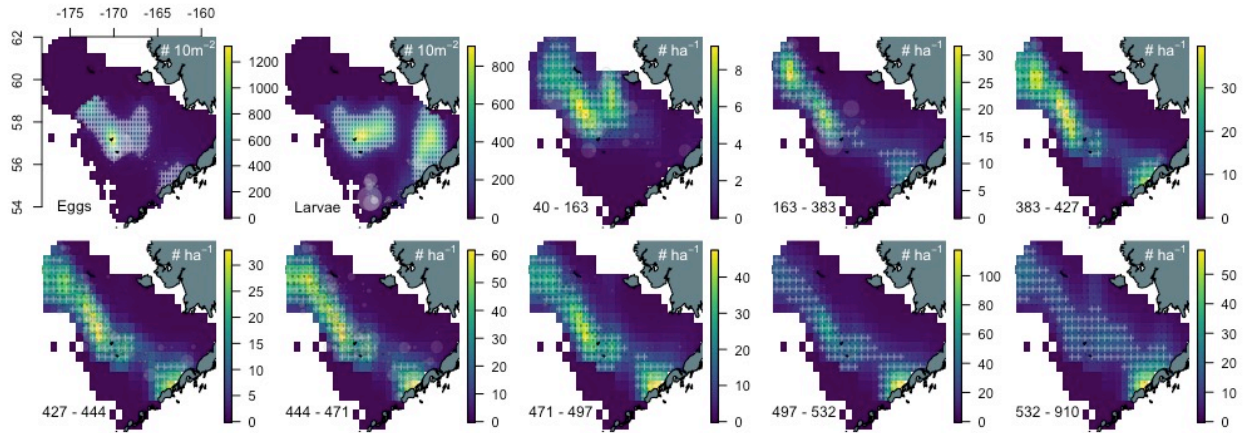
Figure 2. Spatial distribution of walleye pollock in the Bering Sea over different ontogenetic stages and size groups. Predictions are shown as color image in the units of number of individuals $10m^{-2}$ (eggs and larvae), or numbers of individuals per hectare (ha^{-1}) for all other size groups. Predictions were obtained from presence/absence and presence only GAM models (delta method, equation 3). Semitransparent grey bubbles are observ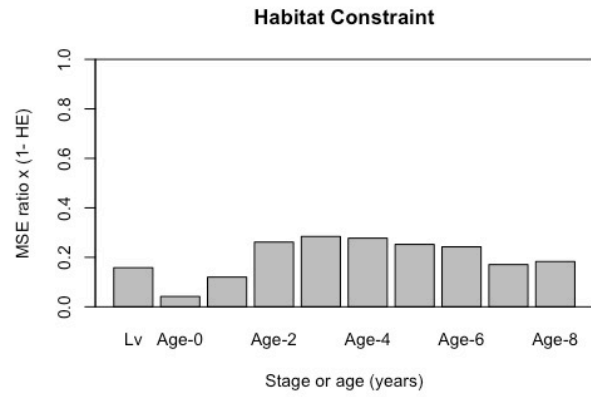ed densit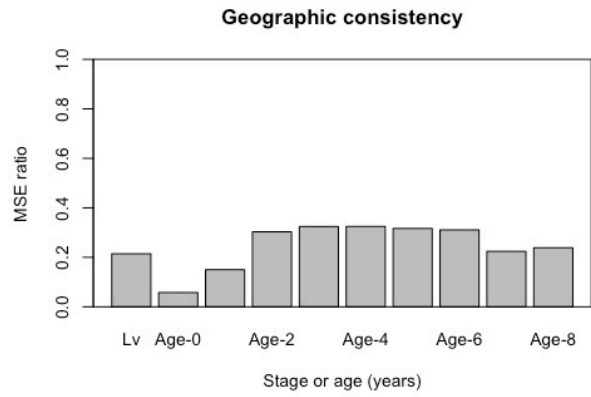i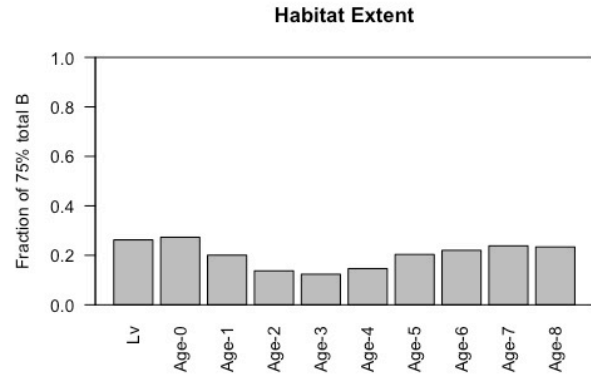es and the region delineated by a white cross ('+') represents the estimated habitat extent, or the portion of the surveyed area that contains 75% of the estimated total abundance. The stage or size range (in mm) examined is indicated in the lower left corner of each plot. The 200m depth isobath is shown.

Explained spatio-temporal variance

Habitat Extent

Geographic consistency

Habitat Constraint

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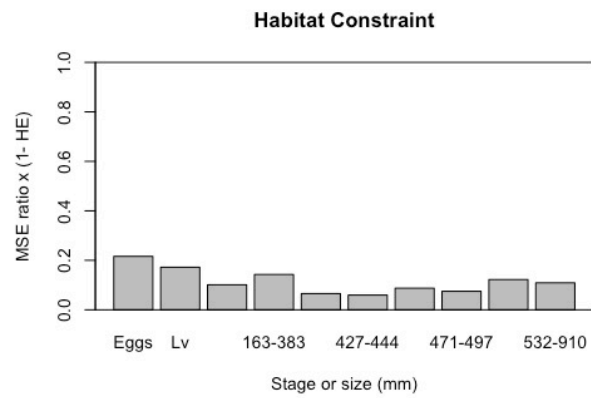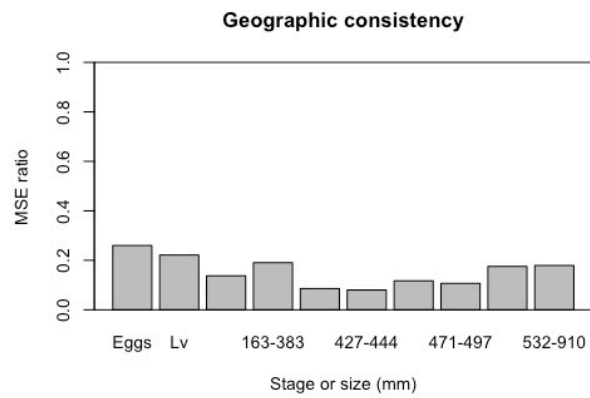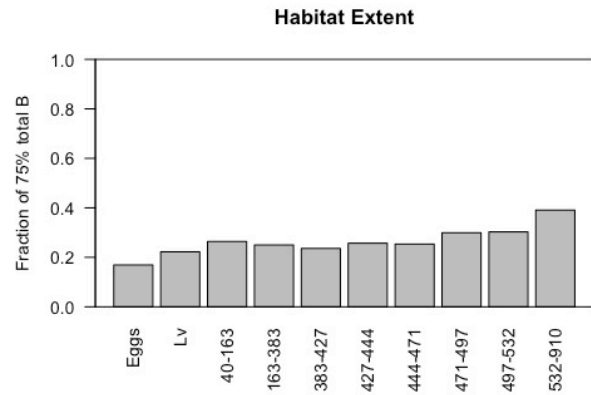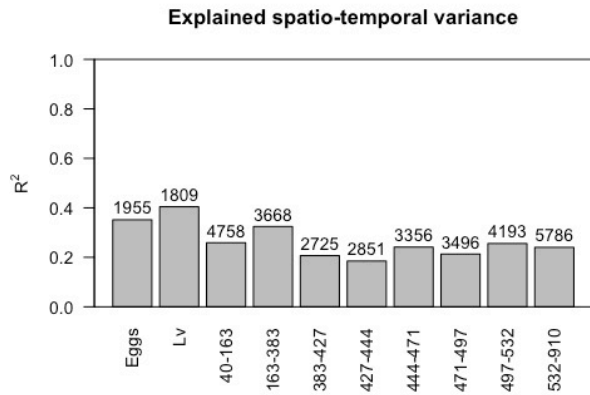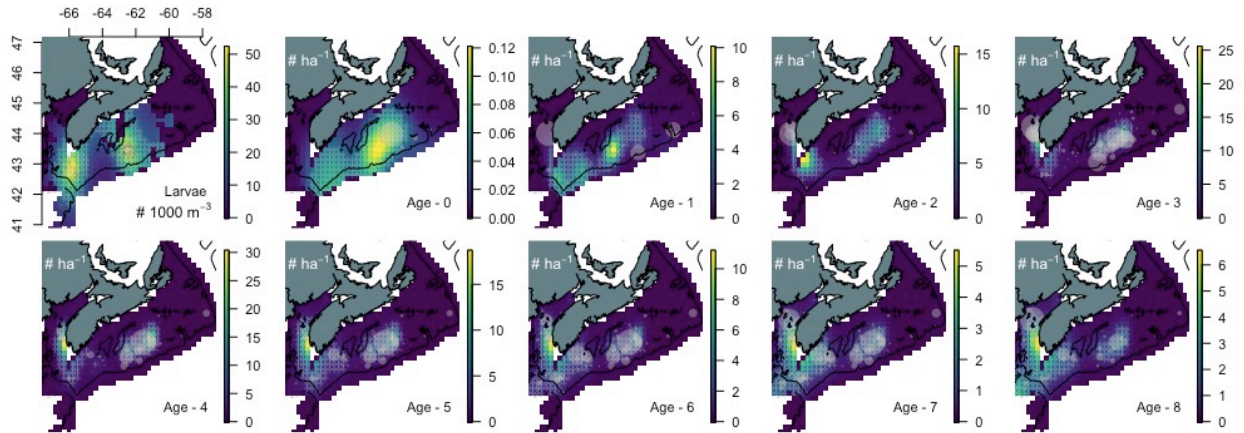
Figure 4. Spatial distribution of haddock in the Scotian Shelf over different ontogenetic stages and age groups. Predictions are shown as color image in the units of number of individuals m^{-3} (larvae), or numbers of individuals per hectare (ha^{-1}) for all other age groups. Predictions were obtained from presence/absence and presence only GAM models (delta method, equation 3). Grey bubbles are observed d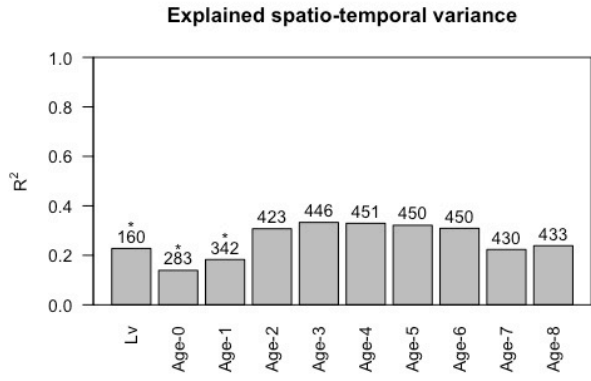ensities and the region delineated by a white cross ('+') represents the estimated habitat e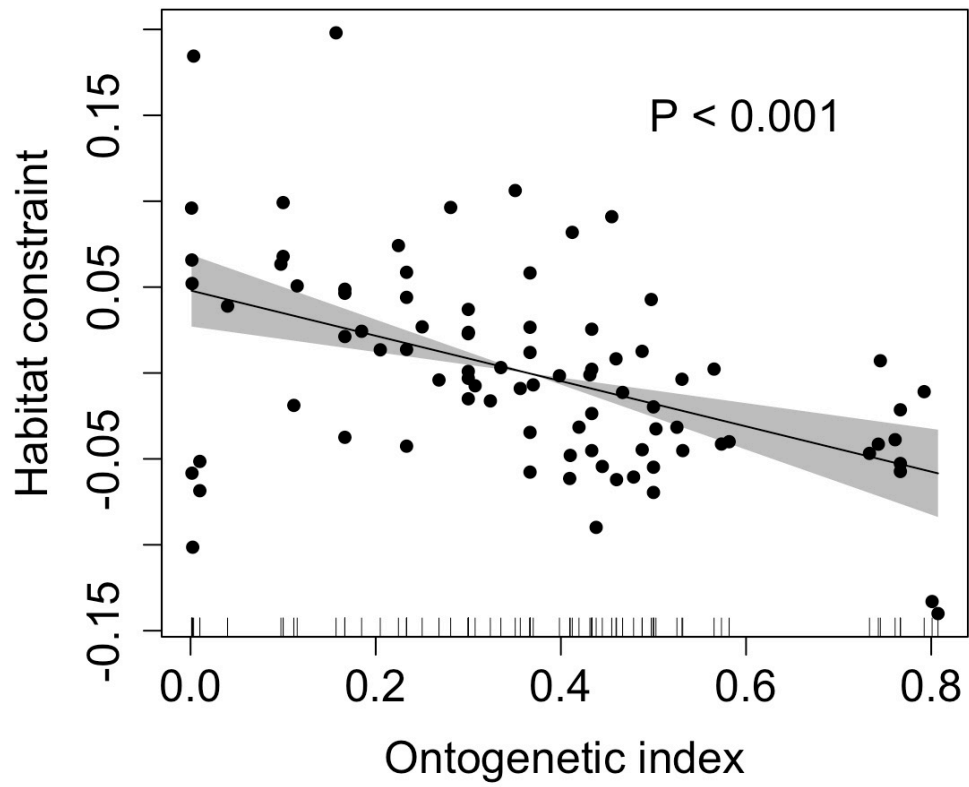xtent, or the portion of the surveyed area that contains 75% of the estimated total abundance. The stage or age (in years) examined is indicated in the lower left corner of each plot. The 200m depth isobaths is shown.
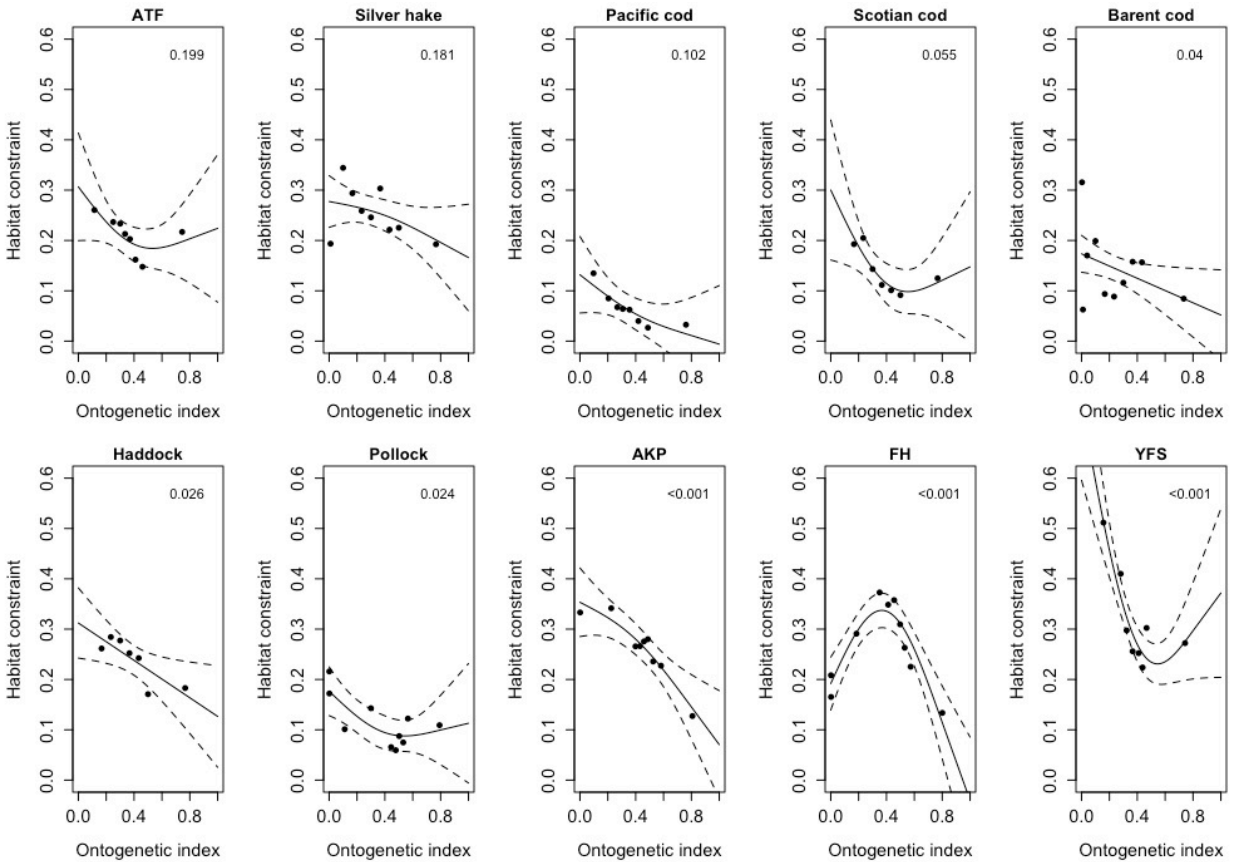
Explained spatio-temporal variance

Habitat Extent

Geographic consistency

Habitat Constraint

964

Ontogenetic Constraints   49/51

P < 0.001

Figure 7. Relationship between the habitat constraint metrics and the ontogenetic index for the ten populations examined in this study (Equation 7). The smooth solid lines are average relationships determined by a fixed effect GAM between constraint and the linear ontogeny index. Dashed lines are 95% confidence intervals. The scale of the y-axis represents the response variable. Species are sorted in decreasing order of their p-value for the ontogenetic index (upper right corner on each plot). For species abbreviations see Table 1.