

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

Published in:
Restoration Ecology

DOI:
[10.1111/rec.13327](https://doi.org/10.1111/rec.13327)

Publication date:
2021

Document Version
Peer reviewed version

Citation for published version (APA):

Vilas, D., Coll, M., Pedersen, T., Corrales, X., Filbee-Dexter, K., & Wernberg, T. (2021). Future trajectories of change for an Arctic deep-sea ecosystem connected to coastal kelp forests. *Restoration Ecology*, 29(S2), Article e13327. <https://doi.org/10.1111/rec.13327>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the public portal.

Take down policy

If you believe that this document breaches copyright please contact rucforsk@kb.dk providing details, and we will remove access to the work immediately and investigate your claim.

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>.

This article may be used for non-commercial purposes in accordance with
Wiley Terms and Conditions for Use of Self-Archived Versions.

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

Running head:

Future changes in Arctic ecosystem

Authors

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

Affiliations

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

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

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

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

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

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

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

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

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

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

*Corresponding author: danielvilasgonzalez@gmail.com

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.

Abstract

Environmental stressors related to climate change and other anthropogenic activities are impacting Arctic marine ecosystems at exceptional rates. Within this context, predicting future scenarios of deep-sea ecosystems and their consequences linked with the fate of coastal areas is a growing need and challenge. We used an existing food-web model developed to represent the outer basin of the Malangen fjord, a Northern 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. We considered four major drivers (kelp particulate organic matter (POM) production entering the deep sea, fishing effort, king crab invasion, and ocean warming) to project 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 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 and the king crab invasion. Yet, the cumulative impacts are predicted to be more important than non-cumulative since some stressors acted synergistically. These results illustrate the vulnerability of sub-Arctic and Arctic marine ecosystems to climate change and consequently call for conservation, restoration, and adaptation measures in deep-sea and adjacent ecosystems. Results also highlight the importance of considering additional stressors affecting deep-sea communities to predict cumulative impacts in an ecosystem-based management and global change context and the interlinkages between coastal and deep-sea environments.

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

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.

Introduction

Within the current scenario of a changing planet, environmental stressors related to climate change, together with other human impacts, are increasingly affecting marine 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 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 communities (Smale et al. 2019). Under this context, predicting future scenarios and their consequences, and providing effective tools to policymakers, is a growing need and challenge. To respond to current global climate challenges, beneficial management strategies must be carried out such as increasing connectivity to ensure resilience to 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 control of other anthropogenic threatening processes and ecological restoration (Gann et al. 2019).

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).

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

In response to degradation and all stressors affecting kelp forests, there is an increasing interest in their conservation, protection, and restoration of these systems (Bekkby et al. 2020). Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration International Science & Policy Working Group 2004) and it is globally recognized as a fundamental component for conservation (Aronson & Alexander 2013). When ecological restoration is enforced adequately and sustainably, it contributes to manifold beneficial outcomes including the protection of diversity, increasing ecosystem quality, delivering services, and supporting climate change adaptation and mitigation (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 appropriate referenced ecosystem states using measurable ecological indicators (Gann et al. 2019). For instance, kelp ecosystem restoration experiences showed that selective relocation of herbivores, rebuilding of their predators, cleaning sediment of rock surfaces, and transplanting of kelp plants, are successful in restoring kelp forests and specially, when involving stakeholders (e.g. fishermen and local community) (Fujita 2011). Restoration and conservation efforts should be focus on maintaining kelp species and preserving ecosystem services and functioning (Hobbs & Harris 2001; Vergés et al. 2019) as well as increasing ecosystem connectivity (Hodgson et al. 2009; Coleman et al. 2020).

Besides, the benefits of kelp forests to adjacent ecosystems, kelp forests provide shelter and habitat for multiple marine species, and associated with these habitats are organisms such as marine mammals, crustaceans, echinoderms, fish, and algae (Steneck et al. 2002). These ecosystems likely also contribute to large carbon sink and 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 considered a nature-based defence upon coastal erosion and extreme storm events (Rebecca L. Morris et al. 2020). From a social and economic perspective, kelp forests provide important ecosystem services through harvesting to extract food, and pharmaceutical components (Vea & Ask 2011).

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

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

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

Material and methods

- Study area

The Arctic deep ecosystem associated with kelp exports (ADEAKE) of the northern Norway model (Vilas et al. 2020) represents the outer basin of the Malangen Fjord (69.529° N, 18.021° E). This fjord is in Troms and Finnmark county, Arctic Norway, and it is connected to the open sea by a sill (180 meters deep) (Fig. 1). Thus, its morphology provides a potentially excellent accumulation site for kelp POM from the surrounding 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 species distribution, including invasive species such as the king crab, and consequently altering the whole food-web of the ADEAKE (IPCC 2018).

- 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:

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

where dB_i/dt is the growth rate of group i during time t in terms of its biomass B_i ; $(P/Q)_i$ is the net growth efficiency of group i ; Q_{ij} is the consumption rate; M_i is the non-predation mortality rate; F_i is the fishing mortality rate; e_i is the emigration, and I_i is the immigration 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-vulnerable fraction and the transfer rate of vulnerability between the two fractions determines the trophic flow between the predator and the prey (Ahrens et al. 2012). The vulnerability concept incorporates density-dependent processes and expresses how far a group is from its carrying capacity (Christensen et al. 2008; Christensen & Walters 2004). For each predator-prey interaction, consumption rates are calculated as:

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

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

We used the temporal dynamic module Ecosim to evaluate the effect of plausible 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 the lack of specific time-series data and consequently, vulnerabilities could not be estimated as recommended (Christensen et al. 2008). Similar to previous temporal dynamic simulations (Vilas et al. 2020), we increased kelp POM vulnerability ($v = 100$) to allow a notable increase in consumption on detritus if the biomass of consumers increases and default values were set ($v = 2$). Four drivers (fishing, kelp POM production, red king crab invasion, and temperature) were selected to condition the scenarios. Among these drivers, we selected twelve plausible future scenarios in the study area considering the knowledge of a group of regional experts (Table 1).

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).

Regionally, we selected four scenarios, three of which were driven by kelp POM production drivers and one by a possible future biological invasion. Scenario 4 (Scn4) 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 forced to decrease their biomass by 50% (Fig. 2b). The second and third regional scenarios (Scn5 and Scn6, respectively) included kelp POM production as the main driver due to changing sea urchins (*Strongylocentrotus droebachiensis*) biomass in surrounding areas. Scn5 simulated a decrease in sea urchin population and recovery of barrens, so coarse kelp POM biomass was forced to increase while fine kelp POM biomass was forced to decrease (50%) because of the non-grazing process (Fig. 2b). 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.

In contrast, Scn6 reflected a regime shift to barrens caused by an increase in sea urchins and destructive grazing of kelp, during which the biomass of coarse kelp POM decreased until negligible, and the amount of fine kelp POM biomass increased at first (due to the high grazing intensity of urchins on attached kelp (Filbee-Dexter et al. 2019) and then decreased as the urchins consumed the entire standing stock (Fig. 2b). The last regional scenario (Scn7) included the future invasion of the red king crab invasion, which is 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 until achieving the same biomass as other Ecopath models in a similar study area (Pedersen et al. 2018). This increase applied the same trend showed in other Norwegian fjords which the red king crab invaded (Oug et al. 2018) (Fig. 2c) while keeping fishing and kelp POM production constant.

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

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

- Model analysis and indicators

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

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

The ECOIND plug-in (Coll & Steenbeek 2017) allowed us to extract ecological indicators related to species traits (biomass, catch, trophic, size, and species-based). We focused on biomass-based indicators, trophic-based and catch-based indicators. 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, biomass of fish species, and the Kempton's diversity index. Next, four trophic-based indicators four indicators were selected based on the trophic level (TL): TL of the community (TLcom), TL of the community including organisms with $TL \geq 2$ (TLcom2), TL

of the community including organisms with $TL \geq 3.25$ ($TL_{com3.25}$) and TL of the community including organisms with $TL \geq 4$ (TL_{com4}). 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

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

Results

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), both scenarios showed similar biomass trends for all selected functional groups between them and with respect to the baseline scenario (Fig. 3, 4, 5, and 6). Coinciding with that, 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 trends on FD/TST were less strong for Scn2 and Scn3 than Scn1 (Fig. 7), and Scn3 showed less strong decreasing trends for Fish C although it was significant too (Fig. 8 and Table S7).

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).

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

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

Red king crab invasion scenario – Scn7

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).

Under this scenario, significant changes in ENA indicators were found for TST, Ex/TST, and FCI. Contrarily, the model did not predict any significant change in FD/TST, A/C, AML, and APL (Fig. 7). A notable increasing trend for Commercial B, Invertebrates 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 and Fish C decreased over time (Fig. 8). Despite ECOIND indicators showed the same trends compared with the baseline scenario, most of these indicators responded weaker over time (Fig. 8).

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 this scenario.

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).

Considering ENA indicators, Scn10 showed a decreasing trend for TST and an 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 trends for TST, Ex/TST, A/C, FCI, and APL, and decreasing trends for FD/TST and AMI (Fig. 7). Ecological indicators obtained similar predicted trends under Scn10 and 12 (Fig. 8). Both of them showed increasing trends for Fish B, TLcom, TL C, and Fish C, while decreasing trends for Commercial B, Demersal B, Invertebrates B, Total B, Kempton's Index, TLcom2, TLcom3.25, Invertebrates C, and Total C. Scn11 showed decreasing trends for commercial B, invertebrates B, total B, Kempton's Index, TLcom2, TLcom3.25, TLcom4, Invertebrates C and Total C and increasing trends for Fish B, TLcom, TL C and Fish C (Fig. 8).

Common patterns

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

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

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

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

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

on benthic invertebrates such as crustaceans, echinoderms, and mollusks and thus it 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).

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

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

Our model predicted ecosystem impacts in an Arctic ecosystem under multiple future scenarios including climate change effects, which, can contribute to the knowledge needed towards deep-sea ecosystems and how ecological restoration in coastal areas can impact adjacent ecosystems. The ADEAKE model displayed a decreasing resilience and ecosystem state under warming and cumulative impacts scenarios, highlighting the 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 impact on deep-sea adjacent ecosystems, which highlights the relevance of ecosystem protection and restoration of such important areas. Ecological restoration, in fact, is recognized as a critical tool for mitigating and adapting to the impacts of climate change (Gann et al. 2019). A recent study (Eger et al. 2020) highlighted that a more holistic approach form of restoration that incorporates species interaction could increase the likelihood of success. Our modelling approach could be a suitable tool to further explore potential restoration scenarios through an integrated view (Frisk et al. 2011), for example, by extending the deep-sea model to the coastal areas and explicitly modelling the kelp bed – deep-sea ecosystem together.

Performing future simulations in ecology is considered an arduous task, especially without any calibration process under long-term scenarios (Dietze & Lynch 2019). Although results are helpful to indicate trends in future changes, these should be interpreted with caution since several limitations were found in this study. For instance, fishing scenarios (Scn2 and Scn3) as well as changes in kelp POM production scenarios (Scn4, Scn5 and Scn6) resulted in similar outputs which may indicate low sensitivity of 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 drivers during future simulations. One of the main hurdles was the inability to fit the model due to the lack of specific time-series data that could affect the model application. This caused high uncertainty for most projections results and could strongly influence the intensity of biomass and ecological indicators changes. Despite this, we consider that our approach included methods to minimize as much as possible the negative effects of 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 as the strongest driver in the study area. Another limitation was the lack of SBT projections under scenarios of greenhouse emissions, which if available could make future simulations more realistic in deep ecosystems. The model represents a deep ecosystem ranging from 400-450 metres depth and we used similar rates of change between reconstructed SST and SBT over time (Husum & Hald 2004). There is evidence that the upper ocean (above 700 metres) is warming similarly with climate change (Llovel et al. 2014). Despite the fact that predicting future deep-sea temperature changes is difficult (Klemas & Yan 2014), SBT projections were estimated taking into account the best available data. Additionally, new species could be incorporated into the food-web due to their migration into the system because of increasing sea temperature and thus it could represent a limitation on this study. These incoming species from southern areas, in the hemisphere north, could forage and interact with other species and alter the food-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 trajectories of change in order to include all species in the analysis. In addition, response functions to sea temperature were included from *AquaMaps* a global database using trapezoid shape (Kaschner et al. 2016), because we lacked specific response functions in the study area. Local sea temperature response functions would improve predictions under global warming scenarios, for example, alternative shapes and statistical models are increasingly used in order to define environmental response functions (Coll et al. 2019; Serpetti 2019). Lastly, future analysis on the same ecosystem may include 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 deep-sea ecosystems, increasing the resilience on deep-sea systems and alleviate the negative effects of sea warming and species invasions.

Acknowledgments

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 Pedersen, Kjell Magnus Norderhaug, Stein Fredriksen, and Eva Ramírez-Llodra for their helpful comments. We want to thank Nina Mikkelsen, Emma Källgren, Freija Hauquier, Margo Van Gyseghem, and Ann Vanreusel for their help during the scientific survey where the input data of the food-web model come from. Also, the authors want to thank the crew of the R/V Johan Ruud. MC acknowledges partial funding by the European Union's Horizon research program grant agreement No 689518 for the MERCES project. This research is part of POLARCSIC activities.

References

- Ahrens RNM, Walters CJ, Christensen V (2012) Foraging arena theory. *Fish 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
- 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 consensus 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 Colléter M, Valls A, Guitton J, Gascuel D, Pauly D, Christensen V (2015) Global
 682 overview of the applications of the Ecopath with Ecosim modeling approach
 683 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 Dietze M, Lynch H (2019) Forecasting a bright future for ecology. *Frontiers in*
 691 *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

696 (Laminaria solidungula) carbon in an arctic kelp community: $\delta^{13}\text{C}$
697 evidence. Marine Biology 93:615–625

698 Eger AM, Marzinelli E, Gribben P, Johnson CR, Layton C, Steinberg PD, et al.
699 (2020) Playing to the Positives: Using Synergies to Enhance Kelp Forest
700 Restoration . Frontiers in Marine Science 7:544

701 Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable
702 states of collapsed kelp ecosystems. Marine ecology progress series
703 495:1–25

704 Filbee-Dexter K, Wernberg T (2018) Rise of turfs: A new battlefield for globally
705 declining kelp forests. BioScience 68:64–76

706 Filbee-Dexter K, Wernberg T Substantial blue carbon in overlooked Australian
707 kelp forests. Scientific Reports

708 Filbee-Dexter K, Wernberg T, Fredriksen S, Norderhaug KM, Pedersen MF
709 (2019) Arctic kelp forests: Diversity, resilience and future. Global and
710 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

714 Finn JT (1976) Measures of ecosystem structure and function derived from
715 analysis of flows. Journal of theoretical Biology 56:363–380

716 Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov
717 A V. (2015) Recent warming leads to a rapid borealization of fish
718 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
721 fish communities. Proceedings of the National Academy of Sciences
722 114:12202–12207

723 Fredriksen S, Filbee-Dexter K, Norderhaug KM, Steen H, Bodvin T, Coleman
724 MA, et al. (2020) Green gravel: a novel restoration tool to combat kelp
725 forest decline. Scientific Reports 10:1–7

726 Free CM, Thorson JT, Pinsky ML, Oken KL, Wiedenmann J, Jensen OP (2019)
727 Impacts of historical warming on marine fisheries production. *Science*
728 363:979–983

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

732 Froese R, Winker H, Coro G, Demirel N, Tsikliras AC, Dimarchopoulou D, et al.
733 (2018) Status and rebuilding of European fisheries. *Marine Policy* 93:159–
734 170

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

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

740 Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al.
741 (2019) International principles and standards for the practice of ecological
742 restoration. *Restoration Ecology* 27:S1–S46

743 Halpern BS, Frazier M, Potapenko J, Casey KS, Koenig K, Longo C, et al.
744 (2015) Spatial and temporal changes in cumulative human impacts on the
745 world's ocean. *Nature Communications* 6:1–7

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

748 Haug T, Bogstad B, Chierici M, Gjøsæter H, Hallfredsson EH, Høines ÅS, et al.
749 (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
754 ecosystem-based management. *Ecological Modelling* 331:173–184

755 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 Kesner-Reyes K, Kaschner K, Kullander S, Garilao C, Barile J, Froese R (2016)
775 AquaMaps: algorithm and data sources for aquatic organisms. In: 2012.
776 FishBase. World Wide Web electronic publication. www.fishbase.org,
777 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

786 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

789 Layton C, Coleman MA, Marzinelli EM, Steinberg PD, Swearer SE, Vergés A, et
790 al. (2020) Kelp Forest Restoration in Australia. *Frontiers in Marine Science*
791 7:74

792 Leslie HM, McLeod KL (2007) Confronting the challenges of implementing
793 marine ecosystem-based management. *Frontiers in Ecology and the*
794 *Environment* 5:540–548

795 Llovel W, Willis JK, Landerer FW, Fukumori I (2014) Deep-ocean contribution to
796 sea level and energy budget not detectable over the past decade. *Nature*
797 *Climate Change* 4:1031–1035

798 Mankettikkara R (2013) Hydrophysical characteristics of the northern
799 Norwegian coast and fjords. PhD thesis, University of Tromsø, Tromsø.

800 Merzouk A, Johnson LE (2011) Kelp distribution in the northwest Atlantic Ocean
801 under a changing climate. *Journal of Experimental Marine Biology and*
802 *Ecology* 400:90–98

803 Morris Rebecca L, Hale R, Strain EMA, Reeves SE, Vergés A, Marzinelli EM, et
804 al. (2020) Key Principles for Managing Recovery of Kelp Forests through
805 Restoration. *BioScience* 70:688–698

806 Morris Rebecca L., Graham TDJ, Kelvin J, Ghisalberti M, Swearer SE (2020)
807 Kelp beds as coastal protection: Wave attenuation of *Ecklonia radiata* in a
808 shallow coastal bay. *Annals of Botany* 125:235–246

809 Oug E, Sundet JH, Cochrane SKJ (2018) Structural and functional changes of
810 soft-bottom ecosystems in northern fjords invaded by the red king crab
811 (*Paralithodes camtschaticus*). *Journal of Marine Systems* 180:255–264

812 Pedersen MF, Filbee-Dexter K, Norderhaug KM, Fredriksen S, Frisk NL, Fagerli
813 CW, et al. (2019) Detrital carbon production and export in high latitude kelp
814 forests. *Oecologia* 192:227–239

815 Pedersen T, Fuhrmann MM, Lindstrøm U, Nilssen EM, Ivarjord T, Ramasco V,
816 et al. (2018) Effects of the invasive red king crab on food web structure and
817 ecosystem properties in an Atlantic fjord. *Marine Ecology Progress Series*
818 596:13–31

819 Pedersen T, Ramsvatn S, Nilssen EM, Nilsen M, Morissette L, Ivarjord T, et al.
820 (2016) Species diversity affects ecosystem structure and mass flows in
821 fjords. *Regional Studies in Marine Science* 3:205–215

822 Poloczanska ES, Burrows MT, Brown CJ, Molinos JG, Halpern BS, Hoegh-
823 Guldberg O, et al. (2016) Responses of marine organisms to climate
824 change across oceans. *Frontiers in Marine Science* 3:3–62

825 Ramirez-Llodra E, Rinde E, Gundersen H, Christie H, Fagerli CW, Fredriksen S,
826 et al. (2016) A snap shot of the short-term response of crustaceans to
827 macrophyte detritus in the deep Oslofjord. *Scientific reports* 6:23800

828 Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, Escobar E, et
829 al. (2011) Man and the last great wilderness: human impact on the deep
830 sea. *PLoS One* 6:e22588

831 Rocha J, Yletyinen J, Biggs R, Blenckner T, Peterson G (2015) Marine regime
832 shifts: drivers and impacts on ecosystems services. *Phil. Trans. R. Soc. B*
833 370:20130273

834 Serpetti N (2019) Ecosystem impacts of cumulative effects from climate and
835 fisheries. Lecture presented December 5th in Ecopath 35 years
836 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
839 informs the Ecosystem Approach to Fisheries. *Scientific reports* 7:1–15

840 Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control
841 of community structure on temperate reefs. *Oecologia* 132:131–142

842 Skants KD (2019) Species composition, distribution and ecology of the
843 demersal fish community along the Norwegian coast north of Stad under
844 varying environmental conditions. The University of Bergen

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

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.

902
903
904
905

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

FIGURES

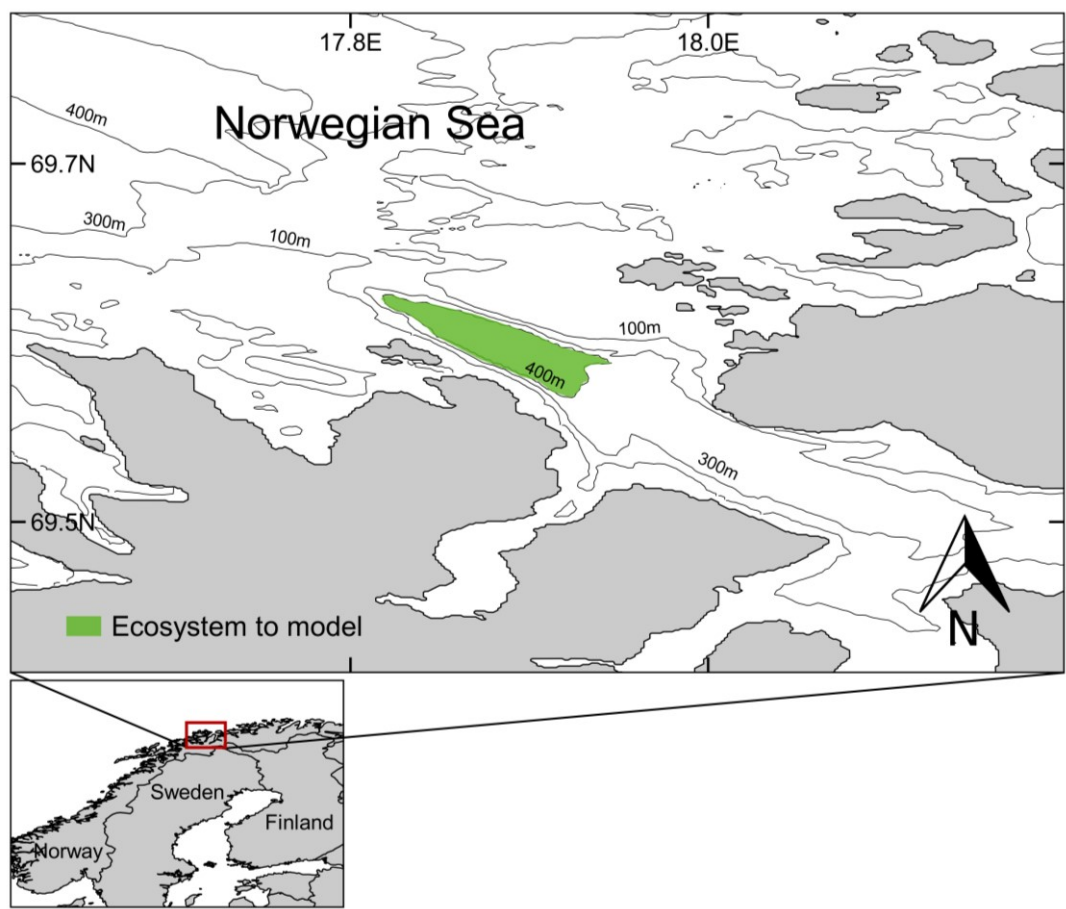


Figure. 1. Study area located in Malangen fjord, northern Norway, and the Arctic deep ecosystem associated with kelp exports (ADEAKE) (green polygon).

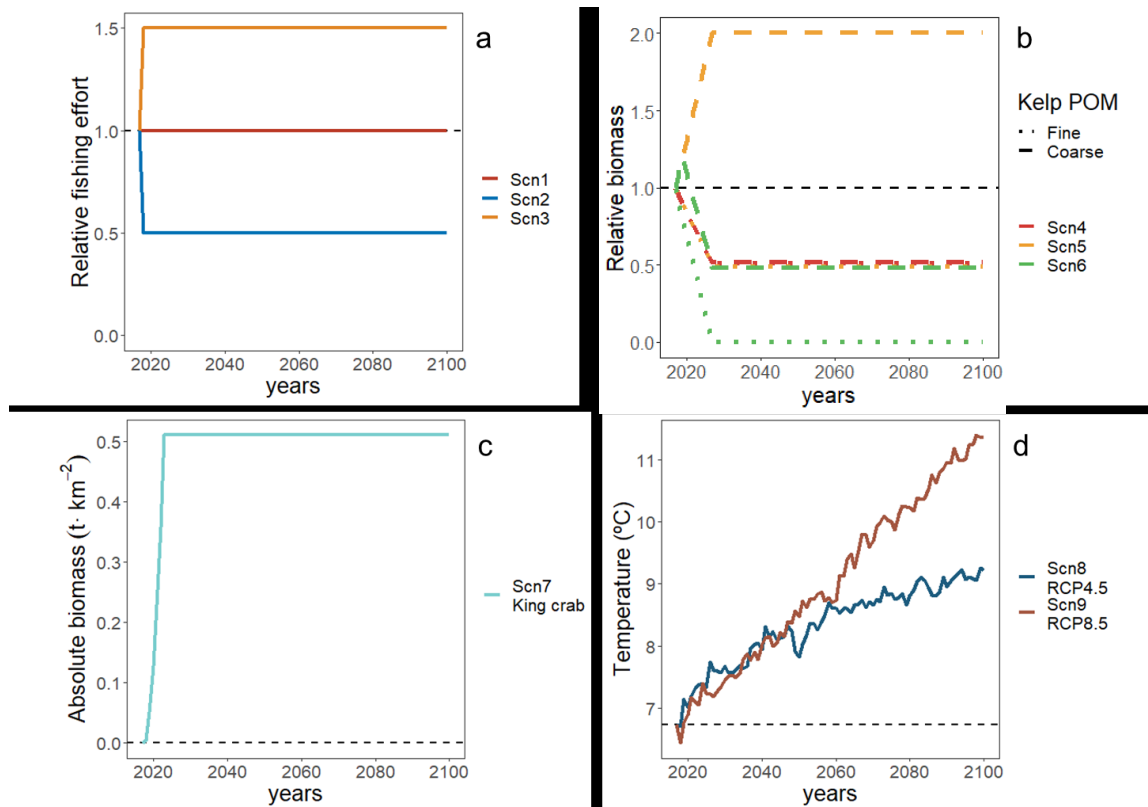


Figure 2. Stressors in the ADEAKE model for the simulation period 2017-2100: (a) relative fishing effort; (b) fine and coarse kelp POM production; (c) invasive species in terms of absolute biomass (t·km⁻²) of king crab; and (d) annual sea bottom temperature (°C) under the two scenarios of IPCC projections.

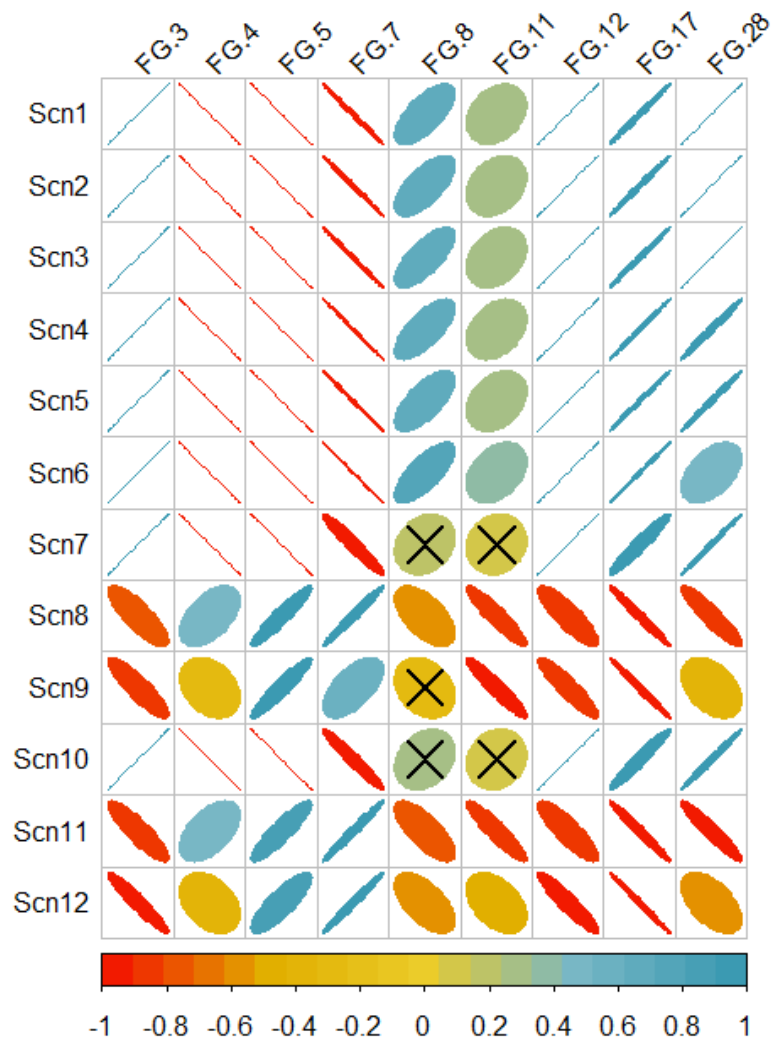
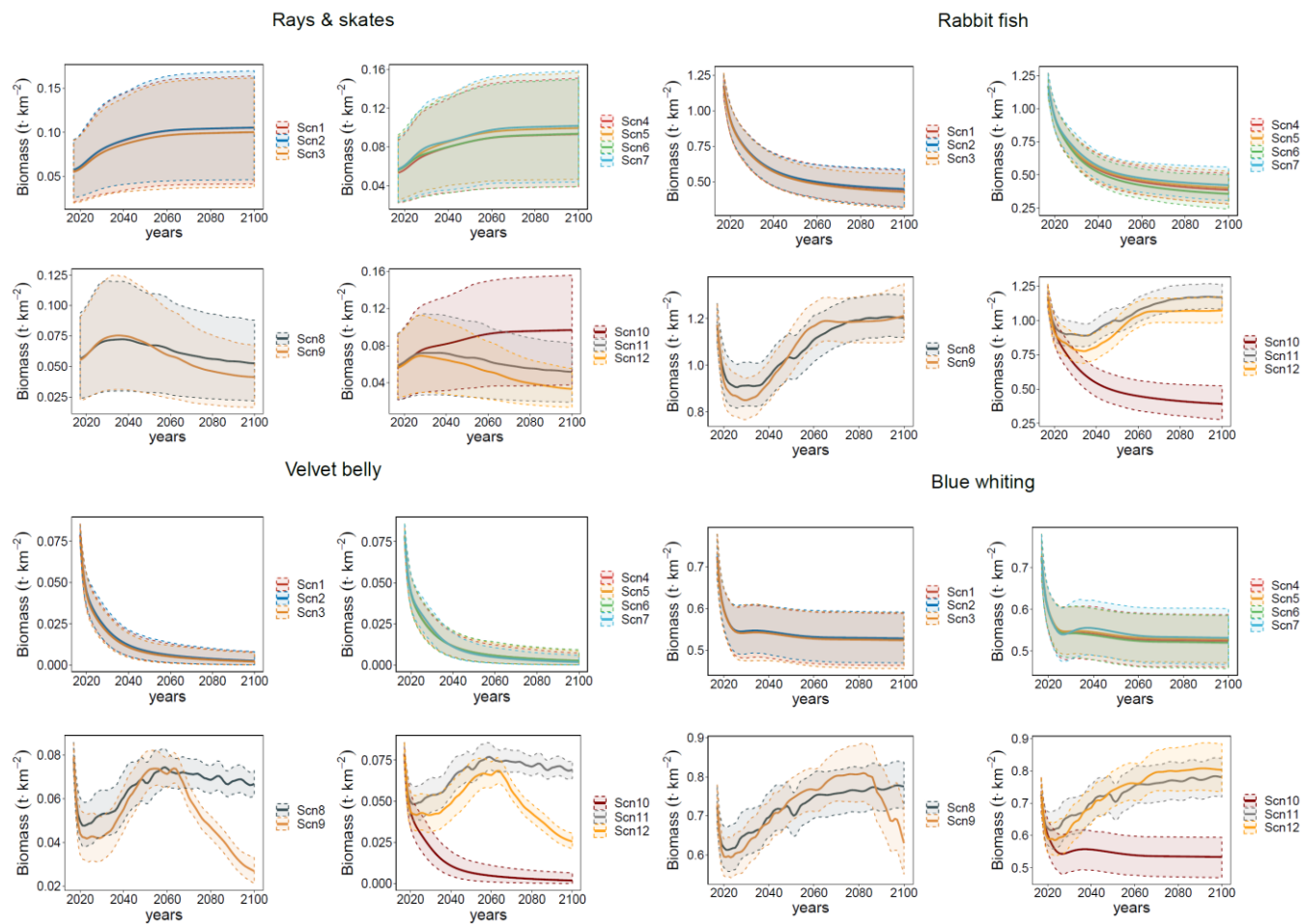


Figure 3. Spearman's rank correlation between selected biomasses of functional groups (FG) and time for the 12 future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the strength correlation coefficient (rho-value) and its corresponding colour 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 supplemental Table S2) (FG.3: rays and skates; FG.5: rabbit fish; FG.7: blue whiting; FG.8: large fish feeders; FG.11: other commercial demersal fishes; FG.12: redfishes; FG.17: benthopelagic shrimps; FG.28: suprabenthos).

941
942
943
944
945
946
947
948
949
950
951
952
953
954
955
956
957
958



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.

961

962

963

964

965

966

967

968

969

970

971

972

973

974

975

976

977

978

979

980

Large fish feeders

Other commercial demersal fishes

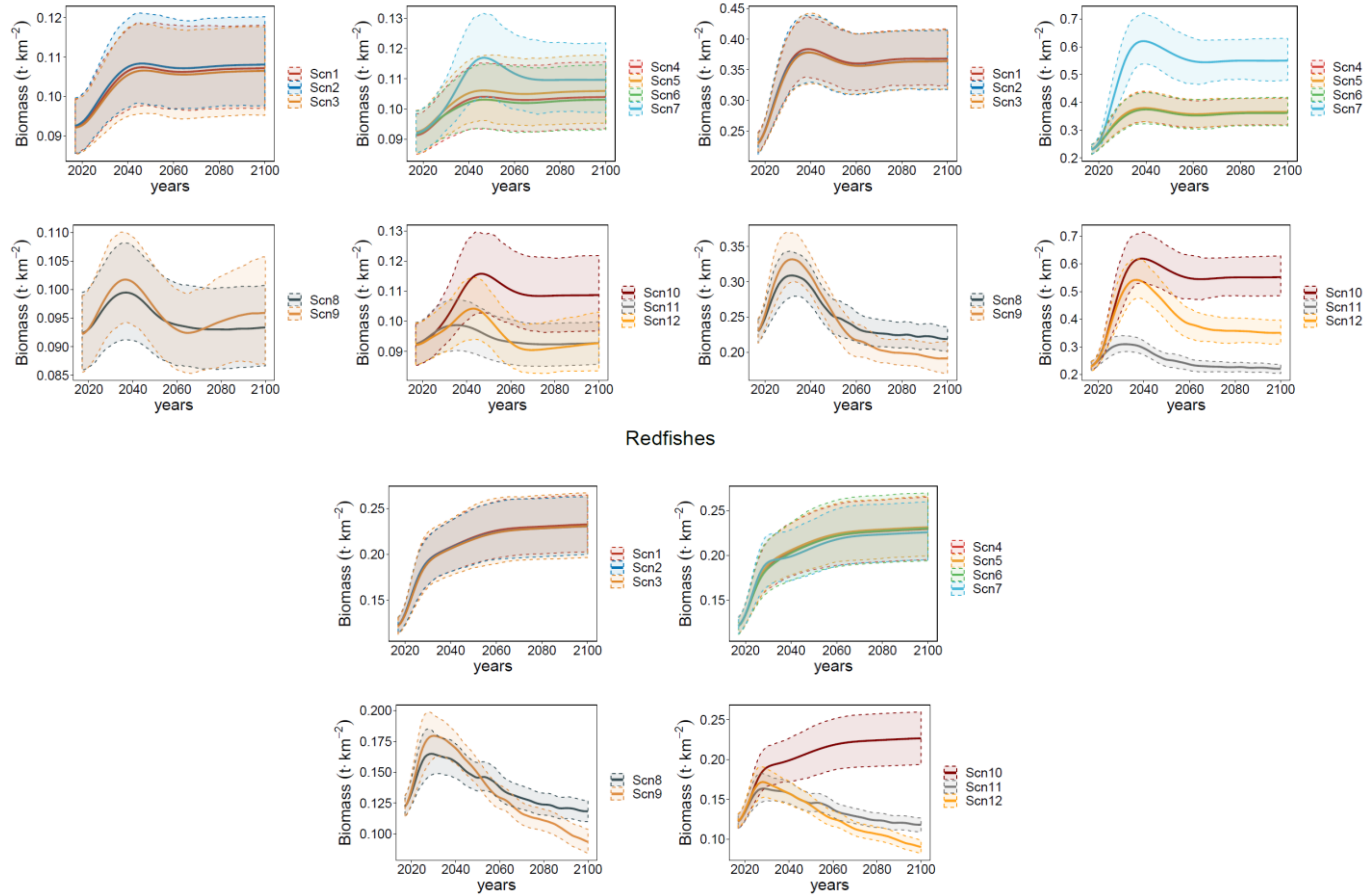
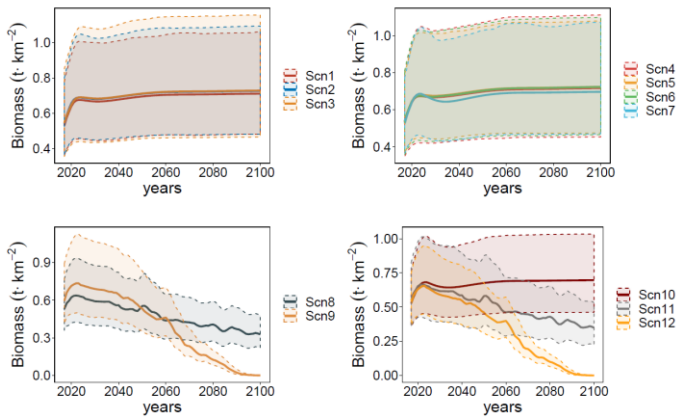


Figure 5. Predicted time series of mean absolute biomass (t·km⁻²) (solid line) for large fish feeders, other commercial demersal fishes and redfishes' functional groups under 12 future scenarios (Table 1). Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Benthopelagic shrimps



Suprabenthos

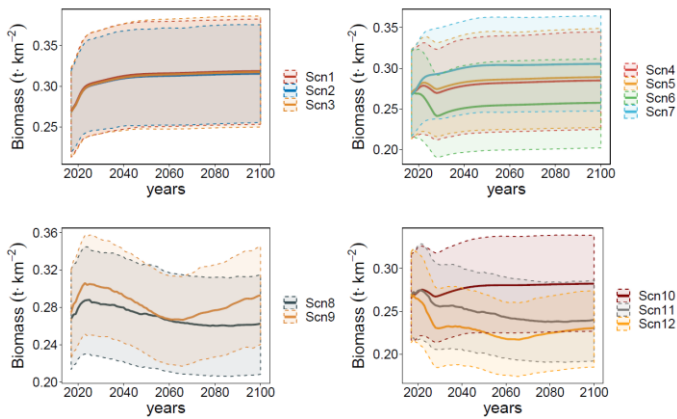


Figure 6. Predicted time series of mean absolute biomass ($\text{t} \cdot \text{km}^{-2}$) (solid line) for benthopelagic shrimps and suprabenthos functional groups under 12 future scenarios (Table 1). Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

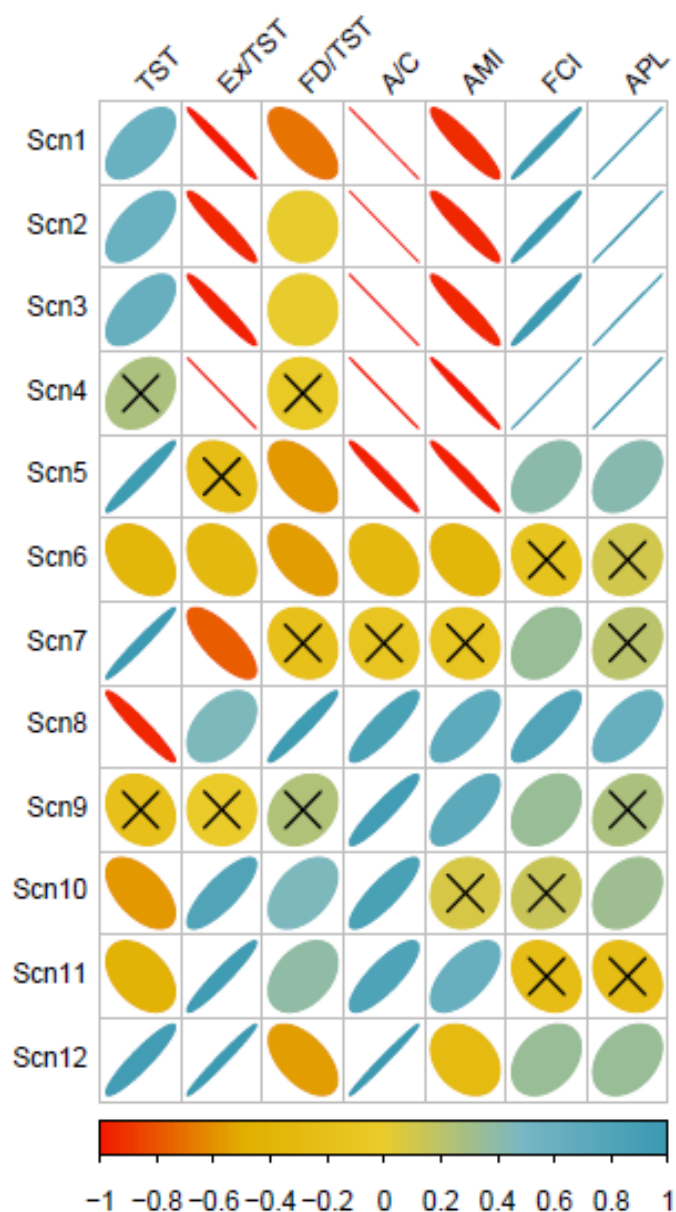


Figure 7. Spearman's rank correlation between selected ENA indicators and time for the 12 future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the strength correlation coefficient (rho-value) and its correspondent colour gradient. Colour 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 S3).

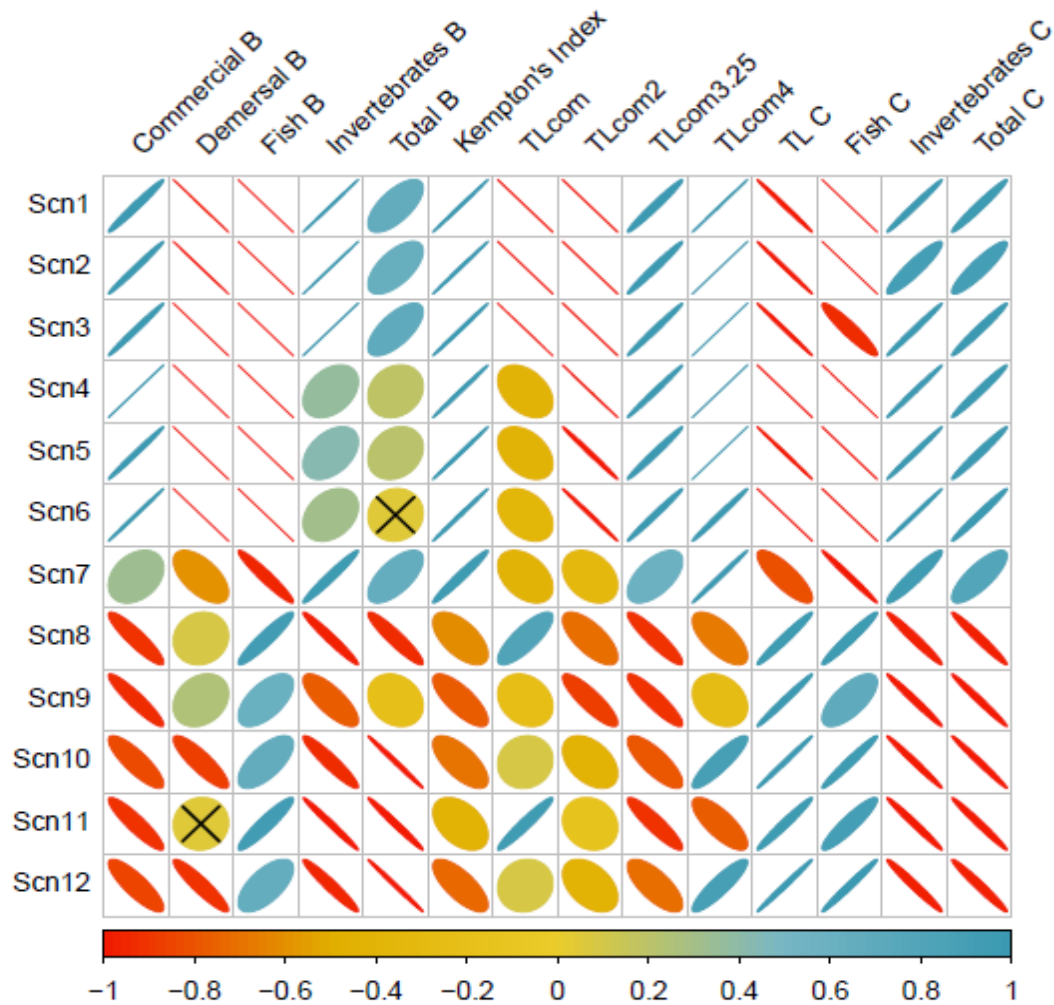


Figure 8. Spearman's rank correlation between selected ECOIND indicators and time for the 12 future scenarios (Table 1). Positive correlations are in blue and negative correlations in red. Legend colour shows the strength correlation coefficient (rho-value) and its correspondent colour gradient. Colour 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 ($p > 0.01$), it is represented with an "X" symbol (rho and p-values are included in suppl. material Table S4).

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

Appendix 1 Supplementary figures: Revised environmental preference functions of each functional 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.