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2

3 **Trophic interactions affecting a key ecosystem component: a multi-stage**
4 **analysis of the recruitment of the Barents Sea capelin**

5

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29

30 **Abstract**

31 The Barents Sea stock of capelin (*Mallotus villosus*) has suffered three major collapses of
32 the stock (>90% reduction) since 1985, due to recruitment failures. As capelin is a key
33 species in the area, these population collapses had major ecosystem consequences. By
34 analysing data on spawner biomass and three recruitment stages (larvae, zero-group and
35 1-year-olds), we demonstrate that much of the recruitment failures are caused by
36 predation from herring (*Clupea harengus*), zero-group cod (*Gadus morhua*) and adult
37 cod. Recruitment is furthermore positively correlated with the sea temperature in winter
38 and spring. Harvesting of maturing capelin on the way to the spawning grounds reduced
39 the abundance of larvae significantly, but this reduction is to a large extent compensated
40 later in life, as mortality is strongly density-dependent between the larval stage and age 1.
41 Altogether, our study indicates a very high importance of trophic interactions, consistent
42 with similar findings in other high-latitude marine ecosystems.

43

44 **Keywords:** Capelin, herring, cod, Barents Sea, General Additive Models (GAM),
45 bottom-up, top-down

46

47 **Introduction**

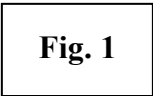
48 It is well recognized that in addition to fishing, fish stocks are affected by interactions
49 with other species (predators, prey and competitors) and climate, which should therefore
50 ideally be taken into account when managing fish stocks (Botsford et al. 1997, Collie and
51 Gislason 2001). However, the management of most fish stocks mainly considers the
52 effect of fisheries due to lack of estimates of other effects. In particular, fishing relies on
53 the natural ability of the fish population to replace itself, and a crucial question is to
54 which degree fisheries on the spawning stock reduces recruitment (Needle 2001).
55 However, the potentially large number of interacting factors (prey availability, predator
56 abundance and the abiotic environment) affecting recruitment conspire to make
57 development of predictive recruitment models difficult (Fogarty et al. 1991, Myers 1998).
58 Also, traditional recruitment studies analyse the transition from spawning stock biomass
59 to recruits, the two endpoints of a very diverse process which encompass several stages
60 where different mechanisms may operate (Bjorkstedt 2000, Brooks and Powers 2007). By
61 using data from several stages during the recruitment process, the chance of uncovering
62 the mechanisms behind recruitment variations should increase, and also some spurious
63 correlations could be avoided (as one often can *a priori* rule out some mechanisms for a
64 specific stage). Also, while the classic spawner-recruitment relationships (such as
65 Beverton-Holt and Ricker) all imply some form of density-dependence (compensation),
66 Brooks and Powers (2007) have pointed out the importance of whether compensation
67 occurs early or late during the recruitment process.

68 The approach of viewing recruitment as a step-wise process, using abundance at
69 one stage as a function of abundance at the previous stage, is well recognized in

70 theoretical studies (Paulik 1973, Bjorkstedt 2000, Brooks and Powers 2007) but has been
71 less common in empirical studies (exceptions include Ciannelli et al. 2005 and Dingsør et
72 al. 2007). First, there are often lack of data for such studies; second, the studies utilizing
73 indices of abundance during several phases of recruitment have focused on different
74 questions, e.g., searching for the "stage of year-class determination" by correlating the
75 abundance at each pre-recruitment phase with the abundance at the age of recruitment to
76 the fishery (e.g., Helle et al. 2000).

77 In this paper, we analyse the recruitment of Barents Sea capelin (*Mallotus*
78 *villosus*) during three phases of recruitment. Capelin is a key species in several
79 ecosystems in the North Atlantic (e.g., Carscadden et al. 2001). In the Barents Sea
80 ecosystem, it is a critical food source for some of the largest populations of predators,
81 such as North-East Arctic cod (*Gadus morhua*) (Marshall et al. 1999, Hjermann et al.
82 2007, Bogetveit et al. 2008) and the common guillemot (*Uria aalge*) (Barrett and
83 Krasnov 1996, Bogstad et al. 2000). Also, it is the most effective grazer on zooplankton
84 in the central and northern parts of the Barents Sea (Gjøsæter 1998, Hassel et al. 1991).
85 As huge numbers of mature capelin migrate southwards to the coast to spawn in the
86 spring, large amounts of energy are effectively transported southwards, making the
87 energy produced in the open northern Barents Sea accessible for species confined to
88 southern and coastal areas (Fig. 1).

89 The Barents Sea capelin stock has gone through strong fluctuations during the last
90 couple of decades, including three collapses of >90% reduction of stock size (ICES
91 2006a). The first of these collapses had large ecosystem effects (Gjøsæter et al. 2009),
92 including decreased growth (Mehl and Sunnanå 1991) and increased cannibalism (ICES

**Fig. 1**

93 2006b, Fig. 3.10) among cod, invasions of harp seal (*Phoca groenlandica*) along the
94 Norwegian coast (Haug et al. 1991), and a loss of 85-90% (more than 200 000 pairs) of
95 the common guillemot breeding colony at Bear Island (Vader et al. 1990, Strøm 2005).
96 Through the effects on cod, the collapses have also had substantial economic effects
97 (Hamre 1994).

98 The first of the three recorded collapses came as a surprise both for scientists and
99 managers, and Hamre (1994) suggested that the main mechanism was massive mortality
100 of capelin larvae during summer due to predation from 1-2 year old Norwegian Spring-
101 Spawning (NSS) herring (*Clupea harengus*). NSS herring spends most of its life cycle in
102 the Norwegian Sea and along the Norwegian west coast, but partly uses the Barents Sea
103 as a nursery area (mainly for 0-2 year olds). The hypothesis proposed by Hamre (1994)
104 has later been supported by statistical analyses of the stock-recruitment relationship of
105 capelin (Gjøsæter and Bogstad 1998, Hjermann et al. 2004a, Mikkelsen and Pedersen
106 2004) as well as by field studies (Godiksen et al. 2006, Hallfredsson 2006). On the other
107 hand, Dingsør et al. (2007) analyzed recruitment to the zero-group stage as a function of
108 spawner biomass and covariates, and found no effect of herring abundance. Moreover,
109 predation on larvae by zero-group cod (Hallfredsson and Pedersen 2007), as well as
110 climate and climate-related changes in prey abundance (Gjøsæter 1998), can be of
111 importance. The role of capelin fisheries has been a matter of discussion. During the
112 1970s, capelin landings were high (up to 3.0 million tonnes) but capelin recruitment was
113 nevertheless good, and Gjøsæter (1995), analysing data on larval production, concluded
114 that there was no substantial effect of the capelin fishery on the collapses of the 1980s
115 and 1990s. In contrast, others have claimed that the capelin fishery was an important

116 cause of the 1980s collapse (Hopkins and Nilssen 1991, Ushakov and Prozorkevich 2002,
117 Hjermann et al. 2004a).

118 Data on capelin abundance exists for several early stages: early larval (in June,
119 spawning takes place around April 1st), zero-group (in September; i.e., right after the
120 presumptive period of herring predation), and as 1-year olds (in September-October the
121 year after spawning). This paper reports the results of a comprehensive analysis of these
122 data, making us able to pinpoint the effect of different factors at different stages. The only
123 previous analysis of these data is by Gundersen and Gjørseter (1998), who did not
124 explicitly analyse the effect of covariates and whose data only included capelin year
125 classes 1981-1994. Using four different transition models, we clarify the importance of
126 different stages and factors for recruitment. Specifically, we evaluate the role of predation
127 and to what extent harvesting of mature capelin contributed to the recruitment failure
128 during the mentioned three collapses. We also evaluate whether mechanisms may have
129 changed over time. Through a systematic evaluation of the recruitment process on the
130 different life stages of the capelin, we show how the dynamics of this keystone species is
131 affected by predation from other species, fishing, and indirectly and directly by climate.

132 **Materials and Methods**

133 Data on four stages (Fig. 2, Fig. 3) for year-classes 1981-2006 were used in our analysis:

134 (1) Abundance index of the parental generation of capelin, given as maturing stock
135 biomass (*MSB*, measured in 1000 t) approximately half a year before spawning,
136 based on acoustic measurements in September of year $t-1$ (the survey is described
137 by Gjørseter et al. 1998). Individuals larger than 14.0 cm are assumed to spawn
138 the next spring (Gjørseter 1998).

Fig. 2

Fig. 3

139 (2) The abundance of capelin larvae (10^{12} individuals) in June year t (*Larvae*) (ICES
 140 2006a). In some years there were restrictions on entering the Russian Exclusive
 141 Economic Zone (EEZ), which have lead to incomplete coverage to a smaller or
 142 larger degree (depending on the distribution of larvae that year). Based on larvae
 143 distribution maps, the abundance might potentially have been significantly
 144 underestimated in the years 1996-1999, 2001-2002 and 2004. While a correction
 145 of the data may be possible using spatial analyses, it is quite difficult because
 146 there is large between-year variation in both the capelin's spatial extent as well as
 147 in the spatial pattern of density within the capelin distribution. We have
 148 considered such an analysis to be outside the scope of this paper.

149 (3) Abundance indices (unit: 10^9 individuals) of zero-group capelin calculated using
 150 the stratified sample mean of pelagic trawl data from the international zero-group
 151 survey in September year t (*Zero*; see Dingsør 2005 and ICES 2007).

152 (4) Estimates of the number of one-year old capelin (unit: 10^9 individuals) in
 153 September year $t+1$ (*Age1*), based on the same acoustic survey as in (1). For the
 154 years prior to 1981, we use back-calculated values of survey abundance at age 2
 155 the following year, since survey coverage of 1-year-old fish was poor during this
 156 period (Gjøsæter et al. 1998).

157 We used regression analyses to analyse stage-to-stage survival, investigating the
 158 effects of a number of covariates on survival (Tab. 1, 2) based on the following (see also
 159 Fig. 2):

160 (1) During the winter (after *MSB* is estimated, and before spawning), maturing
 161 capelin on their spawning migration are subject to predation by several fish,

Tab. 1

Tab. 2

162 mammal and bird species. Of these, especially cod is of importance (Bogstad and
163 Gjøsaeter 2001); because of its large biomass, it is the dominant predator of
164 capelin of this ocean (Bogstad et al. 2000, Dolgov 2002). The cod's predation is
165 mainly due to subadult (3-6 year old) cod (*CodSubad*; Dolgov 2002). Adult cod
166 (ca. age 7 and up) are on their annual spawning migration west and south of the
167 capelin's distribution (Bogstad and Gjøsaeter 2001), and younger cod (age 1-2) are
168 less piscivorous. Moreover, capelin is also targeted by fisheries during this stage,
169 which here is taken into account using the log-transformed biomass of the catch
170 (*LogCatch*).

171 (2) Between the larval and zero-group stage (i.e., in summer), capelin is eaten by
172 several planktivorous predators. In years when 1-2 year-old herring (*Herr12*) are
173 abundant, this is the dominant planktivorous fish in the coastal areas in summer.
174 Analyses of these time series (Gjøsaeter and Bogstad 1998) together with stomach
175 samples of herring, (Hallfredsson and Pedersen 2009) have indicated a significant
176 impact on the capelin. Also the density of zero-group cod (*CodZero*) may be high,
177 and they can eat a significant amount of capelin according to field studies
178 (Hallfredsson and Pedersen 2007).

179 (3) Between the zero-group and one-year stage, capelin might be affected by
180 predation by cod in winter/spring (mostly subadult cod, *CodSubad*) as well as in
181 summer (in this case, all piscivorous cod, *Cod*). Although capelin overlaps with
182 young herring only to a small degree during this stage, there is a possibility for a
183 competition effect by herring depleting advecting plankton resources.

184 (4) During all stages, food availability (plankton abundance) may be an important

185 factor. Russian plankton data during spring and summer (May-July) is available
186 but exists only until 1990. For the stagewise analyses we used sea temperature as
187 a proxy, which affects in situ biological productivity positively. In addition, high
188 temperatures indicate a high inflow of Atlantic, zooplankton-rich water to the
189 Barents Sea (Wassmann et al. 2006). We use Kola section temperatures, depth 0-
190 200 m (Tereshchenko 1996) which have been shown to be a good indicator of the
191 climate of the Barents Sea as a whole (e.g., Ottersen and Sundby 1995, Wassmann
192 et al. 2006).

193 We did not try to include the predation by birds and mammals. Minke whales
194 (*Balaenoptera acutorostrata*) and harp seals (*Phoca groenlandica*) are important
195 predators. Based on diet samples, it has been estimated that average annual consumption
196 of capelin is 140 000 metric tons and 260-410 000 metric tons for minke whales and harp
197 seals, respectively (Bogstad et al. 2000). There is, however, not enough data on neither
198 diet or abundance of mammals to estimate the consumption for each specific year .
199 However, cod clearly consumes even more capelin than mammals do (up to 3 million
200 metric tons annually; ICES 2007). Also, mammal populations can be considered to be
201 changing relatively slowly compared to the fast fluctuations of capelin population. The
202 same applies to birds, which are less important as predators (annual consumption of
203 capelin: around 100 000 metric tons; Barrett et al. 2002). Although the total annual
204 removal of capelin caused by these predators may change little from year to year, the
205 removal relative to the total stock, and thereby the predatory impact, may change
206 considerably.

207 We used Generalized Additive Models (GAM) models on the form

208

209 eq. 1
$$\log(\text{Stage}_{i,j}) = a + G(\log(\text{Stage}_{i-1,j})) + H(X_j) + \dots + \varepsilon_j$$

210

211 where $\text{Stage}_{i,j}$ is the abundance at stage i ($i = 2,3,4$) in cohort j ($j = 1981,1982, \dots,2006$)212 and X is a covariate. The functions G and H may be linear (i.e., $b \cdot \text{LogMSB}_{t-1}$), or non-

213 linear (e.g., a spline function), and there may be several covariate terms (see below).

214 Note that if mortality is density-independent, we expect G to be linear with a slope of 1.215 If G has a slope of 0, mortality is highly density-dependent, exactly compensating for

216 changes in density (abundance of one stage is independent of abundance at the previous

217 stage). We used the package `mgcv` (Wood 2006) of R, where the degrees of freedom of

218 the smooth function is chosen automatically based on the General Cross-Validation

219 (GCV) score, including $\text{d.f.}=1$ (i.e., a linear effect). We used thin plate regression splines220 (Wood 2006) and specified the maximum dimension of the smooth term to 3 ($k=3$) to

221 avoid overly "wiggly" regression lines.

222 We searched for the optimal model by searching through combinations of

223 biologically plausible explanatory variables for each stage (Tab. 2) using GCV score

224 (Wood 2006) as a guide. Young herring abundance was log-transformed to reduce the

225 influence of outliers. Due to a relatively high ratio between numbers of potential

226 variables and sample size we did not check for interaction effects. The exception was that

227 we tested for interaction between herring and zero-group cod in the stage 2-3 transition,

228 based on inspection of the plotted residuals of a model with additive effect of herring and

229 zero-group cod. For the models involving larvae (transitions 1-2 and 2-3), we tried to

230 include a dummy variable for the years when larval abundance might have been

231 significantly underestimated owing to restrictions on entering the Russian EEZ (see
 232 above). We checked whether the residuals were autocorrelated by plotting the partial
 233 autocorrelations of the residuals.

234 The flexibility of GAM increases the probability of achieving spurious results. To
 235 reduce this problem, we considered non-monotonous relationships explaining an
 236 unrealistically high fraction of deviance, likely to be spurious results. When a GAM
 237 model produced such a relationship, we replaced it with a monotonous relationship using
 238 "hockey stick GAM" (HSGAM), the GAM equivalent of hockey stick regression (e.g.,
 239 Maceina 2007). That is, we restricted the relationship to be flat (slope zero) below or
 240 above some threshold (chosen by minimizing residual variance). For instance, a HSGAM
 241 model with the restriction that Y has no effect below the threshold Y_{th} may look like this:

242

$$243 \text{ eq. 2a} \quad \log(\text{Stage}_{i,j}) = a_1 + G(\log(\text{Stage}_{i-1,j})) + H(X_j) + \dots + \varepsilon_j \quad \text{for } Y_j \leq Y_{th}$$

$$244 \text{ eq. 2b} \quad \log(\text{Stage}_{i,j}) = a_2 + G(\log(\text{Stage}_{i-1,j})) + H(X_j) + H(Y_j) + \dots + \varepsilon_j \quad \text{for } Y_j > Y_{th}$$

245

246 where coefficients a_1 and a_2 are set so that the function is continuous. The threshold Y_{th} is
 247 found using a routine to search for the global minimum of the deviance. Because of this
 248 approach, GCV values are not representative; we therefore also give Akaike's
 249 Information Criterion (AIC) adjusted for small sample size (Burnham and Anderson
 250 2002), as this criterion can correctly take the extra threshold variable into account.

251 We wanted to evaluate the effect of plankton abundance during spring and
 252 summer during the larval stage, but this could not be done within the stagewise analyses
 253 since the data were available only for 1959-1990. In order to obtain a long enough time

254 series, we made a simple model for recruitment at age 1 (stage 4) as a function of *MSB*
255 (stage 1) for a different period than the rest of the analysis, the cohorts 1974-1990. As
256 covariates we used those found to be important in the stagewise analyses. We then added
257 plankton abundance to evaluate the additional effect of this variable. We used data either
258 from only the western ("North Cape") transect closest to main spawning areas
259 (*ZooNCSouth_t*) or both transects (including *ZooSouth_t*). In any case we used data from
260 the southern part of the covered area in order to restrict to the area covered by capelin
261 larvae (Tab. 1).

262 Finally, the robustness of the models was tested using k-fold cross-validation
263 (Fielding and Bell 1997): the time series (length *N*) is divided in *k* (more or less) equally
264 long parts. For each part of the time series, the model parameters are estimated excluding
265 this part from the data. Then these parameters are used to predict the response for the
266 other part. We used *k* = 5 or 6 (for time series starting in 1981 or 1974, respectively).

267 **Results**

268 For all transitions, we found models that were able to explain over half of the variation
269 (56-80% of the deviance explained, Tab. 3). Model residuals were not significantly
270 autocorrelated at lag 1 and 2 years; overall, there were not more autocorrelations with
271 $p < 0.05$ than expected by chance (Suppl. Fig. 1). The k-fold cross-validation tests (Suppl.
272 Fig. 2) showed that the models were quite robust, i.e. returned quite good out-of data
273 predictions in most cases, except for the stage 2 to 3 (larvae to zero-group) transition
274 (commented further below).

275 **Stage 1 (maturing biomass) to 2 (larvae)**

276 The best GAM models for larval abundance as a function of *MSB* (Tab. 3) had a positive

Tab. 3

Tab. 4

Fig. 4

277 effect of *MSB* ($p < 0.001$) as well as negative effects of cod age 3-6 biomass (*CodSubad*,
278 $p < 0.001$) and the proportion of capelin caught in the fisheries between survey time and
279 spawning (*LogCatch*, $p = 0.007$), and a weaker positive effect of temperature in the winter
280 and spring (*TempWintspr*, $p = 0.05$). A model with these four explanatory variables
281 explained a large part (72%) of the deviation in larvae abundance (Tab. 3a, Fig. 4a-d).
282 The effect of $\log(\text{MSB})$ was weakly non-linear; if it was forced to be linear, the estimated
283 slope was 1.33 (SE 0.30), i.e., not significantly different from a straight line with a slope
284 of 1. Thus, there was no evidence of density-dependent mortality at this stage (Tab. 4a).
285 The effect of harvesting is mostly due to the high harvest in the years 1982-1986, when
286 68-87 % of the mature biomass was harvested. After 1986, the harvest has been
287 maximum 44 % of the biomass. A dummy variable for coverage of the larval distribution
288 (complete/incomplete) was on the border of significance ($p = 0.10$) and reduced the GCV
289 value somewhat (1.5 units). However, the effect of the dummy variable was opposite of
290 what was expected (positive effect of incomplete coverage), and we concluded this was a
291 spurious effect.

292 **Stage 2 (larvae) to 3 (zero-group)**

293 Surprisingly (in view of existing literature), the effect of young herring biomass (*Herr₁₂*)
294 alone on survival through this stage was not very strong ($p = 0.062$). In fact, the
295 abundance of zero-group cod (*CodZero*) had a much more consistent negative effect on
296 survival ($p = 0.002$). However, there was a significant interaction between *Herr₁₂* and
297 *CodZero* ($p = 0.006$; Tab. 3b). A model including this interaction (Fig. 5) indicates that
298 high abundance of one predator increases the negative effect of the other. Fig. 5b also
299 shows that the abundance of the two predators is correlated, which makes it difficult to

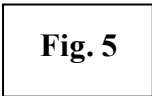


Fig. 5

300 separate the effects of the two. The slope of $\log(Larvae)$ was significantly lower than 1
 301 (Tab. 4b), indicating strong density-dependent mortality. A dummy variable for years
 302 with incomplete coverage of the larval distribution did not improve the model ($p = 0.23$).
 303 Compared to the other transitions, this model showed poor results for the k-fold cross-
 304 validation test (Suppl. Fig. 2b): the second collapse (start of the 1990s) is not well
 305 predicted based on the data of the other periods. The cross-validation results were not
 306 much affected if zero-group cod was deleted from the model, but worse in some periods
 307 (the late 1990s) if we deleted herring from the model (Suppl. Fig. 2b)

308 **Stage 3 (zero-group) to 4 (age 1)**

309 For this stage, we found two alternative sets of covariates (denoted model 1 and model 2)
 310 that could explain the variation in survival (Tab. 3c): (1) abundance of herring ($Herr_{12}$)
 311 and temperature during winter and spring ($TempWintspr$), and (2) abundance of subadult
 312 cod ($CodSubad$). The effects of the covariates were also non-linear in both cases; we used
 313 HSGAM models (Fig. 6). In any case, the slope of $\log(Zero)$ indicated strong density-
 314 dependent survival, especially at low abundance (see Tab. 4c and Fig. 6; for model 1,
 315 slope varies from approx. 0.25 to 0.5).

316 **Effects of zooplankton abundance and other covariates on recruitment**

317 We made a baseline model where stage 4 abundance (age 1, year $t+1$) was
 318 modeled as a function of stage 1 (MSB , year $t-1$) $Herr_{12}$ (in year t), $CodSubad$ (year t or
 319 $t+1$) and $TempWintspr$ (year t or $t+1$) based on model fit. The explanatory variables were
 320 selected on basis of the stagewise regression results (see above), but the model was fitted
 321 to the longest time series covering stage 1, stage 4 and zooplankton data, i.e., cohorts
 322 1974-1990. The best fit (explaining 72% of the deviance) was obtained by using



Fig. 6

323 *TempWintspr* for year $t+1$ and *CodSubad* for year t . $Herr_{12}$ (with a threshold effect) and
324 *TempWintspr* were statistically significant ($P = 0.003$ and $P = 0.006$, respectively), while
325 the effect of *MSB* ($P = 0.26$) and *CodSubad* ($P = 0.19$) was not. When zooplankton was
326 added to this baseline model, there was no improvement in model fit, neither for
327 zooplankton in the western transect ($P=0.41$) or for both transects ($P=0.99$). See suppl.
328 Fig 3 for graphs of showing the covariate effects.

329 **Discussion**

330 This study supports that capelin, a key species in the food-web of the Barents Sea, is
331 heavily affected by predation (i.e., top-down control) on every stage of recruitment.
332 However, mortality also appears to be density- and climate-dependent, which may
333 indicate bottom-up effects. While the results of model selection based on retrospective
334 analyses of time series data always has some uncertainty (i.e., the possibility of spurious
335 relationships), we tried to keep the number of potential variables relatively low (Tab. 2),
336 and as the results are in line with field studies (e.g., Hallfredsson 2006, Hallfredsson and
337 Pedersen 2007, Fossheim et al. 2006) we have quite high confidence in the results. The
338 high impact of predation is consistent with studies from other northerly ecosystems (e.g.,
339 Frank et al. 2005, Savenkoff et al. 2007). Petrie et al. (2009) suggest that the tendency for
340 strong top-down effects stem from the lower diversity and higher species specificity of
341 predation in northerly ecosystems, a view that is supported by the highly species-specific
342 predation effects found in the present study.

343 From stage 1 to 2, subadult (3-6 year old) cod has the largest impact. Stage 1
344 marks the end of the feeding season of the matures (i.e. before the maturing capelin
345 separates from the rest of the stock in the central Barents Sea and start the spawning

346 migration towards the coast). During this migration, they are followed by large amounts
347 of predatory fish, as well as birds, seals and whales, which by these results have a
348 substantial impact on the biomass that survives until spawning and thereby on the
349 abundance of larvae. This impact is substantially larger than the impact of fishing, at least
350 since 1990, when fisheries have been relatively small compared to the stock abundance
351 (22-31 % of the mature biomass in all years when fishing has been allowed except one).
352 It is likely that the variations in cod abundance has had a larger effect on this stage
353 transition. According to the model estimates, a 3-fold increase in the biomass of subadult
354 cod – similar to the increase from 1990 to 1993 - is associated with a reduction in
355 $\log(Larvae)$ of 3.23, i.e., a reduction in larval abundance of 96%. Although this is likely
356 to be an overestimate of the effect, it clearly is an indication that cod predation can be
357 highly influential.

358 During the next relatively short phase over the summer, the capelin larvae are
359 strongly affected by the abundance of young herring as well as zero-group cod. The effect
360 of young herring was first suggested by Hamre (1994) and later supported by the stock-
361 recruitment analysis of Gjørseter and Bogstad (1998) as well as field data (Hallfredsson
362 and Pedersen 2009). However, we found a less clear-cut effect of herring than expected.
363 What the data tell us is that survival during summer is likely to be high if there is low
364 abundance of both predators, and low if there is a high abundance of both. If there is
365 much young herring but little zero-group cod, the outcome is highly variable; survival
366 can be good (as in 2006) or bad (as in 1998). Statistically, the best model indicates that
367 mortality is affected by an interaction between the two types of predators, herring and
368 zero-group cod. However, the interaction effect is uncertain as it depends on quite few

369 data points and especially as we lack the combination of little herring and much zero-
370 group cod. The apparent interaction effect may also be an artefact resulting from leaving
371 out confounding parameters, such as climate (affecting spatial distribution of the
372 predators) and abundance of alternative prey for the herring and zero-group cod.
373 Godiksen et al. (2006) found that individual herring switches between selectively eating
374 either copepods or krill and capelin larvae, which indicates that krill and capelin larvae
375 occur together in the same patches. Therefore, the effect of the two predators also
376 depends on the abundance of copepods. Time series on copepod abundance at this time of
377 the year are unfortunately not available. Since copepod abundance is also related to
378 predator abundance (both are linked to climate), this may disturb the apparent effects of
379 predators.

380 Capelin larvae are rapidly digested in herring stomachs (Huse and Toresen 2000),
381 but by using the anterior part of the stomach and using the presence of larval eyes
382 (Godiksen et al. 2006) it has been made possible to estimate predation rates based on
383 predator stomachs. Hallfredsson and Pedersen (2007, 2009) tried to estimate mortality
384 rates of capelin due to herring and zero-group cod predation. For herring, they found a
385 predation mortality of 7 and 10% per day (in 2001 and 2003, respectively) at the stations
386 where herring was found (Hallfredsson and Pedersen 2009). Averaged over all stations,
387 the daily mortality rates were 2.6% (2001) and 0.004% (2003); the latter estimate is
388 extremely uncertain as the herring was highly aggregated that year, being difficult to
389 sample using a regular sampling grid. For cod, the daily mortality rate, averaged over all
390 stations was 1.7% in 2002 and 1.5% in 2003 (Hallfredsson and Pedersen 2007). For
391 comparison, the mortality rate of capelin larvae in predator-free bag experiments was 1%

392 per day (Fossheim 2006).

393 Finally, this analysis indicates that either cod or herring abundance affects
394 survival in the one-year period following the zero-group stage. Of these two alternative
395 models, we believe, based on the size and spatial distribution of the capelin at this stage,
396 that the model with cod has most credibility. During summer the year after spawning, cod
397 and capelin often overlap substantially in the capelin's feeding grounds; hence cod
398 predation in this area may have a substantial impact. (The same conclusion was drawn by
399 Dingsør et al. 2007, using the same data). These feeding grounds are situated far north of
400 the herring's northern limit, and also the capelin at this stage is too large to be a preferred
401 prey of herring. The shape of the density-dependent survival may also be linked to
402 predation: as capelin becomes scarce, cod may switch to other prey and thereby capelin
403 survival increases. This is of course speculation; also note that the shape of this curve
404 depends a lot on two years with low capelin abundance and high survival.

405 While reproduction and mortality until the larval stage is not significantly density-
406 dependent, mortality is strongly density-dependent from the larval stage onwards. Eq. 1
407 contains measurement error in the abundance estimates of both stages, which leads to a
408 downward bias in the slope of abundance at the previous stage (G in eq. 1) (Carroll et al.
409 1995) and thereby an upward bias in the strength of density-dependence (1-slope). This
410 bias is quite small when variation in abundance is large (Suppl. Fig. 4), which it is in
411 capelin: the ratio between the largest and smallest abundance is 154, 366, 762, and 350
412 for stage 1-4, respectively. For stage 1 and 4, Tjelmeland (2002) modelled the uncertainty
413 for the abundance estimates of age 2-3 capelin 1972-2000, the coefficient of variation
414 (CV) was mostly below 20%; it exceeded 20% in 1 and 5 years in the case of 2-year and

415 3-year olds, respectively (maximum CV was ca. 60%). In accordance with this, Løland et
416 al. (2007) found the CV to be 20% in most years for NSS herring, another large stock
417 measured acoustically. For zero-group abundance (stage 3), measurement error CV was
418 32% on average over all years (range 10%-64%; Dingsør 2005). The uncertainty of the
419 stage 2 (larval capelin) abundance estimates have not been estimated. The uncertainty of
420 larval (ichthyoplankton) abundance estimates is generally difficult to estimate. In a
421 comparable oceanic larval survey, Pepin and Anderson (1997) indicated that the CV was
422 around 15%. Using a simulation approach, Voss and Hinrichsen (2003) found that the
423 mean error was 10%-20% (depending on wind stress) without accounting for transport
424 losses out of the surveyed area, which in their case reached up to >10% when winds were
425 strong. As shown in Suppl. Fig. 4c, if we assume that our estimates have a CV of 30%,
426 the bias of the slope of G is 0.05, i.e. quite small compared to the slope values.

427 The strong density-dependence diminishes the effect of processes occurring on
428 early stages, especially before the larval stage. Therefore, although spawner abundance
429 and harvesting mature capelin was found to affect recruitment at the larval stage (stage 1
430 to 2), it has a very small effect on overall recruitment (stage 1 to 4). Density-dependence
431 from the larval stage onwards strongly reduces the effect of spawner abundance. From
432 the larval to the zero-group stage, the slope of G in eq. 1 is estimated to be 0.45 (Tab. 4).
433 For example, if harvest reduces larval abundance by 25%, the change in $\log(\text{Zero})$ is
434 $0.45 \cdot \log(1-0.25) = -0.13$. To get the reduction at the zero-group stage, we back-
435 transform: $1 - \exp(-0.13) = 0.12$. Thus, a 25% reduction at the larval stage is reduced to
436 12% at the zero-group stage, and (by a similar calculation) to only 3-7% at the age of one
437 year.

438 The conclusion is that harvesting probably played only a minor role in the
439 collapses, including the first one in the 1980s, a result which is consistent with Gjørseter's
440 (1995) conclusions based on larval and zero-group abundance prior to the collapse. This
441 contradicts the conclusion of Hjermann et al. (2004a), who, based on a data set consisting
442 of age 1-4 capelin only, suggested that harvest was an important reason for the 1980s
443 collapse. However, the harvest during autumn 1985 and spring 1986 reduced spawner
444 biomass to extremely low levels, which might have delayed the stock's recovery
445 (Gjørseter 1995). The minor role of harvesting in stock collapses corresponds well with
446 anecdotal information going as far back as to the 16th century, which describes that
447 capelin “disappeared” at irregular intervals. From the recent history, it is known that such
448 periods of capelin disappearance are associated with strong year classes of herring
449 (Gjørseter 1995).

450 We also found capelin recruitment to be positively related to sea temperatures
451 both in the case of the spawner-larvae transition and the zero-group-age 1 transition. In
452 this area, high sea temperatures are associated with higher primary production as well as
453 higher influx of zooplankton from the Norwegian Sea (Dalpadado et al. 2003, Wassmann
454 et al. 2006). Being a planktivore, this could suggest that capelin to some degree also is
455 limited by food abundance (bottom-up control). In the case of adult capelin, they are able
456 to deplete local zooplankton stocks in a few days (Haug et al. 1991). However, we found
457 no effect of zooplankton biomass in spring and early summer on recruitment. The reason
458 may be that zooplankton biomass for a large part is determined by the abundance of
459 *Calanus finmarchicus*. In contrast to herring and cod, whose larvae appear to be tightly
460 coordinated in space and time to *C. finmarchicus*, capelin larvae mainly eat other kinds of

461 zooplankton (Fossheim 2006). Indeed, the relationship between temperature and capelin
462 recruitment may instead be linked to oceanographic features such as eddies and coastal
463 jets: Fossheim et al. (2006) suggested that an important factor for capelin recruitment can
464 be the number and timing of short-lived springtime eddies, which carries warm, oceanic
465 and plankton-rich water on to the shelf. However, compared to the beach-spawning
466 capelin populations in Canada (Leggett and Deblois 1994), the effects of climate on the
467 recruitment of this capelin stock seem to be relatively small. However, climate has a
468 strong indirect, lagged effect on this capelin stock by affecting the recruitment of the
469 capelin predators cod and herring (Hjermann et al. 2004b).

470 While this study is largely based on survey data, the data of age 3 and older cod
471 and herring age 1 and 2 are based on VPA estimates. In particular the herring estimates
472 are uncertain, since they are based on assuming a natural mortality for ages 1 and 2 which
473 is constant through time and high (instantaneous mortality $M=0.9$). Also, one source of
474 error is that some cohorts of young herring stay largely in the fjords of Northern Norway
475 or in the Norwegian Sea instead of in the Barents Sea, and therefore do not overlap with
476 larval capelin. This is not conveyed by VPA estimates (since they are back-calculated
477 from catches of the entire herring stock, after the cohorts have migrated to the Norwegian
478 Sea). In addition, some cohorts are mainly found in the Barents Sea also at age 3 (ICES
479 2006a). Acoustic survey estimates of herring in the Barents Sea (ICES 2006a) exist for
480 most, but not all, of the years 1984 and onwards. However, in addition to the holes in the
481 survey data series, the survey estimates from before 1990 are not compatible with later
482 data due to a change in echosounder equipment (Røttingen and Tjelmeland 2003). Also,
483 the young herring has not always been surveyed at the same time of the year, and they are

484 generally difficult to survey since they are often located near the surface. Thus we
485 decided that using the VPA estimates was the best choice.

486 Some additional information can, however, be derived from the survey data. In
487 some years with large overall abundance of 1-2 year old herring (according to VPA
488 estimates), the survey indicated a relatively low herring density in the Barents Sea
489 (probably because much of the herring was in the fjords). This is the case for one of the
490 years where the survival of larvae was unexpectedly high (2003). However, in two other
491 years with high capelin survival (1999 and 2006), both VPA estimates and survey data
492 show that the Barents Sea contained much young herring. The good survival of capelin in
493 this period may have been due to little spatial overlap between capelin larval drift routes
494 from the spawning grounds (which varies strongly from year to year) and young herring.
495 For instance, in 2006, the capelin had an extreme westerly spawning, and the larvae
496 probably overlapped to a limited degree with herring while drifting north- and eastwards.

497 Direct measurements of the capelin spawning stock are not available and could
498 not be included in the present analysis. Such estimation has been attempted by acoustic
499 surveys in spring, but such surveys have been discontinued since they were not able to
500 cover the capelin stock properly during the capelin migration to the coast. Therefore, the
501 spawning stock estimates used for instance for management purposes are modelled based
502 on the MSB (Gjøsæter et al. 2002).

503 After the disastrous collapse of the capelin stock in the mid-1980s, and the second
504 collapse in the early 1990s, the leading hypothesis has been that a high abundance of
505 young herring causes massive larval mortality, recruitment failure and stock collapse. Our
506 analysis supports that herring is an important cause, as herring abundance alone explains

507 21-23 % of the deviance in the abundance of age 1 capelin. All observed capelin
508 collapses have happened in connection with high abundance of young herring; however,
509 there have also been some years with high herring abundance but good recruitment of
510 capelin. This indicates that a high abundance of young herring is necessary but not a
511 sufficient condition for capelin collapse. The present results point out the importance of
512 cod predation (both from zero-group and older cod), as well as a certain influence of
513 climate. These results could be incorporated in the management advice of capelin, e.g. by
514 indicating the probability of major changes in stock size in the medium term (3-4 years).

515 Erroneous conclusions due to spurious correlations is always a hazard when
516 investigating environment- recruitment relationships, and the flip side of the versatility of
517 GAMs non-linear functions is that it makes GAM even more prone to such errors
518 (Megrey et al. 2005). By analysing intermediate stages of recruitment, and by using
519 HSGAM when this appears more adequate, we are better able to pinpoint which factors
520 that affect which stages. Through careful assessment of our statistically derived results,
521 we can conclude that not only herring but also cod at various stages, as well as climate,
522 appear to play a key role in determining the population dynamics of the capelin living in
523 the Barents Sea.

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- 711

712 **Table 1.** Overview of explanatory variables used in this paper. The data series marked
 713 with (*), were only available for the period 1981-2006 and therefore not used for the
 714 stage 1-stage 4 transition. The data series marked with (†) were only used for the stage 1-
 715 stage 4 transition.

Covariate	
<i>LogCatch_t</i>	Log-transformed harvested biomass (tons·10 ³) of maturing (>14 cm) capelin, based on the catch between the September survey in year <i>t-1</i> and spawning in year <i>t</i> . Because many years had zero catch, $\text{LogCatch} = \log(\text{Harvest} + \text{constant})$ where <i>constant</i> was quite arbitrarily set to 39 (half the minimum non-zero value of <i>Harvest</i>).
<i>Herr12_t</i>	Biomass (tons·10 ⁶) of young (age 1-2) herring based on the SeaStar assessment (ICES 2006b), estimated for 1 January year <i>t</i> . SeaStar is based on several sources of data including age-specific catch statistics and survey data.
<i>CodSubad_t</i>	Biomass (tons·10 ⁶) of cod age 3-6 (i.e., subadult piscivorous cod, expected to overlap with capelin in the winter months) assessed by VPA/XSA (ICES 2006a), estimated for 1 January year <i>t</i> . The assessment is primarily based on age-specific catch statistics with additional input from survey data.
<i>CodAll_t</i>	Biomass (tons·10 ⁶) of cod age 3-13 (i.e., all piscivorous cod) assessed by VPA/XSA (ICES 2006a), estimated for 1 January year <i>t</i>
<i>*CodZero_t</i>	Abundance index of zero-group cod (unit: 10 ⁹ individuals) based on the stratified sample mean from the international zero-group survey in

	September year t (Dingsør 2005, revised values given by ICES 2007). The survey is performed using pelagic trawling.
<i>TempWintspr_t</i>	Average sea temperature (°C) at 0-200 m depth in the Kola section in winter/spring (December year $t-1$ to June year t). The Kola section goes from 70°30' N to 72°30' N along 33°30' E; See Tereshchenko (1996). Data from recent years were kindly provided by PINRO, Murmansk.
<i>TempSummer_t</i>	Average sea temperature (°C) at 0-200 m depth in the Kola section in summer (June-August year t)
<i>†ZooSouth_t</i>	Average biomass of zooplankton in the six innermost stations of both transects of Nesterova (1990) (i.e., the North Cape transect and the Kola transect). Positions are 25°29'-23°12' E, 71°26'-72°27' N and 33°30'E, 69°30'-70°45' N for the two sets of stations.
<i>†ZooNCSouth_t</i>	Average biomass of zooplankton in the six innermost stations of the North Cape transect (25°29'-23°12' E, 71°26'-72°27' N). In most years, this transect is most representative for capelin larval distribution, as there is little spawning as far east as the Kola transect.

716

717

718 **Table 2.** Potential explanatory variables tested for each transition. For each transition, the
 719 left column gives the a priori expectation of the sign of the relationship; e.g., predators
 720 are expected to have negative effects (an empty cell indicates that the variable was not
 721 considered). The second column gives the number of times the coefficient was
 722 statistically significant ($P < 0.05$, regardless of sign) and the number of times it was tested
 723 during model selection. We never considered *CodSubad* and *CodAll* together in the same
 724 model, nor *TempWintspr* and *TempSummer*. Incomplete = 1 for years with incomplete
 725 coverage of the larval distribution, and 0 for years with complete coverage. The bottom
 726 line gives the total number of models tested in each case.

Covariate	Transition between stages					
	1-2 (MSB to larvae)		2-3 (larvae to zero)		3-4 (zero to age 1)	
	A priori	P<0.05	A priori	P<0.05	A priori	P<0.05
<i>LogCatch_t</i>	-	7/12				
<i>Herr12_t</i>			-	0/12	-	6/18
<i>CodSubad_t</i>	-	8/8			-	3/12
<i>CodAll_t</i>	-	7/8			-	0/12
<i>CodZero_t</i>			-	8/12	-	4/18
<i>Herr12_t*CodZero_t</i>			+/-	4/4		
<i>TempWintspr_t</i>	+/-	8/12			+/-	5/12
<i>TempSummer_t</i>			+/-	0/10	+/-	5/12
<i>ZooSouth_t</i>						
<i>ZooNCSouth_t</i>						
<i>Incomplete</i>	-	4/12	+	0/10		
Number of models	23		19		34	

727

728

729 **Table 3.** Model selection using GAM, showing the three best models for each procedure
730 as measured by the general cross-validation criterion (GCV). Only models where all
731 covariates had a $p < 0.15$ are shown. The table shows the proportion of deviance explained
732 by the model (Dev. expl.), approximate number of degrees of freedom (d.f), GCV, and
733 Akaike's Information criterion adjusted for small sample size ($\Delta AICc$) relative to the top
734 model. For some GAM models (marked with footnotes in the GCV column), some of the
735 effects were non-monotonic, and these were re-estimated using HSGAM (see footnotes).
736 Differences in $AICc$ can be considered significant when they exceed 2. The models
737 shown in Table 4 and Figure 4-6 are marked by an asterisk in the left column.
738

739

		Dev.	d.f.	GCV	$\Delta AICc$
		expl.			
(a) Stage 1 (spawners) to stage 2 (larvae)					
*	$\log(MSB_{t-1}) + \text{CodSubad}_t + \text{LogCatch}_{t-1} +$ TempWintspr_t	0.72	4.07	1.147	0
	$\log(MSB_{t-1}) + \text{CodSubad}_t + \text{LogCatch}_{t-1}$	0.68	3.43	1.260	2.73
	$\log(MSB_{t-1}) + \text{CodAll}_t + \text{LogCatch}_{t-1} +$ TempWintspr_t	0.67	4.05	1.373	4.69
(b) Stage 2 (larvae) to stage 3 (zero-group)					
*	$\log(\text{Larvae}_t) + \text{CodZero}_t + \log(\text{Herr12}_t) +$ $\text{CodZero} * \log(\text{Herr12}_t)$	0.64	4.66	1.725	0
	$\log(\text{Larvae}_t) + \text{CodZero}_t$	0.54	2.84	1.861	3.63
	$\log(\text{Larvae}_t) + \log(\text{Herr12}_t)$	0.42	2.00	2.197	3.70
(c) Stage 3 (zero-group) to stage 4 (one-year olds)					
	$\log(\text{Zero}_t) + \text{CodZero}_t + \text{TempSummer}_{t+1}$	0.70	4.48	1.020 ¹⁾	4.26
*	$\log(\text{Zero}_t) + \log(\text{Herr12}_t) + \text{TempWintspr}_{t+1}$	0.72	4.97	1.027 ²⁾	0
*	$\log(\text{Zero}_t) + \text{CodSubad}_{t+1}$	0.66	3.25	1.029 ³⁾	2.93

740 ¹⁾ The effect of CodZero_t was strongly non-monotonic; with HSGAM, $p > 0.20$ for CodZero or
741 TempSummer

742 ²⁾ The effects of $\log(\text{Herr12})_t + \text{TempWintspr}_{t+1}$ were non-monotonic; with HSGAM, $p < 0.001$ for
743 $\log(\text{Herr12})_t$ and $p = 0.016$ for TempWintspr_{t+1} , 0.75 of the deviance explained, $GCV > 0.782$

744 ³⁾ The effect of $\log(\text{Zero}_t)$ was non-monotonic; with HSGAM, $p = 0.010$ for $\log(\text{Zero}_t)$,
745 0.66 of the deviance explained, $GCV > 0.942$

746

747 **Table 4.** Model estimates for the selected models (marked with an asterisk in Table 2).
 748 Estimated degrees of freedom (edf) equal 1 indicates a linear term, for which the estimate
 749 and standard error (SE) of the slope is given. F and p values are approximate in the case
 750 of non-linear terms. The importance of each term is indicated by ΔDev , the decrease in
 751 proportion of deviance explained when the term is deleted from the model (when the term
 752 was involved in an interaction term, this term was deleted too). The intercept is only
 753 included when it includes meaningful information, i.e. in models without non-linear (and
 754 non-parametric) terms. Also see Figures 4-6.
 755

(a) Stage 1 (spawners) to stage 2 (larvae)

	edf	Estimate	SE	F	p	ΔDev
$\log(\text{MSB}_{t-1})$	1.07			10.39	<0.001	0.26
CodSubad_t	1	-2.94	0.60	23.90	<0.001	0.32
LogCatch_{t-1}	1	-0.81	0.28	8.65	0.007	0.11
TempWintspr_t	1	0.84	0.40	4.49	0.046	0.05

756 **(b) Stage 2 (larvae) to stage 3 (zero-group)**

	edf	Estimate	SE	F	p	ΔDev
$\log(\text{Larvae}_t)$	1	0.45	0.15	9.09	0.007	0.13
$\log(\text{Herr}12_t)$	1.66			1.54	0.238	0.22
CodZero_t	1	-0.039	0.013	9.33	0.006	0.22
$\log(\text{Herr}12_t)*\text{CodZero}_t$	1	-0.049	0.016	9.47	0.006	0.17

757

758

759 (c) Stage 3 (zero-group) to stage 4 (one-year olds)

	edf	Estimate	SE	F	<i>p</i>	
<u>Model 1</u>						
$\log(\text{Zero}_t)$	1.52			6.86	0.005	0.12
$\log(\text{Herr}12_t)$ (when < -0.24)		0				
$\log(\text{Herr}12_t)$ (when ≥ -0.24)	1	-1.41	0.31	20.60	0.000	0.21
TempWintspr_{t+1} (when < 3.79)		0				
TempWintspr_{t+1} (when ≥ 3.79)	1.09			5.05	0.016	0.09
<u>Model 2</u>						
Intercept	1	5.19	1.01	26.40	0.000	
$\log(\text{Zero}_t)$ (when < 1.81)		0				
$\log(\text{Zero}_t)$ (when ≥ 1.81)	1	0.61	0.22	7.94	0.010	0.12
CodSubad_{t+1}	1	-1.92	0.74	6.69	0.017	0.10

760

Figure captions

761

762

763 **Fig. 1.** Simplified map showing the migrations of the capelin (dark grey) as well as the
764 distribution of North-East Arctic cod in winter (dotted) and young herring in summer
765 (hatched). In winter, the capelin distribution is split; immatures overwinter in the central
766 Barents Sea, while matures migrate towards the coast and spawn there in early spring
767 (April). Distributions vary greatly between years depending on, for instance, climate. The
768 red line shows the position of the Kola transect (temperature data).

769 **Fig. 2.** The capelin recruitment process and the capelin survey data used in this paper. In
770 the acoustic surveys (in September), capelin abundance is estimated by both age and
771 length. Capelin larger than 14 cm at the time of the acoustic survey (maturing stock
772 biomass, MSB) are assumed to mature during the winter and to spawn the following
773 spring, and thereafter die. Abundance is furthermore estimated at the larval stage, the 0-
774 group stage and in the September acoustic survey as 1-year olds.

775 **Fig. 3.** Abundance of capelin cohorts 1974-2006 (year of spawning) on stages 1-4. Note
776 logarithmic y-axes of capelin estimates. Parent generations are represented by biomass of
777 maturing fish in September (MSB_{t-1} , filled circles). The two bar plots on the bottom show
778 the annual biomass of the capelin predators cod (3-6: black; age 7-13: grey) and young
779 herring.

780

781

782 **Fig. 4.** Stage 1 (maturing biomass) to stage 2 (larvae). Significant and non-significant
783 effects of maturing biomass (MSB_{t-1}) and covariates on the abundance of larvae given the
784 models in Tab. 4a. Spawning stock biomass is represented by MSB_{t-1} . In this figure and
785 in Figures 5-7, the vertical axis shows the abundance of $\log(Stage_{i,j})$ adjusted for the
786 effect of the other explanatory variables (letting all other variables be equal to the mean
787 value). In these figures, the dotted lines indicate the confidence interval (CI; here defined
788 as standard error times two).

789 **Fig. 5.** Stage 2 (larvae) to stage 3 (zero-group); effects given the model in Tab. 4b. a)
790 Vertical axis shows the abundance of $\log(Stage_{i,j})$ adjusted for the effect of the other
791 explanatory variables (letting all other variables be equal to their respective mean value).
792 Dotted lines indicate the confidence interval (CI; here defined as standard error times
793 two). b) Effects of predation by herring and cod, showing the interaction between these
794 two predatory species (change in abundance of one of them has a high impact on the
795 effect of the other). The contour lines indicate the predicted abundance of zero-group
796 capelin ($\log(Zero_t)$) assuming $\log(Larvae_t)$ to be equal to $\text{mean}(\log(Larvae_t))$. Abundance
797 of zero-group is high in the upper right corner, i.e., when both herring and zero-group cod
798 abundance is high. The symbols show the observed values of $\log(Zero_t)$ adjusted for
799 variation in larval abundance, i.e., adjusted by the deviance of $\log(Larvae_t)$ from
800 $\text{mean}(\log(Larvae_t))$. Symbols denote low survival (crosses; $\log(Zero_t) < 2$), average
801 survival (open circles; $\log(Zero_t)$ between 2 and 3), and high survival (closed circles;
802 $\log(Zero_t) > 3$).

803 **Fig. 6.** Stage 3 (zero-group) to stage 4 (one-year olds). Effects of zero-group abundance
804 and explanatory variables on the abundance of one-year old capelin, as given by the

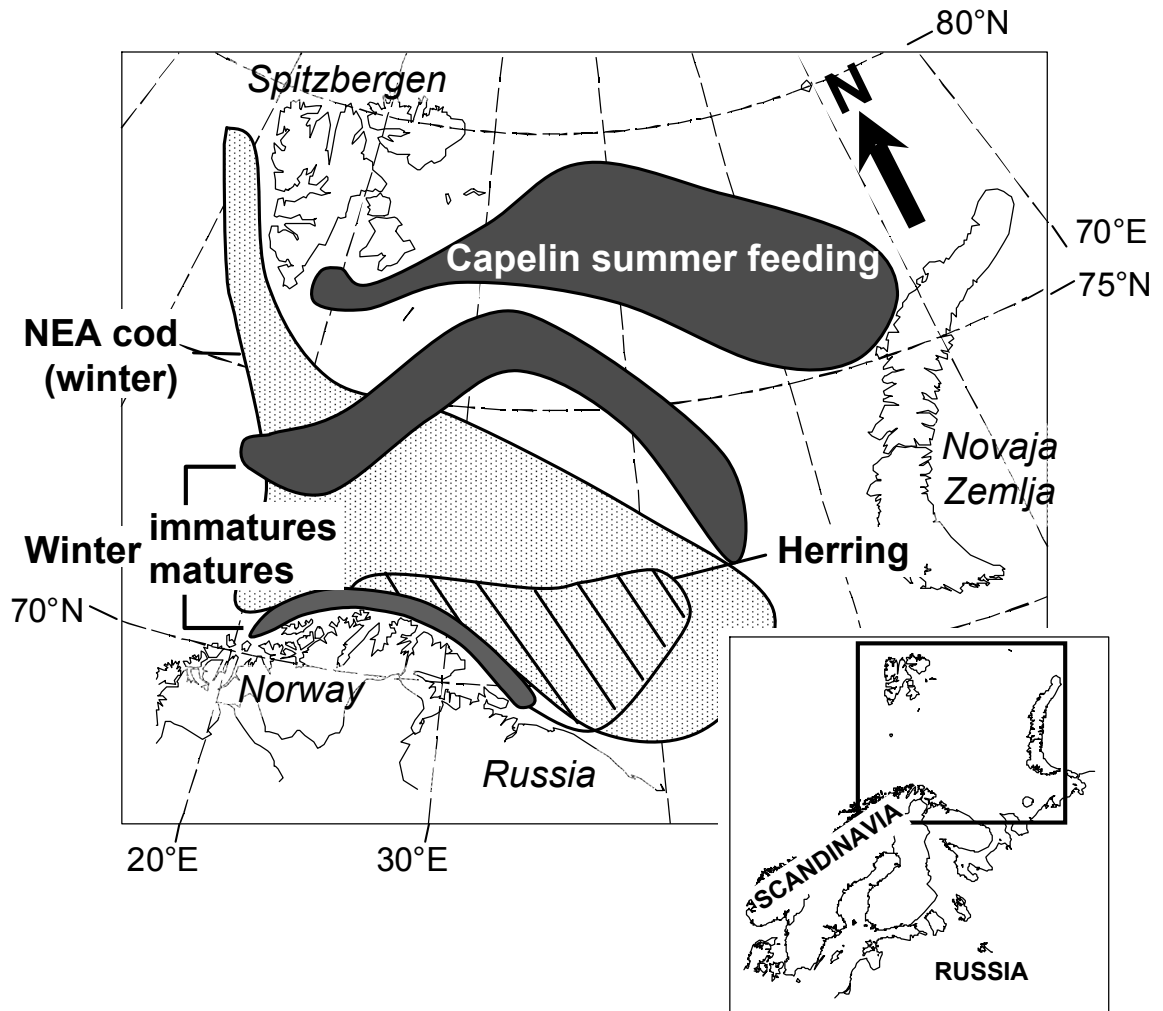
805 models in Tab. 4c. Panel a-c and d-e represent the two alternative models (denoted Model
806 1 and 2 in Tab. 4c). For further explanation, see Fig. 4. Vertical axis is abundance of
807 $\log(Stage_{i,j})$ adjusted for the effect of the other explanatory variables (letting all other
808 variables be equal to the mean value). Dotted lines indicate the confidence interval (CI;
809 here defined as standard error times two).
810

811 **Fig. 1**

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815 **Fig. 2**

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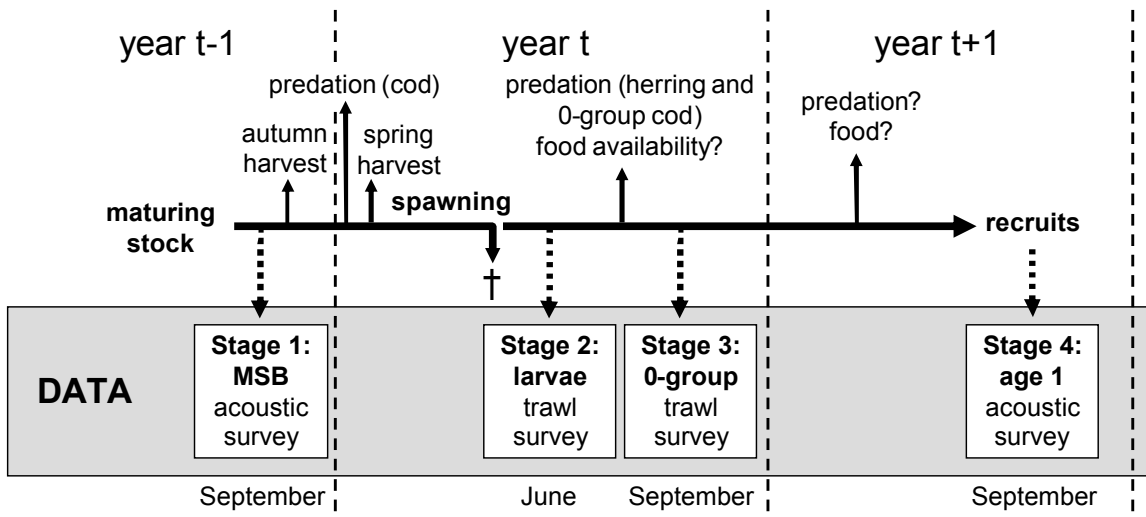
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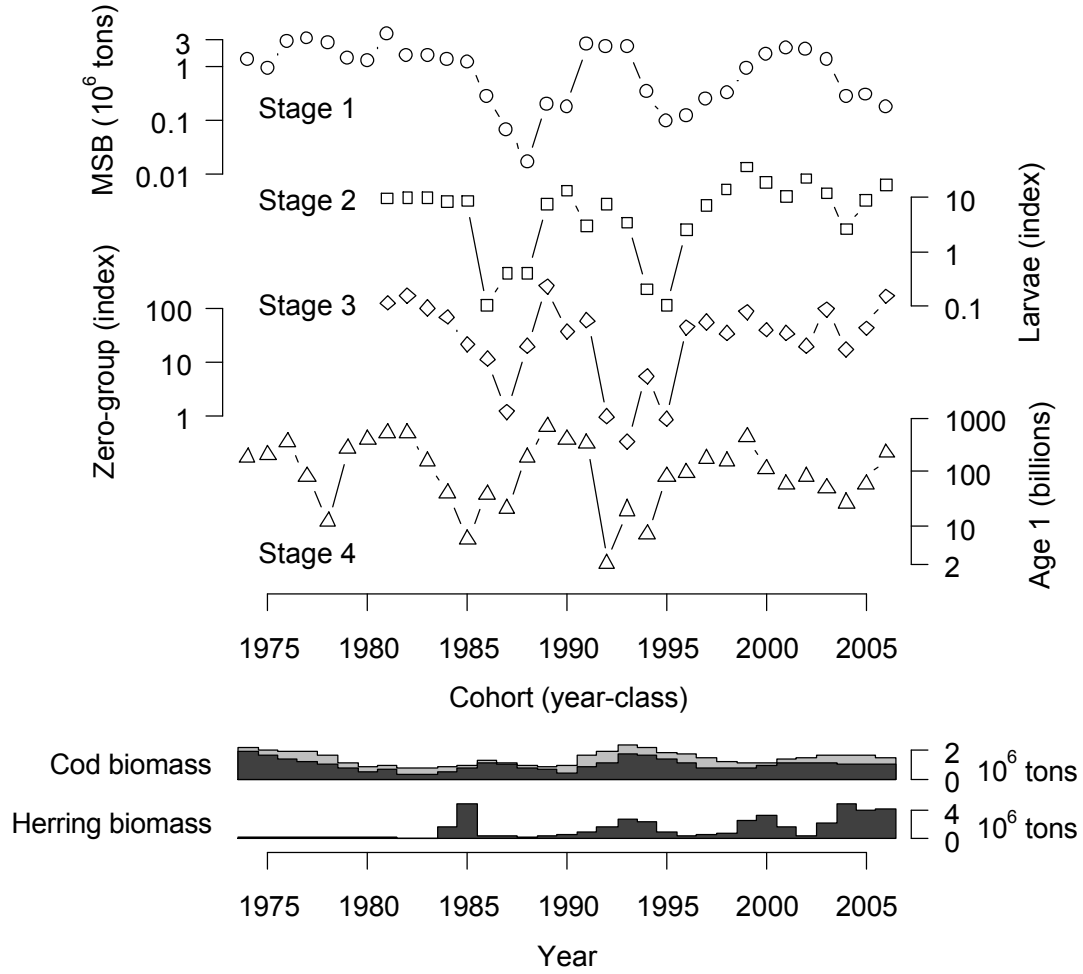
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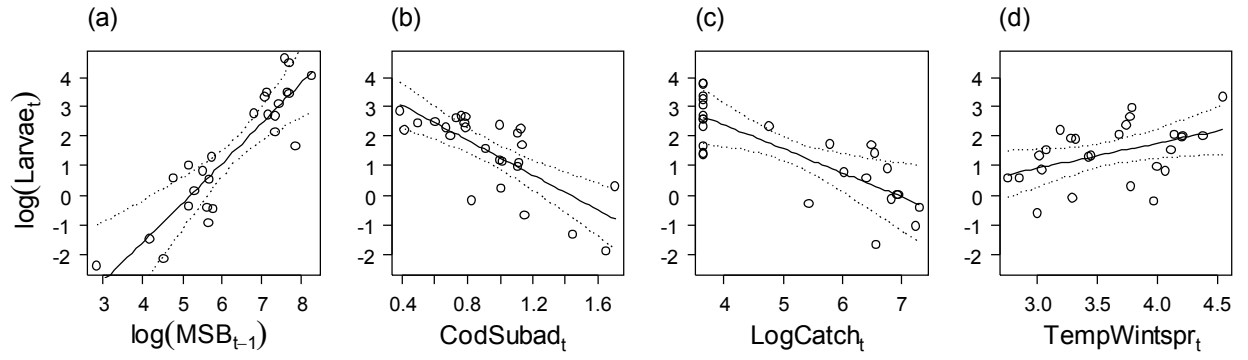
823 **Fig. 3**
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827 **Fig. 4**

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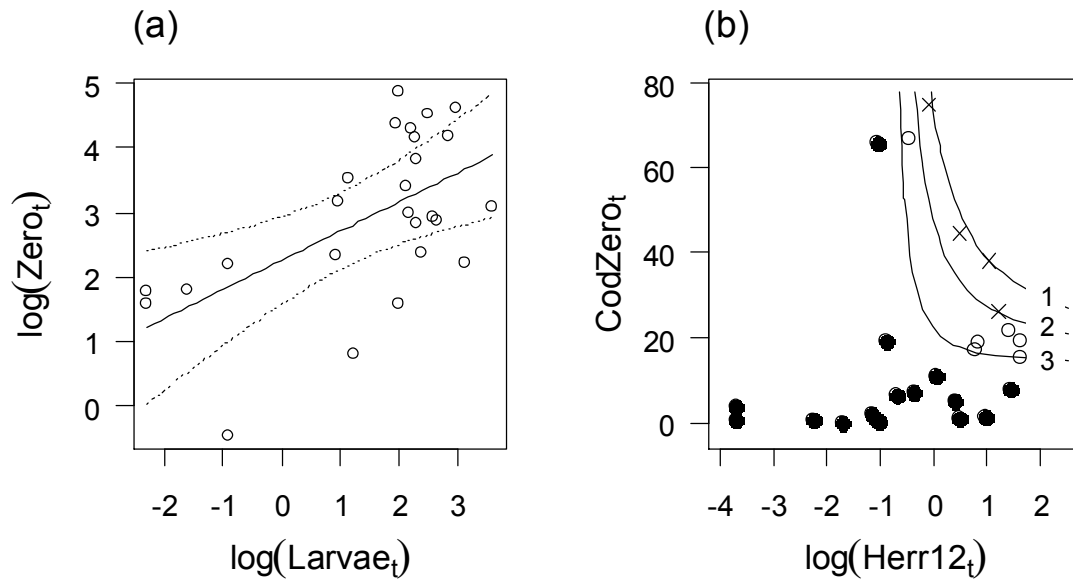
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832 **Fig. 5**

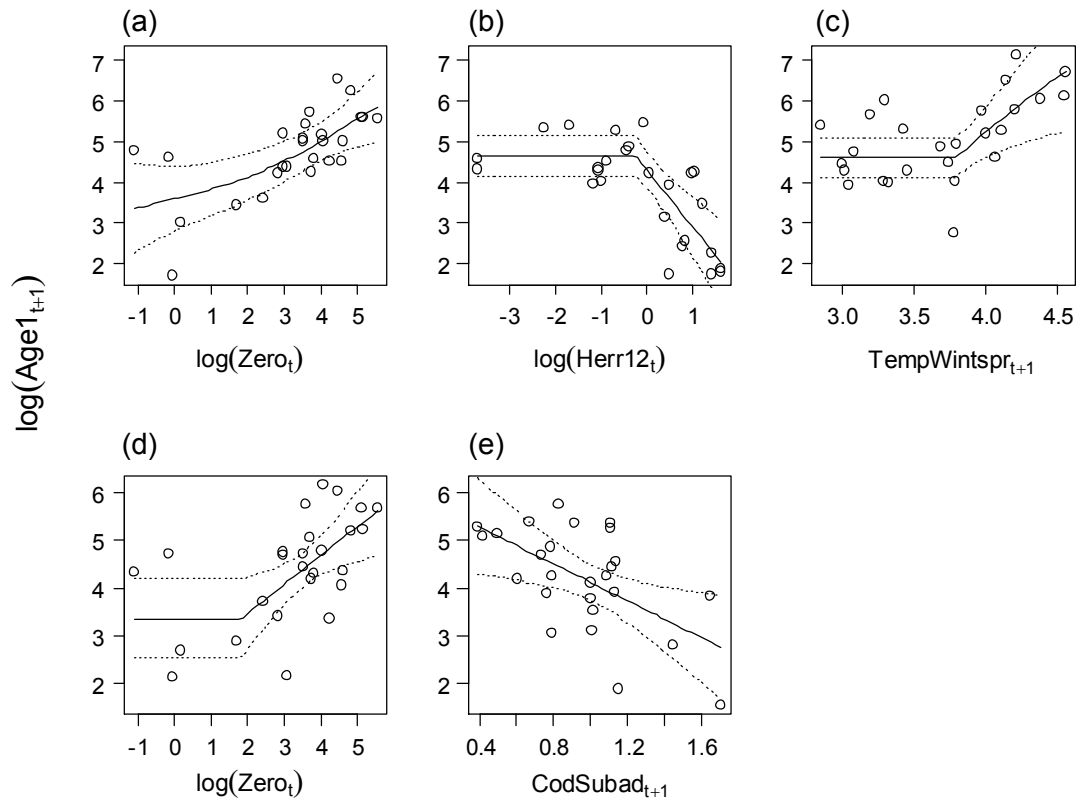
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837 **Fig. 6**
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844 **FOR ELECTRONIC SUPPLEMENT**

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846 **Supplementary Fig. 1.** Partial autocorrelations (denoted "Partial ACF" in figures) of

847 residuals from the models. The dotted line represents the critical correlation level

848 ($p=0.05$). (a) Stage 1 (spawners) to stage 2 (larvae); (b) Stage 2 (larvae) to stage 3 (zero-

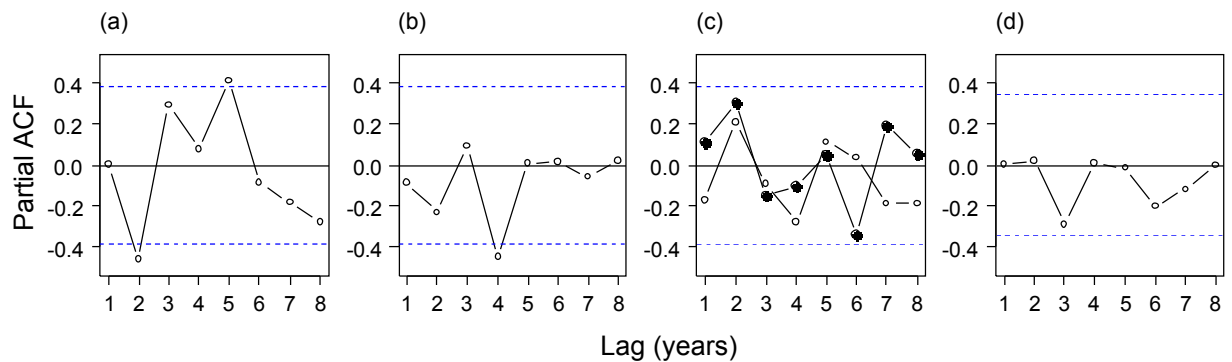
849 group); (c) Stage 3 (zero-group) to stage 4 (one-year olds); (d) Overall recruitment (stage

850 1 to 4). In figure (c), autocorrelations are shown for both model 1 (open circles;

851 covariates are herring and temperature) and model 2 (filled circles; subadult cod is the

852 covariate)

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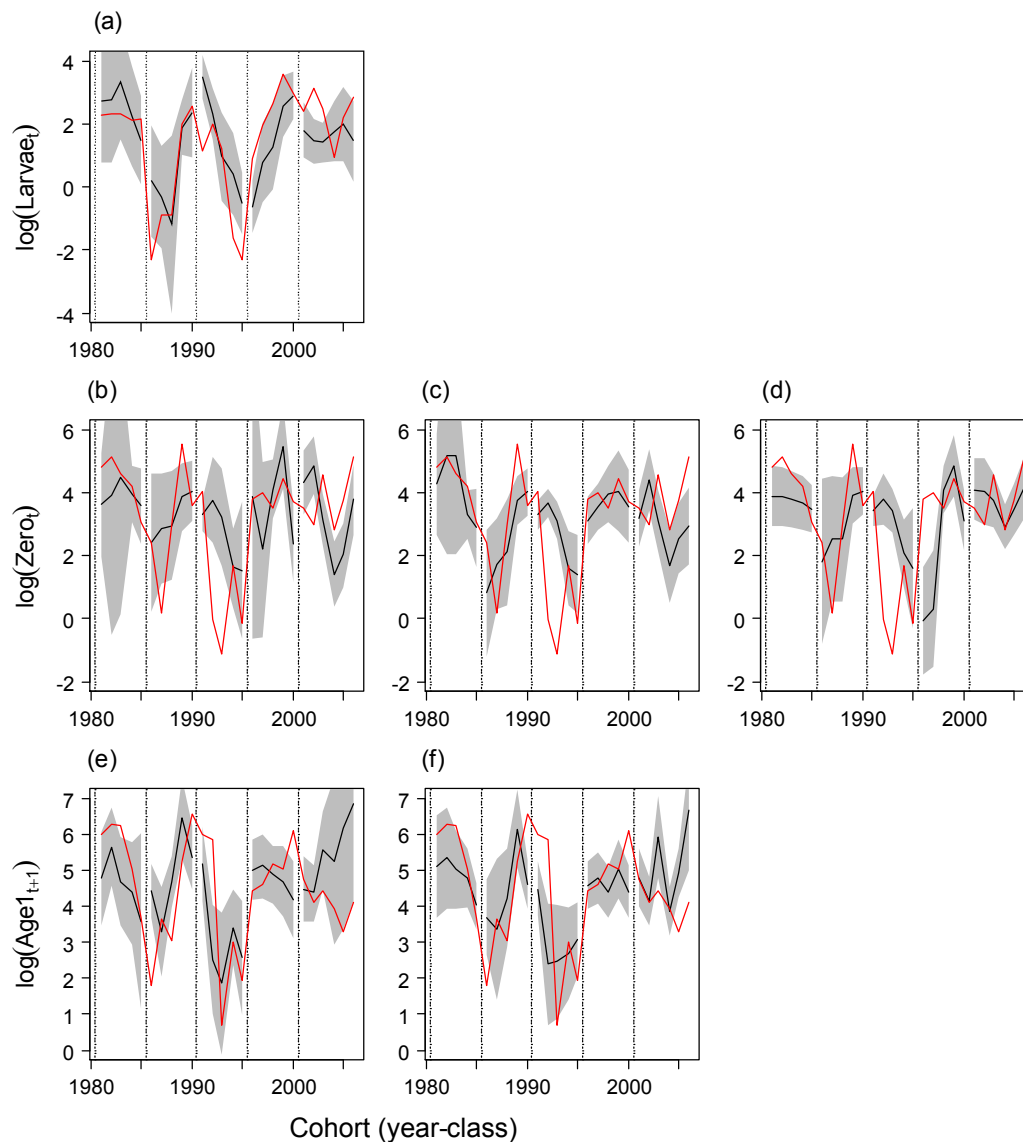
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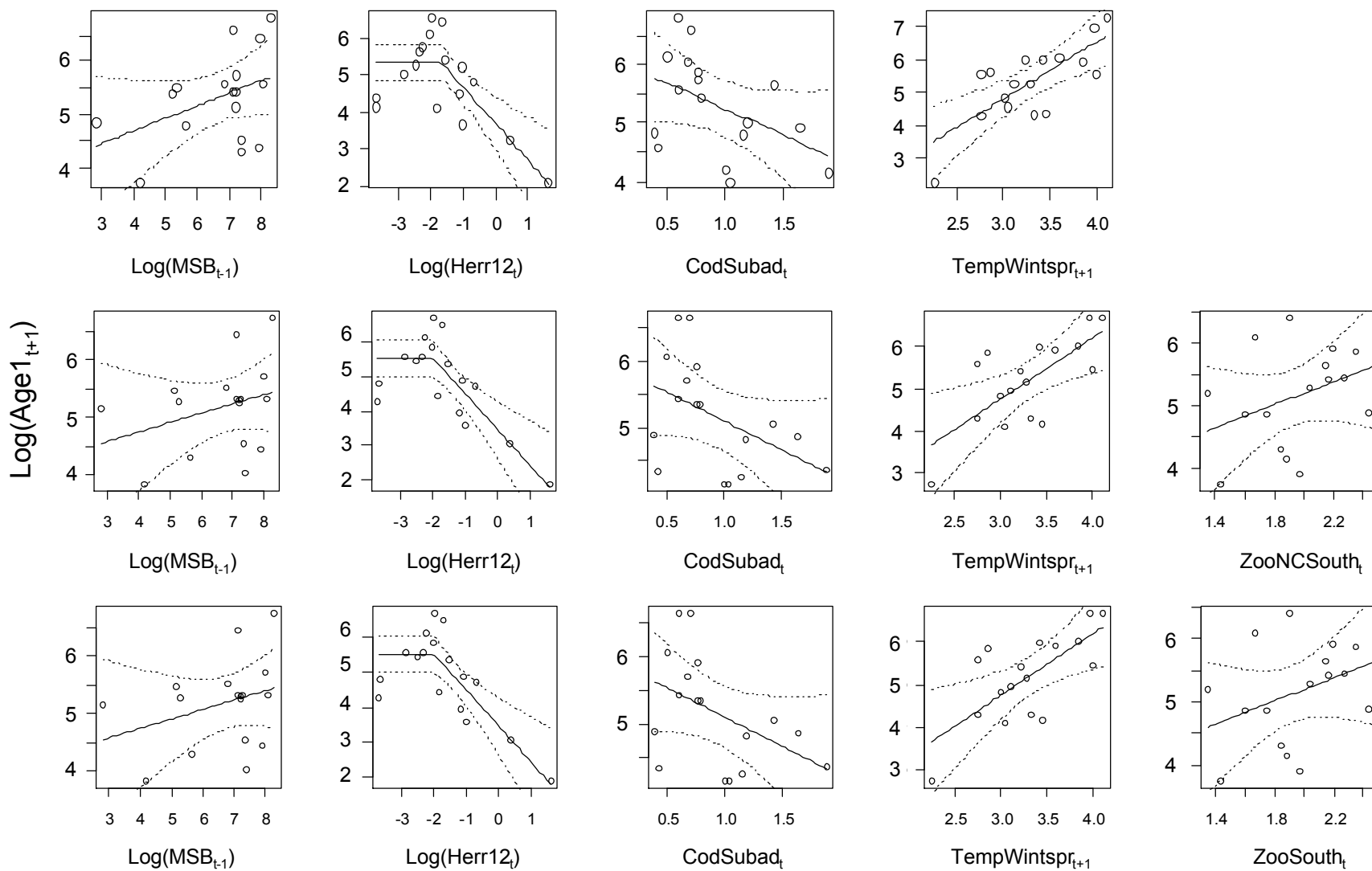
858 **Supplementary Figure 2.** Results from k-fold cross-validation. The figures show cross-
 859 validation predictions (black line) with 95% confidence interval (grey area) as well as
 860 observations (red line). Row 1-4 shows models for stage 1-2 (a), 2-3 (b-d), 3-4 (e-f) and
 861 1-4 (g), respectively. For the stage 2-3 transition (larvae to zero-group), the graphs shows
 862 results from the "best" model (b), a model with only herring as covariate (c) and a model
 863 with only zero-group cod as covariate (d). For the stage 3-4 transition, model 1 (e) and 2
 864 (f) are shown (see text).

865



873 **Supplementary Figure 3.** Recruitment models: age 1 (stage 4) as a function of maturing stock biomass (stage 1) and covariates
 874 that were found to be significant in the stagewise analyses. Each row represents one model: the best models without zooplankton
 875 (top row), the best model with zooplankton in the North Cape transect as a covariate (middle row), the best model with zooplankton
 876 in the both transects as a covariate (bottom row). Models were fitted to data for the cohorts 1974-1990. Tests for the factors used in
 877 the models are shown on next page (Supplementary Table 1).

878



879 **Supplementary Table 1.** the recruitment models shown in Supplementary Figure 3
 880 (previous page).

881 **a. Recruitment without zooplankton as covariate:**

882		edf	Ref.df	F	p-value
883	s(log.msb)	1	1.5	1.491	0.259
884	s(log.herr12)	1	1.5	10.808	0.003
885	s(cod.subad1)	1	1.5	1.920	0.192
886	s(temp.wintspr2)	1	1.5	8.971	0.006
887	Dev. expl.= 0.722		GCV= 1.082		n = 17

888 **b. Recruitment with zooplankton abundance in western transect as covariate:**

889		edf	Ref.df	F	p-value
890	s(log.msb)	1	1.5	1.349	0.289
891	s(var.thresh)	1	1.5	6.813	0.016
892	s(cod.subad1)	1	1.5	1.618	0.239
893	s(temp.wintspr2)	1	1.5	5.992	0.023
894	s(zoopl.nc.south)	1	1.5	0.002	0.991
895	Dev. expl.= 0.722		GCV= 1.287		n = 17

896

897 **c. Recruitment with zooplankton abundance in both transects as covariate:**

898		edf	Ref.df	F	p-value
899	s(log.msb)	1	1.5	0.632	0.506
900	s(var.thresh)	1	1.5	10.595	0.004
901	s(cod.subad1)	1	1.5	1.806	0.210
902	s(temp.wintspr2)	1	1.5	5.029	0.035
903	s(zoopl.south)	1	1.5	0.881	0.412
904	Dev. expl.= 0.742		GCV= 1.194		n = 17

905 **Supplementary Figure 4.** The effect of observation error on estimates of density
906 dependence: results of simulation. Let the abundance at two stages be X and Y ,
907 respectively. We simulated that Y depend on X by the following formula:
908 $\log(Y) = b \cdot \log(X) + \varepsilon$ (where ε represents random variation in survival; ε is normally
909 distributed around zero). Then we simulated a measurement error in X , so we observe not
910 X but $X' = X + \gamma$ (γ is measurement error), and estimated b using linear regression
911 between Y and X' . We let the standard deviation of $\log(X)$, the real value of b , and the
912 degree of measurement (observation) error γ vary. The figures show the estimated values
913 of b (ordinate axis) compared to the real values (abscissa axis); unbiased estimates should
914 lie on the dashed line (indicating ordinate=abscissa). In panel a-c, we show the result when
915 three levels of measurement error (γ) are used, given as the coefficient of variation (CV;
916 standard deviation in γ as percentage of X ; i.e., a coefficient of variation of 30% means
917 that 95% of the measured X values are within +/- 60% of the real X values). It is clear
918 that as long as the variation of X is modest, b is underestimated when there is
919 measurement error (and density dependence, given as $1-b$, is overestimated). However, if
920 the variation in X is large (standard deviation of $\log(X) \geq 1$), bias is small even when
921 measurement error is considerable. Panel (d) shows that due to the inclusion of
922 measurement error, the variation in measured X , i.e., $\text{sd}(\log(X'))$, is slightly higher than
923 the variation in the real X . Horizontal lines indicate $\text{sd}(\log(X'))$ for the capelin data,
924 which is 1.38, 1.67 and 1.75 for the transitions between stages 1-2, 2-3 and 3-4,
925 respectively. For these values, $\text{sd}(\log(X)) \approx \text{sd}(\log(X'))$ even if measurement error is large
926 (CV=30%). Therefore, the bias in b (panel a-c) can also be expected to be small.
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