Accepted Manuscript

This is the peer reviewed version of the following article:

Daniel Vilas, Marta Coll, Torstein Pedersen, Xavier Corrales, Karen Filbee-Dexter, Thomas Wernberg. 2021. Future trajectories of change for an Arctic deep-sea ecosystem connected to coastal kelp forests. Restoration Ecology. 29 (S2): e13327, which has been published in final form at https://doi.org/10.1111/rec.13327.

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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
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30 Author Contributions

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

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35 Abstract

Environmental stressors related to climate change and other anthropogenic activities 36 37 are impacting Arctic marine ecosystems at exceptional rates. Within this context, predicting future scenarios of deep-sea ecosystems and their consequences linked with 38 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 trajectories of change for major drivers in the area, including links to coastal kelp forests. 42 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 approach. Overall, we found that the impact of warming on the deep-sea ecosystem 46 47 structure and functioning, as well as on ecosystem services, are predicted to be greater than changes in kelp forest dynamics and their POM production entering the deep-sea 48 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.

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

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63 Implications for practice:

- Increasing temperature may cause high impacts at species level due to their
 thermal optimum ranges, triggering impacts at the ecosystem level.
- Ecological indicators showed the strongest impacts when increasing temperature
 was included in future predictions. These effects emphasize the vulnerability of
 Arctic marine ecosystems to climate change.
- Regime shifts in kelp organic matter production and a king crab invasion may
 produce more reduced but noticeable impacts at the deep-sea ecosystem level.
- In addition to temperature, considering additional stressors affecting deep-sea
 communities such as changes in kelp forest from coastal areas are important to
 predict cumulative impacts of the deep sea in an ecosystem-based management
 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 al. 2011; Sweetman et al. 2017; Danovaro et al. 2017). The 20 years of warmer 80 81 temperatures at the beginning of the twenty-first century have affected the phenology of organisms, the range, and distribution of species, and the composition and dynamics of 82 communities (Smale et al. 2019). Under this context, predicting future scenarios and their 83 84 consequences, and providing effective tools to policymakers, is a growing need and 85 challenge. To respond to current global climate challenges, beneficial management strategies must be carried out such as increasing connectivity to ensure resilience to 86 87 climate change (e.g. through the maintenance and increase of the area of high-quality habitats), the conservation of areas that have high environmental heterogeneity, the 88 control of other anthropogenic threatening processes and ecological restoration (Gann 89 et al. 2019). 90

Worldwide, numerous ecosystems are at risk of severe impacts. Warming events are predicted to be exaggerated in the Arctic, which is undergoing the most rapid change in climate (IPCC 2018), which may increase instances of storm surge or extreme weather (Cohen et al. 2020). Several studies have examined and assessed the impacts on ecosystem services caused by climate change in Arctic systems and highlighted the need for a better understanding of these impacts to reduce the risk of marine regime shifts (Rocha et al. 2015; Wernberg et al. 2019; Merzouk & Johnson 2011). Arctic fjords may be particularly vulnerable to climate change because sea surface temperature is
expected to increase faster in Arctic ecosystems than other ecosystems (IPCC 2018).
Environmental changes are impacting the condition and distributions of Arctic species
and ousting them from current food-webs (Frainer et al. 2017).

102 Kelp forests are phyletically diverse, structurally complex, and highly productive 103 ecosystems of cold-water rocky marine coastlines (Wernberg et al. 2019). Particularly, Laminaria hyperborea, which forms extensive kelp forests in the northeastern Atlantic, 104 105 has a very high annual production 500 - 2,000 g C · m⁻² · 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 conditions remains a challenge (Filbee-Dexter et al. 2018). Climate change is expected 113 114 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 Restoration International Science & Policy Working Group 2004) and it is globally 128 129 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

range of stakeholders and using available scientific and local knowledge to achieve 134 135 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, when involving stakeholders (e.g. fishermen and local community) (Fujita 2011). 139 140 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 organisms such as marine mammals, crustaceans, echinoderms, fish, and algae 146 147 (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-Jensen et al. 2018; Filbee-Dexter & Wernberg in press). In addition, kelp forests are 149 150 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). Understanding how these multiple stressors, marine organisms, and ecosystems 158 159 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,

such as climate change, in an ecosystem-based management approach. In this study, 169 170 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

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179 Material and methods

180 - Study area

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

190 - Modelling approach

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

The existing EwE model represents an annual average situation in 2017, ranging from 400 to 450 meters depth and covering an area of 11.8 km² (Vilas et al. 2020). The Ecopath model was developed using Ecopath version 6.6, and it consisted of 36 functional groups (FGs) with special emphasis on kelp POM because the model was built to assess the ecological role of kelp export into the deep-sea system. Two out of four detritus groups (marine snow, coarse kelp POM, fine kelp POM, and benthic detritus) represented the kelp secondary production. A functional group consists of ontogenic fractions of a species, individual species, or groups of species that perform a
similar function in the ecosystem, i.e. have similar growth rates, consumption rates, diets,
habitats, and predators (Heymans et al. 2016).

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

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

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210 where dB/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 'foraging arena' theory, which divides the biomass of prey into a vulnerable and a non-214 vulnerable fraction and the transfer rate of vulnerability between the two fractions 215 determines the trophic flow between the predator and the prey (Ahrens et al. 2012). The 216 vulnerability concept incorporates density-dependent processes and expresses how far 217 218 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:

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

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

The environmental response functions ($f(Env_{function},t)$), which link the species or FGs dynamics with the environmental drivers, were first obtained from *AquaMaps* (Kesner-Reyes et al. 2016), a global database on species distribution. These environmental response functions are given as curves showing the minimum and maximum tolerance levels and 10th and 90th preferable quantiles to the environmental parameters (in our case, temperature). As a second step, these functions were modified using expert
 opinion from scientists to incorporate local knowledge. The final environmental
 preference functions for each FG (Fig. S1.1) were obtained by weighting the values of
 the species included in a FG to their relative biomass.

- 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 (2017-2100) (Table 1). Future scenarios were simulated without fitting the model to data due to 241 242 the lack of specific time-series data and consequently, vulnerabilities could not be estimated as recommended (Christensen et al. 2008). Similar to previous temporal 243 244 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 considering the knowledge of a group of regional experts (Table 1). 249

In the first scenario (Scn1) fishing effort, kelp POM production and sea water temperature were kept constant from 2017, which was the year for the Ecopath baseline model (Vilas et al. 2020). Fishing effort was modified in the second and third scenarios: the relative fishing effort was reduced to 50% for both operating fleets (gillnetters and shrimp trawlers) (Scn2), or increased 50% on gillnetters (Scn3) in order to reduce large fish feeders group biomass while keeping constant kelp POM production and 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 rising activity in northern Norway (Stévant et al. 2017), and both kelp POM groups were 260 forced to decrease their biomass by 50% (Fig. 2b). The second and third regional 261 262 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 keeping constant fishing and temperature and without the invasion of the red king crab. 268

In contrast, Scn6 reflected a regime shift to barrens caused by an increase in sea urchins 269 270 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 ADEAKE model with very small biomass and then it was forced to increase in the model 276 277 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 extract the trend of these projections. SST projections under two contrasting scenarios 284 285 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 that rates of increasing SST are equal for SBT. The scenarios conducted to simulate 291 potential impacts of ocean warming were RCP4.5 (Scn8) and RCP8.5 (Scn9), and they 292 293 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 projection of SST – RCP8.5 (Scn9). 304

- 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 structuring importance in the deep-ecosystem and/or vulnerability under future scenarios 308 309 (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 System Throughput (TST, t km⁻² year⁻¹), export (Ex/TST), flow to detritus (FD/TST), the 319 relative Ascendancy (A/C), the average mutual information (AMI), Finn's Cycling Index 320 321 (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 (Christensen 1995) so it decreases after being impacted. The AMI indicates the 326 327 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). We focused on biomass-based indicators, trophic-based and catch-based indicators. 334 335 Biomass-based indicators are based on the abundance of organisms in the food-web and we considered: biomass of commercial species, biomass of invertebrates' species, 336 337 biomass of fish species, and the Kempton's diversity index. Next, four trophic-based indicators four indicators were selected based on the tropic level (TL): TL of the 338 community (TLcom), TL of the community including organisms with TL \geq 2 (TLcom2), TL 339

of the community including organisms with $TL \ge 3.25$ (TLcom3.25) and TL of the community including organisms with $TL \ge 4$ (TLcom4). We also selected 4 catch-based indicators: TL of the catch (TL C), fish catch (Fish C), invertebrates catch (Invertebrates C) and total catch (Total C).

- Assessing uncertainty

345 Temporal dynamic simulations require quantifying uncertainties inherent in the 346 simulations in order to facilitate decision-making. We performed an uncertainty assessment based on the pedigree values that describe the origin and uncertainty of 347 348 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 uniform distributions, with the width of distributions corresponding to the pedigree-355 356 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 with time and its strength were measured using the nonparametric Spearman correlation 361 362 (Spearman 1904). Additionally, changes of model outputs with time were checked using unlagged cross-correlation analysis (Venables & Ripley 2013). 363

364

365 **Results**

366 Baseline Scenario – Scn1

Under the baseline simulation (Scn1) in which fishing effort, kelp POM production, and sea water temperature were kept constant from 2017, the Ecosim model predicted changes in biomass trends for several FGs. This is due to the addition of the temperature effects to the baseline mass-balance model and the sensitivity of different species to the temperature range that was introduced when we moved to the temporal model. This impact of sub-optimal temperatures in the consumption rates of some FGs had cascading effects through the food web. For example, velvet belly was negatively impacted by a sub-optimal temperature condition and this caused predation release on
benthopelagic shrimps and suprabenthos, which biomass increased. In any case, we
perform a relative comparison of scenarios to the baseline, thus this initial change is not
affecting the comparison.

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

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

Fishing scenarios – Scn2 and Scn3

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

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

Under scenarios with changes in kelp POM import, model results delivered similar
biomass trends for most functional groups (Fig. 3, 4, 5, and 6) except for suprabenthos,
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).

Similar to the baseline scenario, ECOIND indicators showed an increasing trend for 408 409 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** – *Scn*7

Applying the king crab scenario (Scn7), the model predicted an increasing trend for rays and skates, redfishes, benthopelagic shrimps, and suprabenthos, while it predicted a decreasing trend for velvet belly, rabbit fish, and blue whiting (Fig. 3, 4, 5 and 6). Despite the similarity with the baseline scenario on FG biomass trend, changes in blue 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, AMI, 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 Total C was observed, while Demersal B, Fish B, TL community, TL community 2, TL C 426 and Fish C decreased over time (Fig. 8). Despite ECOIND indicators showed the same 427 trends compared with the baseline scenario, most of these indicators responded weaker 428 429 over time (Fig. 8).

430 Impacts of ocean warming scenarios – Scn8 and Scn9

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

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

showed similar trends for these indicators, except for TLcom which decreased under thisscenario.

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

In Scn10 biomass of velvet belly, rabbit fish and blue whiting decreased, while
increased on rays and skates, redfishes, benthopelagic shrimps, and suprabenthos (Fig.
3, 4, 5, and 6). On the contrary, Scn11 showed opposite biomass trends similarly to
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 decreased, while Ex/TST, FD/TST, A/C, and AMI increased. Scn12 showed increasing 451 trends for TST, Ex/TST, A/C, FCI, and APL, and decreasing trends for FD/TST and AMI 452 (Fig. 7). Ecological indicators obtained similar predicted trends under Scn10 and 12 (Fig. 453 8). Both of them showed increasing trends for Fish B, TLcom, TL C, and Fish C, while 454 455 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**

In general, scenarios that included temperature increasing (Scn8, Scn9, Scn11, and 461 Scn12) showed opposite biomass trends in most functional groups compared to the 462 baseline scenario (Fig. 3). The rest of the scenarios (fishing effort, kelp POM production, 463 464 and king crab invasion scenarios) showed similar biomass trends of most functional groups compared to the baseline (Fig. 3). Most scenarios showed increasing trends for 465 466 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

Under the baseline scenario, most functional groups increased in biomass, including all commercial functional groups, while important FGs in terms of biomass decreased (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).

Overall, the fishing scenarios did not show noticeable impacts at species levels nor at ecosystem level. These results likely reflect the sustainability of current fishing activities and their moderate impact in this study area, which has also been pointed out in adjacent areas (Pedersen et al. 2016). A general study carried out in EU waters (Froese et al. 2018) identified the Norwegian Sea and the Barents Sea as the European 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 suprabenthos under Scn6 showed an opposite trend compared to the baseline scenario, 488 with lower biomass correlation results. Small crustaceans are considered one of the most 489 490 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, functioning, and resilience. This finding is especially interesting given the ubiquitous 500 501 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.

Local and regional stressors (fishing effort, kelp POM production, and invasive species) have been previously highlighted as potentially important for impacting at species and ecosystem level (Pedersen et al. 2018; Ramirez-Llodra et al. 2016). However, this study showed that these changes may have limited impacts in the ADEAKE at their modelled level in comparison with the global stressors (ocean 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 (Fossheim 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 it could be explained by trophic interactions processes like predation or competition 533 534 (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-Arenas 1997) under global warming scenarios, which is in line with the decreasing trend 538 539 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

production. Scn10 results suggested that the synergic effect of king crab and change on 544 545 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 correlations over time compared to the warming scenario (Scn9). This scenario 558 559 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 shows that what may happen in coastal areas, in this case in kelp beds, can have an 569 570 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.

Performing future simulations in ecology is considered an arduous task, especially 579 580 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 these drivers on the modelled ecosystem (i.e. low fishing impact) or slight changes on 586 587 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 intensity of biomass and ecological indicators changes. Despite this, we consider that 590 591 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 functional groups are likely to be artifacts of sea water temperature which was highlighted 593 594 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 species in the study area should be performed to complement the analysis of future 607 608 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 trapezoid shape (Kaschner et al. 2016), because we lacked specific response functions 610 611 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

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

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

625

626 Acknowledgments

627 This work was funded by the Norwegian Research Council through the KELPEX project (NRC Grant no. 255085/E40). The authors wish to acknowledge Morten Foldager 628 629 Pedersen, Kjell Magnus Norderhaug, Stein Fredriksen, and Eva Ramírez-Llodra for their helpful comments. We want to thank Nina Mikkelsen, Emma Källgren, Freija Hauquier, 630 Margo Van Gyseghem, and Ann Vanreusel for their help during the scientific survey 631 where the input data of the food-web model come from. Also, the authors want to thank 632 633 the crew of the R/V Johan Ruud. MC acknowledges partial funding by the European 634 Union's Horizon research program grant agreement No 689518 for the MERCES project. 635 This research is part of POLARCSIC activities.

637 **References**

638	Ahrens RNM, Walters CJ, Christensen V (2012) Foraging arena theory. Fish
639	and fisheries 13:41–59

- Aronson J, Alexander S (2013) Ecosystem restoration is now a global priority:
 Time to roll up our sleeves. Restoration Ecology 21:293–296
- Aschan M, Fossheim M, Greenacre M, Primicerio R (2013) Change in Fish
 Community Structure in the Barents Sea. PLoS ONE 8:e62748
- Assis J, Araújo MB, Serrão EA (2018) Projected climate changes threaten
 ancient refugia of kelp forests in the North Atlantic. Global change biology
 24:e55--e66
- Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic
 predator abundances. Journal of Animal Ecology 78:699–714
- Bekkby T, Papadopoulou N, Fiorentino D, McOwen CJ, Rinde E, Boström C, et
 al. (2020) Habitat Features and Their Influence on the Restoration Potential
 of Marine Habitats in Europe. Frontiers in Marine Science 7:184
- Bentley JW, Serpetti N, Heymans JJ (2017) Investigating the potential impacts
 of ocean warming on the Norwegian and Barents Seas ecosystem using a
 time-dynamic food-web model. Ecological Modelling 360:94–107
- Blanchard JL (2015) Climate change: A rewired food web. Nature 527:173–174
- Christensen V (1995) Ecosystem maturity towards quantification. Ecological
 Modelling 77:3–32
- 658 Christensen V, Coll M, Steenbeek J, Buszowski J, Chagaris D, Walters CJ
- (2014) Representing variable habitat quality in a spatial food web model.
 Ecosystems 17:1397–1412
- Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities
 and limitations. Ecological Modelling 172:109–139
- Christensen V, Walters CJ, Pauly D, Forrest R (2008) Ecopath with Ecosim
 version 6: user guide. November 2008. Fisheries Centre, University of
 British Columbia, Vancouver, Canada 235

666	Christiansen JS, Sparboe M, Sæther B-S, Siikavuopio SI (2015) Thermal
667	behaviour and the prospect spread of an invasive benthic top predator onto
668	the Euro-Arctic shelves. Diversity and Distributions 21:1004–1013
669	Cohen J, Zhang X, Francis J, Jung T, Kwok R, Overland J, et al. (2020)
670	Divergent consensuses on Arctic amplification influence on midlatitude
671	severe winter weather. Nature Climate Change 1–10
672	Coleman MA, Wood G, Filbee-Dexter K, Minne AJP, Goold HD, Vergés A, et al.
673	(2020) Restore or redefine: future trajectories for restoration. Frontiers in
674	Marine Science 7:237
675	Coll M, Pennino MG, Steenbeek J, Sole J, Bellido JM (2019) Predicting marine
676	species distributions: Complementarity of food-web and Bayesian
677	hierarchical modelling approaches. Ecological Modelling 405:86–101
678	Coll M, Steenbeek J (2017) Standardized ecological indicators to assess
679	aquatic food webs: The ECOIND software plug-in for Ecopath with Ecosim
680	models. Environmental Modelling & Software 89:120–130
681 682 683	Colléter M, Valls A, Guitton J, Gascuel D, Pauly D, Christensen V (2015) Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. Ecological Modelling 302:42–53
684	Corrales X, Coll M, Ofir E, Heymans JJ, Steenbeek J, Goren M, et al. (2018)
685	Future scenarios of marine resources and ecosystem conditions in the
686	Eastern Mediterranean under the impacts of fishing, alien species and sea
687	warming. Scientific reports 8:1–16
688	Danovaro R, Corinaldesi C, Dell'Anno A, Snelgrove PVR (2017) The deep-sea
689	under global change. Current Biology 27:R461–R465
690 691	Dietze M, Lynch H (2019) Forecasting a bright future for ecology. Frontiers in Ecology and the Environment 17:1–3
692	Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N (2013) The role of
693	coastal plant communities for climate change mitigation and adaptation.
694	Nature Climate Change 3:961–968
695	Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal

- (Laminaria solidungula) carbon in an arctic kelp community: δ13C
 evidence. Marine Biology 93:615–625
- Eger AM, Marzinelli E, Gribben P, Johnson CR, Layton C, Steinberg PD, et al.
 (2020) Playing to the Positives: Using Synergies to Enhance Kelp Forest
 Restoration . Frontiers in Marine Science 7:544
- Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable
 states of collapsed kelp ecosystems. Marine ecology progress series
 495:1–25
- Filbee-Dexter K, Wernberg T (2018) Rise of turfs: A new battlefront for globally
 declining kelp forests. BioScience 68:64–76
- Filbee-Dexter K, Wernberg T Substantial blue carbon in overlooked Australian
 kelp forests. Scientific Reports
- Filbee-Dexter K, Wernberg T, Fredriksen S, Norderhaug KM, Pedersen MF
 (2019) Arctic kelp forests: Diversity, resilience and future. Global and
 Planetary Change 172:1–14
- 711 Filbee-Dexter K, Wernberg T, Norderhaug KM, Ramirez-Llodra E, Pedersen MF
- 712 (2018) Movement of pulsed resource subsidies from kelp forests to deep
- 713 fjords. Oecologia 187:291–304
- Finn JT (1976) Measures of ecosystem structure and function derived from
 analysis of flows. Journal of theoretical Biology 56:363–380
- Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov
- A V. (2015) Recent warming leads to a rapid borealization of fish
- communities in the Arctic. Nature Climate Change 5:673–677
- 719 Frainer A, Primicerio R, Kortsch S, Aune M, Dolgov A V, Fossheim M, et al.
- 720 (2017) Climate-driven changes in functional biogeography of Arctic marine
- fish communities. Proceedings of the National Academy of Sciences114:12202–12207
- Fredriksen S, Filbee-Dexter K, Norderhaug KM, Steen H, Bodvin T, Coleman
 MA, et al. (2020) Green gravel: a novel restoration tool to combat kelp
 forest decline. Scientific Reports 10:1–7

Free CM, Thorson JT, Pinsky ML, Oken KL, Wiedenmann J, Jensen OP (2019)
Impacts of historical warming on marine fisheries production. Science
363:979–983

Frisk MG, Miller TJ, Latour RJ, Martell SJD (2011) Assessing biomass gains
 from marsh restoration in Delaware Bay using Ecopath with Ecosim.
 Ecological Modelling 222:190–200

Froese R, Winker H, Coro G, Demirel N, Tsikliras AC, Dimarchopoulou D, et al.
(2018) Status and rebuilding of European fisheries. Marine Policy 93:159–
170

Fuhrmann MM, Pedersen T, Nilssen EM (2017) Trophic niche of the invasive
red king crab Paralithodes camtschaticus in a benthic food web. Marine
Ecology Progress Series 565:113–129

Fujita D (2011) Management of kelp ecosystem in Japan. CBM-Cahiers de
Biologie Marine 52:499

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al.

(2019) International principles and standards for the practice of ecological
 restoration. Restoration Ecology 27:S1–S46

Halpern BS, Frazier M, Potapenko J, Casey KS, Koenig K, Longo C, et al.

(2015) Spatial and temporal changes in cumulative human impacts on the
 world's ocean. Nature Communications 6:1–7

Harvey CJ (2014) Mediation functions in Ecopath with Ecosim: handle with
 care. Canadian journal of fisheries and aquatic sciences 71:1020–1029

Haug T, Bogstad B, Chierici M, Gjøsæter H, Hallfredsson EH, Høines ÅS, et al.

(2017) Future harvest of living resources in the Arctic Ocean north of the

750 Nordic and Barents Seas: A review of possibilities and constraints.

751 Fisheries Research 188:38–57

752 Heymans JJ, Coll M, Link JS, Mackinson S, Steenbeek J, Walters C, et al.

753 (2016) Best practice in Ecopath with Ecosim food-web models for

ecosystem-based management. Ecological Modelling 331:173–184

Hobbs RJ, Harris JA (2001) Restoration ecology: Repairing the earth's

756	ecosystems in the new millennium. Restoration Ecology 9:239–246				
757	Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change,				
758	connectivity and conservation decision making: back to basics. Journal of				
759	Applied Ecology 46:964–969				
760	Husum K, Hald M (2004) A continuous marine record 8000-1600 cal. yr BP from				
761	the Malangenfjord, north Norway: Foraminiferal and isotopic evidence. The				
762	Holocene 14:877–887				
763	IPCC (2018) Global warming of 1.5°C. An IPCC Special Report on the impacts				
764	of global warming of 1.5°C above pre-industrial levels and related global				
765	greenhouse gas emission pathways, in the context of strengthening the				
766	global response to the threat of climate change.				
767	Jørgensen LL, Nilssen EM (2011) The invasive history, impact and				
768	management of the red king crab Paralithodes camtschaticus off the coast				
769	of Norway. In: In the Wrong Place-Alien Marine Crustaceans: Distribution,				
770	Biology and Impacts. Springer pp. 521–536.				
771	Kaschner K, Kesner-Reyes K, Garilao C, Rius-Barile J, Rees T, Froese R				
772	(2016) AquaMaps: Predicted range maps for aquatic species. World wide				
773	web electronic publication, www.aquamaps.org, Version 08/2016.				
774 775 776 777	 Kesner-Reyes K, Kaschner K, Kullander S, Garilao C, Barile J, Froese R (2016) AquaMaps: algorithm and data sources for aquatic organisms. In: 2012. FishBase. World Wide Web electronic publication. www.fishbase.org, version (04/2012). 				
778	Klemas V, Yan XH (2014) Subsurface and deeper ocean remote sensing from				
779	satellites: An overview and new results. Progress in Oceanography 122:1–				
780	9				
781	Kortsch S, Primicerio R, Fossheim M, Dolgov A V, Aschan M (2015) Climate				
782	change alters the structure of arctic marine food webs due to poleward				
783	shifts of boreal generalists. Proc. R. Soc. B 282:20151546				
784	Krause-Jensen D, Lavery P, Serrano O, Marbà N, Masque P, Duarte CM, et al.				
785	(2018) Sequestration of macroalgal carbon: the elephant in the Blue				

- Carbon room. Biology Letters 14:20180236
- 787 Krause-Jensen D, Duarte CM (2016) Substantial role of macroalgae in marine
 788 carbon sequestration. Nature Geoscience 9:737
- Layton C, Coleman MA, Marzinelli EM, Steinberg PD, Swearer SE, Vergés A, et
 al. (2020) Kelp Forest Restoration in Australia. Frontiers in Marine Science
- 791 7:74
- Leslie HM, McLeod KL (2007) Confronting the challenges of implementing
 marine ecosystem-based management. Frontiers in Ecology and the
 Environment 5:540–548
- Llovel W, Willis JK, Landerer FW, Fukumori I (2014) Deep-ocean contribution to
 sea level and energy budget not detectable over the past decade. Nature
 Climate Change 4:1031–1035
- 798 Mankettikkara R (2013) Hydrophysical characteristics of the northern
- Norwegian coast and fjords. PhD thesis, University of Tromsø, Tromsø.
- Merzouk A, Johnson LE (2011) Kelp distribution in the northwest Atlantic Ocean
 under a changing climate. Journal of Experimental Marine Biology and
 Ecology 400:90–98
- 803 Morris Rebecca L, Hale R, Strain EMA, Reeves SE, Vergés A, Marzinelli EM, et
- al. (2020) Key Principles for Managing Recovery of Kelp Forests through
 Restoration. BioScience 70:688–698
- Morris Rebecca L., Graham TDJ, Kelvin J, Ghisalberti M, Swearer SE (2020)
 Kelp beds as coastal protection: Wave attenuation of Ecklonia radiata in a
 shallow coastal bay. Annals of Botany 125:235–246
- 809 Oug E, Sundet JH, Cochrane SKJ (2018) Structural and functional changes of
- soft-bottom ecosystems in northern fjords invaded by the red king crab
- 811 (Paralithodes camtschaticus). Journal of Marine Systems 180:255–264
- Pedersen MF, Filbee-Dexter K, Norderhaug KM, Fredriksen S, Frisk NL, Fagerli
 CW, et al. (2019) Detrital carbon production and export in high latitude kelp
 forests. Oecologia 192:227–239

- Pedersen T, Fuhrmann MM, Lindstrøm U, Nilssen EM, Ivarjord T, Ramasco V,
 et al. (2018) Effects of the invasive red king crab on food web structure and
 ecosystem properties in an Atlantic fjord. Marine Ecology Progress Series
 596:13–31
- Pedersen T, Ramsvatn S, Nilssen EM, Nilsen M, Morissette L, Ivarjord T, et al.
 (2016) Species diversity affects ecosystem structure and mass flows in
 fjords. Regional Studies in Marine Science 3:205–215
- Poloczanska ES, Burrows MT, Brown CJ, Molinos JG, Halpern BS, HoeghGuldberg O, et al. (2016) Responses of marine organisms to climate
 change across oceans. Frontiers in Marine Science 3:3–62
- Ramirez-Llodra E, Rinde E, Gundersen H, Christie H, Fagerli CW, Fredriksen S,
 et al. (2016) A snap shot of the short-term response of crustaceans to
 macrophyte detritus in the deep Oslofjord. Scientific reports 6:23800
- Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, Escobar E, et
 al. (2011) Man and the last great wilderness: human impact on the deep
 sea. PLoS One 6:e22588
- Rocha J, Yletyinen J, Biggs R, Blenckner T, Peterson G (2015) Marine regime
 shifts: drivers and impacts on ecosystems services. Phil. Trans. R. Soc. B
 370:20130273
- Serpetti N (2019) Ecosystem impacts of cumulative effects from climate and
 fisheries. Lecture presented December 5th in Ecopath 35 years
 conference.
- 837 Serpetti N, Baudron AR, Burrows MT, Payne BL, Helaouet P, Fernandes PG, et
 838 al. (2017) Impact of ocean warming on sustainable fisheries management
- informs the Ecosystem Approach to Fisheries. Scientific reports 7:1–15
- Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control
 of community structure on temperate reefs. Oecologia 132:131–142
- 842 Skants KD (2019) Species composition, distribution and ecology of the
- demersal fish community along the Norwegian coast north of Stad under
- varying environmental conditions. The University of Bergen

Smale DA, Wernberg T, Oliver ECJ, Thomsen M, Harvey BP, Straub SC, et al. 845 (2019) Marine heatwaves threaten global biodiversity and the provision of 846 ecosystem services. Nature Climate Change 9:306-312 847 848 Society for Ecological Restoration International Science & Policy Working 849 Group (2004) The SER International Primer on Ecological Restoration. 850 Spearman C (1904) The proof and measurement of association between two 851 things. American journal of Psychology 15:72–101 Steenbeek J, Corrales X, Platts M, Coll M (2018) Ecosampler: A new approach 852 to assessing parameter uncertainty in Ecopath with Ecosim. SoftwareX 853 854 7:198-204 Steneck RS, Graham MH, Bourgue BJ, Corbett D, Erlandson JM, Estes JA, et 855 856 al. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental conservation 29:436-459 857 858 Stévant P, Rebours C, Chapman A (2017) Seaweed aquaculture in Norway: recent industrial developments and future perspectives. Aquaculture 859 International 25:1373–1390 860 861 Sweetman A, Thurber A, Smith C, Levin L, Mora C, Wei C-L, et al. (2017) Major impacts of climate change on deep-sea benthic ecosystems. Elem Sci Anth 862 5:4 863 Timpane-Padgham BL, Beechie T, Klinger T (2017) A systematic review of 864 ecological attributes that confer resilience to climate change in 865 environmental restoration. PLOS ONE 12:e0173812 866 Ulanowicz RE (2004) Quantitative methods for ecological network analysis. 867 Computational Biology and Chemistry 28:321-339 868 Ulanowicz RE, Abarca-Arenas LG (1997) An informational synthesis of 869 ecosystem structure and function. Ecological Modelling 95:1-10 870 Vea J, Ask E (2011) Creating a sustainable commercial harvest of Laminaria 871 hyperborea, in Norway. Journal of Applied Phycology 23:489–494 872 873 Venables WN, Ripley BD (2013) Modern applied statistics with S-PLUS.

- 874 Springer Science & Business Media
- Vergés A, McCosker E, Mayer-Pinto M, Coleman MA, Wernberg T, Ainsworth T, et al. (2019) Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. Functional Ecology 33:1000-1013 Vilas D, Coll M, Pedersen T, Corrales X, Filbee-Dexter K, Pedersen MF, et al. (2020) Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role in maintaining ecosystem structural and functional traits. Journal of Marine Systems 203:103268 Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2019) Status and trends for the world's kelp forests. In: World Seas: an Environmental Evaluation. Elsevier pp. 57–78. **TABLES** Table 1. Summary of drivers and scenarios for the ADEAKE model from 2017 to 2100.

Scale	Driver/s	Scenario	Description
Baseline		1	Constant fishing effort, constant kelp production, and constant temperature
	Fishing	2	Decreasing fishing effort (reducing 50% relative fishing effort)
Loodi		3	Increasing fishing effort (reducing 50% large benthic fish feeders' biomass)
	Kelp POM production	4	50% decline of coarse and fine kelp biomass due to direct harvesting
Regional		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
Clabal	Temperature	8	Moderate increasing of sea bottom temperature (scenario RCP4.5)
Giobal		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)

FIGURES



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



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



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 negative correlations in red. Legend colour shows the strength correlation coefficient 932 (rho-value) and its corresponding colour gradient. Colour intensity and the size of the 933 ellipses are proportional to the correlation coefficients, with more diffused and wider 934 ellipses representing lower correlation strengths. When the indicator is non-significant 935 (>0.01), it is represented with an "X" symbol (rho and p-values are included in suppl. 936 937 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: benthopelagic shrimps; FG.28: suprabenthos. 939



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



Figure 5. Predicted time series of mean absolute biomass (t·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.



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



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

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

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

Appendix 1 Supplementary figures: Revised environmental preference functions of eachfunctional group (Fig. S1).

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