

1 **Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous**
2 **fishes in the Barents Sea**

3 Leif Christian Stige^{1*}, Elena Eriksen², Padmini Dalpadado², Kotaro Ono^{1,3}

4 ¹ Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, P.O. Box 1066
5 Blindern, N-0316 Oslo, Norway.

6 ² Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway.

7 ³ Centre for Coastal Research (CCR), University of Agder, N-4604 Kristiansand, Norway.

8 * Corresponding author. Telephone: +47 2285 4608. E-mail: l.c.stige@ibv.uio.no.

9 **Abstract**

10 Large areas of the Arctic are being transformed from seasonally ice-covered to ice-free zones. These
11 changes in physical conditions affect the primary production regime and the higher trophic levels
12 through a multitude of direct and indirect effects. We here analysed interannual variability in autumn
13 biomasses of the main zooplankton groups and planktivorous fishes in the central and northern
14 Barents Sea from 1980 to 2015, a period with a dramatic decrease in winter sea ice in the region. The
15 analysed zooplankton groups were copepods, krill, and amphipods and the planktivorous fishes were
16 capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*). By building a Bayesian state-space
17 model, we estimated the direct associations between winter sea ice cover and year-to-year change in
18 biomass of each key zooplankton group and fish species, as well as the indirect and delayed effects of
19 winter sea ice cover through the other zooplankton groups and fish species. We found that low sea
20 ice cover in winter was associated with increased population biomass of capelin and reduced
21 biomasses of copepods and amphipods in the following autumn. Furthermore, results suggested
22 strong predator-prey interactions, with capelin playing a central role. We found positive bottom-up
23 effects by krill on capelin and by copepods on amphipods and negative top-down effects by capelin
24 on krill and on copepods and by polar cod on amphipods. These predator-prey interactions led to
25 indirect and delayed effects of sea ice cover, which were of comparable magnitudes as the direct
26 associations. The indirect effects were of same sign as the direct associations and amplified the
27 effects of sea ice cover on capelin, copepods and amphipods, whereas for krill, results indicated that
28 reduction in sea ice increased biomass in the short-term but reduced biomass at longer terms
29 because of increased predation pressure. These findings suggest that both bottom-up and top-down
30 processes need to be taken into account when projecting the effects of future climate change on
31 ecosystems.

32 **Keywords:** Copepods; Krill; Amphipods; Capelin; Polar cod; Multi-species dynamics

33 **Introduction**

34 Climate variability and change affect organisms directly as well as indirectly, via effects on predators,
35 competitors and prey (Drinkwater *et al.*, 2010; Pörtner and Peck, 2010). In general, the indirect
36 effects appear to be quantitatively more important than the direct effects in driving changes in
37 marine ecosystems (Ockendon *et al.*, 2014). Identification of which direct and indirect effects are
38 quantitatively important is therefore fundamental to understanding and predicting ecosystem
39 changes.

40 Arctic marine ecosystems are rapidly changing because of global warming. The maximum
41 extent of the Arctic sea ice (which usually occurs in late winter) is decreasing at a rate of about 2.5 %
42 per decade, transforming large areas from seasonally ice-covered to ice-free zones (Comiso *et al.*,
43 2017). One of the areas with the fastest declines in winter sea ice is the Barents Sea, located north of
44 Norway and Russia, where the present-day extent of winter ice has been reduced to less than a third
45 of the pre-satellite (1850–1978) mean (Comiso *et al.*, 2017; Onarheim and Årthun, 2017).

46 Most of the sea ice in the Barents Sea is formed seasonally, but multi-year ice is found in the
47 northern Barents Sea (Vinje, 2001). The extent of ice cover is highly variable depending on climate
48 conditions, and an area of about half the Barents Sea (around 0.7 million km²) can either be ice
49 covered in cold years or remain open in warm years. The seasonal growth of phytoplankton is
50 different in ice covered and ice free areas. In ice covered regions, the growth is highly influenced by
51 ice melting causing vertical stability and thereby driving a short spring/summer phytoplankton bloom
52 with low (about 50 g C m⁻²) primary production (Rey *et al.*, 1987; Wassmann *et al.*, 2006). In contrast,
53 the spring blooms in the ice free regions are driven by seasonal warming, which result in deeper and
54 less pronounced stratification intermittently broken up by strong winds; the spring blooms are
55 therefore slower and prolonged but with considerably higher primary production (about 100 g C m⁻²
56 per year, Wassmann *et al.*, 2006). Thus in the ice free regions there is a more effective coupling to
57 the next level in the pelagic food web, allowing more time for zooplankton to exploit the
58 phytoplankton production. The Arctic blooms consist of two distinct categories of primary producers,
59 ice algae growing within and on the underside of the sea ice, and phytoplankton growing in open
60 waters (Søreide *et al.*, 2010). Ice algae contribute only a small proportion of the primary production
61 (around 3 % for the Barents Sea as a whole, Wassmann *et al.*, 2006), but may nevertheless constitute
62 an important food source for Arctic zooplankton when water column phytoplankton are not available
63 during critical periods in their life history (Wang *et al.*, 2015). In the Barents Sea, the reproduction
64 and growth of the key Arctic zooplankton *Calanus glacialis* is dependent on both ice algae and open
65 water phytoplankton production (Søreide *et al.*, 2010). In the Bering Sea, Wang *et al.* (2015) showed

66 by use of compound specific isotopes that a sizable portion (27 – 74%) of the fatty acids in *Calanus*
67 *marshallae*, *Thysanoessa raschii* and *Themisto libellula* are derived from ice algae. These studies
68 indicate the importance of ice algal production (and hence sea ice extent) to some Arctic species.
69 Reductions in the extent of winter sea ice are also correlated with other environmental changes,
70 such as in water temperature, water mass distribution and timing of spring bloom, which may
71 potentially have both positive and negative effects on zooplankton biomass, dependent on
72 zooplankton species composition, area and time scale.

73 The distributions of marine organisms have shifted poleward in response to the warming,
74 causing large changes in species composition and ecosystem functioning (Pinsky *et al.*, 2013; Frainer
75 *et al.*, 2017). In the Barents Sea, many boreal species have increased in biomass and distribution in
76 response to warming, at the expense of Arctic species (Dalpadado *et al.*, 2012; Fosheim *et al.*, 2015;
77 Eriksen *et al.*, 2017). These changes may have occurred through a multitude of mechanisms related
78 to changes in sea ice, light regime, temperature, water column stability, primary production and
79 species interactions, with, e.g., increased dominance of boreal species being associated with
80 increased overall predation rates (Frainer *et al.*, 2017).

81 The focus in this study is the pelagic ecosystem in the central and northern Barents Sea (Fig.
82 1), where the transition from seasonally ice-covered to ice-free conditions is taking place. The
83 dominant planktivorous fishes in this region are capelin, *Mallotus villosus*, and polar cod, *Boreogadus*
84 *saida* (Gjørseter, 1998; Orlova *et al.*, 2009). The capelin is sub-Arctic and has copepods and krill as its
85 main prey (>80 % of diet, Dalpadado and Mowbray, 2013). The polar cod is Arctic and has copepods,
86 pelagic amphipods and, to a lesser extent, krill, as its main prey (Orlova *et al.*, 2009; ICES, 2018). Two
87 largely herbivorous copepod species dominate the mesozooplankton biomass in the Barents Sea, the
88 boreal *Calanus finmarchicus* and the predominantly Arctic *C. glacialis*, with *C. glacialis* being the most
89 abundant of the two in the central and northern regions (Orlova *et al.*, 2011; Aarflot *et al.*, 2017). In
90 addition, the Arctic *Calanus hyperboreus* contributes to the mesozooplankton biomass, as well as
91 several species of smaller copepods and other taxa such as *Clione limacina* (Aarflot *et al.*, 2017). The
92 dominant krill species in the region is the mainly boreal and largely herbivorous *Thysanoessa inermis*,
93 but with, e.g., *T. longicaudata*, *T. raschii* and *Meganyctiphanes norvegica* also contributing to the
94 biomass (Eriksen *et al.*, 2016). The dominant pelagic amphipod is the Arctic *Themisto libellula*, which
95 is carnivorous and has copepods as important parts of the diet (Auel *et al.*, 2002; Dalpadado, 2002).

96 We here build on previous studies that have investigated effects of climate and predator-
97 prey interactions on zooplankton and planktivorous fishes in the Barents Sea (e.g., Skjoldal *et al.*,
98 1992; Orlova *et al.*, 2009; Dalpadado *et al.*, 2012; Stige *et al.*, 2018). In contrast to previous studies,

99 we estimated climate effects as well as bottom-up and top-down effects of species interactions in
100 one state-space statistical framework. This approach allowed us to separate direct climate-species
101 associations from indirect associations mediated by other species, and to account for the effects of
102 observation noise. Our aim was to understand how climate changes, particularly changes in winter
103 sea ice cover, have influenced the biomasses of the main zooplankton groups and planktivorous
104 fishes in the central and northern Barents Sea, either through direct associations or indirectly
105 through effects on the other zooplankton groups or fish species.

106

107 **Material and methods**

108 *Time-series analysed*

109 We focused the analysis on time-series representing three key zooplankton groups in the central and
110 northern Barents Sea, i.e. copepods, krill and amphipods, and the main planktivorous fishes, i.e.
111 capelin and polar cod (Fig. 2A, Table 1). In addition we included time-series of key predators on the
112 fish species, fishing, and climate (Fig. 2B). Please note that, for brevity, we referred to the
113 zooplankton groups as copepods, krill and amphipods, but that the results did not necessarily reflect
114 the dynamics of the smallest species and stages of each group, which were not sampled
115 representatively (see Table 1 and below). It should also be noted that by grouping species and stages,
116 we averaged out within-group and within-species heterogeneity in associations with climate and
117 other species. The two dominant copepods, *C. glacialis* and *C. finmarchicus*, differ for example in
118 their ecological roles by the former being better able than the latter to utilize the ice algae
119 production (Broms *et al.*, 2009; Søreide *et al.*, 2010). *C. glacialis* is distributed in colder waters
120 (Aarflot *et al.*, 2017) and is on average larger (but with similar lipid-content for a given size, Renaud
121 *et al.*, 2018). The grouping of zooplankton species was dictated by data availability but nonetheless
122 resulted in meaningful functional groups in terms of their roles as prey for the fish species.

123 Copepods were represented by biomass (g dry weight m⁻²) of mesozooplankton, for brevity
124 referred to as “copepods” due to their dominance in the mesozooplankton biomass (Orlova *et al.*,
125 2011; Aarflot *et al.*, 2017). Copepods were sampled by the Institute of Marine Research (IMR) from
126 August to early October 1981 and 1984–2015 throughout the water column in the Barents Sea (ICES,
127 2018). The majority of the samples were taken using WP2 plankton nets (56 cm diameter, 180 μm
128 mesh). Copepod biomass time-series were available as annual indices from three areas of the
129 Barents Sea (Stige *et al.*, 2018), as shown in Fig. 1. The three areas were the southwestern
130 (characterized by surface waters >3 °C), central (0–3 °C) and northern (<0 °C) Barents Sea (with
131 temperatures referring to long-term averages for August to early October, see Stige *et al.*, 2014). The

132 copepod biomass time-series were constructed from the spatiotemporal observation data by using a
133 statistical regression approach to account for interannual differences in sampling protocol (sampling
134 location, -day, -gear and -depth, as described in Stige *et al.*, 2014). The indices were on scale
135 $\ln(\text{weight} + 1)$, with 1 added to avoid taking the log of zero (adding, e.g., 0.1 instead of 1 led to more
136 skewed \ln -transformed data, with variability among very small values contributing more to the
137 variance). We here combined the indices for the central (Cop_C) and northern (Cop_N) parts of the
138 Barents Sea into one index (Cop , Fig. 2), using the formula $Cop = \ln([\exp(Cop_C) + \exp(Cop_N)] / 2)$. The
139 two indices (Cop_C and Cop_N) have previously been found to associate similarly to climate variables
140 and planktivorous fish biomass (Stige *et al.*, 2014) and were here combined to reduce model
141 complexity. The central and northern Barents Sea were, for simplicity, weighted equally rather than
142 by their coverage area in the calculation of the index, as the extent of species distributions in the
143 respective areas were uncertain.

144 Krill biomass (g wet weight m^{-2}) was estimated based on pelagic trawl samples in
145 August–September 1980–2015 (Eriksen *et al.*, 2016; ICES, 2018). The pelagic trawl had a 20 × 20-m
146 mouth opening, seven panels, and a codend. Each panel consisted of meshes of different sizes
147 varying from 100 mm in the first to 30 mm in the last and 7 mm in the codend. Sampling was
148 routinely conducted with a trawl head line at 0, 20 m, and 40 m, and thus covered the upper 60 m
149 (Eriksen *et al.*, 2016). Krill conduct diel feeding migrations, migrating to the surface during the night
150 to feed and to near the bottom during the day to avoid predation. To avoid bias from sampling time,
151 we first calculated the annual arithmetic means of day ($Krill_D$) and night ($Krill_N$) catches in the upper
152 60 m in the Barents Sea north of 74 °N and then computed a combined log-scale index, $Krill =$
153 $\ln([\text{Krill}_D + \text{Krill}_N] / 2)$ (Fig. 2).

154 Amphipod biomass (kg wet weight per nautical mile surveyed) was sampled by pelagic trawls
155 (see trawl description and hauling procedure above) in August–September 1985–2015 (Eriksen *et al.*,
156 2016; ICES, 2018). The data in this investigation were restricted to latitudes 74–80 °N of the Barents
157 Sea, as this area was surveyed most years and generally covered most of the non-zero amphipod
158 catches. An annual amphipod index ($Amph$) was constructed from the spatiotemporal observation
159 data by using a statistical regression approach to account for interannual differences in sampling
160 protocol (sampling location, -gear and -depth, as described in Dalpadado *et al.*, 2012). The scale of
161 this index was $\ln(\text{catch}/\text{distance} + 0.1)$, with 0.1 added to avoid taking the logarithm of zero (adding
162 0.1 led to less skewed data than adding 1) (Fig. 2).

163 Population biomasses of age 1+ capelin (Cap , $\ln[1000 \text{ tonnes}]$) between 1980 and 2015 were
164 taken from the ICES report (2016) and calculated from acoustic surveys carried out by IMR and the

165 Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in the Barents Sea during
166 September–October (usually late in September, Gjøsæter, 1998) (Fig. 2).

167 Estimates of age 1+ polar cod biomass (Pol , ln[1000 tonnes]) from 1986 to 2015 were based
168 on acoustic surveys taken from the annual IMR-PINRO survey reports (Skaret and Prozorkevich, 2016)
169 (Fig. 2).

170 Annual biomasses of age 3+ cod (Cod , ln[1000 tonnes]) and age 1–3 herring (Her , ln[1000
171 tonnes]) were obtained from ICES (2016). The estimates were from virtual population analyses,
172 mostly relying on fisheries catch data, and referred to biomass at the beginning of the year. Age 3+
173 cod are key predators on capelin at the central and northern Barents Sea feeding grounds, with
174 highest overlap between cod and capelin in years when the cod stock is large (Gjøsæter, 1998;
175 Johannesen *et al.*, 2012; Fall *et al.*, 2018; ICES, 2018). Age 1–3 herring are predators on capelin larvae
176 and suspected to be responsible for recruitment failures and population collapses of capelin in the
177 1980s, 1990s and 2000s (Gjøsæter *et al.*, 2016). Cod is also a potential predator on polar cod, notably
178 in recent years with extended cod distribution (Johannesen *et al.*, 2012; ICES, 2018). Other potential
179 predators, such as marine mammals (Bogstad *et al.*, 2015), were not explicitly modelled due to
180 scarcer observation data, but were accounted for in a process noise term in the statistical model (see
181 the *Statistical analyses* section).

182 A summer–autumn fishery for capelin occurs in August–December, i.e., both before and after
183 the scientific survey around late September (Gjøsæter, 1998). For each year T , we calculated a crude
184 index of fishing rate (f_{CAP}) as sum of the catch (taken from ICES, 2016) in August–September in year T
185 and October–December in year $T-1$, divided by the population biomass in year $T-1$. We also
186 calculated the transformed variable $F_{CAP} = -\ln(1 - f_{CAP})$, which approximated the reduction in
187 ln(biomass) due to fishing (note, however, that F_{CAP} may have underestimated the fishing mortality
188 rate, because the change in population biomass during the period of fishing was ignored). We did not
189 consider the capelin winter fisheries, as these fisheries target spawning fish, which do not contribute
190 much to next autumn’s biomass due to the likely semelparous life cycle of capelin (Gjøsæter, 1998).
191 Commercial fishing for polar cod in the study period has been negligible (ICES, 2018).

192 We used annual mean winter sea ice concentration as a key climate variable (Ice). We chose
193 to focus on this index as it measures the transition from seasonal ice cover to ice-free conditions,
194 which is thought to have large influence on Arctic organisms (e.g., Søreide *et al.*, 2010; Wang *et al.*,
195 2015). The index was calculated from monthly satellite-derived sea ice concentrations (Nimbus-7
196 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, NSIDC-0051) provided by the National Snow
197 and Ice Data Center (Cavalieri *et al.*, 1996, updated yearly). The index was calculated for a

198 representative area in the central and northern Barents Sea (74–80 °N, 20–50 °E; Fig. 1). *Ice* for year
199 T referred to the average ice cover between December of year $T-1$ and May of year T , which were
200 the six months that had the highest sea ice concentrations for the analysed years, on average.

201 To throw additional light on the mechanisms for the effects of climate and to assess the
202 sensitivity of results to the choice of climate index, we considered six alternative climate indices
203 correlated with *Ice* in a supplementary analysis. The six indices were sea ice cover in April, area of
204 Arctic water masses in autumn, summer sea surface temperature, spring sea surface temperature,
205 previous-autumn sea surface temperature, and previous-autumn water column temperature (Table
206 S1, Fig. S1).

207 *Statistical analyses*

208 The statistical analysis quantified associations between year-to-year variations in winter sea ice cover
209 in the central and northern Barents Sea (*Ice*) and biomasses of key zooplankton groups and
210 planktivorous fish species, i.e. copepods, krill, amphipods, capelin and polar cod. Specifically, we
211 investigated how *Ice* explained the variations in these organism groups either through direct
212 associations or indirectly through associations with the other organism groups. In addition, we
213 accounted for the effects of key fish predators on capelin and/or polar cod (*Cod*, *Her*) and harvesting
214 (F_{CAP}).

215 All time-series were analysed in one statistical model that simultaneously estimated the
216 strengths of bottom-up and top-down effects and the effects of climate (represented schematically
217 in Fig. 3). We predicted that amphipods, capelin and polar cod potentially had negative top-down
218 effects on their copepod prey, and that copepods potentially had positive bottom-up effects on
219 amphipods, capelin and polar cod. Similarly, we predicted potentially negative top-down effects by
220 capelin on krill and by polar cod on amphipods, with corresponding positive bottom-up effects the
221 other way. Furthermore, we predicted that climate conditions, as represented by the sea ice index,
222 potentially affected all five organism groups. We also took into account potential top-down effects
223 by herring, cod and fishing on capelin, and by cod on polar cod. To limit model complexity, we did not
224 analyse how climate or other factors influenced herring or cod, but only used these variables as
225 covariates for explaining the variation in capelin and polar cod biomasses. For the same reason, we
226 only included one climate variable in the model, and considered the alternative climate variables one
227 at a time by replacing *Ice* with each variable in a series of alternative models.

228 The model was fitted in a Bayesian state-space framework, whereby the ecosystem variables
229 and processes shown in Fig. 3 were described by a set of state variables and equations that are
230 jointly referred to as the “process model”. The process model was linked to data by an observation

231 model. This way, uncertainties about biological processes and observation noise were explicitly
 232 accounted for, to provide unbiased parameter estimates and appropriate estimates of confidence
 233 intervals (Clark and Bjørnstad, 2004).

234 *The process model*

235 Equations 1–5 describe the dynamics of copepods (eq. 1), krill (eq. 2), amphipods (eq. 3), capelin (eq.
 236 4) and polar cod (eq. 5).

$$\begin{aligned}
 237 \quad (1) \quad X_{1,T} &= C_{10} + C_{11} X_{1,T-1} && + C_{13} X_{3,T-1} + C_{14} X_{4,T-1} + C_{15} X_{5,T-1} + C_{16} Z_{1,T} && + \delta_{1,T} \\
 238 \quad (2) \quad X_{2,T} &= C_{20} && + C_{22} X_{2,T-1} && + C_{24} X_{4,T-1} && + C_{26} Z_{1,T} && + \delta_{2,T} \\
 239 \quad (3) \quad X_{3,T} &= C_{30} + C_{31} X_{1,T-1} && + C_{33} X_{3,T-1} && + C_{35} X_{5,T-1} + C_{36} Z_{1,T} && + \delta_{3,T} \\
 240 \quad (4) \quad X_{4,T} &= C_{40} + C_{41} X_{1,T-1} + C_{42} X_{2,T-1} && + C_{44} X_{4,T-1} && + C_{46} Z_{1,T} + C_{47} Z_{2,T} + C_{48} Z_{3,T} + C_{49} Z_{4,T} + \delta_{4,T} \\
 241 \quad (5) \quad X_{5,T} &= C_{50} + C_{51} X_{1,T-1} && + C_{53} X_{3,T-1} && + C_{55} X_{5,T-1} + C_{56} Z_{1,T} + C_{57} Z_{2,T} && + \delta_{5,T}
 \end{aligned}$$

242 The state variables $X_{1,\dots}, X_5$ represented the “true” log-biomasses of each of these zooplankton and
 243 fish groups. The state variables $Z_{1,T}, \dots, Z_{4,T}$ were the covariates Ice_T, Cod_T, Her_{T-1} and $F_{CAP,T}$, with the
 244 time-lag for herring included because predation mainly affects larvae (Gjøsæter *et al.*, 2016). The
 245 subscript T represented the year (1980, ..., 2015). In six alternative models Ice was replaced by the
 246 different alternative climate indices. The coefficients C_{10}, \dots, C_{50} were intercepts that represented
 247 average productivity and scaling. Coefficients $C_{11}, C_{22}, C_{33}, C_{44}, C_{55}$ quantified density dependence for
 248 each population, with no compensatory density dependence at $C_{ij} = 1$, complete compensation at $C_{ij} =$
 249 0, and overcompensation at $C_{ij} < 0$. With this formulation, the Gompertz model was written in a linear
 250 form, which simplifies statistical estimation and is also a good first-order approximations of more
 251 complex dynamics (Ives *et al.*, 2003). The support in the data for using a Gompertz model was
 252 assessed for all populations by plotting log-biomass at time T against log-biomass at time $T+1$, which
 253 showed approximately linear relationships, as assumed by the Gompertz model (Fig. S2).

254 The other coefficients C_{ij} quantified effects of biotic and abiotic environmental variables on
 255 log-biomass for each population. Coefficients C_{31}, C_{41}, C_{51} quantified effects of copepods on
 256 amphipods, capelin and polar cod; C_{42} the effect of krill on capelin; C_{13} and C_{53} the effects of
 257 amphipods on copepods and polar cod; C_{14} and C_{24} the effects of capelin on copepods and krill; C_{15}
 258 and C_{35} the effects of polar cod on copepods and amphipods; C_{16}, \dots, C_{56} the effects of sea ice (or the
 259 alternative climate variables) on each population; C_{47} and C_{57} the effects of cod on capelin and polar
 260 cod; C_{48} the effect of herring on capelin; and C_{49} the effect of fishing on capelin. This formulation
 261 assumed linear, additive effects on log-biomass, implying linear effects on instantaneous rate of
 262 change in biomass, which in turn is a function of mortality, growth, fecundity and net migration rates.
 263 The formulation also implied multiplicative effects on biomass. The latter assumption is not

264 necessarily true if, for example, predator effects on prey mortality depend on prey population size, as
265 reported for cod predation effects on capelin (Hjermann *et al.*, 2004). In a previous study, we found
266 that alteration of this assumption for cod predation on capelin was not critically influencing
267 inferences about zooplankton-capelin dynamics (Stige *et al.*, 2018).

268 Finally, $(\delta_1, \dots, \delta_5)$ were process noise terms for each zooplankton and fish group that
269 represented the effects of environmental factors that were not explicitly modelled. The process noise
270 terms $(\delta_1, \dots, \delta_5)$ were jointly drawn from a multivariate normal distribution centred around zero and
271 with a variance-covariance matrix Σ .

272 *The observation model*

273 The state variables for copepods, krill, amphipods, capelin and polar cod were linked to the data by
274 considering the time-series data Cop_T , $Krill_T$, $Amph_T$, Cap_T and Pol_T to be the sums of the state
275 variables $x_{1,T}, \dots, x_{5,T}$ and observation noise terms $\varepsilon_{1,T}, \dots, \varepsilon_{5,T}$. The observation noise terms $\varepsilon_{1,T}, \dots, \varepsilon_{5,T}$
276 were assumed to be independent and normally distributed with means zero and standard deviations
277 $\sigma_{1,T}, \dots, \sigma_{5,T}$. The observation variables Ice , Cod , Her and F_{CAP} were identical to the corresponding state
278 variables z_1, \dots, z_4 , meaning that model parameters did not account for uncertainty in these variables.

279 *Fitting the model*

280 All parameters in the model were estimated jointly using the software Stan and the R interface 'rstan'
281 (Stan Development Team, 2018c; Stan Development Team, 2018a). The model code is given in
282 Appendix S1 and details about the model fitting and choice of prior distributions in Appendix S2. We
283 chose non-informative priors for most model parameters to let the data drive the inferences. An
284 exception was the coefficient for the effect of fishing, c_{49} , for which we chose a narrow prior centred
285 on the expected value of -1 (following the definition of the variable F_{CAP}). Furthermore, due to the
286 inherent difficulties in simultaneously estimating observation and process errors (Ives *et al.*, 2003;
287 Auger-Méthé *et al.*, 2016), we used informative priors for the standard deviations for the observation
288 noise $\sigma_{1,T}, \dots, \sigma_{5,T}$.

289 *Model diagnostics and sensitivity analyses*

290 We used the interactive model diagnostics tool 'shinystan' (Stan Development Team, 2018b) to
291 assess convergence through, e.g., visual inspection of the mixing of the chains and inspection of
292 Gelman and Rubin \hat{R} convergence diagnostics (Gelman and Rubin, 1992).

293 Our main model did not include interaction terms between copepods and krill as we assumed
294 that possible competition for phytoplankton prey resources would happen at daily to weekly rather

295 than interannual time scales. The model further assumed no direct interactions between krill and
296 polar cod, as krill seem to contribute less to the diet of polar cod than what amphipods and
297 copepods do and to have lower spatial overlap (Orlova *et al.*, 2009; ICES, 2018). We assessed the
298 sensitivity to these assumptions by comparing the results of the main model with results of
299 alternative models that included either copepod-krill or krill-polar cod interaction terms.

300 *Calculating indirect and delayed effects of climate*

301 The coefficients c_{16}, \dots, c_{56} for the effects of *Ice* on each zooplankton group and fish species measured
302 the “direct effects” of climate, with direct effects here referring to associations in the same year (and
303 not necessarily to direct, causal relationships). In addition, we estimated how *Ice* affected each
304 zooplankton group and fish species indirectly at different time-lags, through the other organism
305 groups. For example, the indirect, lag-1 effect of *Ice* on capelin through copepods was given by the
306 product $c_{16} c_{41}$, as c_{16} measured the effect of *Ice* on copepods in year T and c_{41} the effect of copepods
307 on capelin in year $T+1$. The total indirect lag-1 effect of *Ice* on capelin was given by $c_{16} c_{41} + c_{26} c_{42}$,
308 where $c_{26} c_{42}$ measured the indirect effect through krill. In similar ways, we calculated indirect lag-1
309 effects of *Ice* on all zooplankton groups and fish species.

310 We calculated the total direct and indirect effects of *Ice* at a range of time lags from 0 to 5
311 years. For example, the total direct and indirect lag-1 effect of *Ice* on capelin is given by $c_{16} c_{41} + c_{26}$
312 $c_{42} + c_{46} c_{44}$, where $c_{46} c_{44}$ measured the density-dependent dampening of the direct effect of *Ice* on
313 capelin. The lag-2 effect was found by replacing c_{16} with the lag-1 effect of *Ice* on copepods, c_{26} with
314 the lag-1 effect of *Ice* on krill, and c_{46} with the lag-1 effect of *Ice* on capelin. Such calculations were
315 done for each time lag for each zooplankton group and fish species. Hence, we estimated how a
316 single year’s anomaly in *Ice* influenced dynamics over several years.

317 To estimate how longer-term changes in *Ice* influenced the zooplankton groups and fish
318 species, we added the direct effects of *Ice* to the delayed effects at all time lags. For example, the
319 estimated effect of a persistent change in *Ice* on capelin after one year is $c_{16} c_{41} + c_{26} c_{42} + c_{46} c_{44} + c_{46}$.
320 Here, $c_{16} c_{41} + c_{26} c_{42} + c_{46} c_{44}$ gave the lag-1 effect of *Ice* and c_{46} the direct effect. This way we
321 estimated how persistent changes in *Ice* would influence the species, all other factors being equal.

322 To estimate uncertainty, these calculations were done for each sample of the joint posterior
323 distribution of the model parameters, and the 2.5 and 97.5 percentiles of the resulting distributions
324 of indirect and lagged effects of *Ice* were used as 95 % credibility intervals. To investigate the
325 sensitivity of these results to the choice of climate variable, we also conducted corresponding
326 calculations for the alternative climate variables.

327 **Results**

328 *Model diagnostics*

329 The model captured the variability in the observed time-series well, with no systematic deviations
330 between fitted and observed values (Fig. 2). Visual inspection of the chains suggested that the model
331 had converged; the four parallel Hamiltonian Monte Carlo chains were well-mixed, had low
332 autocorrelation after thinning and showed no trends after the burn-in iterations. There were no
333 warnings of divergent transitions in the chains (Stan Development Team, 2018c). The Gelman and
334 Rubin scale reduction factor, \hat{R} – which compares within-chain and between-chain variance and is
335 supposed to be close to 1 at convergence (Gelman and Rubin, 1992) – was <1.01 for all model
336 parameters, providing additional support for convergence.

337 *Estimated direct sea ice effects*

338 The analysis showed direct positive associations between ice cover and biomasses of copepods and
339 amphipods (coefficients c_{16} and c_{36}), direct negative association between ice cover and biomass of
340 capelin (coefficient c_{46}) and indications of negative associations with biomasses of krill and polar cod
341 (coefficients c_{26} and c_{56} ; shown on ln-scale in Fig. 4, on a normalized scale in Fig. S3, and tabulated in
342 Table S2). Specifically, each 10 % increase in ice cover was estimated to lead to 9 % higher biomass of
343 copepods (i.e. +0.09 on ln-scale, Fig. 4) with 95 % credibility intervals (c.i.) from 0 to +18 %, 18 %
344 higher biomass of amphipods (c.i.: +3 %, +38 %), 19 % lower biomass of capelin (c.i.: -32 %, -1 %), 15 %
345 lower biomass of krill (c.i.: -33 %, +9 %) and to 7 % lower biomass of polar cod (c.i.: -28 %, +17 %).

346 *Species interactions*

347 Results suggested positive bottom-up effect by krill on capelin (coefficient c_{42}) and, with weaker
348 statistical support, by copepods on amphipods (coefficient c_{31}). Specifically, a doubling in krill (+0.69
349 on ln-scale) was estimated to lead to 53 % increase in capelin biomass (c.i.: +18 %, +100 %) and a
350 doubling in copepods was estimated to lead to 67 % increase in amphipod biomass (c.i.: -8 %, +198 %). We did not find statistical support for bottom-up effects by copepods on capelin or polar
351 cod (coefficients c_{41} and c_{51}) or by amphipods on polar cod (coefficient c_{53}).

353 Results suggested negative top-down effects by capelin on copepods (coefficient c_{14}), by
354 capelin on krill (coefficient c_{24}) and by polar cod on amphipods (coefficient c_{35}). Specifically, a
355 doubling in capelin was estimated to lead to 10 % reduction in copepods (c.i.: -20 %, -1 %) and 21 %
356 reduction in krill (c.i.: -38 %, 0%) and a doubling in polar cod to lead to 26 % reduction in amphipods
357 (c.i.: -48 %, -2 %). The results also suggested significant negative top-down effects by cod and herring

358 on capelin (coefficients c_{47} and c_{48}), but not by cod on polar cod (coefficient c_{57}) or by polar cod or
359 amphipods on copepods (coefficients c_{15} and c_{13}).

360 *Other model parameters*

361 The posterior distributions for the effects of fishing (c_{49}) and magnitudes of observation noise ($\sigma_1, \sigma_2,$
362 $\sigma_3, \sigma_4, \sigma_5$) were nearly identical to the priors (Table S2), suggesting that the data did not contain
363 information to update the values of these parameters. According to the posterior median values of
364 the scale parameters for observation noise, observation noise contributed 6%, 19%, 7%, 3% and 16%,
365 respectively, of the variance in *Cop*, *Krill*, *Amph*, *Cap* and *Pol*.

366 We did not find evidence for correlation in process noise between state variables (i.e., non-
367 zero off-diagonal elements in the process noise correlation matrix Ω , Table S2). By taking the square
368 of the posterior medians of the scales of the process errors at the normalised scale the model was
369 fitted to (τ_1, \dots, τ_5 , Table S2), we found that process noise contributed 42%, 32%, 21%, 9% and 32%,
370 respectively, of the variance in *Cop*, *Krill*, *Amph*, *Cap* and *Pol*. By subtracting the process and
371 observation noise variances from the total variance, we found that the predictor variables accounted
372 for 52%, 48%, 72%, 88% and 50%, respectively, of the variance in *Cop*, *Krill*, *Amph*, *Cap* and *Pol*. Note
373 that the predictor variables included autoregressive terms, which contributed to the high percentage
374 of variance explained in, e.g., *Cap*.

375 Several of the coefficients were correlated, meaning that they were best interpreted pairwise
376 (Fig. S4). We noted, for example, that the density dependence parameters for copepods and
377 amphipods were correlated with parameters for effects of other species on copepods and
378 amphipods, and that narrower credibility intervals for the latter effects were attained when
379 excluding posterior samples that implied overcompensation in copepods and amphipods.

380 *Indirect and delayed climate effects*

381 Because of species interactions, changes in ice cover had a multitude of indirect effects at different
382 time lags. Our results shown in Fig. 5 suggested that the indirect one-year delayed effects of ice cover
383 through the other species were generally of comparable magnitude as the direct effects. However,
384 there was considerable uncertainty associated to the estimates, as the 95 % credibility intervals for
385 the indirect effects included zero for all zooplankton groups and fish species. Interestingly, the direct
386 association between low ice cover and krill biomass was most likely positive (although the 95 %
387 credibility interval included zero), while the indirect was most likely negative.

388 Our results revealed how the effects of a one-year anomaly in ice cover played out over
389 several years, when taking into account the direct as well as indirect effects (Fig. 6A). The shown

390 effects can be thought of as what might happen if ice cover was reduced by 25 % in one winter, e.g.
391 from around the long-term average of 49 % to the observed minimum of 23 %, and then returned to
392 the long-term average the subsequent winters. In reality, these effects could never be observed as
393 “purely” as shown, because for each year, the ice cover as well as other drivers such as cod, herring
394 and fishing changed into new states, and the effects of these changes added to the dynamics shown.
395 The most striking results were found for krill: reduced ice cover in winter possibly led to increased
396 krill biomass in autumn but reduced biomass two to six years later, consistent with the opposite signs
397 of the direct and indirect climate effects (Fig. 5). A single year’s anomaly in ice cover affected capelin
398 biomass for around three to four years. In contrast, there were limited delayed effects of ice cover on
399 copepods and amphipods after one year. Reduced ice cover had uncertain effect on polar cod.

400 We also estimated the effects of a persistent reduction in ice cover (Fig. 6B). These results
401 suggested that under such conditions copepod and amphipod biomasses would be reduced, capelin
402 biomass increased and krill biomass, while initially increasing, would more likely be reduced in the
403 long-term. The effect on polar cod was highly uncertain.

404 *Sensitivity analysis*

405 The main model assumed no direct interactions between polar cod and krill and between copepods
406 and krill. To assess the validity and possible implications of these assumptions, we also fitted
407 alternative models that included such interactions (Fig. S5). The alternative models showed no strong
408 interactions between polar cod and krill or between copepods and krill (95 % credibility intervals for
409 the relevant model parameters included zero). Furthermore, the other parameters in the model
410 were not very sensitive to these alternative model formulations.

411 *Results of models with alternative climate variables*

412 The biotic variables (*Cop*, *Krill*, *Amph*, *Cap* and *Pol*) were similarly associated with area of Arctic water
413 masses in autumn as with *Ice*, i.e., sea ice cover in winter (Fig. S6). The biotic variables also showed
414 similar strengths of associations with previous-autumn water column temperature as with *Ice*, but
415 with opposite sign. The associations of the biotic variables with sea ice cover in April were similar to
416 the associations with *Ice*, but slightly weaker. Sea surface temperature was at most weakly
417 associated with the biotic variables, except negative associations between summer and spring
418 temperatures and amphipod biomass. The estimated bottom-up and top-down effects among
419 zooplankton groups and fish were relatively independent of which climate variable was included in
420 the model (Fig. S6). The finding that the indirect one-year delayed effects of ice cover through the
421 other species were generally of comparable magnitude as the direct effects was also supported by

422 models with area of Arctic water masses in autumn, previous-autumn water column temperature or
423 sea ice cover in April as climate variable (Fig. S7).

424

425 **Discussion**

426 Since the 1980s, increased sea temperatures and reduced sea ice cover in the Barents Sea (e.g., Fig. 2)
427 have led to substantial changes in the ecosystem (Fossheim *et al.*, 2015; Eriksen *et al.*, 2017; ICES,
428 2018). We identified in this study how changes in sea ice cover over the last 36 years were associated
429 with the interannual variations in the biomasses of the main zooplankton groups and planktivorous
430 fishes in the central and northern Barents Sea. Specifically, low winter sea ice cover in warm years
431 was associated with increased biomasses of krill and capelin and reduced biomasses of copepods and
432 amphipods the following autumn. These changes had various indirect effects over the subsequent
433 years because of strong predator-prey interactions. The strongest predator-prey interactions that we
434 identified were positive bottom-up effects by krill on capelin and by copepods on amphipods, and
435 negative top-down effects by capelin on copepods and krill and by polar cod on amphipods.

436 *Direct associations with climate*

437 High biomass of krill and low biomasses of copepods and amphipods in the central and northern
438 Barents Sea followed warm winters with low ice cover. Similar associations between zooplankton
439 biomasses and physical conditions as measured by sea ice cover or correlated factors such as sea
440 temperature or water mass distribution have also been reported previously (e.g., Dalpadado *et al.*,
441 2012; Stige *et al.*, 2014; Orlova *et al.*, 2015, and references therein). The results using alternative
442 climate variables showed that the associations with winter sea ice were alternatively explainable
443 through associations with previous-autumn water column temperature or area of Arctic water
444 masses in autumn. This finding leaves the causal mechanisms behind the associations open for
445 alternative interpretations, involving, e.g., sea ice effects on primary production, temperature effects
446 on metabolic rates, and advection and distribution of water masses and species.

447 Low biomass of copepods following warm winters suggested that possible increase in
448 biomass of the boreal *C. finmarchicus* was not sufficient to compensate for biomass reductions in the
449 predominantly Arctic *C. glacialis* in the central and northern Barents Sea. These two copepod species
450 show opposite associations with ambient temperatures in the Barents Sea: weakly positive for *C.*
451 *finmarchicus* and strongly negative for *C. glacialis* (Aarflot *et al.*, 2017). The reproduction of *C.*
452 *glacialis* is thought to be impeded by loss of sea ice because of a poorer match between the seasonal
453 timing of primary production and the food requirements of *C. glacialis* (Søreide *et al.*, 2010),

454 although *C. glacialis* seem to be able to sustain ice-free conditions in some regions by basing egg
455 production on stored lipids instead of the ice algae bloom (Daase *et al.*, 2013). Warm winters may
456 also cause mortality by elevating the metabolism and exhausting the lipid reserves during diapause,
457 which seems to be a reason for population decline of *Calanus marshallae* in the Bering Sea in warm
458 years (Coyle *et al.*, 2011; Coyle and Gibson, 2017). Low biomass of amphipods following warm
459 winters is consistent with the dominant Arctic amphipod *T. libellula* being nearly absent in Atlantic
460 waters ($T > 3$ °C) in the Barents Sea in autumn (Dalpadado, 2002). The near-absence of *T. libellula* in
461 Atlantic waters could be due to physiological limitations, as metabolic rates increase sharply when
462 temperatures surpass 5 °C (Percy, 1993), but other factors such as match-mismatch with copepod
463 prey could also come into play (Dalpadado, 2002). The association between krill biomass and ice
464 cover or other climate variables did not reach statistical significance but is consistent with
465 observations by Orlova *et al.* (2015), who reported high krill abundance in winter in warm years,
466 possibly caused by inflow of the predominantly boreal *T. inermis* into areas of the Barents Sea that
467 are traditionally covered by Arctic waters. Eriksen *et al.* (2016) suggested that increased krill biomass
468 in the Barents Sea during the last two decades occurred most likely due to increased occurrence of
469 large boreal krill species (*M. norvegica*).

470 Perhaps counter-intuitively, warm winters with low ice cover were also associated with
471 positive biomass growth of the sub-Arctic capelin. The positive association is, however, consistent
472 with stage-resolved data showing that high winter-spring temperatures are associated with high
473 abundance at age 0 and high summer temperatures with high mean body length at age 1 (ICES, 2018;
474 Stige *et al.*, 2018). Several mechanisms can potentially explain these associations. Fast growth at high
475 temperatures is supported by studies of individual capelin and is explainable by temperature effects
476 on metabolic rates (Gjøsæter and Loeng, 1987). Fast growth at high temperatures can also increase
477 abundance, as fish larvae may grow rapidly out of the size range most susceptible to predation
478 (Bailey and Houde, 1989). Temperature and ice cover may also be indicators of feeding conditions for
479 capelin; low ice cover may for example mean a large area and long time period with light and
480 temperature conditions suitable for capelin to feed, and to a large extent of zooplankton-rich Atlantic
481 or mixed water masses (Orlova *et al.*, 2015).

482 Somewhat surprisingly, we found that biomass growth of the Arctic polar cod was neither
483 associated with ice cover in winter nor any of the other climate variables. The biomass growth of
484 polar cod was furthermore not significantly associated with predator (cod) or prey (copepod)
485 biomasses. The lack of significant associations should be interpreted with caution, as observation
486 noise in the acoustic survey estimates of polar cod is of unknown magnitude and the survey did not
487 cover the entire distribution area in all years. However, the strong auto-correlation in polar cod

488 biomass (as reflected in c_{55} between 0.5 and 1) and significant top-down effect by polar cod on
489 amphipods might suggest that the polar cod time-series contains ecologically relevant information.
490 The reasons for the weak associations may be investigated by stage-resolved analysis in later studies,
491 to assess whether contrasting effects of climate at different stages cancel out (as shown for
492 copepods, Persson *et al.*, 2012).

493 *Bottom-up and top-down effects*

494 Positive bottom-up effect by copepods on amphipods is consistent with copepods being the key prey
495 of the dominant amphipod in our samples, *T. libellula* (Auel *et al.*, 2002). This finding complements
496 previous studies based on shorter data time-series, which have not been able to separate the
497 correlated effects of high copepod biomass and large extent of Arctic waters (Dalpadado, 2002;
498 Dalpadado *et al.*, 2012), by suggesting that both factors contributed to explain the variation in
499 amphipod biomass.

500 Positive bottom-up effect by krill on the capelin biomass is consistent with the results of a
501 stage-wise analysis of capelin dynamics showing high survival of capelin to age-2 and age-3 in years
502 with high krill biomass (Stige *et al.*, 2018). The authors proposed that the krill-capelin survival
503 association in the Barents Sea was caused by food limitation in spring causing starvation or increased
504 susceptibility to predation. Similarly, Buren *et al.* (2014) suggested that food conditions for capelin in
505 spring, when the stored energy level is low, might influence starvation or predation mortality and
506 mediate bottom-up climate effects on capelin biomass in the marine ecosystem off the
507 Newfoundland and Labrador Shelf (but see Frank *et al.* 2006 for an alternative interpretation). The
508 stage-wise analysis by Stige *et al.* (2018) also suggested positive bottom-up effect by copepods on
509 capelin, as high copepod biomass was associated with fast growth, which leads to early maturation
510 and subsequently high mortality due to the semelparous life cycle of capelin. The lack of significant
511 association in our analysis of aggregated biomass data should therefore not be taken as evidence for
512 lack of biologically significant effect on population dynamics.

513 The identification of strong top-down effects suggested that the dynamics were not solely
514 driven by bottom-up processes, but also involved feedbacks between bottom-up and top-down
515 effects. The estimated top-down effects by capelin on copepods and krill are consistent with previous
516 studies showing inverse correlations of capelin with copepod and krill time-series in the Barents Sea
517 (e.g., Skjoldal *et al.*, 1992; Dalpadado *et al.*, 2002; Stige *et al.*, 2014). Capelin schools appear to be
518 able to forage down the zooplankton biomass in an area in a matter of 3–4 days (Hassel *et al.*, 1991).
519 Moreover, capelin form density-dependent migratory waves that move out from the central
520 distribution area as the zooplankton prey are depleted locally (Fauchald *et al.*, 2006). We note that

521 our results support that capelin may have an indirect, negative effect on amphipods caused by
522 asymmetric competition for copepod prey (as proposed by Orlova *et al.*, 2005), and that krill may
523 have an indirect, negative effect on copepods caused by apparent competition mediated by their
524 shared predator, capelin (Stige *et al.*, 2018). There is also a negative feedback between capelin and
525 krill, whereby krill abundance (and size distribution, Dalpadado and Skjoldal, 1996) is reduced in high-
526 capelin years, which contributes to reduce biomass growth of capelin; this negative feedback is,
527 however, not strong enough to cause predator-prey cycles (Stige *et al.*, 2018). Negative top-down
528 effect by polar cod on amphipods has, to our knowledge, not been shown before but is consistent
529 with amphipods being a key prey of polar cod (Orlova *et al.*, 2009; ICES, 2018) and the population
530 biomass of polar cod and capelin being of comparable magnitudes (range approximately 0.1 – 2
531 compared to 0.1 – 8 million tonnes, Fig. 2).

532 Strong top-down effects on zooplankton biomass have also been reported for other
533 ecosystems dominated by relatively few species and with extreme environmental conditions such as
534 cold temperatures or low salinities, including the Baltic Sea and the Norwegian Sea (reviewed by
535 Daewel *et al.*, 2014) and the Black Sea (Daskalov *et al.*, 2007). In contrast, bottom-up processes
536 appeared equally or more important than top-down processes in shaping zooplankton dynamics in
537 ecosystems with high to intermediate species diversity and moderate environmental conditions,
538 including the North Sea, the Bay of Biscay, the Georges Bank and Gulf of Maine region and the
539 southern Benguela upwelling system (Daewel *et al.*, 2014). Similarly, fish populations appeared
540 particularly prone to being top-down controlled by their predators in species-poor and cold
541 ecosystems (Frank *et al.*, 2007; Boyce *et al.*, 2015).

542 *Indirect and delayed climate effects*

543 We identified mechanisms for indirect effects of climate on the main zooplankton groups and
544 planktivorous fish species in the central and northern Barents Sea through the other analysed
545 organism groups (summarised in Fig. 3). For copepods and krill, the indirect effects appeared to occur
546 mainly through their main predator, capelin. For amphipods, the indirect effects potentially operated
547 through copepods, their main prey, as well as through polar cod, their main predator. However, the
548 bottom-up effect through copepods was quantitatively most important for our results as we found
549 no association between sea ice cover and polar cod biomass. For capelin, indirect effects on biomass
550 might have occurred through krill (prey), cod (predator) and herring (predator), although climate
551 effects on cod and herring were not modelled in this study. For polar cod, we did not find evidence
552 that species interactions led to indirect climate effects.

553 Climate warming has been associated with “borealization” of demersal fish communities in
554 the Barents Sea in recent decades, with the distribution of boreal species expanding northwards and
555 the distribution of Arctic species retracting (Fossheim *et al.*, 2015). Our findings suggested that
556 warming, in our study expressed as reduced ice cover, had a corresponding direct effect on the main
557 zooplankton groups, with the boreal krill most likely increasing in biomass in the central and northern
558 Barents Sea and predominantly Arctic copepods and amphipods decreasing. However, the longer-
559 term effects of warming are not necessarily the same as the direct effects because of species
560 interactions.

561 Our results showed the importance of predator-prey interactions among key zooplankton
562 and fish groups for indirect and delayed climate effects at different time-scales. The indirect effects
563 were of same sign as and amplified direct effects of sea ice cover on capelin, copepods and
564 amphipods. For these groups the short- and long-term effects of a change in ice cover were of same
565 sign, but the magnitude of the effects varied over time. For krill, results indicated that reduction in
566 sea ice increased biomass in the short-term but reduced biomass at longer terms because of
567 increased predation pressure. For krill, the effect of ice cover therefore depended critically on the
568 time-scale. These results should be interpreted cautiously because important mechanisms, such as
569 climate effects on the predators of capelin, were not modelled. The results nonetheless demonstrate
570 quantitatively how predator-prey interactions have led to indirect and delayed climate effects in the
571 past, which need to be accounted for to realistically project future changes.

572 *Implications*

573 By simultaneously estimating climate effects and strengths of species interactions in one statistical
574 model, we have identified likely pathways of direct and indirect effects of climate. Our results
575 showed that the indirect effects may be similarly important as the direct effects to understand how
576 the anticipated reductions in Arctic sea ice might influence the pelagic ecosystems. The ecosystem
577 changes can therefore not be understood as a straight-forward bottom-up process driven by changes
578 in physical conditions and lower trophic levels. In contrast, the changes are better understood by
579 considering the interplay between bottom-up and top-down effects, with the main planktivorous fish,
580 capelin, playing a key role in the changes in the central and northern Barents Sea. We propose that
581 top-down effects should be considered to understand and predict how climate influences also other
582 ecosystems, especially ecosystems with low species diversity and extreme environmental conditions,
583 which appear to be particularly susceptible to top-down control (Frank *et al.*, 2007; Daewel *et al.*,
584 2014; Boyce *et al.*, 2015).

585

586 **Acknowledgements**

587 This work was funded by the Research Council of Norway (RCN) through the project The Nansen
588 Legacy (RCN # 276730). K.O. was funded by the Skagcore project (RCN #255675). E.E. and P.D. were
589 funded by the TIBIA project (Trophic Interactions in the Barents Sea – steps towards Integrated
590 Assessment, RCN # 228880). We thank George L. Hunt Jr. and an anonymous referee for constructive
591 comments on a previous version of the manuscript.

592

593 **Literature**

- 594 Aarflot, J. M., Skjoldal, H. R., Dalpadado, P., and Skern-Mauritzen, M. 2017. Contribution of *Calanus*
595 species to the mesozooplankton biomass in the Barents Sea. *ICES Journal of Marine Science*,
596 75: 2342-2354.
- 597 Auel, H., Harjes, M., da Rocha, R., Stübing, D., and Hagen, W. 2002. Lipid biomarkers indicate
598 different ecological niches and trophic relationships of the Arctic hyperiid amphipods
599 *Themisto abyssorum* and *T. libellula*. *Polar Biology*, 25: 374-383.
- 600 Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., and Flemming,
601 J. M. 2016. State-space models' dirty little secrets: even simple linear Gaussian models can
602 have estimation problems. *Scientific Reports*, 6: 26677.
- 603 Bailey, K. M., and Houde, E. D. 1989. Predation on eggs and larvae of marine fishes and the
604 recruitment problem. *Advances in Marine Biology*, 25: 1-83.
- 605 Bogstad, B., Gjøsæter, H., Haug, T., and Lindstrøm, U. 2015. A review of the battle for food in the
606 Barents Sea: cod vs. marine mammals. *Frontiers in Ecology and Evolution*, 3: 29.
- 607 Boyce, D. G., Frank, K. T., Worm, B., and Leggett, W. C. 2015. Spatial patterns and predictors of
608 trophic control in marine ecosystems. *Ecology Letters*, 18: 1001-1011.
- 609 Broms, C., Melle, W., and Kaartvedt, S. 2009. Oceanic distribution and life cycle of *Calanus* species in
610 the Norwegian Sea and adjacent waters. *Deep-Sea Research II*, 56: 1910-1921.
- 611 Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N., et al.
612 2014. Bottom-up regulation of capelin, a keystone forage species. *PLoS One*, 9: e87589.
- 613 Cavalieri, D. J., Parkinson, C. L., Gloersen, P., and Zwally, H. J. 1996, updated yearly. Sea Ice
614 Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data,
615 Version 1. [Monthly averaged sea ice concentrations for the north polar region]. NASA
616 National Snow and Ice Data Center Distributed Active Archive Center. doi:
617 <http://dx.doi.org/10.5067/8GQ8LZQVL0VL>. [Accessed 12.01.2018]. Boulder, Colorado USA. .
- 618 Clark, J. S., and Bjørnstad, O. N. 2004. Population time series: Process variability, observation errors,
619 missing values, lags, and hidden states. *Ecology*, 85: 3140-3150.
- 620 Comiso, J. C., Meier, W. N., and Gersten, R. 2017. Variability and trends in the Arctic Sea ice cover:
621 Results from different techniques. *Journal of Geophysical Research: Oceans*, 122: 6883-6900.
- 622 Coyle, K. O., Eisner, L. B., Mueter, F. J., Pinchuk, A. I., Janout, M. A., Ciciel, K. D., Farley, E. V., et al.
623 2011. Climate change in the southeastern Bering Sea: Impacts on pollock stocks and
624 implications for the oscillating control hypothesis. *Fisheries Oceanography*, 20: 139-156.
- 625 Coyle, K. O., and Gibson, G. A. 2017. *Calanus* on the Bering Sea shelf: probable cause for population
626 declines during warm years. *Journal of Plankton Research*, 39: 257-270.
- 627 Daase, M., Falk-Petersen, S., Varpe, Ø., Darnis, G., Sørreide, J. E., Wold, A., Leu, E., et al. 2013. Timing
628 of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective.
629 *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 871-884.

630 Daewel, U., Hjøllø, S. S., Huret, M., Ji, R., Maar, M., Niiranen, S., Travers-Trolet, M., et al. 2014.
631 Predation control of zooplankton dynamics: a review of observations and models. ICES
632 Journal of Marine Science, 71: 254-271.

633 Dalpadado, P. 2002. Inter-specific variations in distribution, abundance and possible life-cycle
634 patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biology, 25: 656-666.

635 Dalpadado, P., Bogstad, B., Gjørseter, H., Mehl, S., and Skjoldal, H. R. 2002. Zooplankton-fish
636 interactions in the Barents Sea. In Large marine ecosystems of the North Atlantic, pp. 269-
637 291. Ed. by K. Sherman, and H. R. Skjoldal. Elsevier, Amsterdam.

638 Dalpadado, P., Ingvaldsen, R. B., Stige, L. C., Bogstad, B., Knutsen, T., Ottersen, G., and Ellertsen, B.
639 2012. Climate effects on the Barents Sea ecosystem dynamics. ICES Journal of Marine Science,
640 69: 1303-1316.

641 Dalpadado, P., and Mowbray, F. 2013. Comparative analysis of feeding ecology of capelin from two
642 shelf ecosystems, off Newfoundland and in the Barents Sea. Progress in Oceanography, 114:
643 97-105.

644 Dalpadado, P., and Skjoldal, H. R. 1996. Abundance, maturity and growth of the krill species
645 *Thysanoessa inermis* and *T. longicaudata* in the Barents Sea. Marine Ecology Progress Series,
646 144: 175-183.

647 Daskalov, G. M., Grishin, A. N., Rodionov, S., and Mihneva, V. 2007. Trophic cascades triggered by
648 overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the
649 National Academy of Sciences, USA, 104: 10518-10523.

650 Drinkwater, K. F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R. I., Pörtner, H. O., et al.
651 2010. On the processes linking climate to ecosystem changes. Journal of Marine Systems, 79:
652 374-388.

653 Eriksen, E., Rune Skjoldal, H., Gjørseter, H., and Primicerio, R. 2017. Spatial and temporal changes in
654 the Barents Sea pelagic compartment during the recent warming. Progress in Oceanography,
655 151: 206-226.

656 Eriksen, E., Skjoldal, H. R., Dolgov, A. V., Dalpadado, P., Orlova, E. L., and Prozorkevich, D. V. 2016.
657 The Barents Sea euphausiids: methodological aspects of monitoring and estimation of
658 abundance and biomass. ICES Journal of Marine Science, 73: 1533-1544.

659 Fall, J., Ciannelli, L., Skaret, G., and Johannesen, E. 2018. Seasonal dynamics of spatial distributions
660 and overlap between Northeast Arctic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) in
661 the Barents Sea. PLoS One, 13: e0205921.

662 Fauchald, P., Mauritzen, M., and Gjørseter, H. 2006. Density-dependent migratory waves in the
663 marine pelagic ecosystem. Ecology, 87: 2915-2924.

664 Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. 2015.
665 Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature
666 Climate Change, 5: 673-677.

667 Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A., Fossheim, M., and Aschan, M. 2017.
668 Climate-driven changes in functional biogeography of Arctic marine fish communities.
669 Proceedings of the National Academy of Sciences of the United States of America.

670 Frank, K. T., Petrie, B., and Shackell, N. L. 2007. The ups and downs of trophic control in continental
671 shelf ecosystems. Trends in Ecology and Evolution, 22: 237-242.

672 Frank, K. T., Petrie, B. D., Shackell, N. L., and Choi, J. S. 2006. Reconciling differences in trophic control
673 in mid-latitude ecosystems. Ecology Letters, 9: 1096-1105.

674 Gelman, A., and Rubin, D. B. 1992. Inference from iterative simulation using multiple sequences.
675 Statistical Science, 7: 457-472.

676 Gjørseter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the
677 Barents Sea. Sarsia, 83: 453-496.

678 Gjørseter, H., Hallfredsson, E. H., Mikkelsen, N., Bogstad, B., and Pedersen, T. 2016. Predation on
679 early life stages is decisive for year-class strength in the Barents Sea capelin (*Mallotus villosus*)
680 stock. ICES Journal of Marine Science, 73: 182-195.

681 Gjørseter, H., and Loeng, H. 1987. Growth of the Barents Sea capelin, *Mallotus villosus*, in relation to
682 climate. *Environmental Biology Of Fishes*, 20: 293-300.

683 Hassel, A., Skjoldal, H. R., Gjørseter, H., Loeng, H., and Omli, L. 1991. Impact of grazing from capelin
684 (*Mallotus villosus*) on zooplankton: a case-study in the northern Barents Sea in August 1985.
685 *Polar Research*, 10: 371-388.

686 Hjermann, D. Ø., Ottersen, G., and Stenseth, N. C. 2004. Competition among fishermen and fish
687 causes the collapse of Barents Sea capelin. *Proceedings of the National Academy of Sciences*,
688 USA, 101: 11679-11684.

689 ICES 2016. Report of the Arctic fisheries working group (AFWG), 19-25 April 2016, ICES HQ,
690 Copenhagen, Denmark, ICES CM 2016/ACOM:06. 621 pp.

691 ICES 2018. Interim Report of the Working Group on the Integrated Assessments of the Barents Sea
692 (WGIBAR), 9-12 March 2018, Tromsø, Norway, ICES CM 2018/IEASG:04. 210 pp.

693 Ives, A. R., Dennis, B., Cottingham, K. L., and Carpenter, S. R. 2003. Estimating community stability
694 and ecological interactions from time-series data. *Ecological Monographs*, 73: 301-330.

695 Johannesen, E., Lindstrøm, U., Michalsen, K., Skern-Mauritzen, M., Fauchald, P., Bogstad, B., and
696 Dolgov, A. 2012. Feeding in a heterogeneous environment: spatial dynamics in summer
697 foraging Barents Sea cod. *Marine Ecology Progress Series*, 458: 181-197.

698 Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E., et al.
699 2014. Mechanisms underpinning climatic impacts on natural populations: altered species
700 interactions are more important than direct effects. *Global Change Biology*, 20: 2221-2229.

701 Onarheim, I. H., and Årthun, M. 2017. Toward an ice-free Barents Sea. *Geophysical Research Letters*,
702 44: 8387-8395.

703 Orlova, E. L., Boitsov, V. D., Dolgov, A. V., Rudneva, G. B., and Nesterova, V. N. 2005. The relationship
704 between plankton, capelin, and cod under different temperature conditions. *ICES Journal of*
705 *Marine Science*, 62: 1281-1292.

706 Orlova, E. L., Dalpadado, P., Knutsen, T., Nesterova, V. N., and Prokopchuk, I. P. 2011. Zooplankton. *In*
707 *The Barents Sea. Ecosystem, resources, management.*, pp. 90-119. Ed. by T. Jakobsen, and V.
708 K. Ozhigin. Tapir Academic Press, Trondheim, Norway.

709 Orlova, E. L., Dolgov, A. V., Renaud, P. E., Greenacre, M., Halsband, C., and Ivshin, V. A. 2015. Climatic
710 and ecological drivers of euphausiid community structure vary spatially in the Barents Sea:
711 relationships from a long time series (1952-2009). *Frontiers in Marine Science*, 1: doi:
712 10.3389/fmars.2014.00074.

713 Orlova, E. L., Dolgov, A. V., Rudneva, G. B., Oganin, I. A., and Konstantinova, L. L. 2009. Trophic
714 relations of capelin *Mallotus villosus* and polar cod *Boreogadus saida* in the Barents Sea as a
715 factor of impact on the ecosystem. *Deep-Sea Research II*, 56: 2054-2067.

716 Percy, J. A. 1993. Energy consumption and metabolism during starvation in the Arctic hyperiid
717 amphipod *Themisto libellula* Mandt. *Polar Biology*, 13: 549-555.

718 Persson, J., Stige, L. C., Stenseth, N. C., Usov, N., and Martynova, D. 2012. Scale-dependent effects of
719 climate on two copepod species, *Calanus glacialis* and *Pseudocalanus minutus*, in an Arctic-
720 boreal sea. *Marine Ecology Progress Series*, 468: 71-83.

721 Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., and Levin, S. A. 2013. Marine taxa track local
722 climate velocities. *Science*, 341: 1239-1242.

723 Pörtner, H. O., and Peck, M. A. 2010. Climate change effects on fishes and fisheries: towards a cause-
724 and-effect understanding. *Journal of Fish Biology*, 77: 1745-1779.

725 Renaud, P. E., Daase, M., Banas, N. S., Gabrielsen, T. M., Søreide, J. E., Varpe, Ø., Cottier, F., et al.
726 2018. Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of
727 resilience. *ICES Journal of Marine Science*, 75: 1871-1881.

728 Rey, F., Skjoldal, H. R., and Slagstad, D. 1987. Primary production in relation to climatic changes in the
729 Barents Sea. *In The effect of oceanographic conditions on distribution and population*
730 *dynamics of commercial fish stocks in the Barents Sea.*, pp. 29-46. Ed. by H. Loeng. Institute
731 of Marine Research, Bergen, Norway.

732 Skaret, G., and Prozorkevich, D. 2016. Chapter 5.7. Pelagic fish abundance and distribution. *In* Survey
733 report from the joint Norwegian/Russian ecosystem survey in the Barents Sea and adjacent
734 waters, August – October 2015, pp. 54-72. Ed. by D. Prozorkevich, and K. Sunnanå.
735 IMR/PINRO Joint Report Series, No. 1/2016, 147 pp. ISSN 1502-8828.

736 Skjoldal, H. R., Gjøsæter, H., and Loeng, H. 1992. The Barents Sea ecosystem in the 1980s: ocean
737 climate, plankton, and capelin growth. ICES Marine Science Symposium, 195: 278-290.

738 Stan Development Team 2018a. *RStan: the R interface to Stan*. R package version 2.17.2, [http://mc-
740 stan.org](http://mc-

739 stan.org).

740 Stan Development Team 2018b. *ShinyStan: Interactive Visual and Numerical Diagnostics and
741 Posterior Analysis for Bayesian Models*. R package version 2.5.0, <http://mc-stan.org>.

742 Stan Development Team 2018c. *Stan Modeling Language Users Guide and Reference Manual*,
743 Version 2.18.0, <http://mc-stan.org>. <http://mc-stan.org> pp.

744 Stige, L. C., Dalpadado, P., Orlova, E., Boulay, A.-C., Durant, J. M., Ottersen, G., and Stenseth, N. C.
745 2014. Spatiotemporal statistical analyses reveal predator-driven zooplankton fluctuations in
746 the Barents Sea. *Progress in Oceanography*, 120: 243-253.

747 Stige, L. C., Kvile, K. Ø., Bogstad, B., and Langangen, Ø. 2018. Predator-prey interactions cause
748 apparent competition between marine zooplankton groups. *Ecology*, 99: 632-641.

749 Søreide, J. E., Leu, E., Berge, J., Graeve, M., and Falk-Petersen, S. 2010. Timing of blooms, algal food
750 quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change
751 Biology*, 16: 3154-3163.

752 Vinje, T. 2001. Anomalies and Trends of Sea-Ice Extent and Atmospheric Circulation in the Nordic
753 Seas during the Period 1864–1998. *Journal of Climate*, 14: 255-267.

754 Wang, S., Budge, S., Iken, K., Gradinger, R., Springer, A., and Wooller, M. 2015. Importance of
755 sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable
756 isotope analyses. *Marine Ecology Progress Series*, 518: 31-50.

757 Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., Gabrielsen, G. W., et al. 2006.
758 Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, 71: 232-287.

759

760

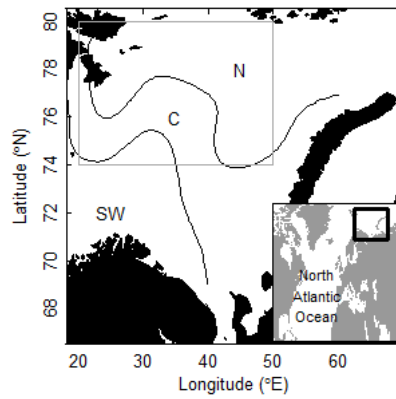
761 **Table 1. Summary of the main biological time-series analysed (Fig. 2A).**

Index	Description
Copepods	Mesozooplankton in C and N Barents Sea (Fig. 1), sampled from whole water column with 180 μ m mesh plankton nets. Dominant taxa were <i>Calanus glacialis</i> , <i>Calanus finmarchicus</i> , <i>Calanus hyperboreus</i> , smaller copepod species and <i>Clione limacina</i> (Aarflot <i>et al.</i> , 2017).
Krill	Large krill north of 75N in the Barents Sea, sampled from 0 to 60 m with 7–100 mm mesh pelagic trawl. Dominant taxa were <i>Thysanoessa inermis</i> , <i>Thysanoessa raschii</i> , <i>Thysanoessa longicaudata</i> and <i>Meganyctiphanes norvegica</i> . Smaller <i>T. longicaudata</i> and juvenile euphausiids were not sampled representatively due to escapement through the mesh (Eriksen <i>et al.</i> , 2016; ICES, 2018).
Amphipods	Large pelagic amphipods north of 75N in the Barents Sea, sampled from 0 to 60 m with 7–100 mm mesh pelagic trawl. Dominant taxon was <i>Themisto libellula</i> , while smaller amphipods such as <i>Themisto abyssorum</i> were not sampled representatively (ICES, 2018).
Capelin	Age 1+ capelin (<i>Mallotus villosus</i>) in the Barents Sea, estimated by acoustic surveys (ICES, 2016). The survey usually covered the entire distribution area.
Polar cod	Age 1+ polar cod (<i>Boreogadus saida</i>) in the Barents Sea, estimated by acoustic surveys (Skaret and Prozorkevich, 2016). The survey covered the distribution area to variable extents.

762

763

764 **FIGURES**



765

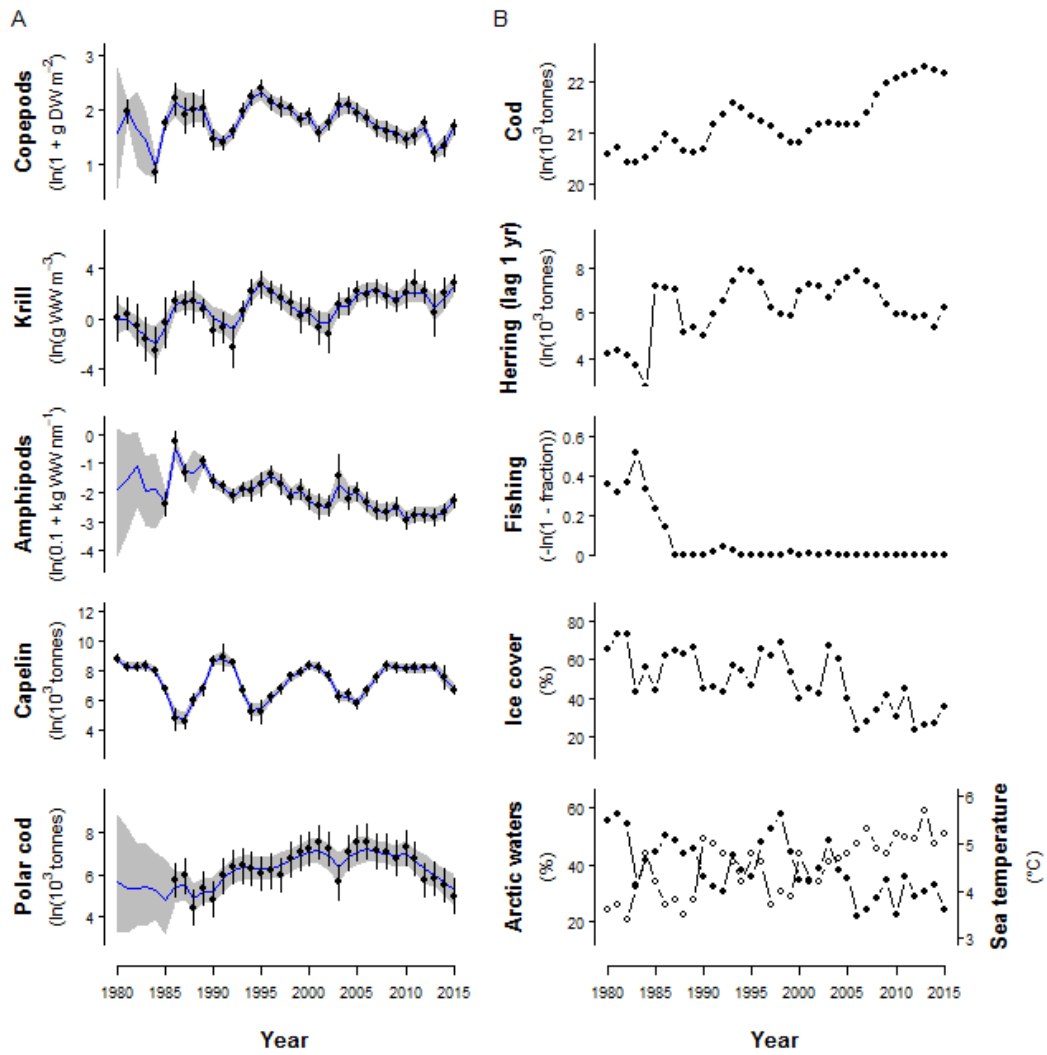
766

767

768

769

Figure 1. The Barents Sea study region. The curved lines separate southwestern (SW), central (C) and northern (N) areas dominated by different water masses and zooplankton species. The coverage of winter sea ice in the grey box (74–80 °N, 20–50 °E) was used as a main climate variable.



770

771

772

773

774

775

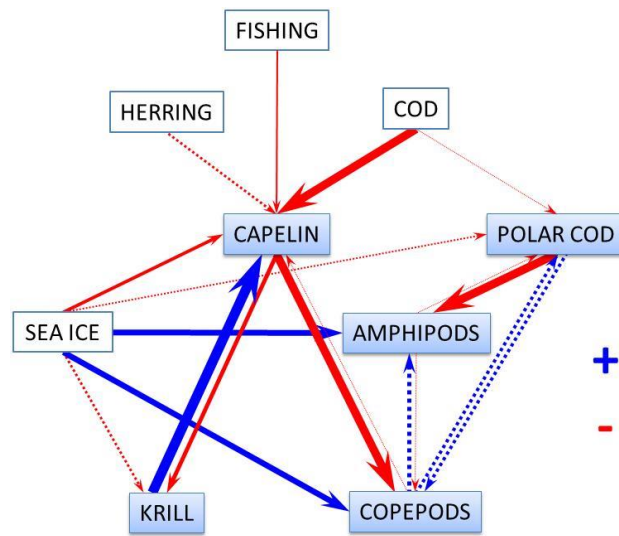
776

777

778

Figure 2. Time-series analysed. (A) Biomasses of main zooplankton groups and planktivorous fishes (referred to by acronyms *Cop*, *Krill*, *Amph*, *Cap*, *Pol* in text). Points and bars show observation time-series ± 2 standard errors. Blue lines and grey shading show the mean and 95% credibility intervals of state variables from the posterior distributions. (B) Covariates thought to potentially influence biomasses of main zooplankton groups and planktivorous fishes (*Cod*, *Her*, *F_{CAP}*, *Ice*, and two alternative climate variables, filled circles: area of Arctic water masses in autumn, open circles: previous-autumn water column temperature, Table S1; see Fig. S1 for all alternative climate variables).

779



780

781

782

783

784

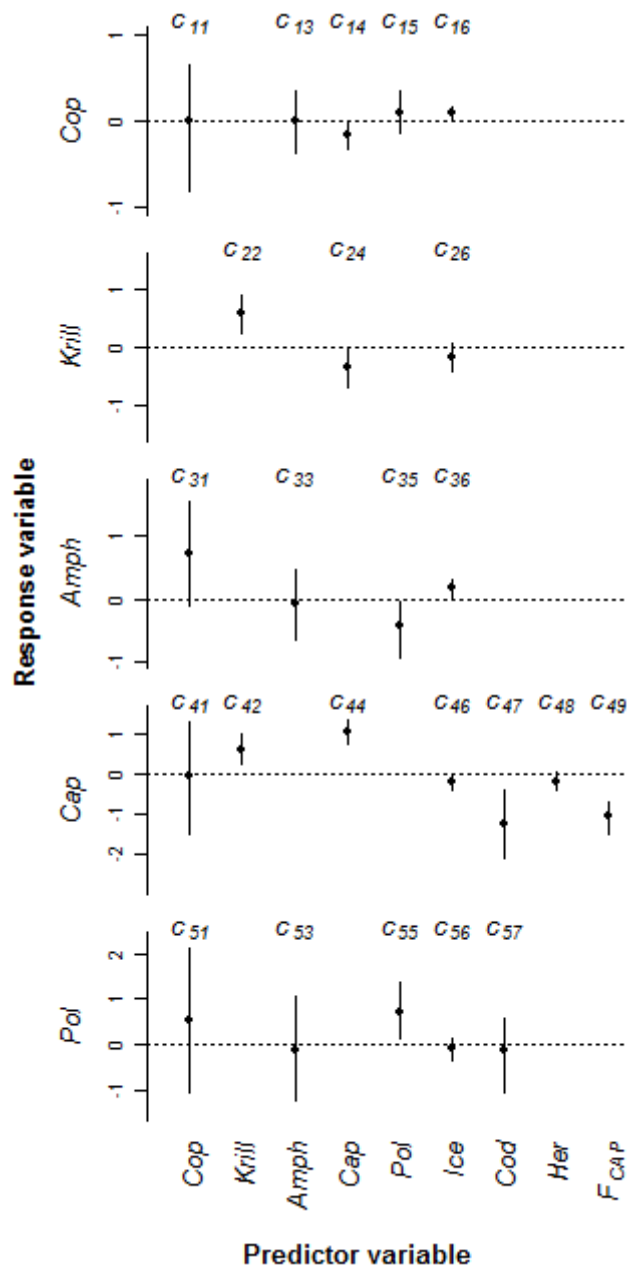
785

786

787

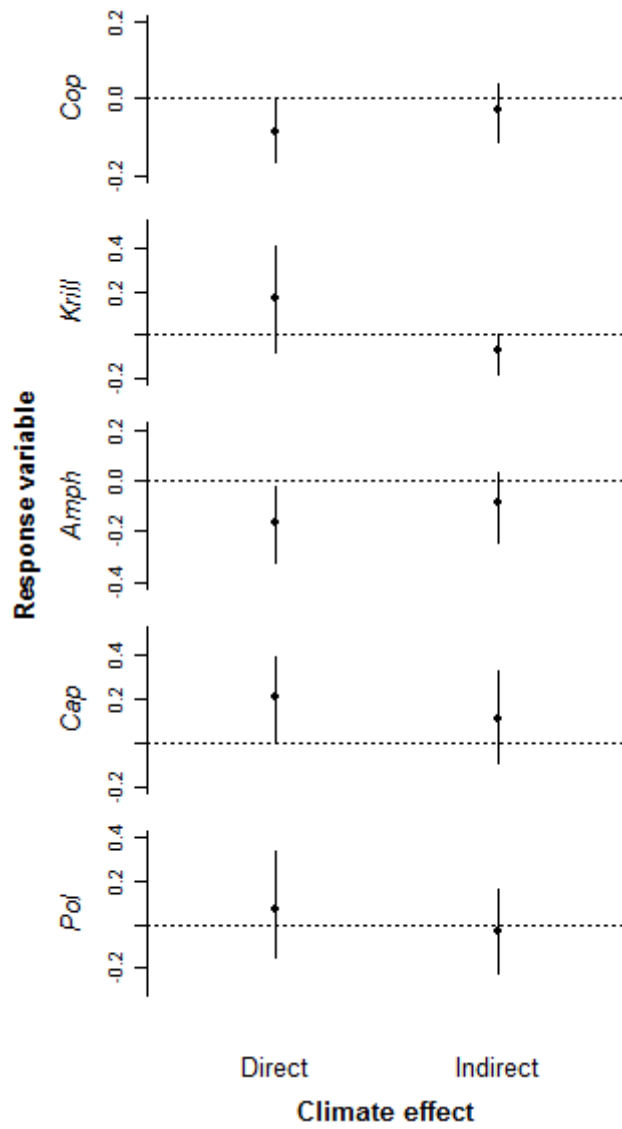
788

Figure 3. Schematic representation of the analysed multi-species dynamics in the central and northern Barents Sea. Blue-shaded boxes represent focal species or species groups, for which strengths of both bottom-up and top-down effects were estimated (arrows). Open boxes represent other key abiotic or biotic variables that we estimated effects of. Arrow widths are approximately proportional to estimated effect sizes (posterior means, Table S2), with colours indicating sign (blue: positive, red: negative) and line types statistical significance (whole lines: 95 % credibility intervals exclude zero) of effects.



789
790
791
792
793
794
795
796
797

Figure 4. Estimated model coefficients. Points and bars show posterior means and 95 % credibility intervals. The coefficients show the ln-scale change in the response variable per ln-unit increase in the predictor variable. Exceptions are coefficients for the arithmetic scale predictor variable *Ice*, which show the ln-scale change in the response variable per 10 % increase in ice cover. Furthermore, the coefficient for F_{CAP} is scaled to be -1 if reported catch and stock biomasses are correct and natural mortality during the period of fishing is ignored. Figure S3 and Table S2 give coefficient values at the normalized scale the model was fitted to.



798

Figure 5. Direct and indirect climate effects. Points and bars show posterior means and 95 % credibility intervals for the ln-scale change in the response variable of a 10 % decrease in ice cover. The direct effects are the estimated effects of *Ice* on each organism. The indirect effects are the estimated effects of *Ice* through the other analysed organisms and occur with a 1-year time lag.

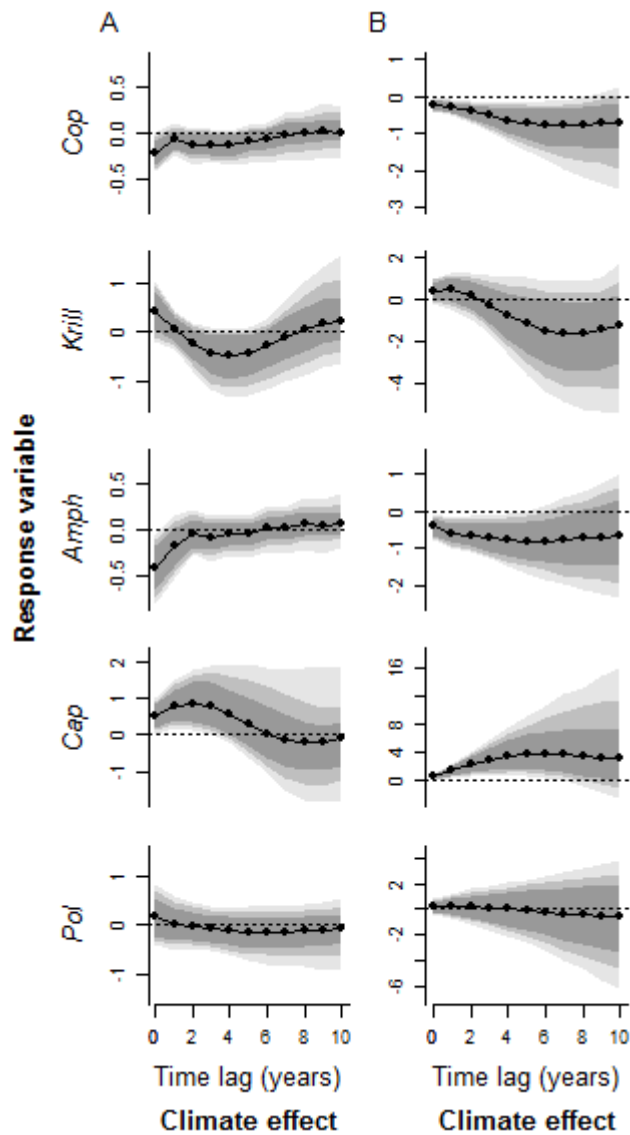


Figure 6. Direct and delayed effects of a transient (A) or persistent (B) change in climate. Points and light-to-dark-grey shading show posterior means and 95 %, 90 % and 80 % credibility intervals for the ln-scale change in the response variable of either a 25 % decrease in ice cover in a single year (A) or a persistent 25 % decrease in ice cover (B). The delayed effects at different time lags include both density-dependent dampening of the direct effect of *Ice* over time and indirect effects of *Ice* through other organisms.