

Future trajectories of change for an Arctic deep-sea ecosystem connected to coastal kelp forests

Vilas, Daniel; Coll, Marta; Pedersen, Torstein; Corrales, Xavier; Filbee-Dexter, Karen; Wernberg, Thomas

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1 **Title:** Future trajectories of change for an Arctic deep-sea ecosystem connected
2 to coastal kelp forests

3 **Running head:**

4 Future changes in Arctic ecosystem

5 **Authors**

6 Daniel Vilas*^{1,2,3}, Marta Coll^{1,4}, Torstein Pedersen⁵, Xavier Corrales^{1,6}, Karen
7 Filbee-Dexter^{7,8} and Thomas Wernberg^{7,9,10}

8 **Affiliations**

9 ¹ Institut de Ciències del Mar (ICM-CSIC), P. Marítim de la Barceloneta, 37-49, 08003
10 Barcelona, Spain.

11 ² Nature Coast Biological Station, Institute of Food and Agricultural Sciences,
12 University of Florida, Cedar Key, FL 32625, United States.

13 ³ Fisheries and Aquatic Sciences Program, School of Forest Resources and
14 Conservation, University of Florida, Gainesville, FL 32611, United States.

15 ⁴ Ecopath International Initiative (EII), Barcelona, Spain.

16 ⁵ Department of Arctic and Marine Biology, UiT–The Arctic University of Norway, 9037
17 Tromsø, Norway.

18 ⁶ AZTI, Marine Research, Basque Research and Technology Alliance (BRTA),
19 Txatxarramendi Ugarteia z/g, 48395, Sukarrieta, Spain.

20 ⁷ Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway.

21 ⁸ Institute of Marine Research, Nye Flødevigveien 20, 4817 His, Norway.

22 ⁹ Department of Science and Environment (DSE), Roskilde University, Roskilde,
23 Denmark.

24 ¹⁰ UWA Oceans Institute & School of Biological Sciences, University of Western
25 Australia, Perth, WA, Australia.

26

27 *Corresponding author: danielvilasgonzalez@gmail.com

28

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30 **Author Contributions**

31 DV, MC conceived and designed the research; DV performed the simulations; DV, MC
32 analyzed the data; DV, MC, TP, XC contributed materials and analysis tools; DV, MC,
33 TP, XC, KF, TW wrote and edited the manuscript.

34

35 **Abstract**

36 Environmental stressors related to climate change and other anthropogenic activities
37 are impacting Arctic marine ecosystems at exceptional rates. Within this context,
38 predicting future scenarios of deep-sea ecosystems and their consequences linked with
39 the fate of coastal areas is a growing need and challenge. We used an existing food-web
40 model developed to represent the outer basin of the Malangen fjord, a Northern
41 Norwegian deep-sea ecosystem, to assess the potential effects of plausible future
42 trajectories of change for major drivers in the area, including links to coastal kelp forests.
43 We considered four major drivers (kelp particulate organic matter (POM) production
44 entering the deep sea, fishing effort, king crab invasion, and ocean warming) to project
45 12 future scenarios using the temporal dynamic module of Ecopath with Ecosim
46 approach. Overall, we found that the impact of warming on the deep-sea ecosystem
47 structure and functioning, as well as on ecosystem services, are predicted to be greater
48 than changes in kelp forest dynamics and their POM production entering the deep-sea
49 and the king crab invasion. Yet, the cumulative impacts are predicted to be more
50 important than non-cumulative since some stressors acted synergistically. These results
51 illustrate the vulnerability of sub-Arctic and Arctic marine ecosystems to climate change
52 and consequently call for conservation, restoration, and adaptation measures in deep-
53 sea and adjacent ecosystems. Results also highlight the importance of considering
54 additional stressors affecting deep-sea communities to predict cumulative impacts in an
55 ecosystem-based management and global change context and the interlinkages
56 between coastal and deep-sea environments.

57

58 **Key words:** Arctic ecosystem, ecological indicators, Ecopath with Ecosim, future
59 management scenarios, kelp detritus, restoration

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62

63 **Implications for practice:**

- 64 - Increasing temperature may cause high impacts at species level due to their
65 thermal optimum ranges, triggering impacts at the ecosystem level.
- 66 - Ecological indicators showed the strongest impacts when increasing temperature
67 was included in future predictions. These effects emphasize the vulnerability of
68 Arctic marine ecosystems to climate change.
- 69 - Regime shifts in kelp organic matter production and a king crab invasion may
70 produce more reduced but noticeable impacts at the deep-sea ecosystem level.
- 71 - In addition to temperature, considering additional stressors affecting deep-sea
72 communities such as changes in kelp forest from coastal areas are important to
73 predict cumulative impacts of the deep sea in an ecosystem-based management
74 context, and calls for urgent conservation, adaptation, and restoration actions.

75

76 **Introduction**

77 Within the current scenario of a changing planet, environmental stressors related to
78 climate change, together with other human impacts, are increasingly affecting marine
79 communities from shallow water to bathyal and abyssal ecosystems (Ramirez-Llodra et
80 al. 2011; Sweetman et al. 2017; Danovaro et al. 2017). The 20 years of warmer
81 temperatures at the beginning of the twenty-first century have affected the phenology of
82 organisms, the range, and distribution of species, and the composition and dynamics of
83 communities (Smale et al. 2019). Under this context, predicting future scenarios and their
84 consequences, and providing effective tools to policymakers, is a growing need and
85 challenge. To respond to current global climate challenges, beneficial management
86 strategies must be carried out such as increasing connectivity to ensure resilience to
87 climate change (e.g. through the maintenance and increase of the area of high-quality
88 habitats), the conservation of areas that have high environmental heterogeneity, the
89 control of other anthropogenic threatening processes and ecological restoration (Gann
90 et al. 2019).

91 Worldwide, numerous ecosystems are at risk of severe impacts. Warming events are
92 predicted to be exaggerated in the Arctic, which is undergoing the most rapid change in
93 climate (IPCC 2018), which may increase instances of storm surge or extreme weather
94 (Cohen et al. 2020). Several studies have examined and assessed the impacts on
95 ecosystem services caused by climate change in Arctic systems and highlighted the
96 need for a better understanding of these impacts to reduce the risk of marine regime
97 shifts (Rocha et al. 2015; Wernberg et al. 2019; Merzouk & Johnson 2011). Arctic fjords

98 may be particularly vulnerable to climate change because sea surface temperature is
99 expected to increase faster in Arctic ecosystems than other ecosystems (IPCC 2018).
100 Environmental changes are impacting the condition and distributions of Arctic species
101 and ousting them from current food-webs (Frainer et al. 2017).

102 Kelp forests are phylogenetically diverse, structurally complex, and highly productive
103 ecosystems of cold-water rocky marine coastlines (Wernberg et al. 2019). Particularly,
104 *Laminaria hyperborea*, which forms extensive kelp forests in the northeastern Atlantic,
105 has a very high annual production $500 - 2,000 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (Pedersen et al. 2019). As
106 much as 90% of this production is exported as particulate organic matter (POM) to
107 adjacent ecosystems (Krause-Jensen & Duarte 2016). In this ecosystem, kelp POM
108 connects coastal areas with deep-sea ecosystems and can provide shelter, substrate,
109 or even food source for these deep-sea benthic communities (Ramirez-Llodra et al.
110 2016). A recent study highlighted that changes in kelp POM biomass could produce
111 noticeable changes in lower trophic levels in Arctic deep ecosystems (Vilas et al. 2020).
112 Predicting changes to arctic kelp forests under rapidly changing environmental
113 conditions remains a challenge (Filbee-Dexter et al. 2018). Climate change is expected
114 to produce local losses of suitable habitats at low latitude ranges where climatic refugia
115 are projected to be located (Assis et al. 2018). Warming sea temperature has direct and
116 indirect impacts on kelp, and it promotes that kelp forests are increasing in northern
117 latitudes, while they are declining in southern latitudes (Filbee-Dexter & Wernberg 2018).
118 Therefore, climate change can alter distributions, densities, and behavior of herbivorous
119 sea urchins and fish whose grazing action can strongly influence the abundance and
120 distribution of kelp species (Filbee-Dexter & Scheibling 2014). It can also influence the
121 likelihood of the establishment of invasive species through climate forcing distributions.
122 For example, the King crab (*Paralithodes camtschaticus*) has expanded westwards from
123 the Barents Sea to the northeastern Norwegian coast (Jørgensen & Nilssen 2011).

124 In response to degradation and all stressors affecting kelp forests, there is an
125 increasing interest in their conservation, protection, and restoration of these systems
126 (Bekkby et al. 2020). Ecological restoration is the process of assisting the recovery of an
127 ecosystem that has been degraded, damaged, or destroyed (Society for Ecological
128 Restoration International Science & Policy Working Group 2004) and it is globally
129 recognized as a fundamental component for conservation (Aronson & Alexander 2013).
130 When ecological restoration is enforced adequately and sustainably, it contributes to
131 manifold beneficial outcomes including the protection of diversity, increasing ecosystem
132 quality, delivering services, and supporting climate change adaptation and mitigation
133 (Gann et al. 2019). Its standards highlight the importance of effectively engage a wide

134 range of stakeholders and using available scientific and local knowledge to achieve
135 appropriate referenced ecosystem states using measurable ecological indicators (Gann
136 et al. 2019). For instance, kelp ecosystem restoration experiences showed that selective
137 relocation of herbivores, rebuilding of their predators, cleaning sediment of rock surfaces,
138 and transplanting of kelp plants, are successful in restoring kelp forests and specially,
139 when involving stakeholders (e.g. fishermen and local community) (Fujita 2011).
140 Restoration and conservation efforts should be focus on maintaining kelp species and
141 preserving ecosystem services and functioning (Hobbs & Harris 2001; Vergés et al.
142 2019) as well as increasing ecosystem connectivity (Hodgson et al. 2009; Coleman et
143 al. 2020).

144 Besides, the benefits of kelp forests to adjacent ecosystems, kelp forests provide
145 shelter and habitat for multiple marine species, and associated with these habitats are
146 organisms such as marine mammals, crustaceans, echinoderms, fish, and algae
147 (Steneck et al. 2002). These ecosystems likely also contribute to large carbon sink and
148 so playing an important role for mitigation and adaptation to climate change (Krause-
149 Jensen et al. 2018; Filbee-Dexter & Wernberg in press). In addition, kelp forests are
150 considered a nature-based defence upon coastal erosion and extreme storm events
151 (Rebecca L. Morris et al. 2020). From a social and economic perspective, kelp forests
152 provide important ecosystem services through harvesting to extract food, and
153 pharmaceutical components (Vea & Ask 2011).

154 Kelp forests are increasingly threatened by a variety of impacts, including species
155 invasions, ocean warming, and direct harvest (Wernberg et al. 2019). Those stressors
156 affect kelp POM production, and consequently, they affect adjacent ecosystems where
157 several marine organisms interact and feed on kelp POM (Ramirez-Llodra et al. 2016).
158 Understanding how these multiple stressors, marine organisms, and ecosystems
159 interact, connect, and influence each other is an issue of relevant importance. To
160 address this challenge, a shift towards a more comprehensive analysis and management
161 of human activities is needed, as underlined by the ecosystem-based management
162 (EBM) approach (Leslie & McLeod 2007).

163 The modelling approach “Ecopath with Ecosim” (EwE) is being widely used as a tool
164 for the analysis of marine ecosystems (Christensen et al. 2008; Colléter et al. 2015).
165 Among these analyses, several studies used the temporal module of EwE (Ecosim) to
166 assess cumulative impacts and predict future scenarios including climate change on
167 marine systems (Bentley et al. 2017; Corrales et al. 2018; Serpetti et al. 2017). These
168 studies illustrated the importance of including multiple stressors other than fisheries,

169 such as climate change, in an ecosystem-based management approach. In this study,
170 we used a previously developed Ecopath food web model of an Arctic deep ecosystem
171 associated with kelp exports (ADEAKE) of northern Norway (Vilas et al. 2020), to
172 evaluate the potential effect of plausible future scenarios for major drivers in the study
173 area. Four drivers accounting for local, regional, and global stressors were used in order
174 to test twelve plausible future trajectories of change (or scenarios) that were conceived
175 and prioritized considering experts' knowledge. Specifically, we considered fishing, kelp
176 POM production, king crab invasion, ocean warming, and the cumulative effects of these
177 changes

178

179 **Material and methods**

180 - Study area

181 The Arctic deep ecosystem associated with kelp exports (ADEAKE) of the northern
182 Norway model (Vilas et al. 2020) represents the outer basin of the Malangen Fjord
183 (69.529° N, 18.021° E). This fjord is in Troms and Finnmark county, Arctic Norway, and
184 it is connected to the open sea by a sill (180 meters deep) (Fig. 1). Thus, its morphology
185 provides a potentially excellent accumulation site for kelp POM from the surrounding
186 coastal dense kelp forests (Filbee-Dexter et al. 2018). This ecosystem is considered
187 particularly vulnerable in face of warming due to its location, which could cause shifts in
188 species distribution, including invasive species such as the king crab, and consequently
189 altering the whole food-web of the ADEAKE (IPCC 2018).

190 - Modelling approach

191 Ecopath with Ecosim (EwE) modelling approach was used to develop the ADEAKE
192 model. The EwE approach is composed by three main modules: the ecosystem trophic
193 mass balance analysis (Ecopath), and the temporal (Ecosim), and spatial-temporal
194 dynamic (Ecospace) modules (Heymans et al. 2016; Christensen et al. 2014)

195 The existing EwE model represents an annual average situation in 2017, ranging
196 from 400 to 450 meters depth and covering an area of 11.8 km² (Vilas et al. 2020). The
197 Ecopath model was developed using Ecopath version 6.6, and it consisted of 36
198 functional groups (FGs) with special emphasis on kelp POM because the model was
199 built to assess the ecological role of kelp export into the deep-sea system. Two out of
200 four detritus groups (marine snow, coarse kelp POM, fine kelp POM, and benthic
201 detritus) represented the kelp secondary production. A functional group consists of

202 ontogenic fractions of a species, individual species, or groups of species that perform a
 203 similar function in the ecosystem, i.e. have similar growth rates, consumption rates, diets,
 204 habitats, and predators (Heymans et al. 2016).

205 The Ecosim module consists in a set of differential equations to describe biomass
 206 dynamics:

207

$$208 \quad \frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum Q_{ji} - \sum Q_{ji} + I_i - (M_i + F_i - e_i) \cdot B_i$$

209

210 where dB_i/dt is the growth rate of group i during time t in terms of its biomass B_i ; $(P/Q)_i$
 211 is the net growth efficiency of group i ; Q_{ij} is the consumption rate; M_i is the non-predation
 212 mortality rate; F_i is the fishing mortality rate; e_i is the emigration, and I_i is the immigration
 213 rate (Christensen & Walters 2004). Consumption rates (Q_{ij}) are calculated based on the
 214 ‘foraging arena’ theory, which divides the biomass of prey into a vulnerable and a non-
 215 vulnerable fraction and the transfer rate of vulnerability between the two fractions
 216 determines the trophic flow between the predator and the prey (Ahrens et al. 2012). The
 217 vulnerability concept incorporates density-dependent processes and expresses how far
 218 a group is from its carrying capacity (Christensen et al. 2008; Christensen & Walters
 219 2004). For each predator-prey interaction, consumption rates are calculated as:

220

$$221 \quad Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot T_j / D_j} \cdot f(Env_{function}, t),$$

222 where a_{ij} is the rate of effective search for i by j ; T_i represents prey relative feeding time;
 223 T_j the predator relative feeding time; M_{ij} is the mediation forcing effects; v_{ij} is the
 224 vulnerability parameter; D_j represents the effects of handling time as a limit to
 225 consumption rate (Ahrens et al. 2012; Christensen et al. 2008); and $f(Env_{function}, t)$ is the
 226 environmental response function that restricts the size of the foraging arena (C_{rcj}) to
 227 account for external environmental drivers changing over time, such as temperature
 228 (Ahrens et al. 2012; Christensen et al. 2014).

229 The environmental response functions ($f(Env_{function}, t)$), which link the species or FGs
 230 dynamics with the environmental drivers, were first obtained from *AquaMaps* (Kesner-
 231 Reyes et al. 2016), a global database on species distribution. These environmental
 232 response functions are given as curves showing the minimum and maximum tolerance
 233 levels and 10th and 90th preferable quantiles to the environmental parameters (in our

234 case, temperature). As a second step, these functions were modified using expert
235 opinion from scientists to incorporate local knowledge. The final environmental
236 preference functions for each FG (Fig. S1.1) were obtained by weighting the values of
237 the species included in a FG to their relative biomass.

238 - Simulations of future scenarios

239 We used the temporal dynamic module Ecosim to evaluate the effect of plausible
240 future scenarios for major drivers in the study area after 83 years of simulation (2017-
241 2100) (Table 1). Future scenarios were simulated without fitting the model to data due to
242 the lack of specific time-series data and consequently, vulnerabilities could not be
243 estimated as recommended (Christensen et al. 2008). Similar to previous temporal
244 dynamic simulations (Vilas et al. 2020), we increased kelp POM vulnerability ($v = 100$)
245 to allow a notable increase in consumption on detritus if the biomass of consumers
246 increases and default values were set ($v = 2$). Four drivers (fishing, kelp POM production,
247 red king crab invasion, and temperature) were selected to condition the scenarios.
248 Among these drivers, we selected twelve plausible future scenarios in the study area
249 considering the knowledge of a group of regional experts (Table 1).

250 In the first scenario (Scn1) fishing effort, kelp POM production and sea water
251 temperature were kept constant from 2017, which was the year for the Ecopath baseline
252 model (Vilas et al. 2020). Fishing effort was modified in the second and third scenarios:
253 the relative fishing effort was reduced to 50% for both operating fleets (gillnetters and
254 shrimp trawlers) (Scn2), or increased 50% on gillnetters (Scn3) in order to reduce large
255 fish feeders group biomass while keeping constant kelp POM production and
256 temperature and without the invasion of the red king crab (Fig. 2a).

257 Regionally, we selected four scenarios, three of which were driven by kelp POM
258 production drivers and one by a possible future biological invasion. Scenario 4 (Scn4)
259 considered direct harvesting of kelp in the surrounding areas, which it is considered a
260 rising activity in northern Norway (Stévant et al. 2017), and both kelp POM groups were
261 forced to decrease their biomass by 50% (Fig. 2b). The second and third regional
262 scenarios (Scn5 and Scn6, respectively) included kelp POM production as the main
263 driver due to changing sea urchins (*Strongylocentrotus droebachiensis*) biomass in
264 surrounding areas. Scn5 simulated a decrease in sea urchin population and recovery of
265 barrens, so coarse kelp POM biomass was forced to increase while fine kelp POM
266 biomass was forced to decrease (50%) because of the non-grazing process (Fig. 2b).
267 These scenarios (Scn4, 5, and 6) included changes in kelp POM production while
268 keeping constant fishing and temperature and without the invasion of the red king crab.

269 In contrast, Scn6 reflected a regime shift to barrens caused by an increase in sea urchins
270 and destructive grazing of kelp, during which the biomass of coarse kelp POM decreased
271 until negligible, and the amount of fine kelp POM biomass increased at first (due to the
272 high grazing intensity of urchins on attached kelp (Filbee-Dexter et al. 2019) and then
273 decreased as the urchins consumed the entire standing stock (Fig. 2b). The last regional
274 scenario (Scn7) included the future invasion of the red king crab invasion, which is
275 predicted for this region (Christiansen et al. 2015). The red king crab was added to the
276 ADEAKE model with very small biomass and then it was forced to increase in the model
277 until achieving the same biomass as other Ecopath models in a similar study area
278 (Pedersen et al. 2018). This increase applied the same trend showed in other Norwegian
279 fjords which the red king crab invaded (Oug et al. 2018) (Fig. 2c) while keeping fishing
280 and kelp POM production constant.

281 To predict the impact of warming waters on the ADEAKE, future sea surface
282 temperature (SST) projections of the study area were obtained from the Royal
283 Netherlands Meteorological Institute Climate explorer (<http://climexp.knmi.nl>) in order to
284 extract the trend of these projections. SST projections under two contrasting scenarios
285 of greenhouse emissions (RCP4.5 and RCP8.5) were used to calculate annual rates of
286 SST change for both scenarios for each year from 2017 to 2100. Similar historical trends
287 have been observed between SST and sea bottom temperature (SBT) in the area
288 (Husum & Hald 2004). Therefore, estimated annual rates of SST change were applied
289 to SBT values in the study area (Mankettikkara 2013). This method allowed us to
290 calculate SBT projections under both scenarios of greenhouse emissions and assumed
291 that rates of increasing SST are equal for SBT. The scenarios conducted to simulate
292 potential impacts of ocean warming were RCP4.5 (Scn8) and RCP8.5 (Scn9), and they
293 both included a constant fishing and kelp POM production and did not include the
294 invasion of the red king crab (Fig. 2d).

295 In addition, three combinations of multiple impacts were performed in order to obtain
296 combined scenarios. In the first combined scenario (Scn10), we merged the decreasing
297 of sea urchin population (Scn5) and a red king crab invasion (Scn7) (Table 1).
298 Afterwards, the least impacting combined future scenario (Scn11) was obtained adding
299 the reduction of fishing effort (Scn2), the decreasing of sea urchin population (Scn5), and
300 one the conservative SBT projection of SBT – (RCP4.5) (Scn8), without the invasion of
301 the red king crab (Table 1). The most impacting combined future scenario (Scn12) was
302 produced combining the increasing of fishing effort (Scn3), the increase of sea urchin
303 population (Scn6), the red king crab invasion (Scn7), and the most extreme SBT
304 projection of SST – RCP8.5 (Scn9).

305 - Model analysis and indicators

306 Biomass trends of selected functional groups were analyzed in order to test potential
307 effects of plausible future scenarios. The groups were chosen considering their
308 structuring importance in the deep-ecosystem and/or vulnerability under future scenarios
309 (Vilas et al. 2020) and their relevance to show the change in ecosystem structure,
310 functioning, and ecosystem services. A total of eight functional groups were included in
311 the analysis: rays and skates, velvet belly, rabbit fish, blue whiting, large fish feeders,
312 other commercial demersal fish, benthopelagic shrimps, and suprabenthos (see Vilas et
313 al. 2020 for more information regarding the food-web structure and their functional
314 groups).

315 Additionally, ecological indicator trends were obtained for each simulation in order to
316 describe the ecosystem structure and functioning and were computed with two plug-ins
317 commonly used: Ecological Network Analysis (ENA) and ECOIND. ENA indicators were
318 extracted with ECOSAMPLER module (Steenbeek et al. 2018) and included: the Total
319 System Throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$), export (Ex/TST), flow to detritus (FD/TST), the
320 relative Ascendancy (A/C), the average mutual information (AMI), Finn's Cycling Index
321 (FCI, %) and the Average Path Length (APL). The TST is the sum of all flows in the
322 model and represents an overall measure of the "ecological size" of the system (Finn
323 1976). Food-web model flows are expected to change under ecosystem impacts, so the
324 TST, Ex/TST, and FD/TST would shift. The A/C is a measure of the food-web
325 organization (Ulanowicz 2004) and its value is highly correlated with ecosystem maturity
326 (Christensen 1995) so it decreases after being impacted. The AMI indicates the
327 distribution of links in the food-web and the higher its value the more vulnerable becomes
328 the ecosystem (Ulanowicz 2004). The FCI is the fraction of the ecosystem's throughput
329 that is recycled to the TST and it decreases after ecosystem impacts (Finn 1976). The
330 APL is the average number of groups through which each inflow passes weighted by the
331 size of the inflows and its decreasing is an indicator of stress (Christensen 1995).

332 The ECOIND plug-in (Coll & Steenbeek 2017) allowed us to extract ecological
333 indicators related to species traits (biomass, catch, trophic, size, and species-based).
334 We focused on biomass-based indicators, trophic-based and catch-based indicators.
335 Biomass-based indicators are based on the abundance of organisms in the food-web
336 and we considered: biomass of commercial species, biomass of invertebrates' species,
337 biomass of fish species, and the Kempton's diversity index. Next, four trophic-based
338 indicators four indicators were selected based on the trophic level (TL): TL of the
339 community (TLcom), TL of the community including organisms with $TL \geq 2$ (TLcom2), TL

340 of the community including organisms with $TL \geq 3.25$ ($TL_{com3.25}$) and TL of the
341 community including organisms with $TL \geq 4$ (TL_{com4}). We also selected 4 catch-based
342 indicators: TL of the catch ($TL\ C$), fish catch ($Fish\ C$), invertebrates catch ($Invertebrates$
343 C) and total catch ($Total\ C$).

344 - Assessing uncertainty

345 Temporal dynamic simulations require quantifying uncertainties inherent in the
346 simulations in order to facilitate decision-making. We performed an uncertainty
347 assessment based on the pedigree values that describe the origin and uncertainty of
348 input parameters used to parametrize the model based on their type (Christensen et al.
349 2008; Christensen & Walters 2004). Afterwards, we used the pedigree information with
350 associated confidence intervals for the input values in the Monte Carlo routine (MC) in
351 Ecosim to evaluate uncertainty (Table S1) (Christensen & Walters 2004; Heymans et al.
352 2016). MC routine is a statistical approach where random mass-balance models are
353 constructed based on the uncertainty previously defined through pedigree values. For
354 each MC run, input values of the baseline Ecopath models were randomly sampled from
355 uniform distributions, with the width of distributions corresponding to the pedigree-
356 specified input uncertainty level (Christensen & Walters 2004; Heymans et al. 2016).
357 Results obtained from MC runs included probability distributions for the estimated
358 parameters along and ecological indicators. 500 MC simulations were run, and 95% and
359 5% percentile confidence intervals (CIs) were calculated to provide a good idea of the
360 range of outputs. Subsequently, the correlation and significance between model outputs
361 with time and its strength were measured using the nonparametric Spearman correlation
362 (Spearman 1904). Additionally, changes of model outputs with time were checked using
363 unlagged cross-correlation analysis (Venables & Ripley 2013).

364

365 **Results**

366 **Baseline Scenario – Scn1**

367 Under the baseline simulation (Scn1) in which fishing effort, kelp POM production,
368 and sea water temperature were kept constant from 2017, the Ecosim model predicted
369 changes in biomass trends for several FGs. This is due to the addition of the temperature
370 effects to the baseline mass-balance model and the sensitivity of different species to the
371 temperature range that was introduced when we moved to the temporal model. This
372 impact of sub-optimal temperatures in the consumption rates of some FGs had
373 cascading effects through the food web. For example, velvet belly was negatively

374 impacted by a sub-optimal temperature condition and this caused predation release on
375 benthopelagic shrimps and suprabenthos, which biomass increased. In any case, we
376 perform a relative comparison of scenarios to the baseline, thus this initial change is not
377 affecting the comparison.

378 Biomass trend of rays and skates, large fish feeders, other commercial demersal fish,
379 redfishes, benthopelagic shrimps, and suprabenthos increased (Fig. 3, 4, 5, 6 and Table
380 S5). In contrast, the model predicted a decreasing trend for velvet belly, rabbit fish, and
381 blue whiting (Fig. 3 and 4).

382 Under Scn1 a significant increasing trend for TST, FCI, and APL was predicted, while
383 Ex/TST, FD/TST, A/C, and AMI decreased over time (Fig. 7 and Table S6). A significant
384 increasing trend for Commercial B, Invertebrates B, Total B, TL community 3.25, TL
385 community 4, Invertebrates C, and Total C was predicted (Fig. 8). On the other side,
386 Demersal B, Fish B, TL community, TL community 2, TL C, and Fish C decreased over
387 time (Fig. 8, and Table S7).

388 **Fishing scenarios – Scn2 and Scn3**

389 Although both fishing scenarios were antagonists in terms of fishing effort (Table 1),
390 both scenarios showed similar biomass trends for all selected functional groups between
391 them and with respect to the baseline scenario (Fig. 3, 4, 5, and 6). Coinciding with that,
392 ecological indicators showed similar trends between them and with respect to the
393 baseline scenario except for small differences (Fig. 7 and 8). For example, decreasing
394 trends on FD/TST were less strong for Scn2 and Scn3 than Scn1 (Fig. 7), and Scn3
395 showed less strong decreasing trends for Fish C although it was significant too (Fig. 8
396 and Table S7).

397 **Changes kelp POM production scenarios – Scn4, Scn5, and Scn6**

398 Under scenarios with changes in kelp POM import, model results delivered similar
399 biomass trends for most functional groups (Fig. 3, 4, 5, and 6) except for suprabenthos,
400 for which non-significant change over time was found in Scn6 (Table S5).

401 Scn4 showed a significant increasing trend over time for FCI and APL and a
402 significant decreasing trend for Ex/TST, A/C, and AMI, while FD/TST did not show any
403 significant trend over time (Fig. 7 and Table S6). Similarly, the model predicted an
404 increasing trend for TST, FCI, and APL under Scn5 and a decreasing trend for A/C and
405 AMI. In contrast, Ex/TST trend was not significantly correlated under this scenario. Under
406 Scn6, although the model predicted relevant change for all ENA indicators except FCI
407 and APL, changes were less remarkable (Fig. 7).

408 Similar to the baseline scenario, ECOIND indicators showed an increasing trend for
409 Commercial B, Invertebrates B, Total B, Kempton's index, TL community 3.25, TL
410 community 4, Invertebrates C, and Total C under changing on kelp POM production
411 scenarios except for Total B in Scn6 (Fig. 8). On the other hand, the model predicted a
412 decreasing trend for demersal B, Fish B, TL community, TL community 2, TL C, and Fish
413 C for these three scenarios. In contrast to the baseline scenario, changes in
414 Invertebrates B, Total B, and TL community were not as strong under Scn4, Scn5, and
415 Scn6 (Fig. 8).

416 **Red king crab invasion scenario – Scn7**

417 Applying the king crab scenario (Scn7), the model predicted an increasing trend for
418 rays and skates, redfishes, benthopelagic shrimps, and suprabenthos, while it predicted
419 a decreasing trend for velvet belly, rabbit fish, and blue whiting (Fig. 3, 4, 5 and 6).
420 Despite the similarity with the baseline scenario on FG biomass trend, changes in blue
421 whiting and benthopelagic shrimps were smaller for Scn7 (Fig. 3).

422 Under this scenario, significant changes in ENA indicators were found for TST,
423 Ex/TST, and FCI. Contrarily, the model did not predict any significant change in FD/TST,
424 A/C, AML, and APL (Fig. 7). A notable increasing trend for Commercial B, Invertebrates
425 B, Total B, Kempton's index, TL community 3.25, TL community 4, Invertebrates C and
426 Total C was observed, while Demersal B, Fish B, TL community, TL community 2, TL C
427 and Fish C decreased over time (Fig. 8). Despite ECOIND indicators showed the same
428 trends compared with the baseline scenario, most of these indicators responded weaker
429 over time (Fig. 8).

430 **Impacts of ocean warming scenarios – Scn8 and Scn9**

431 Increasing temperature scenarios showed similar predicted effects on FG biomass.
432 Under Scn8, rays and skates, large fish feeders, other commercial demersal fish,
433 redfishes, benthopelagic shrimps, and suprabenthos biomass decreased whereas velvet
434 belly, rabbit fish, and blue whiting biomass increased (Fig. 3, 4, 5, and 6). Scn9 obtained
435 similar predictions except for velvet belly and large fish feeders', for which the biomass
436 decreased and did not show significant change respectively (Fig. 3, 4, 5, and 6).

437 Under Scn8, the model predicted a decreasing trend for TST and increasing trends
438 for the rest of ENA indicators. Contrarily, Scn9 did not show changes for TST, Ex/TST,
439 FD/TST, and APL (Fig. 7). For ECOIND indicators, Commercial B, Invertebrates B Total
440 B Kempton's Index, TLcom2, TLcom3.25 TLcom4, Invertebrate C, and Total C
441 decreased, and Demersal B, Fish B TLcom TL C, and Fish C increased (Fig. 8). Scn9

442 showed similar trends for these indicators, except for TLcom which decreased under this
443 scenario.

444 **Cumulative scenarios – Scn10, Scn11 and Scn12**

445 In Scn10 biomass of velvet belly, rabbit fish and blue whiting decreased, while
446 increased on rays and skates, redfishes, benthopelagic shrimps, and suprabenthos (Fig.
447 3, 4, 5, and 6). On the contrary, Scn11 showed opposite biomass trends similarly to
448 Scn12 except for velvet belly biomass which decreased (Fig. 3, 4, 5, and 6).

449 Considering ENA indicators, Scn10 showed a decreasing trend for TST and an
450 increasing trend for Ex/TST, FD/TST, A/C, and APL (Fig. 7). Likewise, under Scn11, TST
451 decreased, while Ex/TST, FD/TST, A/C, and AMI increased. Scn12 showed increasing
452 trends for TST, Ex/TST, A/C, FCI, and APL, and decreasing trends for FD/TST and AMI
453 (Fig. 7). Ecological indicators obtained similar predicted trends under Scn10 and 12 (Fig.
454 8). Both of them showed increasing trends for Fish B, TLcom, TL C, and Fish C, while
455 decreasing trends for Commercial B, Demersal B, Invertebrates B, Total B, Kempton's
456 Index, TLcom2, TLcom3.25, Invertebrates C, and Total C. Scn11 showed decreasing
457 trends for commercial B, invertebrates B, total B, Kempton's Index, TLcom2, TLcom3.25,
458 TLcom4, Invertebrates C and Total C and increasing trends for Fish B, TLcom, TL C and
459 Fish C (Fig. 8).

460 **Common patterns**

461 In general, scenarios that included temperature increasing (Scn8, Scn9, Scn11, and
462 Scn12) showed opposite biomass trends in most functional groups compared to the
463 baseline scenario (Fig. 3). The rest of the scenarios (fishing effort, kelp POM production,
464 and king crab invasion scenarios) showed similar biomass trends of most functional
465 groups compared to the baseline (Fig. 3). Most scenarios showed increasing trends for
466 FCI, and APL (Fig. 7), while they showed decreasing trends for Demersal B, TLcom,
467 TLcom2, and TLcom4 (Fig. 8). Additionally, catch-based indicators and several biomass-
468 based indicators changed their trends under increasing temperature scenarios (Scn8
469 and Scn9) and cumulative scenarios (Scn10, Scn11, and Scn12) (Fig. 8).

470

471 **Discussion**

472 Under the baseline scenario, most functional groups increased in biomass, including
473 all commercial functional groups, while important FGs in terms of biomass decreased
474 (velvet belly; rabbit fish; and blue whiting). This suggests that current sea bottom

475 temperature is favourable for these species and unfavourable for others or that these
476 species are close to the limits of their thermal niches (Poloczanska et al. 2016). Other
477 FGs showed increasing biomass trends (e.g. benthopelagic shrimps) possibly due to
478 cascading effects since their predators declined in terms of biomass (Baum & Worm
479 2009).

480 Overall, the fishing scenarios did not show noticeable impacts at species levels nor
481 at ecosystem level. These results likely reflect the sustainability of current fishing
482 activities and their moderate impact in this study area, which has also been pointed out
483 in adjacent areas (Pedersen et al. 2016). A general study carried out in EU waters
484 (Froese et al. 2018) identified the Norwegian Sea and the Barents Sea as the European
485 Seas with the highest percentage of sustainably exploited stocks.

486 Similarly, predicted future changes in kelp POM production (Scn4, Scn5, and Scn6)
487 showed limited changes in biomass over time for the investigated FGs. Only
488 suprabenthos under Scn6 showed an opposite trend compared to the baseline scenario,
489 with lower biomass correlation results. Small crustaceans are considered one of the most
490 important feeders on kelp POM (Dunton & Schell 1987). At ecosystem level, these
491 scenarios showed changes in the distribution of the flows (Ex/TST and FD/TST) linked
492 to changes in the kelp POM production in coastal areas. Specifically, Scn6 did not show
493 changes in FCI and APL neither strong decreasing on A/C and AMI like baseline
494 scenario, so no change towards a more complex food-web and more mature ecosystem
495 is expected under this scenario. Although kelp POM production scenarios did not highly
496 impact the deep-sea ecosystem, among all the kelp POM production scenarios, the
497 scenario of increasing sea urchins (Scn6) was the one that caused the highest impact.
498 Therefore, the impacts of a regime shift to barrens caused by overgrazing sea urchins
499 may propagate to surrounding deep ecosystems and negatively impact their structure,
500 functioning, and resilience. This finding is especially interesting given the ubiquitous
501 nature of shifts to sea urchin barrens (Filbee-Dexter & Scheibling 2014). Our modelling
502 application suggests that these marine ecosystem shifts could impact surrounding deep
503 ecosystems and highlights the importance of healthy kelp forest coastal ecosystems an
504 effort to conserve and restore them (Layton et al. 2020; Fredriksen et al. 2020).

505 Under red king crab invasion scenario (Scn7), other commercial demersal fish and
506 large fish feeders did not show relevant changes. These results are in line with those of
507 Pedersen *et al.* (2018), which found small effects of red king crab on fish groups.
508 However, dietary studies (Fuhrmann et al. 2017) indicated that king crab diet is based

509 on benthic invertebrates such as crustaceans, echinoderms, and mollusks and thus it
510 may compete with fish species for the same source of food.

511 Local and regional stressors (fishing effort, kelp POM production, and invasive
512 species) have been previously highlighted as potentially important for impacting at
513 species and ecosystem level (Pedersen et al. 2018; Ramirez-Llodra et al. 2016).
514 However, this study showed that these changes may have limited impacts in the
515 ADEAKE at their modelled level in comparison with the global stressors (ocean
516 warming).

517 Global scenarios (Scn8 and Scn9) that included two global warming projections
518 (RCP4.5 and RCP8.5, respectively) showed opposite trends on most FGs biomass in
519 comparison with previous scenarios. In contrast to the baseline scenario, velvet belly,
520 rabbit fish and blue whiting biomass increased because increasing ocean temperature
521 under global warming scenarios places these species into their thermal tolerance
522 thresholds and thus it rises their fitness. In fact, Arctic fish communities are currently
523 suffering a rapid borealization and expanding their distribution northwards (Fosheim et
524 al. 2015). For instance, blue whiting increased in warm waters in the Barents Sea
525 (Aschan et al. 2013), and demersal species such as rabbit fish and velvet belly registered
526 distribution shifts after increasing sea temperature over time in the Norwegian Sea
527 (Skants 2019). Bentley *et al.* (2017) assessed the impact of ocean warming in the
528 Norwegian and Barents Seas and indicated significant changes in ecosystem biomass
529 composition including the decline of boreal functional groups. Similarly, Serpetti *et al.*
530 (2017) investigated the impact of ocean warming in the West Coast of Scotland and
531 suggested that declines of stock may be due to migration to cooler waters. In our study,
532 other FGs' biomass showed increasing biomass trends like benthopelagic shrimps and
533 it could be explained by trophic interactions processes like predation or competition
534 (Kortsch et al. 2015). At ecosystem level, some of these indicators showed an increasing
535 trend under these scenarios, suggesting a change towards a more chain-web structure
536 and less mature structure. For example, the rise in AMI indicated that the ecosystem is
537 becoming more constrained, efficient, unstable, and vulnerable (Ulanowicz & Abarca-
538 Arenas 1997) under global warming scenarios, which is in line with the decreasing trend
539 obtained in the Kempton's Index. This instability could be driven by biomass changes in
540 important FGs driven by increasing on sea temperature in the ecosystem as previously
541 mentioned.

542 Scn10 showed similar biomass trends as found under red king crab invasion scenario
543 (Scn7), highlighting the impact of king crab biomass over the change on kelp POM

544 production. Scn10 results suggested that the synergic effect of king crab and change on
545 kelp POM due to increasing of sea urchins in coastal areas could cause a change
546 towards a more simplified food-web and immature ecosystem, namely decreasing its
547 resilience and similar to warming scenarios (Scn8 and Scn9) impacts on deep-sea
548 ecosystems. The other two cumulative impacts scenarios (Scn11 and Scn12) reflected
549 the effect of temperature increasing and consequent changes in competition and trophic
550 processes as already highlighted for Scn8 and Scn9. However, some indicators
551 suggested different trends because of the cumulative effect of the different drivers
552 considered under the scenario which complicated more its interpretation. For instance,
553 the decreasing trend of AMI under Scn12 could be due to the cumulative decreasing
554 trend of the impacts considered. Considering ecological indicators, total biomass results
555 under warming scenarios are consistent with previous global studies (Free et al. 2019),
556 which found gains in marine fisheries production/biomass in the Norwegian and Barents
557 Sea for the past decades. Under Scn12, some biomass indicators showed stronger
558 correlations over time compared to the warming scenario (Scn9). This scenario
559 highlighted the importance to consider multiple stressors on future projections to properly
560 assess changes in marine ecosystems. Cumulative impacts scenarios showed higher
561 ecosystem effects than non-cumulative scenarios indicating that some stressors can act
562 synergically and increase their impact when gathering.

563 Our model predicted ecosystem impacts in an Arctic ecosystem under multiple future
564 scenarios including climate change effects, which, can contribute to the knowledge
565 needed towards deep-sea ecosystems and how ecological restoration in coastal areas
566 can impact adjacent ecosystems. The ADEAKE model displayed a decreasing resilience
567 and ecosystem state under warming and cumulative impacts scenarios, highlighting the
568 urgent need of considering the impact of several stressors together. Our study also
569 shows that what may happen in coastal areas, in this case in kelp beds, can have an
570 impact on deep-sea adjacent ecosystems, which highlights the relevance of ecosystem
571 protection and restoration of such important areas. Ecological restoration, in fact, is
572 recognized as a critical tool for mitigating and adapting to the impacts of climate change
573 (Gann et al. 2019). A recent study (Eger et al. 2020) highlighted that a more holistic
574 approach form of restoration that incorporates species interaction could increase the
575 likelihood of success. Our modelling approach could be a suitable tool to further explore
576 potential restoration scenarios through an integrated view (Frisk et al. 2011), for
577 example, by extending the deep-sea model to the coastal areas and explicitly modelling
578 the kelp bed – deep-sea ecosystem together.

579 Performing future simulations in ecology is considered an arduous task, especially
580 without any calibration process under long-term scenarios (Dietze & Lynch 2019).
581 Although results are helpful to indicate trends in future changes, these should be
582 interpreted with caution since several limitations were found in this study. For instance,
583 fishing scenarios (Scn2 and Scn3) as well as changes in kelp POM production scenarios
584 (Scn4, Scn5 and Scn6) resulted in similar outputs which may indicate low sensitivity of
585 our model to changes on these drivers. Poor sensitivity indicates either low impacts of
586 these drivers on the modelled ecosystem (i.e. low fishing impact) or slight changes on
587 drivers during future simulations. One of the main hurdles was the inability to fit the model
588 due to the lack of specific time-series data that could affect the model application. This
589 caused high uncertainty for most projections results and could strongly influence the
590 intensity of biomass and ecological indicators changes. Despite this, we consider that
591 our approach included methods to minimize as much as possible the negative effects of
592 this limitation such as Monte Carlo routine. In addition, biomass predictions for most
593 functional groups are likely to be artifacts of sea water temperature which was highlighted
594 as the strongest driver in the study area. Another limitation was the lack of SBT
595 projections under scenarios of greenhouse emissions, which if available could make
596 future simulations more realistic in deep ecosystems. The model represents a deep
597 ecosystem ranging from 400-450 metres depth and we used similar rates of change
598 between reconstructed SST and SBT over time (Husum & Hald 2004). There is evidence
599 that the upper ocean (above 700 metres) is warming similarly with climate change (Llovel
600 et al. 2014). Despite the fact that predicting future deep-sea temperature changes is
601 difficult (Klemas & Yan 2014), SBT projections were estimated taking into account the
602 best available data. Additionally, new species could be incorporated into the food-web
603 due to their migration into the system because of increasing sea temperature and thus it
604 could represent a limitation on this study. These incoming species from southern areas,
605 in the hemisphere north, could forage and interact with other species and alter the food-
606 web (Blanchard 2015). A complete assessment of the spatiotemporal distribution of
607 species in the study area should be performed to complement the analysis of future
608 trajectories of change in order to include all species in the analysis. In addition, response
609 functions to sea temperature were included from *AquaMaps* a global database using
610 trapezoid shape (Kaschner et al. 2016), because we lacked specific response functions
611 in the study area. Local sea temperature response functions would improve predictions
612 under global warming scenarios, for example, alternative shapes and statistical models
613 are increasingly used in order to define environmental response functions (Coll et al.
614 2019; Serpetti 2019). Lastly, future analysis on the same ecosystem may include
615 mediating effects (Harvey 2014) to verify the potential effects of non-trophic relationships

616 between kelp POM and other marine species following previous findings (Vilas et al.
617 2020).

618 Regardless of these caveats, our results demonstrated the vulnerability of sub-Arctic
619 Arctic deep-sea ecosystems to stressors, especially to sea warming. This calls for
620 climate change mitigation, conservation and restoration of deep-sea ecosystems as well
621 as adjacent ecosystems such as coastal kelp forests. Conservation and restoration of
622 coastal kelp forest would ensure the maintenance of kelp POM inputs on adjacent deep-
623 sea ecosystems, increasing the resilience on deep-sea systems and alleviate the
624 negative effects of sea warming and species invasions.

625

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636

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899 **TABLES**

900

901 Table 1. Summary of drivers and scenarios for the ADEAKE model from 2017 to 2100.

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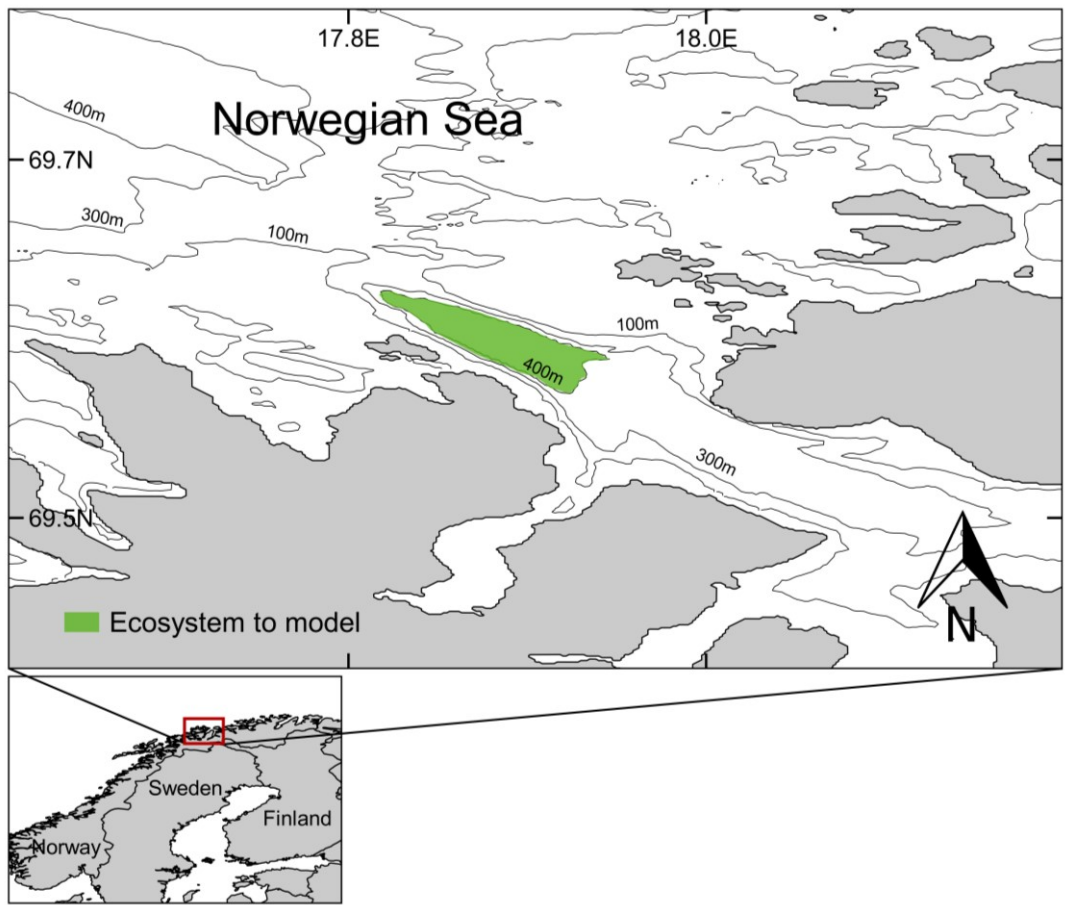
Scale	Driver/s	Scenario	Description
	Baseline	1	Constant fishing effort, constant kelp production, and constant temperature
Local	Fishing	2	Decreasing fishing effort (reducing 50% relative fishing effort)
		3	Increasing fishing effort (reducing 50% large benthic fish feeders' biomass)
Regional	Kelp POM production	4	50% decline of coarse and fine kelp biomass due to direct harvesting
		5	50% increase of coarse kelp POM biomass and 50% decline of fine kelp POM biomass due to decrease of sea urchins
		6	50% decline of coarse and fine kelp biomass due to increase of sea urchins
	Red king crab invasion	7	Invasion of the red king crab into the area
Global	Temperature	8	Moderate increasing of sea bottom temperature (scenario RCP4.5)
		9	Strong increasing of sea bottom temperature (scenario RCP8.5)

Cumulative

	Kelp POM production + red king crab invasion	10	Decreasing sea urchins and red king crab invasion (Scenario 5 + Scenario 7)
	Fishing + kelp POM production + temperature	11	Decreasing effort, decreasing sea urchins and RCP4.5 (Scenario 2 + Scenario 5 + Scenario 8) (Optimistic)
	Fishing + kelp POM production + red king crab invasion + temperature	12	Increasing fishing effort, increasing sea urchins, red king crab invasion and RCP8.5 (Scenario 3 + Scenario 6 + Scenario 7 + Scenario 9) (Pessimistic)

906

907 **FIGURES**



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909 Figure. 1. Study area located in Malangen fjord, northern Norway, and the Arctic deep
910 ecosystem associated with kelp exports (ADEAKE) (green polygon).

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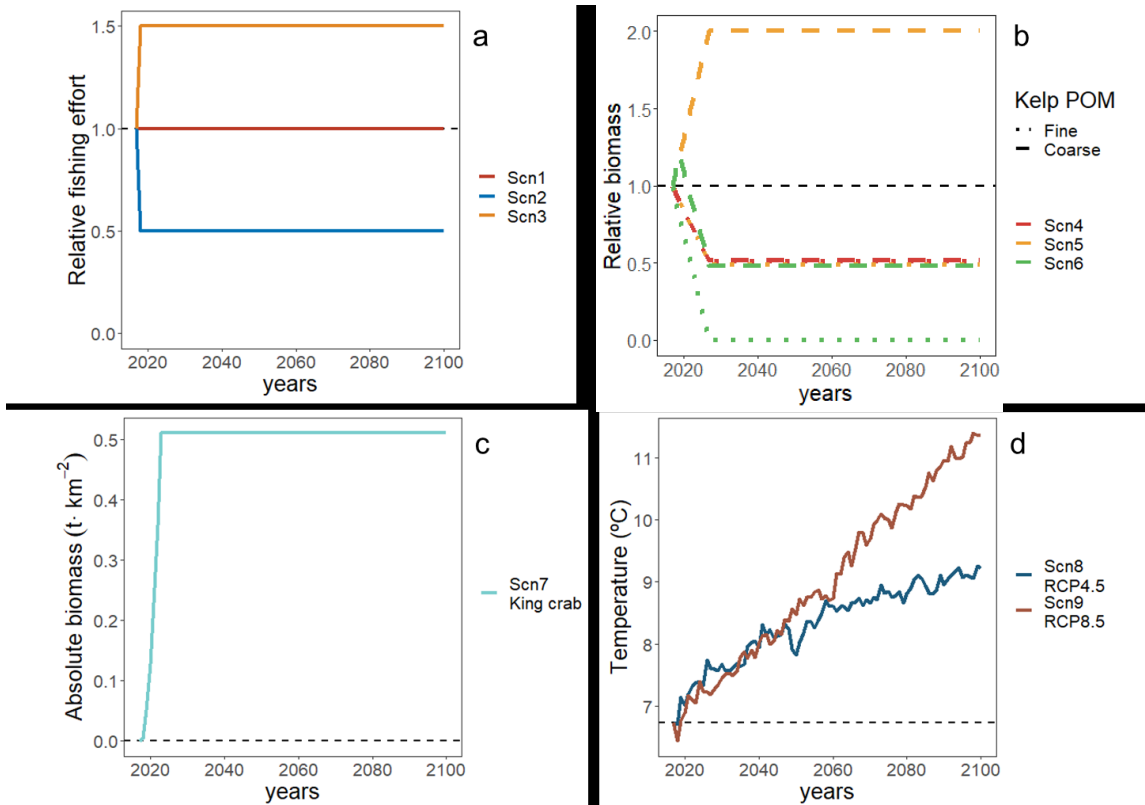
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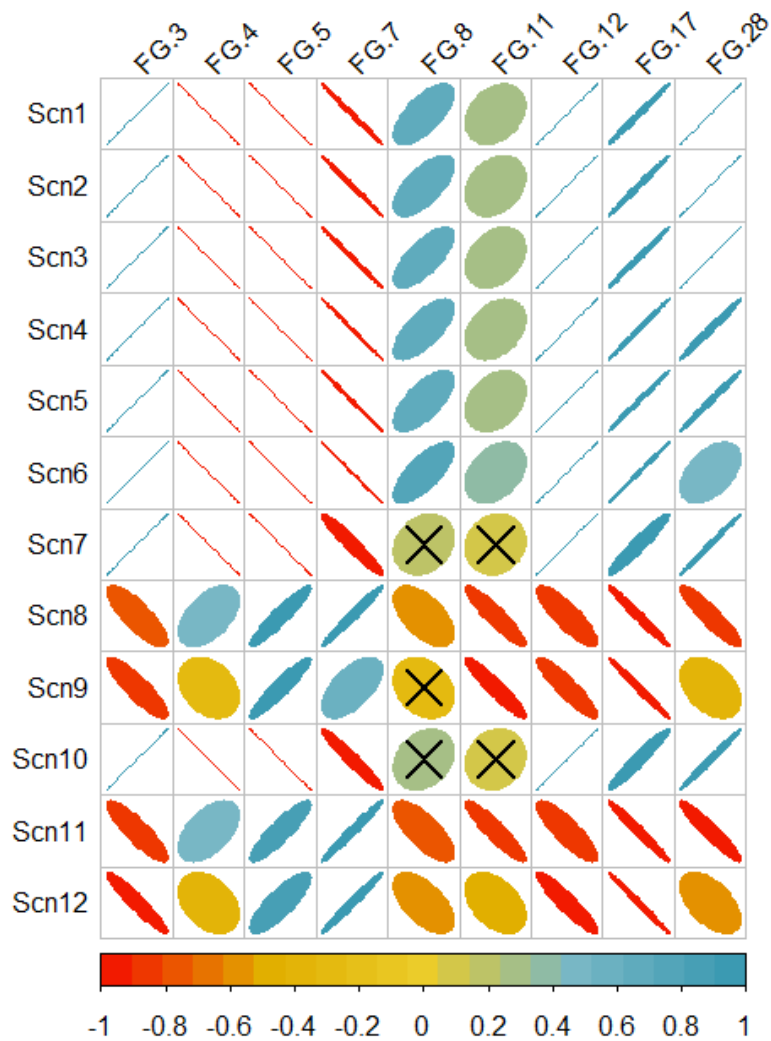
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924 Figure 2. Stressors in the ADEAKE model for the simulation period 2017-2100: (a)
 925 relative fishing effort; (b) fine and coarse kelp POM production; (c) invasive species in
 926 terms of absolute biomass (t·km⁻²) of king crab; and (d) annual sea bottom temperature
 927 (°C) under the two scenarios of IPCC projections.

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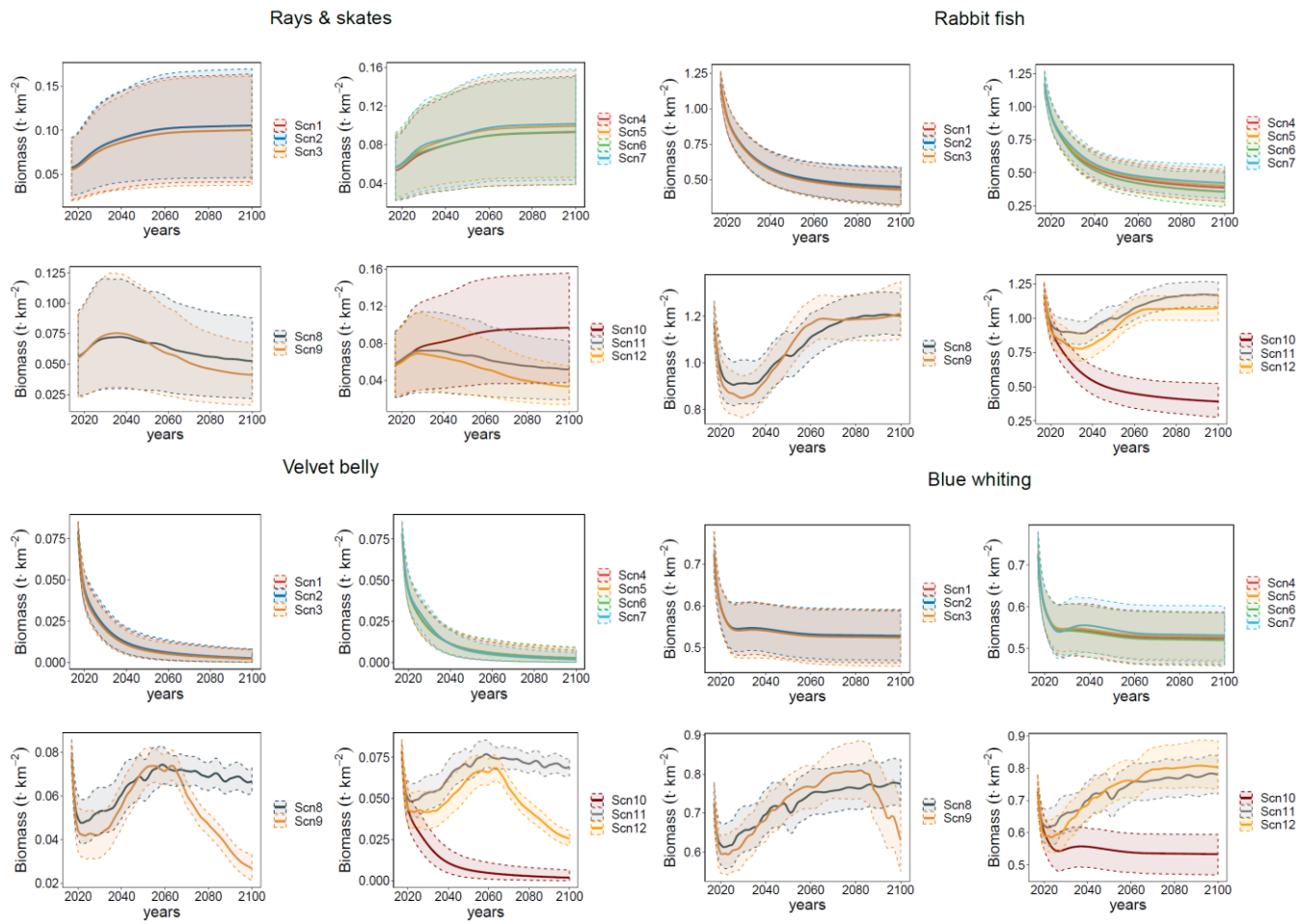


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930 Figure 3. Spearman's rank correlation between selected biomasses of functional groups
 931 (FG) and time for the 12 future scenarios (Table 1). Positive correlations are in blue and
 932 negative correlations in red. Legend colour shows the strength correlation coefficient
 933 (rho-value) and its corresponding colour gradient. Colour intensity and the size of the
 934 ellipses are proportional to the correlation coefficients, with more diffused and wider
 935 ellipses representing lower correlation strengths. When the indicator is non-significant
 936 (>0.01), it is represented with an "X" symbol (rho and p-values are included in suppl.
 937 material Table S2) (FG.3: rays and skates; FG.5: rabbit fish; FG.7: blue whiting; FG.8:
 938 large fish feeders; FG.11: other commercial demersal fishes; FG.12: redfishes; FG.17:
 939 benthopelagic shrimps; FG.28: suprabenthos.

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959 Figure 4. Predicted time series of mean absolute biomass (t·km⁻²) (solid line) for rays and skates, rabbit fish, velvet belly and blue whiting functional
960 groups under 12 future scenarios (Table 1). Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

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Large fish feeders

Other commercial demersal fishes

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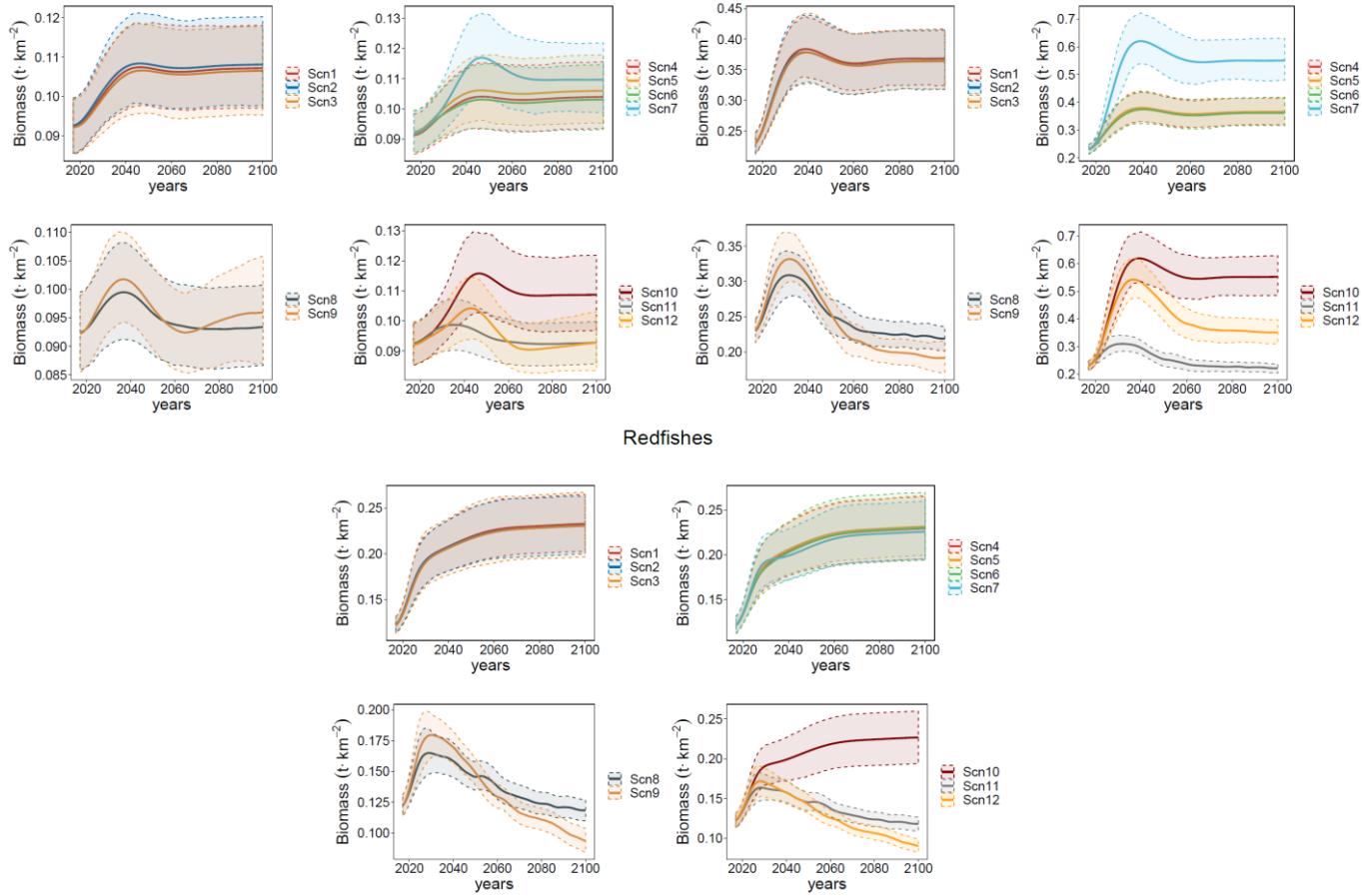
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Figure 5. Predicted time series of mean absolute biomass ($t \cdot km^{-2}$) (solid line) for large fish feeders, other commercial demersal fishes and redfishes' functional groups under 12 future scenarios (Table 1). Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

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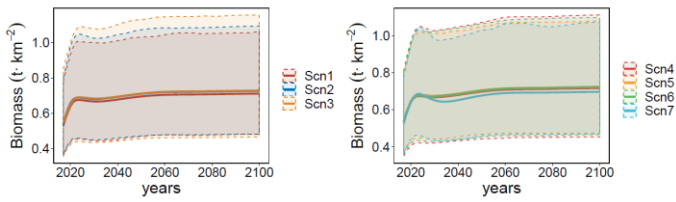
Benthopelagic shrimps

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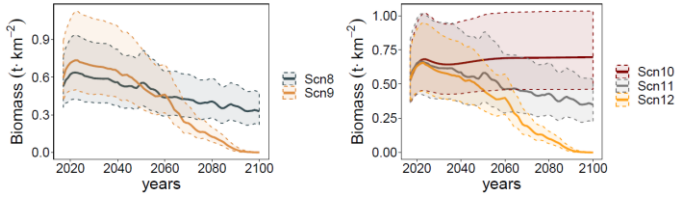


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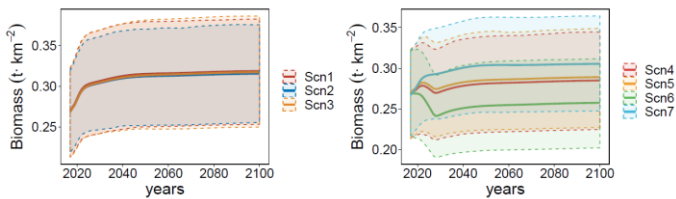
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Suprabenthos

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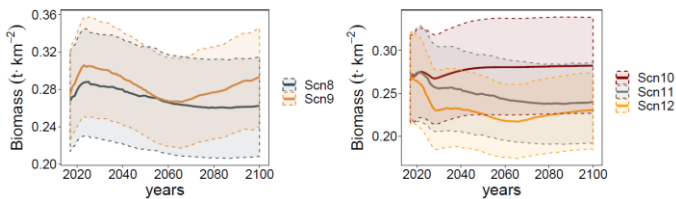


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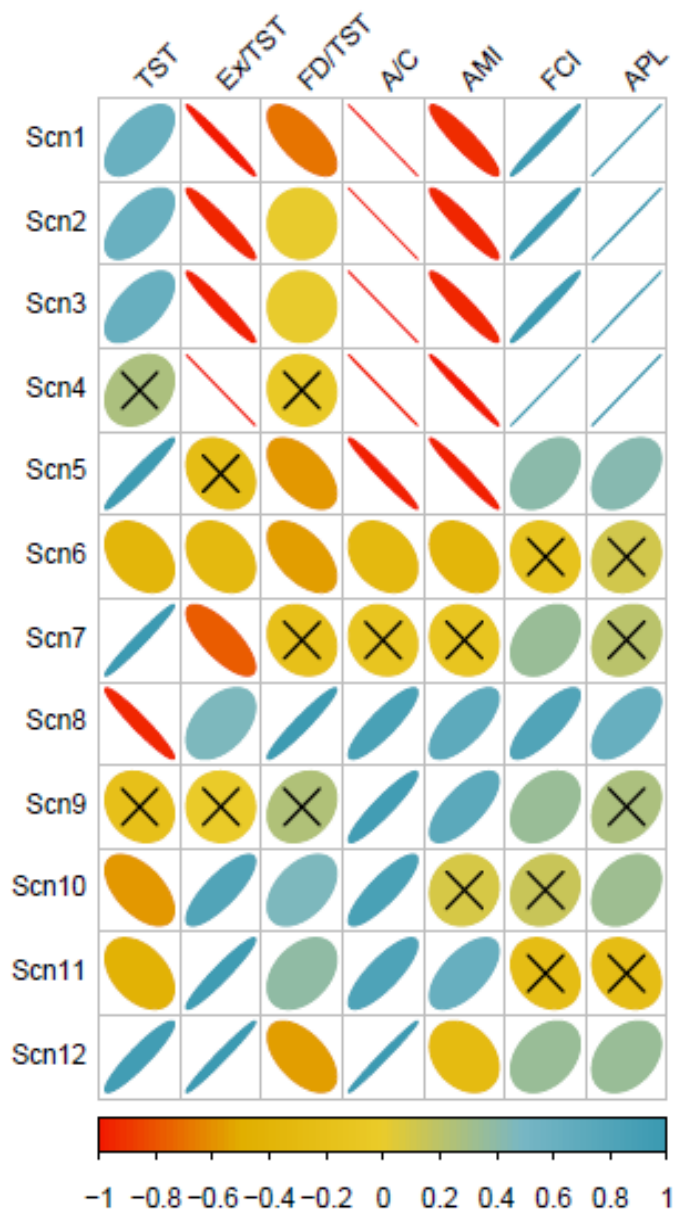
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999 Figure 6. Predicted time series of mean absolute biomass (t·km⁻²) (solid line) for
1000 benthopelagic shrimps and suprabenthos functional groups under 12 future scenarios
1001 (Table 1). Shadows represent the 5% and 95% percentiles obtained using the Monte
1002 Carlo routine.

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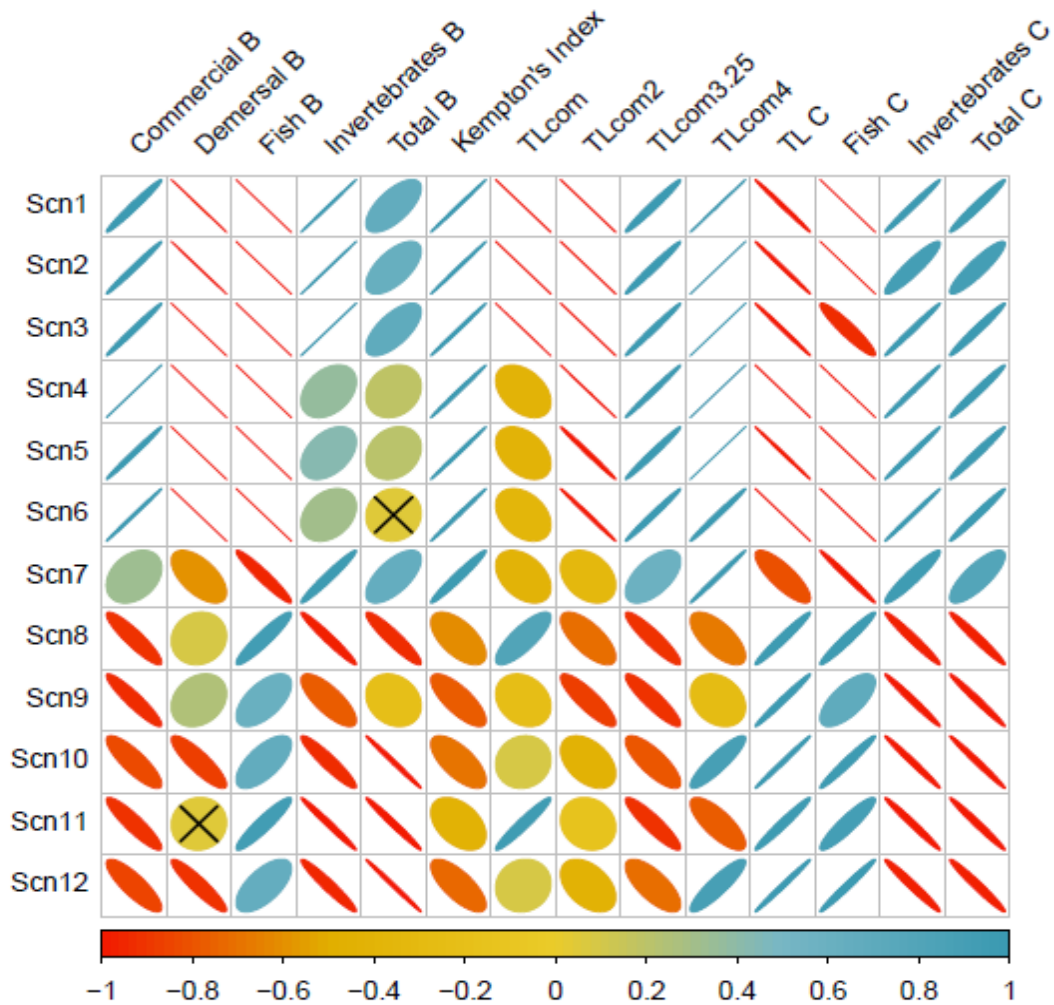


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1005 Figure 7. Spearman's rank correlation between selected ENA indicators and time for the
 1006 12 future scenarios (Table 1). Positive correlations are in blue and negative correlations
 1007 in red. Legend colour shows the strength correlation coefficient (rho-value) and its
 1008 correspondent colour gradient. Colour intensity and the size of the ellipses are
 1009 proportional to the correlation coefficients, with more diffused and wider ellipses
 1010 representing lower correlation strengths. When the indicator is non-significant (>0.01), it
 1011 is represented with an "X" symbol (rho and p-values are included in suppl. material Table
 1012 S3).

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1016 Figure 8. Spearman's rank correlation between selected ECOIND indicators and time for
 1017 the 12 future scenarios (Table 1). Positive correlations are in blue and negative
 1018 correlations in red. Legend colour shows the strength correlation coefficient (rho-value)
 1019 and its correspondent colour gradient. Colour intensity and the size of the ellipses are
 1020 proportional to the correlation coefficients, with more diffused and wider ellipses
 1021 representing lower correlation strengths. When the indicator is non-significant (>0.01), it
 1022 is represented with an "X" symbol (rho and p-values are included in suppl. material Table
 1023 S4).

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1032 Additional Supplementary material may be found in the online version of this article:

1033 **Appendix 1** Supplementary figures: Revised environmental preference functions of each
1034 functional group (Fig. S1).

1035 **Appendix 2** Supplementary tables: Confidence intervals used to describe the
1036 uncertainty for each functional group (FG) and each input parameter of the balanced
1037 Ecopath model (Table S1), Rho and p-values of Spearman correlation of FGs' biomass
1038 (Table S2), Ecological Network Analysis indicators (Table S3) and ECOIND indicators
1039 (Table S4) over time, unlagged cross-correlation validation of FGs' biomass (Table S5),
1040 Ecological Network Analysis indicators (Table S6) and ECOIND indicators (Table S7)
1041 over time.

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