1 **How the spatio-temporal overlap of cod, haddock, and capelin larvae affects their**

2 **recruitment in the Norwegian-Barents Sea system**

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16 **Short title:** Larval fish competition in the NBS system

17 **Abstract**

18 The Norwegian-Barents Sea (NBS) system is very productive. However, the extent at

19 which this productivity varies remains uncertain for many species. Cod (*Gadus morhua*),

20 haddock (*Melanogrammus aeglefinus*), and capelin (*Mallotus villosus*) are three key

21 species overlapping in a large portion of the NBS ecosystem. In this hypothesis-driven

22 study, we investigate the interaction of these three species during their pelagic larval stage

23 and assess the impact of their spatio-temporal overlap on survival. We hypothesise that the

24 spatio-temporal overlap between the larvae of the three species, as they likely drift

25 together, influences their survival at later stages. We calculate the spatio-temporal overlap

26 of each pair of the three studied species and test it against their recruitment. We utilise a

27 multiple linear regression model with temperature, spawning stock biomass, and spatio-

28 temporal overlap among larvae, their food, and competitors as explanatory variables. We

29 explained ~ 43 %, ~ 24 %, and ~ 73 % of the variability in cod, haddock, and capelin

30 recruitment, respectively. The overlaps between larval cod and competing species and/or

31 food have a negative influence on cod recruitment, whereas the sign of the relationships

32 pertaining to haddock and capelin vary. These results improve the understanding of how

33 these fish species use their critical habitats to face emerging environmental stressors.

34 **Keywords:** recruitment dynamics; fish survival; larval competition; and spatio-temporal

35 modelling.

1. INTRODUCTION

37 The Norwegian-Barents Sea (NBS) system is a highly dynamic area with strong physical

38 and biological forcing (Sakshaug et al. 2009, Eide et al. 2013). The NBS is known for its

39 high productivity yet relatively low biological diversity, meaning that the few fish species

40 that take part in the NBS production cycles are present in high abundances (Hamre 1994).

41 Among its most important fish species are the Northeast Arctic cod (*Gadus morhua*, a

42 major predator) and its prey, that are: young stages of the Northeast Arctic haddock

43 (*Melanogrammus aeglefinus*), capelin (*Mallotus villosus*), and juvenile stages of

44 Norwegian spring-spawning herring (*Clupea harengus*) (Hamre 1994).

45 With the collapse of the Barents Sea capelin stock in the mid-late 1980s, the Northeast

46 Arctic cod stock decreased due to lack of food (Hamre 1994, Durant et al. 2021). The

47 factors that influenced their stocks may be directly or indirectly connected (Pálsson 1994).

48 Cod, haddock, and capelin spawn on the Norwegian coast, and drift into the NBS system

49 to feed. In particular, capelin spawns along the Murman coast (although main spawning

50   area is on the Norwegian side, Gjøsæter 1998), while cod and haddock spawn along the

51   continental slope (with different centers of magnitude and depth, with haddock spawning

52   closer to the coast, Jakobsen & Ozhigin 2011). We thus hypothesise that the overlap

53   between cod, haddock, and capelin at the larval stage (and their prey) will play a crucial

54   role in the fish survival at later stages. Furthermore, the degree to which they overlap may

55   differ among years.

56

57   The three species use the oceanic regions of the NBS as feeding grounds, and then migrate

58   closer to the coast to spawn (Olsen et al. 2009). The lives of these species are therefore

59   highly intertwined as they compete for food resources, including the most dominant

60   zooplankton species in the NBS system, *Calanus finmarchicus* (Broms et al. 2009, Orlova

61   et al. 2010, Dalpadado et al. 2012, Aarflot et al. 2017, Prokopchuk & Trofimov 2019). *C.*

62   *finmarchicus* is documented as the main prey item for cod and capelin larvae (Sysoeva

63   1965, Ellertsen et al. 1984, Karamushko & Karamushko 1995, Kvile et al. 2014). For

64   haddock, there is evidence suggesting that *Calanus* spp. importance gradually decreases in

65   the diet of larvae larger than 19 mm long (Sysoyeva et al. 1976). Even if *Calanus* spp. are

66   less important in the diet of haddock larvae than in cod larvae, especially for larger ones, a

67   competition for *C. finmarchicus* may occur for larval cod (all sizes) and haddock (2-19

68   mm) (Sysoyeva et al. 1976, Rowlands et al. 2008). This is supported by the fact that larval

69   haddock exploit a wider range of prey types of smaller and slower moving organisms than

70   other gadoid species (Sysoeva & Bazlova 1967, Economou 1991, Rowlands et al. 2008).

71   Additionally, the three fish species (cod, haddock, and capelin) greatly influence each

72   other's food availability acting as main prey item for each other at later stages (*e.g.* see cod

73   and capelin) (Sundby & Fossum 1990, Hamre 1994, Gjøsæter 1998).

74

75 The place and time where and when these fish spawn and first-feed are thus crucial factors

76 affecting their survival into later stages, yet they are also the most vulnerable to external

77 factors, such as climate change or oil extraction (Olsen et al. 2009). As observed by Olsen

78 et al. (2009), assessing the extent of the spatio-temporal overlap between these species

79 (even though they also considered saithe, *Pollachius virens*) is "imperative to understand

80 the total effects of all human activities in these [vulnerable] areas and to employ a

81 precautionary approach when managing existing and new human activities". These authors

82 acknowledge examples of coastal activities greatly affecting spawning areas, such as

83 fishing, subsurface petroleum installations, offshore wind farms, aquaculture, and noise

84 from seismic exploration.

85

86 As the larval stages of the three species (Northeast Arctic cod, Northeast Arctic haddock,

87 and Barents Sea capelin) are known to overlap in time and space, we ask: what is the effect

88 of spatio-temporal overlap between the larval stages of the three fish species on their

89 survival to later stages? Our objectives are 1) to quantify the spatio-temporal overlap in

90 both space and time, and 2) to assess whether the spatio-temporal overlap affects the

91 survival of the three species.

92 **2. METHODS**

93   2.1. Data

94 Data on larval abundances of the three fish species (cod, haddock, and capelin) were

95 collected during the ichthyoplankton surveys run by the Knipovich Polar Research Institute

96 of Marine Fisheries and Oceanography (PINRO) in both spring (April – May) and summer

97 (June – July) from 1959 to 1993 along the northeastern Norwegian Sea and the

98 southwestern Barents Sea. In this study, we include stations where data were collected by

99   both the ring trawl (150 cm diameter opening, 3 mm mesh size) and the egg net (80 cm

100   diameter opening, 0.505 mm mesh size, Mukhina et al. 2003) (Figure 1). While larvae are

101   also captured in egg nets, the egg nets sample larvae less efficiently than the ring trawls.

102   The main copepod prey of most of the fish larvae species studied here is *C. finmarchicus*.

103   It is also the only zooplankton species which has had the data digitised for this dataset due

104   to lack of current recourses on this specific project (*C. finmarchicus* accounted for 80-90%

105   of zooplankton community) (Aarflot et al. 2018, Prokopchuk & Trofimov 2019). Data on

106   *C. finmarchicus* were collected during the same survey as the fish larvae with a Juday

107   plankton net (37 cm diameter opening, 180 µm mesh size) (Nesterova 1990).

108   Concentration of both fish larvae and copepod data were recorded as individual m^{-3} for

109   each size class (we do not use size class in the present study). In addition, data on herring

110   larvae were collected as the other species. However, because the spatial distribution of

111   these larvae does not match that of the sampling, we exclude herring larvae as a studied

112   species (s), and only considered it as a competitor, thus driving species (D). The herring

113   stock also collapsed in this area in the 1960-1970s, and recruitment was very low until

114   1983, thus no larvae were collected in several of the years.

115

116   Temperature data were from the Nordic Seas 4 km numerical ocean model hindcast

117   archive from 1959 to 1993 (Lien et al. 2013) as in Ferreira et al. (2020). In this study, we

118   use data for the upper 50 m of the water column and match the stations from the fish larvae

119   survey to predict the abundance of the four species of fish at their larval stages.

120

121   We define survival indices as: timeseries of recruitment at age 3 for cod and haddock

122   (1959-1993), and age 1 for capelin (1980-1993); as well as the 0-group timeseries (1980-

123   1993) of the three fish species. Data on recruitment and spawning stock biomass (*SSB*)

124   were collected from the Arctic Fisheries Working Group (AFWG) from ICES (ICES

125   2020).

126

127   The following sections describe the methodology used to estimate the effect of the spatio-

128   temporal overlap between the larval stages and their competitors and/or food. Details are

129   found in Figure 2. We use the larval abundance data to develop a statistical model that fills

130   in the seasonal gaps, and quantifies the spatio-temporal distribution of each species from

131   day of year (DOY) 93 (~ April 3) to 208 (~ July 27, Supplementary Figure S1). DOY 93

132   and 208 are chosen based on data availability. However, we only consider the model

133   predictions within DOY 110 (~ June April 20) to 197 (~ July 16) as that is when the most

134   larvae were present, meaning that there is enough data within this period for the next step

135   (as observed in Supplementary Figure S2). The fish larvae models are based on Stige et al.

136   (2017) and Ferreira et al. (2020), and the copepod model is based on Kvile et al. (2014)

137   and Ferreira et al. (2020). Model equations and scores can be found in Table 1. Since the

138   data are zero-inflated, we use the Tweedie distribution (family=tw(), Dunn & Smyth 2005,

139   2008, Dunn 2017) within the Generalised Additive Models (GAM, mgcv package version

140   1.8-39, Wood 2017) within R version 4.1.2 (2021-11-01) (Team 2021).

141

142   I.   Generalised Additive Models (GAM modelling)

143   The first step of our approach (Figure 2) is to estimate the concentration of fish larvae of

144   cod, haddock, capelin, and herring, across space and time. We use Eq. (1), where Ab_{xt} is

145   the larval concentration at station x and time t (L_{xt}). The coefficient α is the intercept. The

146   smooth, adaptive function f_1 of day of year (*DOY*) estimates the average seasonal change in

147   abundance, whereas f_2 of *DOY* estimated the *DOY*-dependent coefficient for the effect of

148   sea temperature anomaly (*STempA*) calculated as in Kvile et al. (2014) and estimates how

149   the seasonal pattern varies with sea temperature (*STemp*). The two-dimensional smooth

150   function f_3 of longitude (*LON*) and latitude (*LAT*) estimates the time-averaged spatial

151   pattern. *YEAR$_t$* and *STAGE$_{Lt}$* are random effects of year and length-based stage,

152   respectively. There are five length classes for fish larvae: 0-5, 6−10, 11− 15, 16−20, and

153   21+ mm, henceforth referred to as stages. Based on these, the average length per species is

154   as follows: 13.43, 13.40, 11.71, and 18.50 cm for cod, haddock, capelin, and herring,

155   respectively. The higher length of herring confirms the reasoning for excluding it as a

156   studied species (*$_S$*) as these are older individuals, thus with different dynamics. The

157   coefficients β_1 and β_2 account for sample size, with N_{eggnet} being the number of egg net

158   hauls and $N_{ringtrawl}$ the number of ring trawl hauls per station *st*. We use different

159   coefficients for the effects of egg nets and ring trawls because the capture efficiency is

160   likely to differ between the two gears. Finally, ε_{xt} is a normally distributed error term. We

161   also add a weights term that considers the number of data points per *DOY* in logarithmic

162   scale, thus providing less weight on the *DOYs* with less data (except for herring). Eq. (1)

163   (Figure 2) is applied to each of the four fish species separately. The smooth functions

164   applied to *DOY* are used with a single penalty built in smooth classes (*bs*) with an adaptive

165   smoother (*"ad"*) and a dimension of the basis used to represent the smooth term (*k*) of 9.

166   The spatial aspect is included as a tensor product smoother (*te*) with a *bs* set to a low rank

167   isotropic smoother of the *LON* and *LAT* covariates (*"tp"*) and a *k* of 5. *YEAR* is accounted

168   for as a random effect (*"re"*) with a *k* left to default (9) to allow for a smoother interannual

169   variability. A similar approach was used in Ferreira et al. (2020).

170

171   To estimate the concentration of zooplankton across space and time, we use Eq. (1) (Figure

172   2). Here, *Ab$_{xt}$* is copepod concentration in logarithmic scale [log(zoo+1) to account for

173   zero-inflated data] at station *x* and time *t* and represents the prey concentration (*C.*

174   *finmarchicus*, *Z$_{xt}$*) for cod, haddock, and capelin. We analyse 4 stage classes for *C.*

175   *finmarchicus*, where Ns is nauplii, C1 is CI-III, C2 is CIV-V, and C3 is CVIM-F

176   (henceforth referred to as stages). We apply the *C. finmarchicus* model individually for

177   each stage, as opposed to modelling all stages together (as we do for the fish). We use the

178   method="ML" with k set to 5 for stages Nauplii and CVI, and 9 for stages CI-III and CIV-

179   V and bs set to "cr" for a cubic regression spline. All other terms are used as for the fish

180   models (all the R Software syntax used to run all models is available in the Supplementary

181   Table S1). Model results of L_{xt} (larval abundance) and Z_{xt} (*C. finmarchicus* abundance)

182   provide smooth, gap-free seasonal cycles of larval abundance from which we can estimate

183   the areas under the curves (Supplementary Figure S1).

184

185   II.   Area calculation

186   The second step of our approach (Figure 2) is to calculate the area under the Ab_{xt} curves as

187   in Eq. (2). We thus use L_{xt} as the abundance estimates for the fish species and calculated

188   the overlap between each of them and the other competing fish species (competitors); and

189   use Z_{xt} as the food estimate and calculate the overlap between each of the fish species and

190   their food (food). We also consider both factors together (competitors+food). We calculate

191   these using two approaches: an one-by-one and all-competitors-together. We calculate the

192   area under the Ab_{xt} curves as in Ferreira et al. (2020) (Eq. (2), Figure 2), where *A* is defined

193   as the area under the curve of abundance (*L*) for two sets of data: a) the species being

194   studied (A_S), *i.e.* the studied species (henceforth referred to as $_S$); or b) the driving species

195   (A_D), *i.e.* the species that interact, in some form, with the studied species (henceforth

196   referred to as $_D$), either representing the abundance of competitors or of food). For

197   instance, in the case where cod is the studied species, the driving species would be

198   haddock, capelin, and herring as competitors, and *C. finmarchicus* as food. The

199   abundances of relevant species are summed up prior to calculating the area under their

200   curve (A_D) for different combinations: food (*F*), competitors 1 to 3 (*C*), or competitors 1 to

201   3 and food ($C+F$, Figure 2). We calculate the area of the curve (A) for both sets (A_S and

202   A_D), where the seasonal trends in both abundances follow a Gaussian curve defined by the

203   estimated standard deviation (sd) and the timing of the peak (m).

204

205   III.   Spatio-temporal overlap (STO) calculation

206   The third step consists of the calculation of the spatio-temporal overlap metric so that STO

207   provides us the area where two areas (A_S and A_D) overlap: the area under both curves

208   (orange area, Durant et al. 2005, Durant et al. 2019). STO is thus calculated in Eq. (3)

209   (Figure 2) and represents the minimum of the integrals A_S and A_D between DOY_{min} (154)

210   and DOY_{max} (197). STO has no units, as both concentrations cancel each other, therefore,

211   we consider STO a dimensionless metric. Further details on how to calculate STO can be

212   found in Durant et al. (2005) and the R scripts can be found in Durant et al. (2019). See

213   also Table 2 and respective explanation in Ferreira et al. (2020). STO represents the spatio-

214   temporal overlap between each of the studied fish species and their food (STO_F), 1 to 3 of

215   its competitors (driving species, STO_C), or 1 to 3 competitors and their food (driving

216   species, $STO_C + STO_F$).

217

218   IV.   Correlation

219   STO_C, STO_F and $STO_C + STO_F$ are computed annually for 1959-1993 and for each station

220   where data are found. We then test them for their ability to explain variability in the

221   survival index of the studied species. We use recruitment (R) age 3 for cod and haddock,

222   and age 1 for capelin. Results for the 0-group index are shown in the Supplementary

223   Material. We follow Eq. (4) to build a multiple linear regression model (Figure 2). Here, R_t

224   is the recruitment index in year t, STO_i is the Spatio-Temporal Overlap metric that

225   corresponds to STO_C, STO_F or $STO_C + STO_F$ and their correspondent slope (b_1, b_2, or b_{3a}

226   and b_{3b}), Δ is the species-specific lag (in years) of the *STO* in comparison to the year-class

227   of the *R* (age 3 for cod and haddock, and age 1 for capelin), $STemp_t$ is the annual average

228   *STemp*, *a* is the intercept, *c* and *d* are the slopes for $STemp_t$ and SSB_t, respectively, *e* is the

229   slope for the time step (year, *t*) of the regression line, andε_t is the normally distributed

230   error. Estimates of R_t are based on the recent stock assessment (ICES 2020) and then tested

231   against the spatio-temporal overlap indices STO_C, STO_F and $STO_C + STO_F$ with the linear

232   regressions to assess whether any of the overlaps can explain *R* variability. We test for

233   collinearity among all variables using a variance inflation factors (VIF) analysis (Zuur et

234   al. 2007).

235

236   V.   Recruitment variability

237   As a last step, we assess the effect of each of the explanatory variables in explaining the

238   recruitment variability of each of the fish species. We start by analysing both the multiple

239   r^2 and the sign of the multiple regression, linear models assessing recruitment variability,

240   as well as the contribution of the whole model (as shown in Figure 2). To assess the

241   individual contribution of each of the explanatory variables in the multiple regression

242   model explaining the recruitment variability, we use the package relaimpo (Grömping

243   2006) with the "proportional marginal variance decomposition" (pmvd), as in Durant et al.

244   (2021). This result provides information about how much *STO* contributed to the overall

245   variability in recruitment compared to the remaining variables (*SSB*, *STemp*, and *t*).

246   **3. RESULTS**

247   The spatio-temporal overlap between the studied species and its competitors (STO_C,

248   orange) is analysed for each of the three fish species (cod, haddock, and capelin) as the

249   studied species (Figure 3). A similar approach is used to investigate the spatio-temporal

250   overlap between the studied species and its food (STO_F, green) and both together ($STO_C +$

251   STO_F, blue). We here show the correlations between the overlap indices (STO_C, STO_F and

252     $STO_C + STO_F$) and recruitment (R) with each studied species (cod, haddock, and capelin) in

253   detail (Figure 3). We find that all the relationships between the overlap indices of cod

254   larvae (STO_C, STO_F and $STO_C + STO_F$) and its recruitment are statistically significant (p-

255     $value \leq 0.012$, Figure 3), with r^2 ranging from 29.4 to 42.6 % (recruitment at age 3). Only

256   one relationship is statistically significant for haddock with a r^2 of 23.7 % (recruitment at

257   age 3); as well as capelin with a r^2 of 72.5 % (recruitment at age 1). The Supplementary

258   Table S2 shows the parameter estimates for all the linear models as in Eq. (4) in Figure 2.

259   The analyses using the 0-group timeseries show different results (Supplementary Figure

260   S3) perhaps due to the fact of the various lengths in time.

261

262   Most of the relationships between cod R and the overlaps are positive (Supplementary

263   Table S1), meaning that the higher the overlap, the higher the R, except for the effect of the

264   overlap between haddock and cod larvae when compared together with food (STO_C+STO_F,

265   blue Comp 1, Figure 3). The VIF analysis (test of collinearity) detects three issues (marked

266   with an asterisk in Figure 3). The first concerns the cod larvae interaction with the food

267   and haddock, the second is with the cod larvae interaction with food and all the

268   competitors, and the third is with the haddock larvae and all the competitors (cod, capelin,

269   and herring). Therefore, we will not consider these results relevant. The signs of the

270   relationships with haddock R are a mix between negative and positive, but only one is

271   significant: the effect of the overlap between capelin and haddock larvae is positive and

272   significant (orange Comp 2, Figure 3, Supplementary Table S2). Competition alone has no

273   effect on capelin R as none of the STO_C are significant (orange bars, Figure 3,

274   Supplementary Table S2). The effects of $STO_C + STO_F$ are all negative (blue bars, Figure

275   3) meaning that the higher these overlaps, the lower capelin, but only one is significant: the

276   interaction between capelin larvae with food and herring.

277

278   Some of the relationships between STO_F and STO_C+STO_F, and the 0-group are statistically

279   significant (*p-value* ≤ 0.040, Supplementary Figure S3, Supplementary Table S2) with r^2

280   ranging from 69.8 to 78.9 % for cod, and 57.7 to 85.2 % for capelin. The relationships for

281   haddock are not significant (Supplementary Table S2). In terms of the sign of the

282   parameter estimates, the results are very similar to the significant ones found in the

283   analyses using R (Figure 3, Supplementary Table S1 and S2).

284

285   Prior to the calculation of STO, we model the abundance of each fish species (Ab_{xt}, Eq. (3)

286   in Figure 2 and Table 1). We observe that cod larval abundance (L_{xt}) peaks between April

287   20 (DOY 110) and July 9 (DOY 190), even though most of the two-gear sampling

288   occurred in June-July), haddock between May 7 (DOY 127) and July 16 (DOY 197),

289   capelin between April 23 (DOY 113) and July 16 (DOY 197), herring between April 20

290   (DOY 110) and May 26 (DOY 146), whereas *C. finmarchicus* abundance (Z_{xt}) peaks

291   between April 28 (DOY 118) and July 16 (DOY 197). These peak dates suggest that peaks

292   may be multiple in some species and occur in different times, so the sampling may have

293   missed the actual peak dates for these species in some years, as the average peak dates in

294   those years fall on either the first or last date of our predictions (April 20 to July 16).

295

296   Their spatial distributions were considered similar as the four fish species and *C.*

297   *finmarchicus* were collected collectively during the same survey. Since it is only possible

298   to calculate the overlap indices where each pair of species occurrs both spatially

299   (Supplementary Figures S5 and S6) and temporally (Supplementary Figures S7 and S8),

300   the spatio-temporal distribution of the overlap indices are the highest with food and the

301   first competitor and lowest with herring. All these results (Supplementary Figures S5-8)

302   reflect what is shown in Figure 3: higher overlap indices with food and first competitor and

303   lower with herring.

304

4. DISCUSSION

306   In this study, we assess the effect of the spatio-temporal overlap (STO) between the larval

307   stages of three of the most important fish species in the NBS: Northeast Arctic cod,

308   Northeast Arctic haddock, and Barents Sea capelin (Olsen et al. 2009) on their survival to

309   later stages. We find that the overlap with its prey and competitors can explain a

310   substantial part of a fish recruitment variability (~ 24 to ~ 73 %, Figure 3), thus

311   demonstrating that the survival dynamics are, beyond being dependent on the overlap of

312   fish larvae with food, also dependent on the overlap with competitors. We start by

313   quantifying the STO in both space and time, and then assessed whether the STO affects the

314   survival of the three species. Therefore, our results indicate that the survival of the NBS

315   fish is affected by the overlap between their larval stages with their competitors and/or

316   food.

317

318   The combined STO (STO_C+STO_F) proves to be the most successful at explaining the

319   survival indices of the fish species (highest r^2), whereas the least successful is the STO_C,

320   except for haddock. This indicates that the STO between larvae and their prey, *C.*

321   *finmarchicus*, plays a crucial role in the survival of these fish species in the NBS system

322   (Ferreira et al. 2020, Endo et al. 2022). In terms of biomass, *C. finmarchicus* contributes

323   with more than 80 % of biomass to the total zooplankton community in May (personal

324   communication by Irina Prokopchuk). Thus, the presence of competition only makes sense

325   if one considers the prey availability as well. This suggests that these species are likely

326   competing for food and other factors (*e.g.* simultaneously predated on) while sharing the

327 same habitat. These findings can be interpreted in two ways. 1) As suggested by Endo et

328 al. (2022), spatially resolved data is needed in order to understand match-mismatch

329 dynamics. In our study, the overlap metric accounts for the spatial distribution of the

330 larvae, their competitors, and their prey (Supplementary Figures S5 and S6). 2) The same

331 authors suggested that food was not a limiting factor for cod larvae. In our study, we find

332 that food is a very important factor determining cod survival (even more so than the STO

333 with the cod competitors) possibly having a first effect on their growth from larval to

334 recruitment stages (Figure 3). However, we do recognise that food does not appear to be a

335 limiting factor.

336

337 The match-mismatch hypothesis states that the higher the prey-predator overlap in time

338 and space, the higher are the chances of predator survival (Hjort 1914, Cushing 1990,

339 Ferreira et al. 2020, Ferreira et al. 2023). Thus, it is expected that there is a positive

340 relationship between such overlap and survival. In our study, the recruitment of Northeast

341 Arctic cod is positively correlated with most overlaps, except for when their larval stages

342 overlap with those of haddock when food is considered. This negative relationship may

343 indicate a competition for the same food items which, in this case, is *C. finmarchicus*.

344 However, in other cod populations, larvae feed on other copepod species (*Oithona similis*

345 and *Pseudocalanus* spp.), such is the case of Georges Bank's cod or the Atlantic cod off

346 the Gulf of St. Lawrence (Kane 1984, Robert et al. 2011). Furthermore, even though

347 haddock recruitment cannot be explained by the STO with cod larvae, the same STO can

348 explain cod recruitment. This suggests that Northeast Arctic cod larvae are negatively

349 impacted by the presence of haddock larvae when *C. finmarchicus* is present, but not the

350 other way around, possibly because *C. finmarchicus* are less important for haddock than

351 euphausiids for haddock larvae (Sysoeva & Bazlova 1967) but they are for cod (Sysoeva

352 1965).

353

354   The only significant relationship we found to explain the Northeast Arctic haddock

355   recruitment is the STO between haddock larvae and capelin (Figure 3, Supplementary

356   Table S2). As suggested by Gjøsæter et al. (2015), the amount of competition at the early

357   life stages impacts predation mortality. In addition, the presence of a known competitor at

358   the larval stage may lead to increased feeding, especially when haddock are known

359   predators of capelin larvae at larger stages (Gjøsæter et al. 2015). Therefore, it is beneficial

360   for haddock to grow into juveniles when there are capelin larvae present. However, there is

361   no known evidence of this occurring during the stages considered here. It is important to

362   note that the presence of "food" alone (*C. finmarchicus*) did not explain haddock

363   recruitment, which indicates that haddock larvae may not only feed on *C. finmarchicus*:

364   see the case for the North Sea and the Irish Sea (Economou 1991, Rowlands et al. 2008,

365   respectively) as well as in the Barents Sea (Sysoeva & Bazlova 1967).

366

367   The recruitment of Barents Sea capelin is positively impacted by the STO of their larvae

368   with *C. finmarchicus* (positive relationship) and with herring larvae (negative relationship,

369   Figure 3), possibly because these two species may be competing for *C. finmarchicus*. The

370   highest percentages explaining fish recruitment in our study are found for this species,

371   where we explained up to ~ 73 % of capelin recruitment at age 1 with the STO's at the

372   larval stages. However, it is important to note that the recruitment timeseries of capelin is

373   shorter than that of the other species.

374

375   The recruitment of Northeast Arctic haddock is also impacted by increasing temperatures

376   (Bogstad et al. 2013, Landa et al. 2014). Stige et al. (2019) suggested that it is the mean

377   body size of larval and/or juvenile haddock that is associated with high survival during the

378   first winter and with strong recruitment three years later. Their results support the

379   hypothesis that, by having a larger mean body size at age 0, these fish grow more rapidly

380   out of the size range most susceptible to predation by, for instance, adult cod, or by

381   adjusting their winter energy stores. However, these authors acknowledge that it is

382   important to assess the impact of environmental factors on size and abundance during the

383   first growing season. High temperature is linked to, for instance, a high survival of eggs,

384   larvae and early juveniles (Stige et al. 2019), and because egg mortality has been found to

385   be greater for cod than for haddock (Langangen et al. 2013), higher temperatures paired

386   with low egg mortality would thus be expected to lead to higher recruitment. In our study,

387   we do not account for size, egg mortality, or predation by adult fish, which, paired with

388   strong environmental data, would perhaps improve our findings, particularly those of

389   haddock.

390

391   As per our results, haddock recruitment is not affected by the interactions haddock larvae

392   experience, except for when capelin larvae are present (Figure 3). Little is known as to

393   what extent haddock and capelin compete at these stages, but there is evidence that larval

394   haddock compete with cod of similar sizes in Georges Bank (Kane 1984) and the Irish Sea

395   (Rowlands et al. 2008). However, our results suggest that further studies should look at the

396   effects of capelin, not cod, on haddock recruitment dynamics.

397

398   Regarding the recruitment of Barents Sea capelin, Langangen et al. (2013) did not find

399   evidence for the effect of larval length on abundance. Interestingly, capelin recruitment

400   seems to be highly affected by predation, specifically by predation by young herring

401   (Gjøsæter & Bogstad 1998, Hjermann et al. 2010, Gjøsæter et al. 2015), which indicates

402   that future studies of match-mismatch dynamics should account for the overlap dynamics

403   with predators as well. Nevertheless, even though Gjøsæter et al. (2015) acknowledged

404   that other factors may have led to the almost total recruitment failures, the authors still

405   suggest predation as the main factor for these failures. In our study, we explained ~ 73 %

406   of capelin recruitment, where strong evidence was found for the positive impact of food

407   and negative impact of herring on capelin recruitment at age 1 (Figure 3). This means that,

408   when capelin larvae coexist in space and time with one of their main competitors, their

409   chances of survival to age 1 decrease. However, there is no evidence that small capelin

410   larvae are competing for *Calanus* and euphausiids (Pedersen & Fossheim 2008), thus

411   suggesting another mechanism such as competition for another food source or increased

412   predation. Nonetheless, we acknowledge that future studies should include predation by

413   older herring, cod, haddock, red king crab, diving birds, and even capelin (Gjøsæter et al.

414   2015). Again, the length of the capelin timeseries may have impacted our results and thus

415   confirm the previously found fluctuations for capelin (Gundersen & Gjøæster 1998).

416

417   4.1. Room for improvement

418   Regarding the lack of evidence to explain haddock and capelin recruitment in most

419   combinations (Figure 3), the spatio-temporal overlap metric may not have been the ideal

420   approach to assess the match-mismatch dynamics with their competitors and food. There

421   are several reasons as to why. In terms of modelling, our results may have been different if

422   we had used different modelling approaches, as using stage-specific modelling (as in

423   Ferreira et al. 2020). The spatio-temporal abundance distributions of each of the species

424   derived from the models may be lacking detail and patterns that are important, thus

425   weakening the ability to discern relationships in the next step of the analysis. In the next

426   paragraphs, we discuss which biological reasons should be considered further.

427

428　　　　4.1.1. Spatio-temporal coverage

429　Northeast Arctic haddock spawns pelagic eggs from March to June, peaking in late April

430　and early May (Olsen et al. 2009), whereas our study period starts on April 20 and ends on

431　July 16 (Supplementary Figure S1). Even though the dataset shows a peak in mid-May for

432　both haddock and capelin, the temporal coverage of the survey is insufficient during that

433　period (see Supplementary Figures S2 and S4), thus our analysis may be missing the main

434　peak in haddock and capelin larvae which, in turn, affects the relationship with their

435　survival. Our data period (April 20 to July 16) encapsulates an apparent second peak but

436　that may not have been enough to explain more than ~ 24 % of the variability in haddock

437　recruitment.

438

439　The spatial distribution of the survey in which our study is based covers the main transport

440　paths of eggs and larvae from the spawning grounds of the Northeast Arctic cod, Northeast

441　Arctic haddock, and partly Barents Sea capelin (see, for instance, Olsen et al. 2009,

442　Bogstad et al. 2013). However, it does not cover the spawning distribution of Norwegian

443　spring-spawning herring (also evident in the lack of overlap in Supplementary Figures S5

444　and S6). It is also important to note the different lengths of the recruitment and 0-group

445　timeseries in our study. Special attention should be paid to the results due to these

446　differences.

447

448　　　　4.1.2. Other prey, competitors, or predators

449　Northeast Arctic cod and Northeast Arctic haddock compete for the same prey species

450　(Durant et al. 2020) and inhabit the same area, therefore leading to a spatial-temporal

451　overlap between them. *C. finmarchicus* is a high energetic food and dominant species in

452　the area (Broms et al. 2009, Orlova et al. 2010, Dalpadado et al. 2012, Aarflot et al. 2017,

453 Prokopchuk & Trofimov 2019). They also match in time and space with the fish species

454 we study. However, there are indications that haddock larvae may have a wider range of

455 prey species than other gadoids, such as cod (Sysoeva & Bazlova 1967, Economou 1991,

456 Pálsson 1994), which suggests that we may not be accounting for more preferable prey

457 species for haddock larvae in the NBS. The same may be true for capelin.

458

459 In terms of competition, other fish species compete with haddock within the NBS system

460 that our study does not account for. For instance, Norway pout and whiting larvae have

461 been observed as competitors of haddock larvae in the North Sea (Economou 1991), two

462 fish species not covered by our dataset. In addition, adults of the Northeast Arctic cod are

463 also known predators of haddock and capelin early life stages (see Holt et al. 2019 but not

464 necessarily at the larval stage, Durant et al. 2023), which shows that cod adults may affect

465 the survival of haddock and capelin, even though they do not match in water layers. More

466 recently, Yaragina et al. (2022) reported an increasing trend of gelatinous zooplankton

467 (possibly due to an increase in temperature) as bycatch from the same data sampling as the

468 one used in this study. The species they found are known predators of fish eggs and larvae,

469 as well as competitors with the fish larvae for zooplankton prey. The spatial and temporal

470 effects of both such predators as well as competition as investigated here may contribute to

471 the spatially explicit mortality experienced by the fish larvae, which are known to play an

472 important role in survival from different spawning grounds (Langangen et al. 2016). All

473 these interactions are likely to affect the survival and recruitment of fish larvae (Akimova

474 et al. 2019), and should, therefore, be considered when assessing spatio-temporal predator-

475 prey overlap and its effects on recruitment.

476

477   4.1.3. Weak larvae-Recruitment link

478   According to Stige et al. (2019), there is a strong link between the abundances of Northeast

479   Arctic cod larvae to age 1 to 3, whereas the same is not true for Northeast Arctic haddock

480   and capelin (see their Figure 4). These non-significant relationships for haddock and

481   capelin may be the reason why our STO at the larval stages does not explain the

482   recruitment of haddock recruitment at age 3 (Supplementary Table S2). However, as also

483   shown by Stige et al. (2019), the link between the abundances of the larvae and the 0-

484   group is statistically significant for capelin (not for haddock), which may explain the much

485   higher r^2 (between the overlap and the competitors and their food) we find for capelin than

486   for haddock (Supplementary Figure 2). The diet of the Northeast Arctic haddock larvae

487   remains largely understudied. Therefore, we should encourage seeking high-quality diet

488   and prey abundance data for haddock larvae if we want to understand the potential

489   competition with cod or capelin.

490   4.2. <u>Future implications</u>

491   When pairing the effects of food and competitors together, these two factors can explain up

492   to ~ 43 % of the recruitment variability of Northeast Arctic cod, as well as ~ 24 and ~ 73 %

493   of that of haddock and capelin, respectively. Our results suggest a strong link between cod

494   recruitment and its larval stage abundance, which is in accordance with the literature

495   (Helle 1994, Helle et al. 2000, Bogstad et al. 2015, Stige et al. 2019), and should thus be

496   further assessed in future studies. Furthermore, in our study, we account for the effect of

497   *STemp* both on the spatio-temporal distribution of larval abundances (Eq. (1) in Figure 2),

498   and on the interannual variability of recruitment as it may be linked to temperature trends

499   (Eq. (4) in Figure 2). Thus, future studies could benefit from using temperature in

500   predicting future predator-prey relationships and how these affect the future fluctuations of

501   fish recruitment, as temperature is considered a main driver of cod recruitment for various

502   stocks (Planque et al. 2003, Hüssy 2011, Bogstad et al. 2013).

503

504

505   **5.Conclusions**

506   Our study sheds light on a key topic in fish ecology: how recruitment is affected by the

507   first weeks and months of life of fish larvae. We are able to successfully describe the

508   variability in the recruitment of the Northeast Arctic cod, the Northeast Arctic haddock,

509   and the Barents Sea capelin by assessing the overlap with their food and/or competitors at

510   the larval stage. Furthermore, we identify future implications as well as improvements to

511   this type of study: future studies should account for the spatio-temporal overlap between

512   larvae and their predators, as well as for environmental factors, such as temperature, affect

513   earlier life stages, and, subsequently, recruitment.

514

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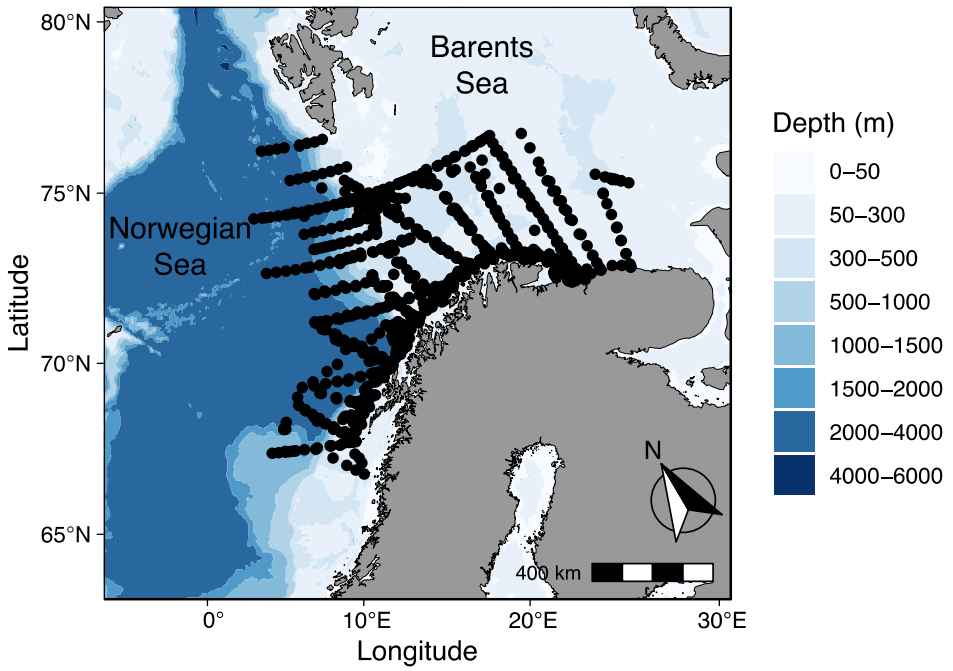684 **Acknowledgements**

687

688 **Tables**

689 **Table 1** – Model equations and deviance explained (%) for each species to use in Eq. (1).

690 The multiple r^2 is shown in brackets. Number of data points in logarithmic scale was used

691 as a weights term in all models except for herring. Species: cod, haddock (had), capelin

692 (cap), herring (her), and *C. finmarchicus* (zoo). x: station; t: time; st: station; Ab:

693 abundance; DOY: day of year; STemp$_A$: sea temperature; Lon: longitude, Lat: latitude,

694 YEAR: year; STAGE$_L$: fish larval stage; N$_{eggnet}$: number of egg net hauls; N$_{ringtrawl}$: number

695 of ring trawl hauls; α: intercept; β_1 and β_2: coefficients accounting for sample size; f$_{1-3}$:

696 adaptive functions; ε_{xt}: normally distributed error term.

| Species	Model formulation		Dev. exp. [%] (r^2)
Cod	$Ab(cod)_{xt} = \alpha + f_1(DOY_t) + f_2(DOY_t) \cdot STemp_{Axt}$ $+f_3(Lon_x, Lat_x) + YEAR_t + STAGE_{Lt}$ $+ \beta_1 \cdot ln(N_{eggnet,st} + 1) + \beta_2 \cdot ln(N_{ringtrawl,st} + 1) + \varepsilon_{xt}$		43.5 (0.05)
Haddock	$Ab(had)_{xt} = \alpha + f_1(DOY_t) + f_2(DOY_t) \cdot STemp_{Axt}$ $+f_3(Lon_x, Lat_x) + YEAR_t + STAGE_{Lt}$ $+ \beta_1 \cdot ln(N_{eggnet,st} + 1) + \beta_2 \cdot ln(N_{ringtrawl,st} + 1) + \varepsilon_{xt}$		25.6 (0.03)
Capelin	$Ab(cap)_{xt} = \alpha + f_1(DOY_t) + f_2(DOY_t) \cdot STemp_{Axt}$ $+f_3(Lon_x, Lat_x) + YEAR_t + STAGE_{Lt}$ $+ \beta_1 \cdot ln(N_{eggnet,st} + 1) + \beta_2 \cdot ln(N_{ringtrawl,st} + 1) + \varepsilon_{xt}$		64.3 (0.05)
Herring	$Ab(her)_{xt} = \alpha + f_1(DOY_t) + f_2(DOY_t) \cdot STemp_{Axt}$ $+f_3(Lon_x, Lat_x) + YEAR_t + STAGE_{Lt}$ $+ \beta_1 \cdot ln(N_{eggnet,st} + 1) + \beta_2 \cdot ln(N_{ringtrawl,st} + 1) + \varepsilon_{xt}$		74.4 (0.05)
Zooplankton	$Ab(zoo)_{xt} = \alpha + f_1(DOY_t)$ $+f_2(DOY_t) \cdot STemp_{Axt}$ $+f_3(Lon_x, Lat_x) + YEAR_t + \varepsilon_{xt}$	Nauplii	36.7 (0.19)
		CI-III	52.5 (-0.50)
		CIV-V	47.5 (0.22)
		CVI	50.5 (0.13)

697

698

699   **Figures**

700

701   **Figure 1 –** Spatial distribution of original larval data for the four species of fish, all years

702   (1959-1993, Mukhina et al. 2003).

703
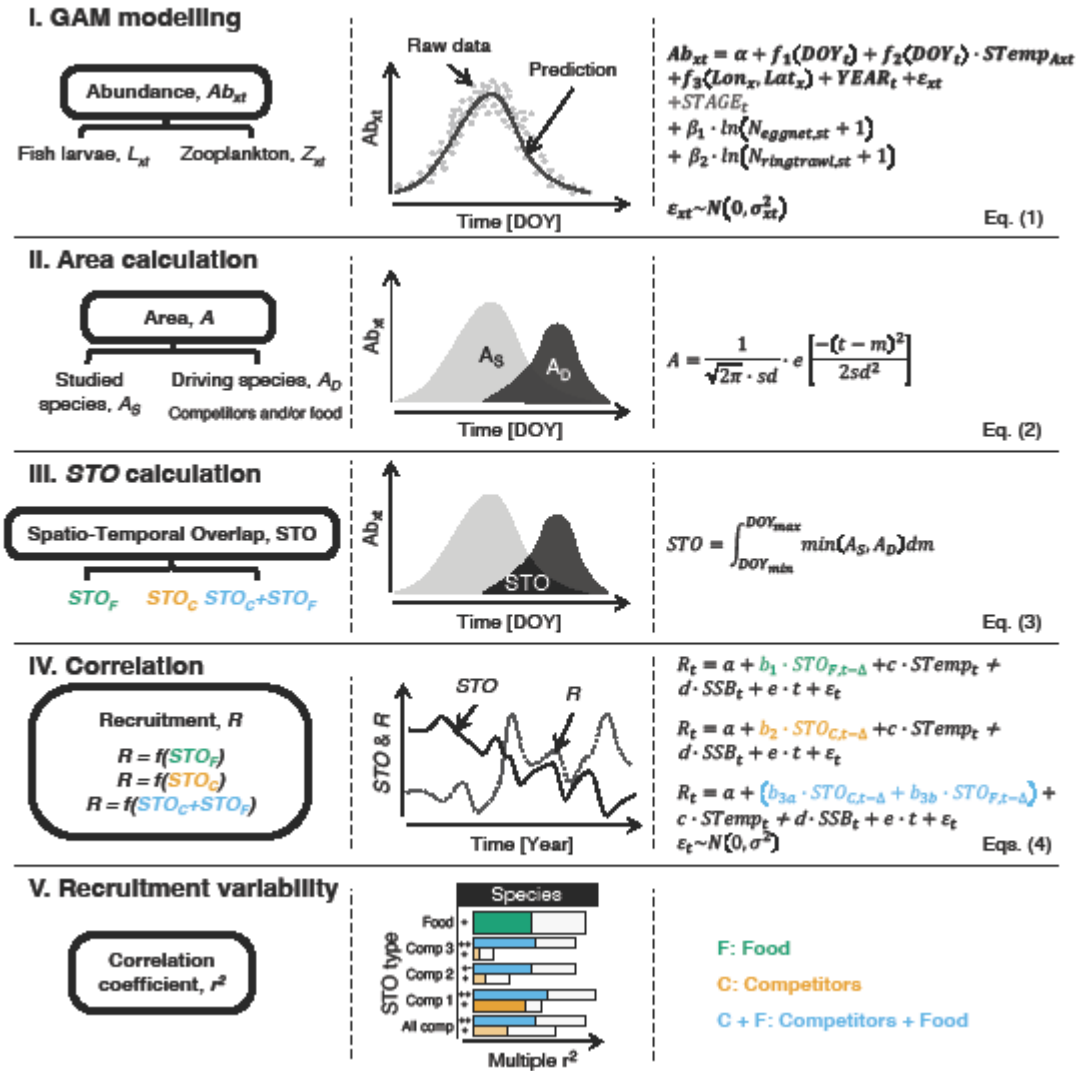
704

705 **Figure 2 –** Schematic of methodology applied within the study. In step "I: GAM
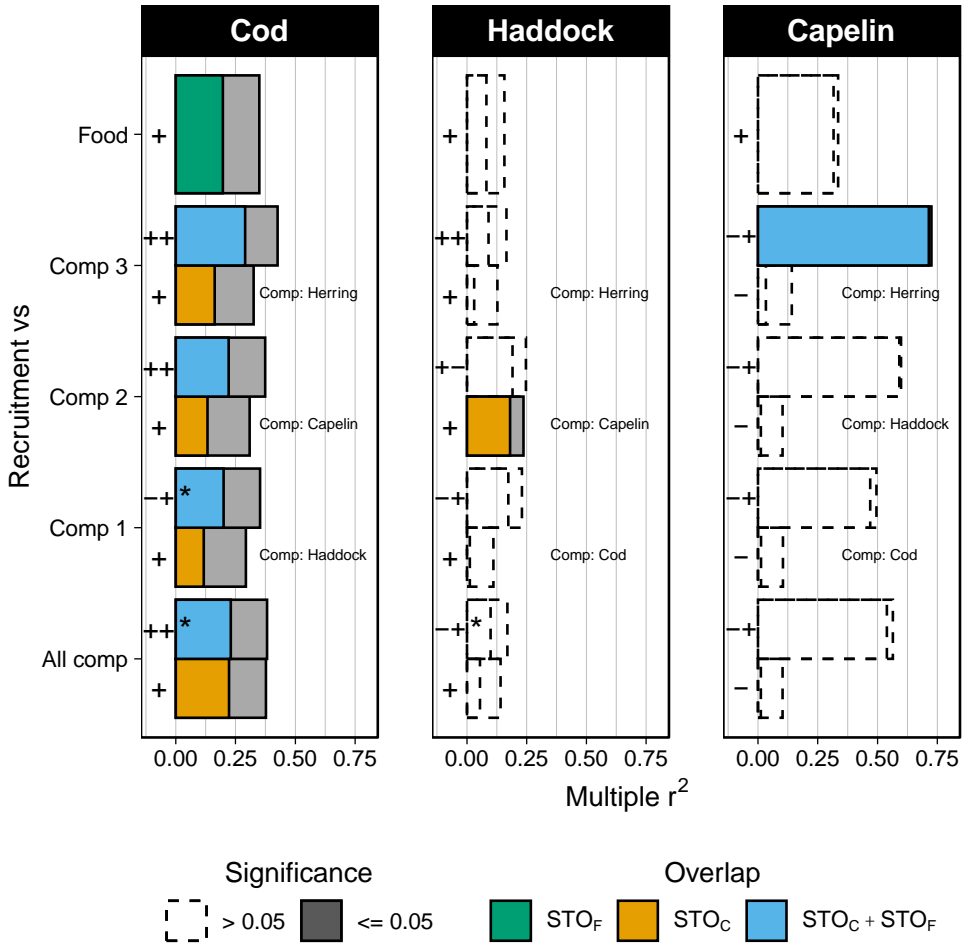
706 modelling", the model framework in bold represents the model for both ichthyoplankton

707 (L_{xt}) and zooplankton (Z_{xt}), whereas the non-bold part of the equation is added to the

708 ichthyoplankton only (see details in Supplementary Table S1).

709

710

Figure 3 – Multiple r^2 between recruitment and the spatio-temporal overlaps: STO_F

(green), STO_C (orange), $STO_C + STO_F$ (blue), and the overall contribution of the multiple

regression, linear model (dark grey) as calculated in step 4 (Figure 2 and Supplementary

Table S1). Dashed borders paired with light grey indicate that the relationship is not

significant. Full borders with full colours indicate significant relationships. The length of

the bar in green (STO_F), orange (STO_C), and blue ($STO_C + STO_F$) indicates the relative

importance of the overlap (STO) on recruitment variability. Recruitment of cod and

haddock is at age 3, and capelin is at age 1. The full length of the bars (colours and grey)

represents the r^2; however, the coloured section represents the percentage of $r2$ that is

explained by the overlap indices. Comp 1-3 refer to haddock, capelin, and herring for cod;

721 cod, capelin, and herring for haddock; and cod, haddock, and herring for capelin. Haddock

722 (had), capelin (cap), herring (her). Full borders paired with light grey indicate a statistically

723 significant relationship (p-$value \leq 0.05$). "*" indicates when the covariate combination

724 failed the collinearity test. "-", "-+", "+", "+-, and "++" indicate the sign of the parameter

725 estimates of the linear relationship between R and each of the STO (Eq. (4) in Figure 2,

726 Supplementary Table S1), where two signs indicate the sign for STO_C coefficient first and

727 then the one for STO_F. * denotes relationships that did not pass the for collinearity test.

728 Competitors (comp) 1 and 2, respectively: haddock and capelin for cod, cod and capelin

729 for haddock, and cod and haddock for capelin.