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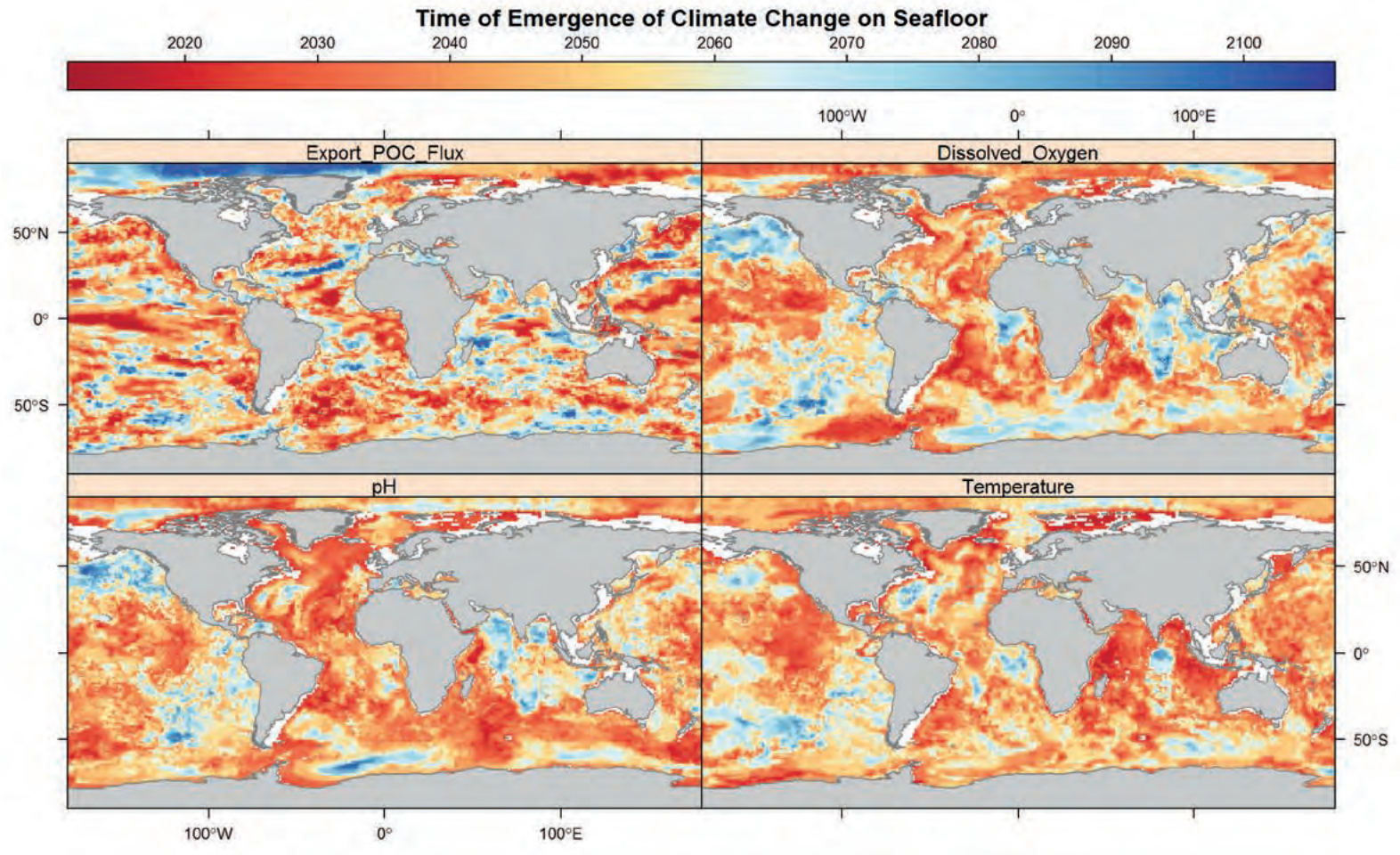
Deep-ocean climate change impacts on habitat, fish and fisheries



Cover image: Time of emergence of seafloor climate changes. Figure 7 in Chapter 8 of this Technical Paper.

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Preparation of this document

The FAO/UNEP Project Sustainable Fisheries Management and Biodiversity Conservation of Deep-sea Living Marine Resources and Ecosystems in the Areas Beyond National Jurisdiction (ABNJ Deep-seas and Biodiversity) aims to achieve efficiency and sustainability in the use of deep-sea living marine resources and improve biodiversity conservation in the ABNJ through systematic application of an ecosystem approach. The project, which started in 2015, covers many aspects of deep-sea fisheries and has many partners. One important activity is an "Assessment of potential interactions between DSF and biodiversity" (Activity 2.1.1.3) in support of demonstrating an "Improved application of management tools for mitigation of threats to sustainable DSF and biodiversity" (Outcome 2.1). An understanding of the likely effects of climate change on the deep oceans is fundamental to the management of deep-sea fisheries. The ABNJ Deep-seas and Biodiversity project partnered with the Deep Ocean Stewardship Initiative (DOSI) to bring together their network of experts and extensive experience to generate predictions on physical, chemical and biological oceanography through a range of approaches under various climate change scenarios. A joint planning workshop was held on 26–27 August 2017 at the WHOI Clark Laboratory, Woods Hole, the United States of America, bringing together DOSI experts and representatives from six deep-seas regional fisheries management organizations. This workshop resulted in the generation of an outline for an FAO Fisheries and Aquaculture Technical Paper and selection of authors for each section. The work was developed over the following six months and is presented in this publication, with the authors of each section identified. The overall compilation was undertaken by Lisa Levin, Maria Baker and Anthony Thompson, who are acknowledged as editors. For providing editorial assistance, the work of Joan Alfaro-Lucas, Bai Li, Olivia Pereira, Sarah Seabrook, Teresa Thomas, Emily Young and Luoliang Xu is gratefully acknowledged. The authors also acknowledge and thank Enzo Luchetti for the layout of the publication.

The Deep Ocean Stewardship Initiative

The Deep Ocean Stewardship Initiative (DOSI) is an international, multidisciplinary network that brings together experts in science, technology, policy, law and economics to provide guidance for decision-making on deep-ocean activities within and beyond national jurisdiction. The DOSI Climate Change Working Group, initiated in August 2015, works to centralize climate scenarios and observations to better assess the impact of climate change on deep-sea ecosystems and to address cumulative pressures. Its goals are to facilitate integration of this information in environmental impact assessment, management of deep-sea ecosystems, and in the design of marine protected areas, to identify high-vulnerability areas and foster interdisciplinary approaches to investigate how deep-sea ecosystems interact with climate on a functional basis. The working group prepares brief and publications, raises awareness about climate change among diverse stakeholders, interacts with the United Nations Framework Convention on Climate Change, contributes to reporting by the Intergovernmental Panel on Climate Change, promotes Sustainable Development Goal (SDG) 14 (including voluntary commitments), provides guidance to the International Seabed Authority, and contributes to deliberations marine biological diversity of areas beyond national jurisdiction. The DOSI Fisheries Working Group works to promote a precautionary approach to deep-ocean management implemented via international cooperation. Focal areas include recovery from fishing disturbance and interaction with mining, application of vulnerable marine ecosystem (VME) concepts across biomes, identification of trends and knowledge gaps in deep-sea fisheries and stocks, differentiating between natural variability and human impacts, and managing expectations on the benefits of marine protected areas. The group has recently hosted a workshop to draft an environmental impact assessment template for use by regional fisheries management organizations (RFMOs) in managing deep-sea bottom-trawl fisheries, and is working towards implementation of SDG 14.2, identification of VMEs related to the implementation of United Nations General Assembly on deep-sea fisheries resolutions, the conservation of biodiversity in areas beyond national jurisdiction in relation to deep-sea fisheries, and facilitating data-poor programmes via RFMOs.

Abstract

This publication presents the outcome of a meeting between the FAO/UNEP ABNJ Deep-seas and Biodiversity project and the Deep Ocean Stewardship Initiative. It focuses on the impacts of climatic changes on demersal fisheries, and the interactions of these fisheries with other species and vulnerable marine ecosystems. Regional fisheries management organizations rely on scientific information to develop advice to managers. In recent decades, climate change has been a focus largely as a unidirectional forcing over decadal timescales. However, changes can occur abruptly when critical thresholds are crossed. Moreover, distribution changes are expected as populations shift from existing to new areas. Hence, there is a need for new monitoring programmes to help scientists understand how these changes affect productivity and biodiversity.

The principal cause of climate change is rising greenhouse gases and other compounds in the atmosphere that trap heat causing global warming, leading to deoxygenation and acidification in the oceans. Three-dimensional fully coupled earth system models are used to predict the extent of these changes in the deep oceans at 200–2500 m depth. Trends in changes are identified in many variables, including temperature, pH, oxygen and supply of particulate organic carbon (POC). Regional differences are identified, indicating the complexity of the predictions. The response of various fish and invertebrate species to these changes in the physical environment are analysed using hazard and suitability modelling. Predictions are made to changes in distributions of commercial species, though in practice the processes governing population abundance are poorly understood in the deep-sea environment, and predicted distributional changes are not always as expected and may be manifested as simple disappearance of species or ecosystems. The publication underscores the fact adaptive monitoring and management mechanisms must be in place to ensure that fisheries are sustainable and the environment remains healthy and productive. Suggestions are provided as to the actions necessary.

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Abbreviations and acronyms

Organizational

ABNJ	Areas Beyond National Jurisdiction
AR5	Fifth Assessment Report (IPCC)
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
DOOS	Deep Ocean Observing Strategy
DOSI	Deep Ocean Stewardship Initiative
DSF	deep-sea fisheries
EEZ	exclusive economic zone
FAO	Food and Agriculture Organization of the United Nations
FAO DSF Guidelines	FAO International Guidelines for the Management of Deep-sea Fisheries in the High Seas (adopted in 2008)
GEBCO	General Bathymetric Chart of the Oceans
GFCM	General Fisheries Commission for the Mediterranean
GO-SHIP	Global Ocean Ship-based Hydrographic Investigations Program
ICES	International Council for the Exploration of the Sea
INDEEP	International Network for Scientific Investigations of Deep-sea Ecosystems
IPCC	Intergovernmental Panel on Climate Change
NAFO	Northwest Atlantic Fisheries Organization
NEAFC	North East Atlantic Fisheries Commission
NPFC	North Pacific Fisheries Commission
OBIS	Ocean Biodiversity Information System
PICES	North Pacific Marine Science Organization
RFMO	regional fisheries management organization or arrangement
SEAFO	South East Atlantic Fisheries Organisation
SPRFMO	South Pacific Regional Fisheries Management Organisation
UNCLOS	United Nations Convention on the Law of the Sea of 10 December 1982
UNFSA	Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks (1995)
UNGA	United Nations General Assembly
UNGA Res.	UNGA resolution
WWF	World Wildlife Fund

Scientific and technical

ASH	aragonite saturation horizon
AUC	area under the curve
CMIP5	Coupled Models Intercomparison Project Phase 5
CO_2	carbon dioxide
GFDL-ESM-2G	Geophysical Fluid Dynamics Laboratory's ESM 2G
IPSL-CM5A-MR	Institut Pierre Simon Laplace's CM6-MR
MLD	mixed layer depths
MPI-ESM-MR	Max Planck Institute's ESM-MR
mya	million years ago
NAO	North Atlantic Oscillation
O_2	oxygen
OMZ	oxygen minimum zone
pCO_2	partial pressure of CO_2
pH	acidity scale
POC	particulate organic carbon
RCP	Representative Concentration Pathway
SAI	significant adverse impact
SDM	species distribution model
SE	standard error
TAC	total allowable catch
thetao	seawater potential temperature
TOE	time of emergence
TRI	terrain ruggedness index
VME	vulnerable marine ecosystem
VMS	vessel monitoring system
Ω	calcium carbonate saturation state (may be calculated for aragonite [$\Omega_{aragonite}$] or calcite [$\Omega_{calcite}$])

Names of fish and shellfish species

English common names for fish and shellfish species have been used throughout the text in this document. Scientific and common names were taken from the FAO ASFIS list of fish and shellfish species[2] and are shown below.

Common name	Scientific name
Alfonsino	*Beryx decadactylus*
American conger	*Conger oceanicus*
American plaice	*Hippoglossoides platessoides*
Anglerfish (blackbellied, black)	*Lophius budegassa*
Anglerfish (white) (= monk)	*Lophius piscatorius*
Antarctic toothfish	*Dissostichus mawsoni*
Argentine	*Argentina sphyraena*
Argentine hake	*Merluccius hubbsi*
Argentine shortfin squid	*Illex argentines*
Atlantic cod	*Gadus morhua*
Atlantic halibut	*Hippoglossus hippoglossus*
Atlantic herring	*Clupea harengus*
Atlantic mackerel	*Scomber scombrus*
Baird's slickhead	*Alepocephalus bairdii*
Beaked redfish	*Sebastes mentella*
Black cardinalfish	*Epigonus telescopus*
Black scabbardfish	*Aphanopus carbo*
Blackbelly rosefish	*Helicolenus dactylopterus*
Blackmouth catshark	*Galeus melastomus*
Blue ling	*Molva dypterygia*
Channeled rockfish	*Setarches guentheri*
Common sole	*Solea solea*
Deepwater rose shrimp	*Parapenaeus longirostris*
Dover sole	*Microstomus pacificus*
European anchovy	*Engraulis encrasicolus*
European conger	*Conger conger*
European hake	*Merluccius merluccius*
European plaice	*Pleuronectes platessa*
Forkbeard	*Phycis phycis*
Giant red shrimp	*Aristaeomorpha foliacea*
Glacier lanternfish	*Benthosema glaciale*
Golden redfish	*Sebastes norvegicus*
Greater argentine	*Argentina silus*
Greater eelpout	*Lycodes esmarkii*
Greater forkbeard	*Phycis blennoides*
Greenland halibut	*Reinhardtius hippoglossoides*

[2] www.fao.org/fishery/collection/asfis/en

Common name	Scientific name
Haddock	*Melanogrammus aeglefinus*
Ling	*Molva molva*
Long-spine thornyhead	*Sebastolobus altivelis*
Longtail southern cod	*Patagonotothen ramsayi*
Megrim	*Lepidorhombus boscii*
Northern shrimp	*Pandalus borealis*
Orange roughy	*Hoplostethus atlanticus*
Pacific armourhead	*Pseudopentaceros richardsoni*
Patagonian scallop	*Zygochlamys patagonica*
Patagonian toothfish	*Dissostichus eleginoides*
Pelagic armourhead (= southern boarfish)	*Pseudopentaceros richardsoni*
Pelagic red crab	*Pleuroncodes planipes*
Portuguese dogfish	*Centroscymnus coelolepi*
Rabbit fish	*Chimaera monstrosa*
Red vermillion crab	*Paralomis virrilli*
Redfish	*Sebastes* spp.
Roughhead grenadier	*Macrourus berglax*
Roughtip grenadier	*Nezumia sclerorhynchus*
Roundnose grenadier	*Coryphaenoides rupestris*
Sablefish	*Anoplopoma fimbria*
Silver scabbardfish	*Lepidopus caudatus*
Slender (north Pacific) armourhead	*Pseudopentaceros wheeleri*
Snow crab	*Chionoectes opilio*
Splendid alfonsino	*Beryx splendens*
Swallowtail bass	*Anthias woodsi*
Tusk	*Brosme brosme*
White hake	*Urophycis tenuis*
Wreckfish	*Polyprion americanus*
Yellowtail flounder	*Limanda ferruginea*
(no common name)	*Laemonema melanurum*
(no common name)	*Dysommina rugosa*

Executive summary

Almost two-thirds of the ocean occurs beyond national jurisdictions (termed the "high seas") where, under the United Nations Convention on the Law of the Sea of 10 December 1982, the commercial fisheries are managed by flagged states individually or through regional fisheries management organizations or arrangements (RFMOs). Most of the high seas are deeper than 200 m and the fish are harvested by bottom and mid-water trawls, seines, bottom-set longlines, gillnets, pots and traps. States have the right to fish the high seas, subject to various provisions relating to the conservation and management of living resources. This includes preventing significant impacts to vulnerable marine ecosystems (VMEs) – areas identified for uniqueness, rarity, functional significance, structural complexity or life-history traits that make recovery from disturbance difficult. Such VMEs can consist of dense aggregations of deepwater corals and sponges on seamounts, canyons, slopes and other bathymetric features, as well as various organisms, e.g. mussels, clams and tube worms around hydrothermal vents and seeps, or xenophyophores (giant protozoa) in multiple settings. They provide complex three-dimensional structural habitat that supports high levels of biodiversity and can provide refuge, food, and spawning and nursery areas for a wide range of organisms, including commercially important fish and crustacean species. In addition to their bioengineering role, coral gardens, sponge grounds and other VME taxa provide important ecosystem services such as carbon storage and nutrient remineralization. While commercial fish can co-occur within or above VME areas, such as seamounts, the functional relationships with VMEs have only been documented for a limited number of fisheries species. Both VME suspension-feeding species and targeted fishery species exploit areas of high productivity, such as sites where there is enhanced flow due to elevated topography and the trapping of migrating zooplankton and micronekton by seamounts and offshore banks.

To help maintain the integrity of VME ecosystems, RFMOs have taken steps to identify existing bottom-fishing areas, create exploratory fishing protocols with impact assessments for new fisheries, generate VME encounter protocols, and close areas containing VMEs. Such VME considerations by RFMOs generally began in about 2006 following the United Nations General Assembly Resolution (UNGA Res.) 61/105. In December 2016, UNGA Res. 71/123 (article 185) called upon states and RFMOs to "take into account the potential impacts of climate change and ocean acidification in taking measures to manage deep-sea fisheries and protect vulnerable marine ecosystems." A first step in addressing this challenge is provided in this technical paper, which represents a collaboration between the Deep Ocean Stewardship Initiative (DOSI) and the FAO's ABNJ Deep-seas and Biodiversity project. Here, climate change is broadly interpreted to encompass the critical effects of atmospheric warming on ocean temperature and oxygen availability, the effects of ocean acidification, and the influence of all three of these on particulate organic matter flux to the seafloor. The information and findings provide an initial attempt to address the manifestations of climate change at the bathyal deep seafloor in the twenty-first century. Exposure to climate hazard is evaluated as the amount of change relative to natural variability. Vulnerability to climate change is underpinned by species' intrinsic sensitivity and adaptive capacity, and risk of impact combines exposure and vulnerability. These were determined for selected VMEs, fish and fisheries at depths of 200–2 500 m in RFMOs. Key methodologies are provided for addressing these complex issues, but the geographic and species-level applications presented here are not exhaustive.

Climate change

Rising levels of greenhouse gases, other compounds and particulates in the atmosphere trap heat and warm the planet. Most of this heat is absorbed by the ocean, representing a massive energy uptake since 1955 and raising temperatures in the upper 2 000 m by 0.09 °C. A major consequence of the warming ocean is loss of oxygen (deoxygenation), through reduced solubility, intensified respiration, and increased stratification. The latter inhibits vertical mixing and re-oxygenation of the ocean interior. Water-borne and airborne anthropogenic nutrient inputs to the ocean from land also exacerbate oxygen loss through stimulation of phytoplankton production and eventual decay and respiration. The open ocean has lost on average 2 percent of its oxygen since the pre-industrial era, although some regional losses may be as high as 20–40 percent. Possible feedbacks include changes in fluxes of greenhouse gases, nutrients, and toxic compounds such as hydrogen sulphide. The ocean is also absorbing about 25 percent of excess atmospheric carbon dioxide (CO_2) directly, leading to declines in seawater pH and reduced concentrations of carbonate ions, a process called ocean acidification. To date, there has been a 26 percent increase in ocean acidity (reduction of 0.1 pH unit), a decline in calcium carbonate saturation state (Ω), and a shoaling of the saturation horizon; these changes are most extreme at the poles. They are likely to stress marine calcifying organisms and enhance dissolution of non-living carbonates, which comprise deepwater reefs and gardens. Changes in temperature, oxygen and pH are greatest in the upper ocean but can be rapidly transferred into or influence the deep sea through large-scale thermohaline circulation, mesoscale features, and small-scale advective events.

Energy transfer to the deep ocean occurs via sinking of particulate organic carbon (POC), which is produced by photosynthesis in surface waters. Ocean warming, stratification, acidification and deoxygenation have complex effects on the flux of POC to the deep ocean enacted through their influence on winds, mixed-layer depths, storms and vertical advection, the intensity and depth of nutrient remineralization, upwelling of inorganic nutrients available for primary production, and the size and ballasting of sinking phytoplankton cells. In general, declines in POC flux (i.e. food supply) to the seafloor are projected for much of the temperate and tropical ocean, with elevated fluxes at the poles.

Rising temperatures, ocean acidification and ocean deoxygenation have been linked to rapid warming in the geological record, with large-scale biological consequences such as extinctions documented. Examples can be found at the Triassic–Jurassic Boundary (200 mya), the Palaeocene–Eocene Thermal Maximum (57 mya), and during glacial–interglacial periods over the last 40 000 years.

Vulnerable marine ecosystems

In a general sense, VMEs include almost all the ecosystems occurring in the sea. However, in 2006, the term acquired a more specific meaning in the context of deep-sea fisheries. There is no unifying definition of VMEs, but the FAO International Guidelines for the Management of Deep-sea Fisheries in the High Seas provide a set of criteria to describe VMEs. They are typically areas rich in structure-forming benthic invertebrates, such as corals and sponges, occurring at great depths down to 2 500 m or more. Their vulnerability is related to the likelihood that a benthic population, community or habitat will experience substantial alteration from short-term or long-term cumulative effects of bottom-fishing disturbance, and refers to the potential slow rate of recovery of the benthic population, community or habitat upon cessation of disturbance. In an ecological context, exposure, sensitivity and adaptive capacity are key to assessing VME vulnerability. Sensitivity is greatest for species with specialized habitat requirements, environmental thresholds or triggers that may be exceeded under climate change, species interactions that may be disrupted under climate change, and low numbers (rarity), whereas adaptive capacity may be limited by poor dispersal ability or

ability to evolve. Life-history traits found in many deep-sea species are likely to increase sensitivity (e.g. habitat specialization, small population size, thermally or nutritionally triggered reproduction, symbiont requirements, narrow environmental tolerances or life near thresholds) or reduce adaptive capacity (e.g. limited larval duration, long lifespans, slow growth and maturation).

Despite limited research on the vulnerability of component species in VMEs to climate change impacts, several key findings emerge. Deepwater corals often occur near carbonate saturation horizons, making them particularly vulnerable to ocean acidification. While a dominant reef-forming stony coral (*Lophelia*) appears resilient to CO_2 stress alone and in combination with warming, *Lophelia* populations in the Mediterranean Sea and the Gulf of Mexico live close to thermal and oxygen thresholds. Changes in temperature and oxygenation may cause mortality, possibly exacerbated by reduced POC flux (food supply). Of possibly greater concern is the effect of undersaturation on the non-living, tissue-unprotected coral matrix underlying the reefs, which will corrode through chemical dissolution and bioerosion by boring organisms. One study suggests gorgonians (octocorals) may be more vulnerable than stony corals to impacts of ocean acidification, and the combined effects of stressors are unknown. Sponges are hypothesized to be more tolerant to ocean acidification than corals, but warming and oxygen loss can threaten sponge reefs in areas such as the northwest Pacific. Xenophyophore distributions suggest potential sensitivities to changes in temperature and oxygenation. Vent and seep taxa are also typically tolerant of extreme temperature, pH conditions and high variability. Their vulnerability may lie with oxygen declines at bathyal depths (a potential problem for oxidizing symbionts), planktonic larvae (e.g. of mussels and shrimp) exposed to warming, pH declines, and altered primary producers at the ocean surface, changes in mesoscale circulation features that transport larvae, as well as declining food supply for those benthic adults that filter feed (e.g. mussels) and are reliant on POC flux.

Future climate change in the deep ocean

Projections for future environmental changes in the deep ocean presented here are based on three three-dimensional fully coupled earth system models, which are part of the Coupled Models Intercomparison Project Phase 5. Projections were made under the current emissions scenario (also known as "business as usual") in Representative Concentration Pathway (RCP) 8.5 for bottom temperature (thetao), oxygen, pH and POC flux to the seafloor. These were made for the ocean from 200–2 500 m, RFMO areas, bottom fishing and VME closed areas within RFMOs, seamounts, canyons and cold-water corals. Change was assessed by subtracting the historical average (1951–2000) from the future average (2041–2060 or 2081–2100). Exposure to climate change hazard was measured as the amplitude of climate change in the unit of historical variability (the ratio between climate change and historical standard deviation). Cumulative impacts were calculated for warming, declines in POC flux, oxygen (O_2) loss, and pH decline together (negative impact), and for the reverse (positive impact). Time of emergences (first and 90 percent) of the climate signal were defined as the dates when the future cumulative standard deviation either **first** exceeds or **90 percent of the time** exceeds the historical standard deviation (1951–2000).

Model predictions indicate that most of the deep seafloor is likely to experience warming by 2041–2060 and 2081–2100, especially at higher latitudes, with greatest effects at bathyal depths of the northwest Atlantic, western Greenland Sea and Barents Sea, Red Sea and Sea of Okhotsk; these areas may see more than 2 °C warming at the seafloor by 2081–2100. Almost the entire seafloor may experience reduced pH by 2041–2060 and 2081–2100; however, the bathyal depths of the north Atlantic, Arctic and Southern Ocean will experience the most severe reductions in pH values with an average decline of 0.08 by 2041–2060 and 0.16–0.18 by 2081–2100. Almost all RFMOs will exhibit ocean

acidification by 2081–2100, with the greatest mean changes in the northwest Atlantic and northeast Atlantic Oceans (~ -0.2 in pH total scale) but the Southern Ocean may have the largest spatial variability in ocean acidification. Large areas of the world's seafloor will simultaneously be exposed to acidification and warming hazards, which are up to 10 times of their historical variability by 2041–2060 and up to 20 times by 2081–2100, respectively; effects may be greatest in the Arctic Ocean (200–2 500 m). The Mediterranean Sea and Southern Oceans may see the highest degree of warming hazard (7.2–9.9 times historical variability), whereas the northwest and northeast Atlantic will probably experience the highest degree of mean acidification hazard (18.2–18.8 times of their historical variability).

Deoxygenation (oxygen loss) is predicted to be greatest in the north Atlantic, part of the Arctic and Southern Oceans, with oxygen losses up to 10–15 µmol kg^{-1} by 2041–2060, and up to 40 µmol kg^{-1} decline by 2081–2100 at high latitudes in the north Atlantic, Norwegian Sea, Greenland Sea and the continental margin of South America, Antarctica and Sea of Okhotsk. Large areas of the world's seafloor will probably experience deoxygenation hazard up to 5 times by 2041–2060, and 10 times by 2081–2100, of their historical variability; hotspots include the Canadian high Arctic, equatorial Atlantic and Pacific and Southern Ocean. On average, the Atlantic bathyal habitats (200–2 500 m) will probably be exposed to the most severe deoxygenation hazard by 2041–2060, followed by the Southern and Arctic Oceans; however, by 2081–2100, the deoxygenation hazard will be most severe in the Arctic Ocean. Among regions, the northwest Atlantic may experience the largest decline in mean dissolved oxygen concentration (-27 µmol kg^{-1}) by 2081–2100, followed by the Southern Ocean (-25 µmol kg^{-1}), northeast Atlantic (-16 µmol kg^{-1}) and the southeast Atlantic (-8 µmol kg^{-1}). The ecological consequences could be greatest not in areas of greatest decline, but where existing oxygen values are already low and could surpass tipping points (e.g. in the southeast Atlantic).

There is expected to be a significant decline in export POC flux at 200–2 500 m in the north and south Atlantic, north Indian and south Pacific Oceans, with the greatest declines on the Atlantic slope (of 1.67 mg C m^{-2} d^{-1} by 2041–2060, and 2.73 mg C m^{-2} d^{-1} by 2081–2100), representing 1.34 and 2.27 times lower than the historic minimums. In contrast, the Antarctic slope might experience an average POC flux increase of 0.61 mg C m^{-2} d^{-1} by 2041–2060 and 1.41 mg C m^{-2} d^{-1} by 2081–2100. Except for the Arctic and Southern Oceans, most of the seafloor will experience declines in export POC flux of up to 2 times (by 2041–2060) and 3 times (by 2081–2100) of its historical variability. All ocean regions at bathyal depths, except the Southern Ocean, are predicted to experience declining export POC flux by 2081–2100, with the largest drop in export POC flux (0.7–8.1 mg C m^{-2} d^{-1}) in the northeast Atlantic.

In terms of signal emergence at bathyal depths (i.e. the ability to detect the global-warming-driven changes from natural variability), the mean time of emergence (TOE) may occur before 2050 in most major ocean basins for all variables except for export POC flux. Almost all regions will probably exhibit signal emergence of each climate change variable before about 2060; however, the TOE of acidification and warming are likely to occur about ten years earlier in most ocean regions.

The northeast Atlantic will probably be exposed to the highest cumulative negative impact of warming, and declines in pH, O_2 and POC flux among all regions under the RCP8.5 climate change scenario. Cold-water corals in the northeast Atlantic and Mediterranean and north Pacific are expected to experience the highest cumulative negative impact by 2081–2100, with mean cumulative negative impact scores over 30, or about 7.5 times over their historical average across the four variables. Although the northeast Atlantic and Southern Ocean may experience cumulative positive impact, the positive effects are small and unlikely to compensate for the overall negative impact caused by climate change. According to this assessment, the northeast Atlantic region is potentially at greatest risk under the RCP8.5 climate change scenario.

Exposure to climate hazard

If long-term changes in environmental conditions exceed the limit to which marine species can adapt, the long-term viability of the population or community may be threatened by these changes. Using current latitudinal and depth distribution ranges for 41 key commercial fishery species, the extent to which each species would be subjected to climate hazards projected by earth system models was determined (based on predicted changes in the physical environment) as exposure to hazard. The levels of exposure to climate hazards were classified as low, medium, high and very high using a fuzzy logic algorithm, allowing for the classification of multiple categories of exposure (temperature, pH, O_2 and POC flux) concurrently. Deepwater species that are likely to be among the most exposed to climate hazards are black scabbardfish, white hake, and beaked redfish. The least exposed species are Patagonian toothfish, sablefish, and Antarctic toothfish; however, exposure to hazard is still considered high to very high even for these relatively less exposed species.

Changes in habitat suitability

In the absence of full *in situ* observations of species' distributions over the area of interest, habitat suitability modelling can provide predictive estimates of species occurrence under existing or projected environmental conditions. Here, the utility of this approach is tested for assessing vulnerability to climate change. Habitat suitability models of three key VME indicator species and three commercially important deep-sea fish species were developed for the northeast and northwest Atlantic Ocean. *Lophelia pertusa*, *Madrepora oculata*, *Desmophyllum* spp., blackbelly rosefish, greater forkbeard and American plaice were assessed for the northeast Atlantic and *Acanella arbuscula*, *Acathogorgia* spp., *Paragorgia arborea*, beaked redfish, blackbelly rosefish and Greenland halibut were assessed for the northwest Atlantic. Predictions of suitable habitat were based on a set of terrain variables (slope, aspect, terrain ruggedness index, topographic position index and roughness) and environmental variables (POC flux to seafloor, dissolved oxygen concentration at the seafloor, pH concentration at the seafloor, and potential temperature at the seafloor) from the analysis described above, along with variation metrics (standard deviation, coefficient variation of the mean and linear detrended standard deviation). The maximum entropy model (Maxent version 3.4.0) was used to predict the habitat suitability of all species in the three different scenarios: 1951–2000, 2041–2060, and 2081–2100.

Habitat suitability under future climate conditions showed contrasting changes among species. Notably, with the exception of *Madrepora oculata* in the northeast Atlantic region, all VME indicator taxa were predicted to have their suitable habitat reduced inside the fisheries management areas by 2100. *Desmophyllum* spp. and *Lophelia pertusa* and all three fish species (blackbelly rosefish, greater forkbeard and American plaice) are likely to experience a decrease in the potential suitable habitat in the northeast Atlantic by 2081–2100, but with an increase in 2041–2060 for *Desmophyllum* spp. and *Lophelia pertusa*. In contrast, *Madrepora oculata* is predicted to experience an increase in suitable habitat for both future periods. In the northwest Atlantic, the model outputs predict a decrease in the suitable habitat for all VME species evaluated (*Acanella arbuscula*, *Acanthogorgia* spp. and *Paragorgia arborea*) in both modelled periods, but with an intermediate period increase in suitable habitat for *Paragorgia arborea*. By 2081–2100, Greenland halibut and blackbelly rosefish are expected to experience a decrease in suitable habitat, but an increase for the intermediate period (2041–2060), whereas beaked redfish suitable habitat should increase over both periods. For five out of the six northwest Atlantic species modelled, outputs predict a distribution shift towards higher latitudes but no marked depth changes.

The POC flux was identified as an important variable for *Desmophyllum* spp., *Lophelia pertusa*, *Madrepora oculata*, *Acanella arbuscula*, *Paragorgia arborea*, American

plaice, Greenland halibut and beaked redfish, while dissolved oxygen was an important variable for *Desmophyllum* spp., *Lophelia pertusa*, *Madrepora oculata*, blackbelly rosefish and American plaice. Temperature was important mostly for deep-sea fish and *Acanella arbuscula* in the northwest Atlantic, and both temperature and pH were important for most species in the northeast Atlantic.

Vulnerability of fisheries species

Vulnerability and risk of impact were determined for 41 deep-sea fishes and invertebrates targeted by commercial fisheries in the 2000s. Calculations were made using a set of heuristic rules that describe a relationship between life-history traits and expected levels of sensitivity, adaptive capacity and vulnerability. All species are predicted to experience a high level of climate hazards, with risk of impacts by 2100 being on average 13 percent higher than the risk by 2050. The most vulnerable taxa were Antarctic toothfish, yellowtail flounder and golden redfish, a result of larger body size and narrow thermal tolerance. Their high vulnerabilities and the high exposure to hazards result in high level of risk of impacts by the middle and end of the twenty-first century. Least vulnerable are argentine shortfin squid, argentine and blackbelly rosefish. Vulnerable species were most concentrated in the northern Atlantic Ocean and the Indo-Pacific region, but also in offshore West Africa and in the south Pacific. High vulnerability in the Antarctic region results from the high vulnerability of Antarctic toothfish.

Gaps and challenges

Key challenges identified in addressing climate impacts on deep-sea habitats, fish and fisheries at 200–2 500 m involve:

- Mismatch in spatial scales of global and regional climate modelling and scales of VME designation.
- Failure of climate models to account for the non-linear response of ecosystems resulting from the combination of stressors and species interactions.
- Scarcity of long-term climate observations in the deep ocean needed to verify models, capture periodicity and short-term events, and to further mechanistic understanding, particularly at the seafloor in areas where VMEs occur.
- Limited availability of oxygen and other biogeochemical sensors on Argo Floats and other platforms.

An integrated oceanographic–ecological approach is essential to predict ecosystem response to climate change at the bathyal depths of concern here, where mesoscale features interact with long-term trends and result in a complex combination of factors generating instabilities. It is necessary to understand taxon response mechanisms and predict future ecosystem responses to the changes occurring, based not only on exposures to climate change stressors, but also the critical roles taxa play in ecosystems. Alterations in physiological state, energy acquisition, growth, reproduction, behaviour, and species interactions of these critical taxa will affect the distribution of species, ecosystem functions and, ultimately, the services they provide. Relevant knowledge may be gained from new tools, such as those revealing gene expression under climate variation, providing geochemical proxies for exposure and condition, or adopting acoustic, environmental DNA and animal tags to evaluate distributions. Manipulative experiments, rate measurements and time-series imaging, enabled through mobile platforms and small-scale observatory facilities, offer new insights. Advances will require combined expertise of deep-sea physical oceanographers, biogeochemists, ecologists and fisheries experts, and potentially integration of large, deep-ocean observing programmes (e.g. Argo, Biogoechemical Argo, Deep Argo, GO-SHIP Sites and cabled observatories). The RFMOs may seek expertise and advice from international "translational" networks, such as DOSI, the Deep Ocean Observing Strategy, and the International Network for

Scientific Investigations of Deep-sea Ecosystems, to meet the management challenges of climate-induced fish migrations, changes in abundance, VME hazards, and maintaining the integrity and resilience of deep ecosystems.

As shifts in fish stock distribution and changes in migratory behaviour occur in response to climate change, fisheries management will face challenges and have adapt in order to maintain the objective of optimum utilization of the fishery resources and safeguarding the marine ecosystems. Fish movements and changing distributions will result in changes to the location of the fisheries, new fisheries, and new impacts on both fish stocks and the biotic environment that require mitigation. This will unavoidably require more adaptive decision-making procedures in RFMOs than are currently in place. Contracting parties within the high-seas and national management bodies will need to work together to ensure joint management. Scientists, in turn, are challenged to deliver proper and adequate information on the ecosystem changes well in advance of the foreseen changes. New approaches are needed to communicate the nature of required information to scientists, and once the science is generated, to facilitate the flow of scientific information to managers and to enhance science–policy communication.

Climate change can be incorporated into RFMO management actions through: (i) more rigorous impact assessments of new fisheries that incorporate climate as a cumulative impact; (ii) a more thorough review process prior to allowing new fisheries to develop; (iii) strengthened monitoring and mapping of bottom-fishing areas by gear and species associated with VMEs vulnerable to climate change; (iv) identification of areas to be more intensely monitored for fishing impacts on the environment; and (v) broadening of VME indicator species reporting to include all encounters, and of bycatch species reporting, with the objectives of preventing further significant impacts and of monitoring the effects of climate change. Science needs include increased deep-ocean observing, particularly around existing and exploratory RFMO fishing areas and VME closures, and more scientific research on the vulnerability and adaptability of key habitat-forming species and fisheries species to changing deep-ocean conditions. Collaboration by RFMOs and state with scientific networks and with industry will be needed to achieve these goals. Ultimately, sustainable management will require cooperation across jurisdictional boundaries, sectors and disciplines, and a forward-looking commitment to sustaining deep-sea ecosystem services.

1. Introduction to deep-sea fisheries, vulnerable marine ecosystems and the science–policy–management interface

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This publication focuses on the effects of climate change in the deep ocean as they might influence benthic ecosystems and associated bottom fisheries in the deep seas. It will assist states in the implementation of United Nations General Assembly (UNGA) resolutions (UNGA Res.) adopted since 2006 calling upon states to manage bottom fisheries in the high seas to prevent significant adverse impacts on vulnerable marine ecosystems (VMEs), and to close areas to bottom fishing where VMEs are known or likely to occur unless the fisheries can be managed to prevent significant adverse impacts on VMEs. The publication also serves to support the FAO International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO DSF Guidelines; FAO, 2009), negotiated under the auspices of FAO to assist states in the implementation of the UNGA resolutions. The UNGA in its resolution 64/72 (and subsequent resolutions) called upon states to implement the FAO DSF Guidelines to sustainably manage fish stocks and protect VMEs from destructive fishing practices (article 113).

Deep-sea fisheries are here regarded as commercial fisheries in waters of about 200–2 500 m depth using types of fishing gear that come into contact with the seafloor during the normal course of fishing operations. This includes bottom trawls, bottom-set longlines, gillnets, pots and traps. Also included here are fisheries using deep mid-water trawls that operate close to the seafloor catching bentho-pelagic species, such as alfonsino, that live in and form part of the deep-sea ecosystem.

These fisheries target a range of fish, shellfish and mollusc species that live on or close to the seafloor. This includes various gadoids, redfish, hake, skate, shrimp, Greenland halibut and other flatfish, toothfish, and many more (Table 1). Most of the species caught in deep-sea fisheries have a relatively high value, and this offsets the relatively high costs of fishing them. Trawls are the most common type of gear used, with the bottom trawls generally contacting the seafloor with the doors, bridles and footropes. In addition, deep mid-water trawls commonly target certain demersal fish species, although these gear types do not have prolonged contact on the seafloor during normal use. Bottom-set longlines, pots and gillnets are also used, although the latter are becoming less common owing to bans to prevent undesirable bycatch and ghost fishing.

TABLE 1
Top 25 demersal fish species caught in the high seas, 2014

Species	Quantity caught (tonnes)
Rockfish *Sebastes* spp. and other sebastids in north Pacific	38 883
Shrimps (deepwater including blue & red shrimp, giant red shrimp, deepwater rose shrimp)	30 500
Longtail southern cod	24 000
European hake	20 400
Argentine hake	19 009
Atlantic cod	15 894
Argentine shortfin squid	15 023
Snow crab	9 354
Greenland halibut	8 622
Alfonsinos	8 158
Northern shrimp	7 210
Roundnose grenadier	4 738
Thorny skate	4 445
Antarctic toothfish	3 738
Orange roughy	3 207
Yellowtail flounder	2 536
Patagonian toothfish	2 115
Pacific armourhead	2 059
Portuguese dogfish	1 265
Roughhead grenadier (rough rattail)	658
Unidentified marine fish	549
Baird's smooth head	490
Black scabbardfish	333
White hake	273
Atlantic halibut	200

Notes: The catches are from various sources and are estimated as actual high seas catches.

The United Nations Convention on the Law of the Sea of 10 December 1982 (UNCLOS) refers to the "high seas" as all parts of the sea that are not included in the exclusive economic zone (EEZ), in the territorial sea or in the internal waters of a state, or in the archipelagic waters of an archipelagic state (article 86). Under UNCLOS, states have the right to fish the high seas subject to various obligations, one of which is to "take into consideration the effects on species associated with or dependent upon harvested species with a view to maintaining or restoring populations of such associated or dependent species above levels at which their reproduction may become seriously threatened." (article 119.1[b]). General concerns about possible negative effects on the seafloor caused by bottom-fishing gear were raised in the 1990s. This eventually led to the pivotal UNGA Res. 61/105, adopted in 2006, that called for regional fisheries management organizations or arrangements (RFMOs) to identify known or likely areas containing VMEs and ensure through a range of bottom-fisheries measures that significant adverse impacts (SAIs) were prevented. The process has been ongoing since 2006 (since 2004 in the case of the North East Atlantic Fisheries Commission (NEAFC)), aided by the FAO DSF Guidelines, with many regions adopting preventive measures. In 2016, the UNGA reviewed the implementation of the previous resolutions committing states to protect deep-sea ecosystems from the harmful impacts of bottom fisheries. In UNGA Res. 71/123, adopted in December 2016, the UNGA reaffirmed the importance of the FAO DSF Guidelines and called for full implementation of its provisions related

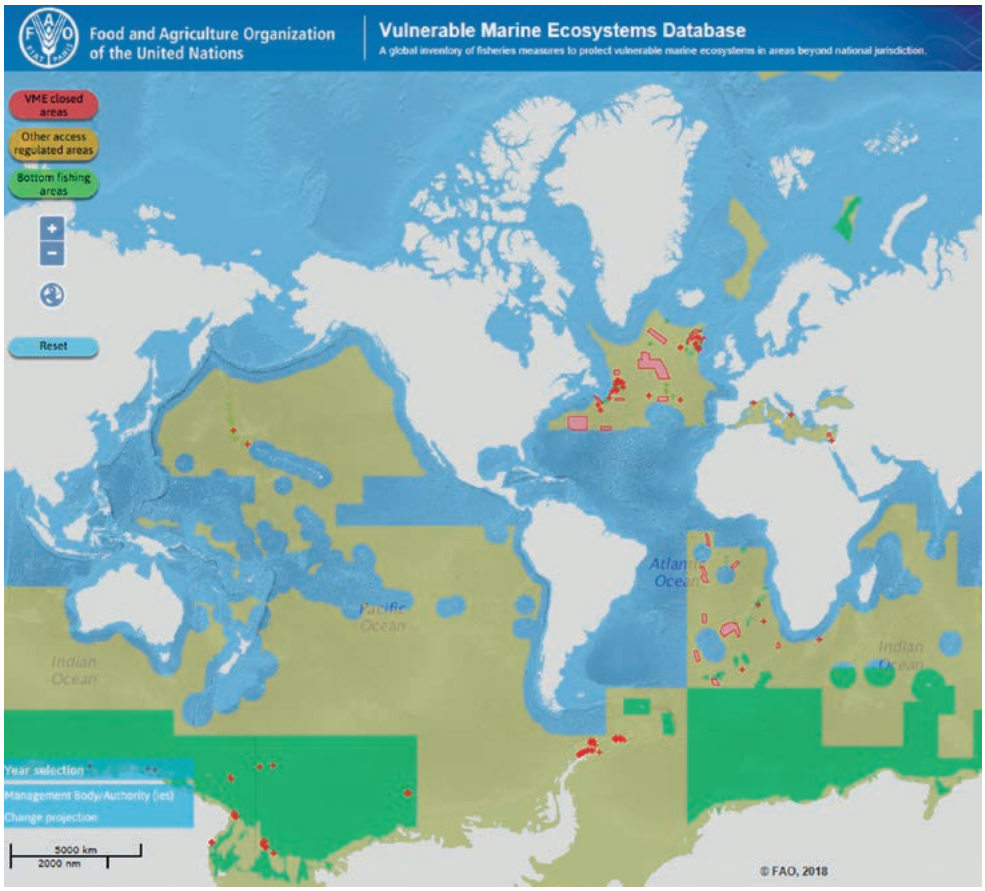
to assessing the impacts of bottom fisheries, including: cumulative impacts, identifying areas where VMEs occur or are likely to occur, and the assessment of SAIs. In addition, among other things, the UNGA called on states and RFMOs to "take into account the potential impacts of climate change and ocean acidification in taking measures to manage deep-sea fisheries and protect vulnerable marine ecosystems" (UNGA Res. 71/123, paragraph 185). Climate change can have both direct and indirect effects on the protection of VMEs from SAIs from fisheries using bottom-contact gear.

Deep-sea fisheries can occur anywhere where the ocean is sufficiently deep, and there is no unified acceptance of where the limits are. The upper limits merge with the fisheries occurring on the continental shelf, and the lower limit is down to where there are effectively no species that can support a commercial fishery. In general, deep-sea fisheries are often associated with the high seas where management is not under the control of any single state (FAO, 2009).

In most regions, the management of bottom fisheries in the high seas is under the control of RFMOs. These bodies operate under multilateral conventions among members that are coastal states, flag states of fishing nations operating in the region, and less commonly, other nations. With the exception of the southwest Atlantic, all regions with significant bottom fisheries are managed by RFMOs (Figure 1). In the Southern Ocean, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has a broader remit and is responsible for the ecosystem in more general terms, including fisheries management. The western and eastern central Atlantic regions have advisory bodies, although they have no significant bottom fisheries in the high seas.

FIGURE 1

Global map of high seas areas managed by RFMOs to protect VMEs



Note: Green = existing bottom-fishing areas; orange = areas outside of existing bottom-fishing areas where bottom fishing is currently closed and exploratory fishing protocols apply; red = VME areas closed to bottom fishing.
Source: FAO VME Database (www.fao.org/in-action/vulnerable-marine-ecosystems/vme-database/en/vme.html).

In a fisheries context, VMEs are areas of seafloor that have some or all of the following characteristics: uniqueness or rarity, functional significance of the habitat, fragility, life-history traits and structural complexity that makes recovery slow (FAO DSF Guidelines, paragraph 42). They are typically in waters of 200–3 000 m depth and are often associated with an underwater topographic feature, usually with associated water currents such as a seamount, canyon, steep slope, seep or vent. The objective for the management of fisheries using bottom-contact gear is to prevent SAI that would compromise the ecosystem integrity of a VME by: (i) impairing the ability of affected populations to replace themselves; (ii) degrading long-term natural productivity; or (iii) causing, on more than a temporary basis, significant loss of species richness, habitat or community types (FAO DSF Guidelines, paragraph 17). In response, RFMOs, with some differences among regions, have adopted the following measures (noting the relevant paragraphs from the FAO DSF Guidelines in each case).

Existing bottom-fishing areas identified and delineated – usually using historical positional information on fishing locations over a period of 4–20 years above some minimum lower threshold limit. This typically includes almost all areas fished at any effort level and with any bottom-fishing gear type. The areas where high levels of fishing activity occur usually occupy less than 5 percent of the existing fishing area. Changes in the areas of high activity can occur seasonally or among years in response to changes in stock abundance and distribution or other factors. Often, considerable knowledge exists within the existing bottom-fishing areas about fish stocks and VMEs. Outside these areas, but still within the convention area of each region (RFMO) are areas that have had little or no bottom fishing, and effectively none within recent years. Generally, little is known about fish stocks (if any) and VMEs in these areas (although benthic surveys have been conducted in some). (FAO DSF Guidelines, paragraphs 21, 23 and 32).

Exploratory fishing protocols (with impact assessments) for new fisheries recognize that limited information is available outside of the existing bottom-fishing areas, and provide for the progressive collection of information to ensure that the fishery does not develop more rapidly than the knowledge available to assess and control it. Protocols usually apply to all bottom fishing outside of the existing fishing areas and to fishing inside the existing fishing areas with a new gear type or with substantially increased effort. The exploratory fishing protocol takes the form of an initial assessment by the contracting party requesting approval to start a new fishery, which is reviewed by the RFMO scientific committee, and then forwarded to the commission for approval. Impact mitigation measures and restrictions may be placed on the new developing fishery. The fishery is subject to strict observer and data collection requirements, and is typically reviewed over a two-year period. If it is found to be sustainable and not causing SAIs to VMEs, then the designation of the new area may be changed to become an existing fishing area. (FAO DSF Guidelines, paragraphs 23, 55, 61 and 65).

VME encounter protocols – are used to identify evidence of VMEs during the course of normal bottom-fishing operations. In the early stages of a fishery, information is generally insufficient to identify, map and close all VMEs; thus, encounter protocols provide for the progressive collection of such information as bottom fishing occurs in unmapped areas. If VME indicator species are taken above a threshold level, this is construed to be evidence of a VME. The vessel may then be required to move away from the location of the capture, although the implementation of such "move-on rules" varies among RFMOs and nations. While VME indicator species cover a wide range of benthic species, they are most commonly species of coral or sponge. The threshold levels have been generally set to indicate that fishing has been through a high density of benthic organisms, although levels do vary greatly by region. (FAO DSF Guidelines, paragraphs 21, 23, 32, 35, 61, 64, 67, 68 and 69).

VME and other benthic closures – areas that are known or likely to contain VMEs are often closed to bottom-fishing activities, and they often include dense aggregations of fauna on topographical features. The early closures adopted around 2006–08 were based on historical catches of corals and sponges, usually from scientific research cruises but sometimes from commercial fisheries. Many of the closures were precautionary, especially when concerning seamounts. Later closures have relied more on extensive dedicated scientific surveys (especially in the north Atlantic). Model predictions provide support information especially in areas that have not been surveyed (notably in the southwest Pacific). However, many of the closures are still precautionary. Usually, only bottom-contact fishing gear types are prohibited, and sometimes only bottom trawling is prohibited. The VME areas can be closed to bottom fishing and deep mid-water trawl gear, recognizing that deep benthic fish species are also part of the demersal community. In some cases, all bottom and pelagic gears are prohibited, which simplifies enforcement. The closures apply only to fisheries controlled by the deep-sea RFMOs; they do not apply, for example, to tuna and other pelagic fisheries that are managed by other international bodies. The purpose of the closures is to prevent SAIs resulting from fishing with gear types that contact the seafloor. The VMEs specifically closed to bottom fishing are shown in Figure 1, although it should be noted that bottom fishing is not allowed in most areas outside historical fishing areas. (FAO DSF Guidelines, paragraphs 14-19, 42–52 and 63).

The management of bottom fisheries by RFMOs is undertaken thorough measures and regulations adopted by a committee of managers, usually called the commission, fisheries commission, or meeting of parties. These are specific to the RFMO and apply to a specific region within the high seas (northeast Atlantic, Southern Ocean, etc.), and are binding on members of that RFMO. Many of these regulations apply to well-established historical issues, such as the assessment of fish stocks and setting of catch limits. However, new issues can be considered by a commission, and these can be initiated by concerns raised through UNGA resolutions, contracting parties and the scientific committees. The VME issue is an example that entered the commissions around 2006 following UNGA Res. 61/105. Once within the commission, the process typically involves a request for advice from its scientific committee (which is usually an internal body, but can be external, for example, as with the NEAFC). The issue is discussed by contracting parties, the scientific committee and the commission until such time that the commission, if appropriate, decides to adopt measures controlling the fisheries under their competence.

Issues relating to climate change were discussed by the commission and scientific committee in the CCAMLR (Southern Ocean) regarding the krill fishery and degree of ice cover as early as 2009 (see commission and scientific committee reports).[2] The CCAMLR also held a Joint Committee for Environmental Protection (of the Antarctic Treaty) – Scientific Committee Workshop on Climate Change and Monitoring in Punta Arenas, Chile, on 19–20 May 2016.[3] In the last few years, the General Fisheries Commission for the Mediterranean (GFCM) has considered the effects of climate change on aquaculture, and to a lesser extent on fish stocks, and held a joint GFCM, FAO Fisheries Department and World Wildlife Fund (WWF) side event on assessing the potential effects of climate change on Mediterranean and Black Sea fisheries and ecosystems, and has a workshop planned on the same topic (FAO, 2017). The deep-seas RFMOs in the other regions have either not discussed climate change or only made general references and a consideration for future work plans. The International Council for the Exploration of the Sea (ICES), which provides scientific advice to the NEAFC upon request, is scheduled to hold a joint symposium in June 2018 with the North Pacific Marine Science Organization (PICES) titled Strategic Initiative on Climate

[2] See: www.ccamlr.org/

[3] See: https://ats.aq/documents/ATCM39/wp/atcm39_wp053_e.pdf

Change Impacts on Marine Ecosystems.[4] The ICES also has a working group with PICES on Climate Change and Biologically-driven Ocean Carbon Sequestration.[5]

This technical paper represents a collaboration between the Deep Ocean Stewardship Initiative (DOSI)[6] and the FAO ABNJ Deep-seas and Biodiversity project. The project was initiated during a workshop held in Woods Hole, the United States of America, on 26–27 August 2017, with representatives from the DOSI Climate Change and Fisheries Working Groups, and multiple RFMOs participating. A workshop summary, agenda and list of participants can be found in Appendix 1.

The objectives of this technical paper are to evaluate the potential impacts of climate change on deep-sea ecosystems and the implications for the management of deep-sea fisheries. To this end, information has been compiled and scenarios modelled that: (i) define major climate change features that affect the deep ocean and its biodiversity, and discuss mechanisms by which these might affect fish and fisheries; (ii) provide paleo examples of deep-sea ecosystem response to climate change; (iii) generate global climate projections of change, variability, exposure hazard and time of signal emergence for temperatures, oxygen, acidity scale (pH) and particulate organic carbon (POC) flux at the seafloor, and across various features (e.g. canyons and seamounts) within RFMOs; (iv) identify VME criteria, traits that define vulnerability to climate change, and which VME indicator species are most vulnerable; (v) quantify exposures and hazard for fisheries species and for VME indicator species; (vi) summarize the linkages between VMEs, fish and fisheries; and (vi) synthesize the implications for management by RFMOs. The publication also summarizes major data gaps and observations needed to fully assess risks and advance management under climate change and identify programmatic linkages that could help fill these gaps. This technical paper is a first step towards incorporating complex changes in the deep-sea environment into international management actions.

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[4] See: www.ices.dk/community/groups/Pages/SICCME.aspx
[5] See: www.ices.dk/community/groups/Pages/WGCCBOCS.aspx
[6] See: http://dosi-project.org/

2. Climate change: overview and drivers

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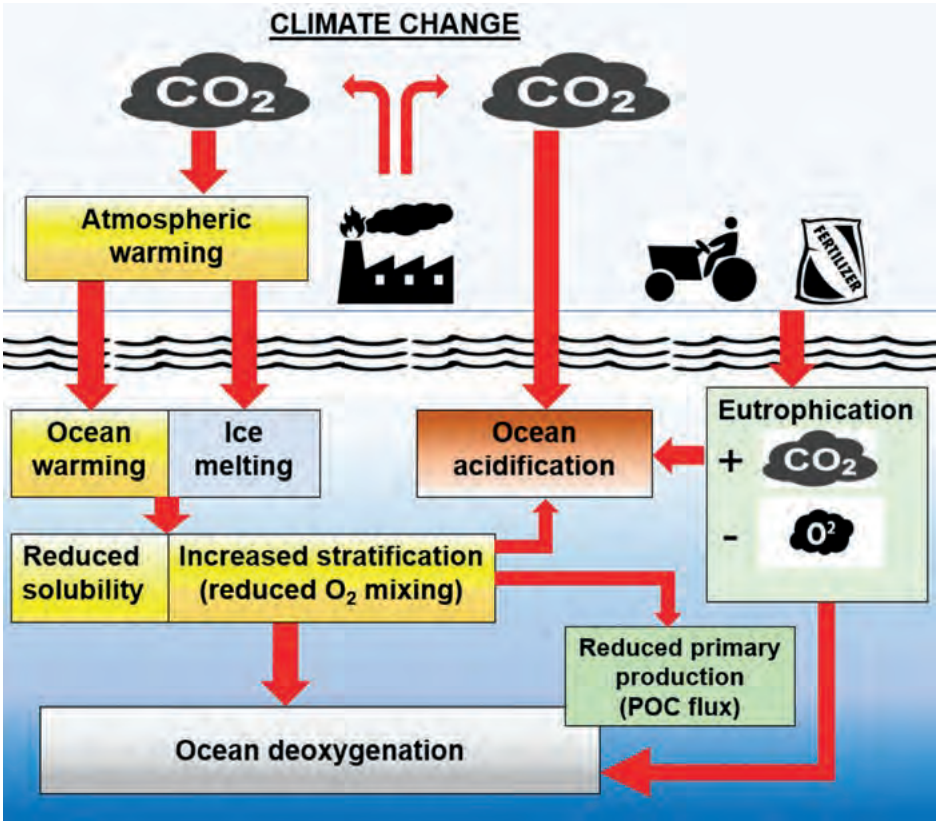
The chapter provides a brief introduction to the underlying causes of climate change in the deep ocean, and the mechanisms by which these affect deep-ocean ecosystems (Figure 2). Climate change is interpreted in the broad sense here and incorporates the many changes in ocean environments linked to atmospheric and ocean warming and/or ocean acidification, including oxygen loss, changes in POC flux to depth, altered hydrodynamics and circulation, as well as bentho-pelagic coupling.

FIGURE 2
Elements of climate change that affect the deep ocean



Ocean warming

Rising concentrations of CO_2 and other greenhouse gases and compounds (such as methane, nitrous oxide, tropospheric ozone, and hydrofluorocarbons) as well as particulates (black carbon) in the atmosphere act to trap heat by absorbing the infrared radiation, resulting in the warming of both the land and the ocean (Doney *et al.*, 2012). The ocean has played a primary role in taking up this excess heat, largely in the surface ocean to 700 m, but with significant uptake and storage in the deep ocean (Purkey and Johnson, 2010; Mauritzen, Melsom and Sutton, 2012). This leads to a large heat imbalance, with ocean warming accounting for 93 percent of this uptake from 1971–2010 (Rhein *et al.*, 2013).

Ventilation processes are key to understanding the changes in conditions in the ocean interior and the pathways, rates and temporal variation responsible (Talley *et al.*, 2016). Transient tracers, such as chlorofluorocarbons, sulphur hexafluoride, bomb tritium, and some radiocarbon, have provided important insights into the relative importance of physical processes such as stratification, solubility and mixing, thermohaline circulation and biological processes such as respiration and remineralization influencing changes since the mid-1900s. Reduction in classical Labrador seawater formation and strength of the subpolar gyre, global air–sea CO_2 exchange rates and ocean ventilation rates provide examples of some of the inferences gained (Talley *et al.*, 2016, and references therein).

The upper ocean (0–2 000 m) warmed between 1955 and 2010 by about 0.09 °C, representing 24.0 ± 1.9 × 1022 J (±2 SE) (Levitus *et al.*, 2012). More than half of this heat uptake has taken place since 1997, with more than one-third of this uptake below 700 m (Glecker *et al.*, 2016). This amount of heat uptake is equivalent to a "16-kiloton TNT" nuclear bomb exploding every second for 100 years. Argo floats, which measure temperature to 2 000 m, reveal that this warming is highly heterogenous, affected by water mass circulation, winds, and natural climate variability (Roemmich *et al.*, 2015). Repeat hydrography (Global Ocean Ship-based Hydrographic Investigations Program (GO-SHIP) – Talley *et al.*, 2016), which surveys the deep ocean every five years, has documented warming in the deep ocean. Warming of about 0.03 °C per decade has occurred in basins around Antarctica, representing 19 percent of the global increase of 183 TW from 1972–2008 (Church *et al.*, 2011). GO-SHIP documents the chemical properties associated with upper ocean ventilation as well as changes in abyssal circulation and transport (Talley *et al.*, 2016).

Ocean deoxygenation

Recent compilations of observational data reveal that, globally, the ocean has lost 2 percent of its oxygen, although regional losses can be much greater (Schmidtko, Stramma and Visbeck, 2017). Warming of the ocean contributes to open-ocean oxygen loss in multiple ways, primarily through changes in solubility and through stratification, which reduces transport of oxygen from surface to subsurface waters (Keeling, Korzinger and Gruber, 2010; Levin, 2018). Warming also raises respiration rates, leading to higher oxygen consumption when organic carbon is not limiting (Levin, 2018).

Less oxygen dissolves in warmer seawater, as per Le Chatelier's principle. For example, a shift from 4 °C to 6 °C can lead to loss of 14.7 µmol kg^{-1} O_2 (Brewer and Pelzer, 2016). Solubility change accounts for about 15 percent of open ocean oxygen loss recorded in the post-industrial era, but almost half in the upper 700 m (Schmidtko, Stramma and Visbeck, 2017).

Warming intensifies ocean stratification by increasing the strength of both thermal density gradients and salinity gradients (via ice melting and elevated freshwater input). Increased stratification reduces vertical mixing of oxygen into the ocean interior, and is attributed with about 85 percent of global open ocean oxygen loss (Helm, Bindoff and Church, 2011). Oxygen inventories are a balance between supply and demand.

Increased stratification also suppresses upwelling and input of nutrients to surface waters. A resulting reduction in surface production can reduce biological oxygen demand from microbial respiration of sinking material, counteracting the stratification effects that reduce ventilation. At the same time, warming will increase respiration rates. For example, a 2 °C increase in temperature can raise respiration rates by 29 percent (Brewer and Pelzer, 2016). The balance among these different processes varies regionally, and how this will affect future oxygen conditions in deep water is still not well understood.

Beyond the direct influence of CO_2-driven warming discussed above, there are less direct influences on ocean oxygenation. Foremost among these are inputs of nutrients associated with human activities. Inputs of nitrogen, phosphorus and organic wastes from watersheds into the coast may be exacerbated by effects of warming on precipitation and vegetation processes, leading to greater eutrophication and oxygen drawdown in coastal waters; but exchanges with waters beyond 200 nautical miles are poorly documented. In contrast, airborne transport of nitrogen and iron from land can act to fertilize the open ocean and ultimately influence oxygenation (Ito *et al*., 2016). Changes in circulation, winds and upwelling can all influence the regional transport of waters with nutrients or low oxygen; such changes may or may not be linked to climate change. Major oxygen losses have been attributed to strengthening of the California undercurrent in southern California, the United States of America (Bograd *et al*., 2015), and to strengthened influence of north Atlantic central waters in the Saint Lawrence Estuary, Canada (Gilbert *et al*., 2005). Warming on margins may act to dissociate buried gas hydrates (James *et al*., 2016); resulting methane release can act to cause oxygen drawdown through aerobic methane oxidation at the seafloor or in the water (Boetius and Wenzhöfer, 2013). Any methane reaching the atmosphere acts as a powerful greenhouse gas, further warming the atmosphere.

Further oxygen reduction in the ocean interior, where oxygen levels are already low, can induce many biogeochemical feedbacks that exacerbate deoxygenation. Examples include release of nitrous oxide via denitrification, which acts to intensify greenhouse conditions, and production of hydrogen sulphide from sediments, which is highly toxic to most life. Warming might raise the rates and alter locations or depths of animal oxygen consumption, while greater hypoxia might suppress the metabolism of some species. However, many questions remain about the magnitudes and even mechanisms of these feedbacks, in part explaining why oxygen projections under future climate scenarios are so variable (Oschlies *et al*., 2017; Levin, 2018).

Carbonate system changes (ocean acidification)

The oceans absorb one-quarter of the anthropogenic CO_2 emitted to the atmosphere, acting as a major sink for anthropogenic carbon (Orr *et al*., 2001; Sabine *et al*., 2004). While this has played an important role in helping to mitigate the atmospheric effects of climate change, it has resulted in significant effects on seawater carbonate chemistry. When dissolved CO_2 reacts with seawater, it reduces seawater pH (resulting from the release of hydrogen ions H^+) and the concentration of carbonate ions (CO_3^{2-}), a process termed ocean acidification.

Since the pre-industrial era, the average surface ocean pH has declined by 0.1 units (corresponding to ~26 percent increase in acidity; Ciais *et al*., 2013), and it is predicted to decline by an additional 0.3–0.4 units by 2100 (100–150 percent increase in acidity) if CO_2 emissions continue in a business-as-usual scenario (Representative Concentration Pathway (RCP) 8.5 CO_2 emission scenario) (Orr *et al*., 2005; Orr, 2011; Ciais *et al*., 2013). The actual change will depend on future CO_2 emissions, with both regional and local variations in the oceanic response (Ciais *et al*., 2013).

While the projected changes are largest at the ocean surface, the penetration of anthropogenic CO_2 at depth will also alter the chemical composition of the deep

ocean (Cao *et al*., 2014; Zheng and Cao, 2014; Sweetman *et al*., 2017). Recent model projections by Sweetman *et al*. (2017) suggest that bathyal depths (200–3 000 m) worldwide will undergo the most significant reductions in pH in all oceans by 2100 (by 0.29–0.37 pH units) as a result of the entrainment of CO_2-rich seawater to the seafloor at sites of bottom-water formation. In addition, subduction of high-CO_2 waters via thermohaline circulation is contributing to acidification in the north Atlantic, with predictions of more than 17 percent of the seafloor area below 500 m depth experiencing pH reductions exceeding 0.2 units by 2100 (Gehlen *et al*., 2014; Sweetman *et al*., 2017).

Model projections also show large decreases in carbonate ion concentrations and, thus, the calcium carbonate saturation state (Ω) in seawater throughout the world oceans (Orr *et al*., 2005; Ciais *et al*., 2013; Zheng and Cao, 2014). In seawater, Ω is the critical parameter with respect to the precipitation and dissolution of calcium carbonate mineral forms (e.g. aragonite and calcite). Solubility increases at higher pressure and lower temperature, which means that Ω decreases with increasing water depths and at higher latitudes. The depth at which $\Omega = 1.0$ is the saturation horizon, a naturally occurring boundary. When $\Omega > 1$, seawater is supersaturated with respect the carbonate ion and carbonate precipitation is favoured; in contrast, when $\Omega < 1$, the seawater is undersaturated and dissolution is favoured. Currently, the vast majority of the surface ocean is supersaturated with respect to calcium carbonate while most of the deep ocean (below 1–2 km) is undersaturated (Ciais *et al*., 2013).

Zheng and Cao (2014) model simulations suggest that the volume of ocean with supersaturated waters will decline from 19 percent in the pre-industrial era to 5–11 percent in 2100 under the business-as-usual scenario (RCP8.5) to the high mitigation scenario (RCP2.6). By 2300, more than 98 percent of the ocean is projected to be undersaturated under the RCP8.5 scenario. The decrease in surface carbonate ion concentrations will be largest at low and mid-latitudes which are naturally rich in this ion, although carbonate undersaturation is projected to occur at high southern latitudes first, where carbonate ion concentration is lower (Ciais *et al*., 2013).

As subsurface saturation state declines, the depth separating undersaturated from oversaturated waters moves upwards (shoals). Averaged over the whole ocean, the aragonite saturation horizon of aragonite (ASH) is projected to increase from a depth of 1 138 m in the pre-industrial period to 308 m in 2100 under the RCP8.5 scenario (Zheng and Cao, 2014). At the oceanic scale, by 2100 the ASH is projected to shoal from 200 m to 40 m in the subarctic Pacific, from 1 000 m to the surface in the Southern Ocean, and from 2 085 m to 150 m in the north Atlantic (Orr *et al*., 2005; Orr, 2011; Ciais, 2013). The undersaturation is more extreme towards the poles, with surface seawater becoming undersaturated in the Arctic and the Southern Ocean as soon as the mid-twenty-first century (Steinacher *et al*., 2009; Zheng and Cao, 2014).

Marine calcifying organisms inhabiting cold waters and deep areas may be particularly sensitive to projected changes in carbonate chemistry. This is because there is low natural availability of the carbonate ion in these areas due to the higher CO_2 and lower pH of deep waters resulting from organic matter microbial respiration (Ciais *et al*., 2013; Roberts, Hennige and Vierros, 2016). Impacts on VMEs such as cold-water coral reefs may be of special concern as they inhabit water depths close to or at the saturation horizon and, thus, may be highly susceptible to ocean acidification (Orr *et al*., 2005; Guinotte *et al*., 2006). According to recent model simulations, during the pre-industrial period, 87 percent of cold-water coral reefs were surrounded by oversaturated seawater, while projections for 2100 suggest that 73 percent of cold-water coral reefs will suffer from undersaturated aragonite seawater due to the shoaling of the aragonite saturation horizon (RCP8.5 scenario, Zheng and Cao, 2014). Dissolution of the non-living matrix of cold-water coral reef habitat will occur in undersaturated waters (Hennige *et al*., 2015).

Changes in primary production and POC flux

Energy in the form of organic carbon is transferred to the deep sea mainly via the sinking of particulate organic carbon (POC), which is largely produced in surface waters as a result of photosynthetic primary production (via phytoplankton) and its consumption by zooplankton, generating secondary production by-products such as metabolites and unassimilated waste (faecal material), dead or dying plankton (Cavan *et al*., 2015). Several processes are considered to modulate the sinking rate of particulates, including aggregation of organic particles and inorganic phytoplanktonic tests forming marine snow. The so-called "ballast effect" resulting from this aggregation is one of the most important factors modulating the sedimentation rate. Another important factor is the size of biological material being exported. Change in the size of dominant plankton cells and occurrence of jellyfish or salp blooms can have profound influence on the export of fresh organic matter to great depths (Smith *et al*., 2014). Rapid sinking of particles indeed means less degraded material arriving on the seafloor, with higher nutritional value. However, the processes that regulate precisely how much of the POC is transported to the deep sea are complex. Thermal stratification can reduce the depth of the surface mixed layer, favouring remineralization in the surface layers, which hinders the export of POC and nutrients to deeper water (Smith *et al*., 2013). As such it has been argued that any intensification in thermal stratification due to climate change would tend to reduce the export of POC from the photic mixed layer to the deep seafloor (Sweetman *et al*., 2017).

In contrast, Smith *et al*. (2013) observe changes in deepwater currents caused by increasing surface wind stress, resulting in greater nutrient upwelling off the coast of California, giving rise to increased primary production and subsequent POC export to the deep sea. More generally, stratification will play a role in regulating the extent of POC fluxes in the deep sea.

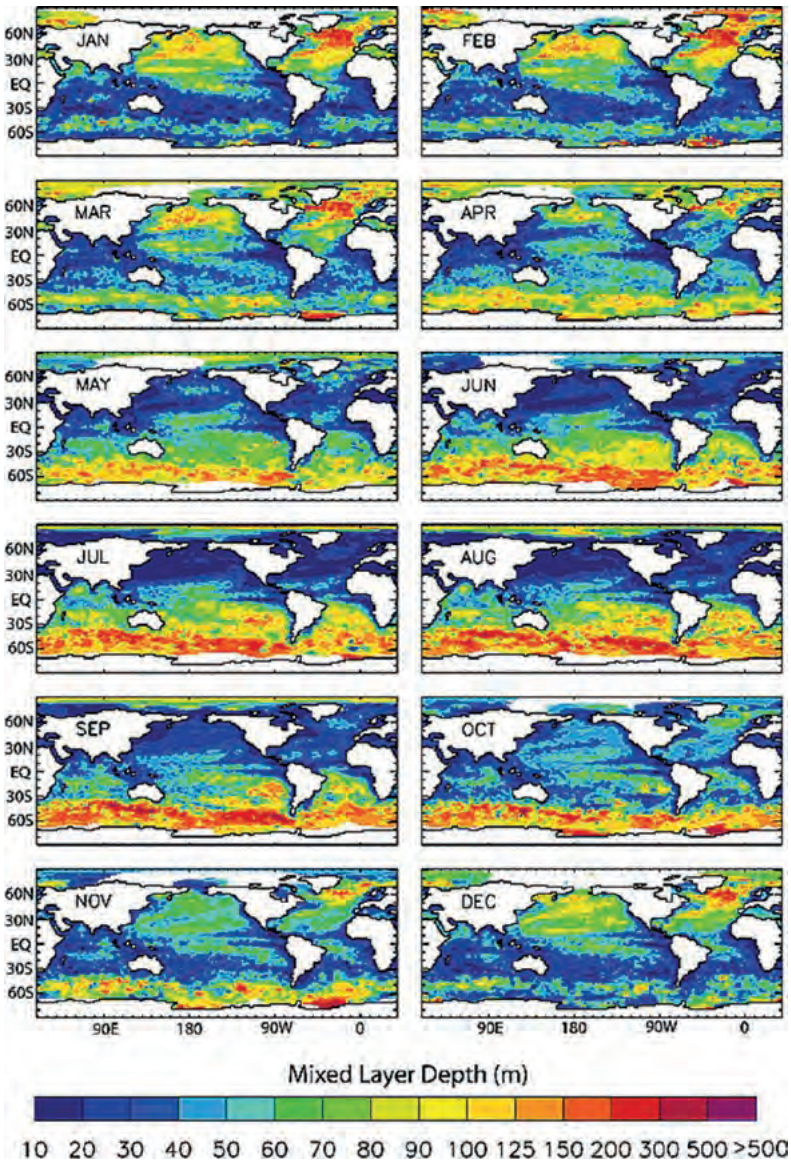
Climatology of the mixed layer depths (MLD) (Figure 3; de Boyer Montégut *et al*., 2004) shows that mixing under the effect of dominant winds exceed 200 m in large regions of the Southern Ocean, Arctic and north Atlantic. Both primary productivity in surface waters and the export of high-quality POC to depth are enhanced by MLD seasonal deepening. Change in ice cover will combine with changes in the wind regime to incr ease stratification and reduce those fluxes. Furthermore, mesoscale oceanographic features (as developed in the following section) can have influence at larger scales on POC exported at depth. In regions where deep abyssal waters are formed by the sinking of dense surface waters (e.g. the Artic and Southern Ocean, Greenland Sea and Mediterranean Sea) deep convection events can reach up to 2 000 m depth. While these extreme events occur on a multiannual basis, they play a significant role in the supply of resources to organic-carbon-limited, deep-sea ecosystems. In the Southern Ocean, fresh diatoms can be rapidly exported to bathyal and abyssal depths (Agusti *et al*., 2015), whereas in stratified areas the degradation of labile material at similar depths will be almost complete.

Change in mesoscale hydrodynamics

In some areas, long-term warming, acidification and deoxygenation trends in deep waters will be superimposed on changes in the mixing of surface and deep waters occurring on shorter timescales. Episodic vertical advection and mixing events exceeding 200 m depth significantly impact deep-sea ecosystems through their influence on: (i) the oxygen content and consumption rate, temperature and pH of deep waters; and (ii) surface primary production and export at depth.

Vertical mixing is regionally modulated on a seasonal basis by the fluctuations of the dominant wind regime (de Boyer Montégut *et al*., 2004), with a strong event-based dimension. Downwelling processes during episodes of strong winds favour the export of surface waters transporting organic material and oxygen to greater depths (Ivanov

FIGURE 3
Seasonal changes in mixed layer depth – an examination of profile data and a profile-based climatology



Source: De Boyer Montégut *et al.* (2004).

et al., 2004; Pusceddu *et al.*, 2013). One single event could lead to abrupt changes in deepwater mass properties, as observed for the East Mediterranean Transient, with major consequences on deep-sea ecosystem functions (e.g. Klein *et al.*, 2003). Changes in the intensity and frequency of the atmospheric regime still need to be assessed in future ocean models (Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5)), but they are expected to strongly influence deep-sea ecosystems in high-latitude regions or semi-enclosed basins and deep archipelagic seas.

On margins, storm events can generate massive transport of organic particles and coarse debris through surface water advection downslope (e.g. Sanchez-Vidal *et al.*, 2012). Strong hydrodynamic disturbances are also generated by dense shelf-water cascading events triggered by the increase in salt content and temperature decrease under cold wind regimes that propagate through canyons and across the slope to the abyssal plain. An extreme cascading event was shown to lead to temporary fishery collapse in the western Mediterranean Sea, followed by an increase in catches after several years (Company *et al.*, 2008). Storm-induced downwelling and dense shelf-

water cascading typically last less than one week and less than one month, respectively, and contribute predominantly to organic matter export to the bathyal and abyssal depths, particularly when they are channelled through submarine canyons (Canals *et al*., 2006; Ulses *et al*., 2008; Palanques *et al*., 2011; Thomsen *et al*., 2017).

In the open sea, abrupt "deep convection" events that follow a similar "pre-conditioning" loss of buoyancy under wind-forcing have been described to break the stratification and generate intense plumes; these are typically a few kilometres in size reaching down to as deep as 2–3 km (Houpert *et al*., 2016). The ventilation of deep layers occurs by replacing old deep waters by waters transported from the surface and is combined with rapid export of fresh planktonic material at depth. At the same time, large amounts of nutrients are brought to the surface, enhancing primary production. Hence, such events have large consequence for deep-sea POC export and the capacity of ecosystems to take advantage of these inputs. Deep convection occurs at high latitudes but also in the Greenland Sea, Labrador Sea, and western Mediterranean Sea in the Northern Hemisphere, and in the Weddell Sea in the Southern Hemisphere.

Another important wind-driven phenomenon expected to change under changing climate is the formation of mesoscale eddies. The consequence of these changes is variable. In oxygen minimum zone (OMZ) regions, these features were shown to transport and enhance mixing of low-O_2, low-pH mode waters at depth to at least 400 m, up to 1 500 km offshore (Stramma *et al*., 2014; Bettencourt *et al*., 2015). An increase in their frequency in a key area may periodically expose sessile organisms to stressful conditions while excluding migrating and mobile fauna. Another consequence of these gyres is the lateral transport of inorganic, organic and biological material (including larvae) across and among key ecosystems (Adams *et al*., 2011). Spatial and seasonal shifts in the formation of these gyres should also be considered, especially if they are expected to superimpose locally with other stressors.

These wind-driven hydrodynamic features combine with local upwelling and downwelling phenomena, as well as eddies formed where the dominant ocean circulation interacts with the seabed topography (such as in the proximity of seamounts and canyons) (Turnewitsch *et al*., 2013). Shoaling or deepening of the MLD results from local upwelling or downwelling processes on the shelf, modulated by seasonal fluctuations in the wind periods.

Bentho-pelagic coupling (physical, chemical and biological transport mechanisms)

Benthic-pelagic coupling is the exchange of energy, mass or nutrients between benthic (seafloor) and pelagic (water column) habitats. This coupling is crucial to functions ranging from nutrient cycling to energy transfer in food webs as well as habitat provision (nursery areas, etc.). Climate change will regulate directly or indirectly bentho-pelagic coupling through effects on the physical (salinity, temperature, turbulence), biogeochemical (nutrients, oxygen, CO_2), and biological (food delivery, species distribution, community composition) components of deep-sea ecosystems, as occurs in coastal and estuarine ecosystems (Griffiths *et al*., 2017).

The physical processes described above affect the quality and quantity of food supply to benthic and bentho-pelagic organisms, larval dispersal, sediment transport and deposition, and are ultimately dependent on the influence of seafloor topography (e.g. abyssal hills, knolls, seamounts, canyons and basins) in the deep sea. The consequences of these processes depend on local conditions, and they may be difficult to forecast as they involve complex mechanisms and non-linear responses. A reduction of periodic ventilation of deep-sea waters due to a reduction in strong vertical mixing will cause oxygen loss in intermediate waters, affecting the availability of oxygen at the sediment/rock-water benthic habitats (i.e. on the seamount or canyon flanks or in slope sediments). Conversely, an increase in intensity and frequency of vertical mixing will increase oxygen availability and the fluxes of labile organic carbon to the

deep layers and ocean floor. Locally, such phenomena, although intermittent and limited in time, may induce rapid shifts of deep-sea ecosystem structure and function. This can only be assessed by establishing the vulnerability of key ecosystem species to these abrupt changes that generate unique combinations of abiotic conditions that depart from seasonal means, and how the combination of changing parameters will affect ecosystem functions. In some cases, attenuation of climate stressor impact can be expected. The challenge is then to understand how these processes play out (e.g. reducing MLD will reduced surface PP and its degradation in deeper layers, reducing oxygen consumption).

Several examples show the effect of temperature increase and pH decrease on phytoplankton blooms, causing decreasing input of organic matter to the benthos, and consequently altering inorganic nutrient release from the sediment (Nixon *et al*., 2009). Taucher *et al*. (2017), showed that ocean acidification under oligotrophic conditions, or with an increased productivity due to upwelling, shifted the plankton community composition. This can have consequences for ecosystem productivity, biomass transfer to higher trophic levels, and biogeochemical elemental cycling in oligotrophic ocean regions, influencing the transport of organic matter to the bottom of the ocean.

A recent study of the Baltic coast and estuaries on how anthropogenic stressors can influence bentho-pelagic coupling showed that during hypoxia or anoxia the flow of organic material from the benthos to the pelagic ecosystem decreases (Griffiths *et al*., 2017). Decreasing the sedimentation (organic fluxes from pelagic primary producers to benthic habitats) will alter species distribution and composition, and, consequently, will also alter nutrient recycling. However, the biologically mediated couplings, such as bioturbation, suspension feeding and predation, will depend on functional traits and species resilience. Projections of changes in carbon export to the deep seafloor related to climate change were made by Jones *et al*. (2014), who predicted decreases in benthic biomass, affecting remineralization, bioturbation, and carbon burial (Smith *et al*., 2008). The biomass decrease will consequently alter the bioturbation capacity and nutrient recycling, which are key functions and services of this environment.

Tecchio *et al*. (2014) showed that both primary and secondary production processes taking place in surface layers are key drivers of deep-sea food web structure. Habitat and nursery provision function of bioengineering species will be affected by climate change, as calcifying structures will become more fragile (see section Carbonate system changes [above] and references therein). However, to fully understand these aspects, there is the need to conduct parallel pelagic and benthic studies at the same temporal and spatial scales.

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3. Lessons from palaeoceanography

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Rapid warming of deep-sea waters has occurred in the past, and this can be instructive to understanding the consequences of such events. The best record, with closely detailed micropaleontological data, is from the later Palaeocene, ~57 million years ago (mya), where the bottom waters at 2 100 m, slightly north of the Weddell Sea, Antarctica, underwent a rapid temperature change, from about 8 °C to 14 °C over a roughly 3 000-year period (Kennett and Stott, 1991). At the same time, oxygen declined to levels that were probably lower than those of the present (Dickson, Cohen and Coe, 2012). This event, known as the Palaeocene–Eocene Thermal Maximum, resulted in a 72 percent loss in benthic foraminifera species, including the loss of several functional groups. Ostracod functional diversity also dropped, with the remaining forms small and thin-walled. Isotopically light 13C values coincident with the rise in water temperature suggests that release of methane gas hydrates added its oxidation product, CO_2, to the atmosphere, which affected the whole ocean–atmosphere reservoir and precipitated a strong global rise in temperature (Bains, Corfield and Norris, 1999). Jenkyns (2003) suggested that similar rapid rises in ocean bottom temperatures have happened as far back as the Triassic–Jurassic boundary (~200 mya), each time accompanied by lighter ^{13}C isotope signatures, indicating increased flux of CO_2 into the atmosphere, subsequent warming of intermediate and deep waters, and concomitant changes in microfauna and nannofloral diversity (see Figure 6 in Jenkyns, 2003).

In the more recent past, Thiagarajan *et al.* (2013) found that populations of the deep-sea solitary coral, *Desmophyllum dianthus*, have waxed and waned over the last 40 000 years as the global ocean has been influenced by glacial advances and retreats. In particular, the concentrations of CO_3^{2-} and, O_2, and surface productivity, strongly influenced the distribution of the corals. From corals recovered at various depths on seamounts in both the north Atlantic and southwest Pacific, they discovered that coral populations responded to changes in the aragonite saturation depth, which has shoaled since the last glacial maximum, and they predict that future increases in atmospheric CO_2 will lead to a further decrease in suitable habitat for deep-dwelling, hard coral species and their associated benthic organisms.

Rapid responses, over a 10–1 000 year period, to warming and ocean deoxygenation have been recorded for both foraminifera and fossilizing invertebrates in cores from the Santa Barbara Basin. Extremophile taxa, including lucinid bivalves with symbiotic, sulphide-oxidizing bacteria and gastropods that graze chemosynthetic bacteria as well as ophiuroids and ostracods show sensitivity to abrupt deoxygenation events over the past 3 000–16 000 years (Moffitt *et al.*, 2015; Myhre *et al.*, 2017). In this system, trophic diversity declines with oxygen loss. As oxygen declines, detrital guilds shift to chemoautotrophy. Carnivory, motile detritivores and suspension feeders are lost at oxygen levels below 0.2–0.5 ml litre^{-1} (Sperling *et al.*, 2013; Moffitt *et al.*, 2015). At the lowest oxygen levels, protozoan (foraminifera) extremophiles (e.g. *Nonionella stella*, *Bolivina tumida*) dominate the benthos.

Current rates of climate change are of major concern because they exceed the rates documented in the historical and paleo record, and conditions are unlike those experienced for hundreds of thousands of years. The rapid translation of changes, often within a six-month period, in the surface environment to responses in the deep-sea means that the deep ocean is far from immune to these changes.

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4. Criteria for vulnerable marine ecosystems

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The FAO DSF Guidelines (FAO, 2009) provide general tools and considerations for the identification of VMEs. The Guidelines indicate that vulnerability is related to the likelihood that a benthic population, community or habitat will experience substantial alteration from short-term or chronic effects of bottom-fishing disturbance, and to the potential rate of recovery of the benthic population, community or habitat upon cessation of disturbance.

Although no formal definitions for VMEs exists, VME **indicator species**, or VME **elements** are provided in the Guidelines (paragraph 42); the FAO DSF Guidelines do state that VMEs should be identified based on the characteristics they possess, for example:

- uniqueness or rarity: habitats consisting of endemic or rare species;
- functional significance of the habitat: necessary for the survival, function, spawning/reproduction, or recovery of fish stocks or rare, threatened or endangered marine species;
- fragility;
- life-history traits: slow growth, late age at maturity, low or unpredictable recruitment, long-lived;
- structural complexity: comprising significant concentrations of biotic and abiotic features.

The FAO DSF Guidelines (paragraph 43) acknowledge that the criteria "should be adapted and additional criteria should be developed as experience and knowledge accumulate." Since publication of the FAO DSF Guidelines, several RFMOs have engaged in fisheries assessments that have identified and mapped VMEs within parts of their area of competence. This has resulted in an enhanced understanding of what constitutes deep-sea VMEs, and a recognition that the FAO criteria should generally (but not always) be viewed in combination, especially when identifying and mapping VMEs in relation to high seas fisheries management and the need to establish VME fishery closures.

For example, the presence of a VME **indicator** species or a habitat feature alone, does not necessarily verify the presence of a VME. Some RFMOs have observed that VMEs typically possess a level of benthic community organization larger than the space occupied by an individual organism, with structural complexity and "significant concentrations" of individuals (or biomass) being an important defining characteristic

of a VME. This is consistent with the criteria listed in the FAO DSF Guidelines taken as a whole.

The aggregating nature of many VME indicator species allows natural discontinuities in the spatial distribution of high species biomass and/or abundance to be assessed and mapped, and VME fishery closures to be established (FAO, 2009, paragraph 42v). However, the extent of VME habitat, within which significant concentrations of VME indicator species occur, often extends spatially beyond the boundary of the area defined by "significant concentration" (Kenchington *et al*., 2015). Such VME habitat is generally structurally complex and may be characterized by higher diversities and/or different benthic communities from those characterizing the area of significant concentration. The VME habitat is also most probably providing ecosystem functions and processes closely linked to the sustainability of the "significant concentrations" and, therefore, should be regarded as an integral part of the VME.

Because information on benthic fauna in the deep ocean is sparse, habitat suitability models have been found to be essential for predicting the probability of occurrence of a VME indicator species, or habitats, beyond areas of observed "significant concentration". Such models generate continuous surfaces of probability (or, more rarely, predicted density) using a suite of environmental variables that are statistically associated with observations of the presence, absence, or concentration of VME indicator species.

From the experience gained by RFMOs since the introduction of the FAO DSF Guidelines, it is therefore evident that two characteristic features of VMEs have emerged that are particularly important when attempting to identify and map VMEs:

- The observation or prediction of "significant concentrations" of VME **indicator species**, which are species that meet one or more of the Guidelines' criteria for potential VMEs. The simple presence of such taxa is not an automatic indication of VME presence, but "significant concentrations" of one or more VME indicator species can be considered to constitute a VME.
- The identification of VME **elements** or habitats that are topographical, hydrophysical or geological features typically associated with VME indicator species in a global context and likely to support VMEs.

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5. Linkage between VME species, fish and fisheries

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Is there a connection of fish and fisheries to VMEs? Deep-sea fisheries have been recorded in areas where there are VMEs, and catches may be higher in VME areas than outside VME areas (Pham *et al.*, 2015). In the case of trawl fisheries especially, the VME species often become victims of the fishery, and are labelled as bycatch (e.g. Anderson and Clark, 2003). As a result, the question needs to be asked, are the targeted fish reliant on the VME species in some way, that is, do the VME species provide habitat for the fish, or do both the fish and the VME indicator species merely prefer the same environmental conditions?

There is some evidence for a functional relationship between deep-sea corals and some fish species, although not necessarily those being targeted by the fishery. For example, Baillon *et al.* (2012) found the larvae of redfish most frequently, but also glacier lanternfish and greater eelpout, nestled among the polyps of sea pens, especially *Anthoptilum grandiflorum* and *Pennatula aculeata*. Three other species of sea pens also harboured some fish larvae. The hosts with fish larvae were found primarily at depths of 400–600 m, where bottom temperatures were in the range of 4–6 °C. Specimens of *Chrysogorgia artospira* were seen to host egg masses of an unidentified fish species collected on the Corner Rise seamounts (Pante and Watling, 2011) at 1 650 m, and the octocoral *Thouarella* on the southeast African margin at 600 m host-attached fish eggs (Levin, Sink and Ven der Meden, personal observations). Some adult fish, such as boarfish, were most often encountered on seamounts in areas of moderately dense gorgonian coral growth (Moore *et al.*, 2008), and orange roughy is routinely seen in and around coral colonies on seamounts (Davies *et al.*, 2015).

There are records of commercially harvested fish and shellfish species aggregating or reaching elevated densities at methane seeps. They include: Patagonian toothfish off Chile (Sellanes, Quiroga and Neira, 2008); long-spine thornyheads, Dover sole, and red vermillion crab off southern California (Grupe *et al.*, 2015; Levin *et al.*, 2016); and orange roughy and other bottom fishes off New Zealand (Baco *et al.*, 2010; Bowden *et al.*, 2013). Seep habitats offer opportunities for use of hard substrate, refuge from predators, enhanced food availability, or parasite protection (e.g. from hydrogen sulphide), but there are few mechanistic studies to confirm which of these explain fish associations with seeps.

Etnoyer and Warrenchuk (2007) observed catshark egg cases attached to the primnoid gorgonian, *Callogorgia americana*, in the deep Gulf of Mexico at 533 m.

Catsharks are known to attach their egg cases to a number of biological structures, but also to derelict fishing gear (Able and Flescher, 1991). Treude *et al.* (2011) found abundant catshark (probably blackmouth catshark and *Bathyraja* sp.) egg cases inside a dense tube-worm field (*Lamellibrachia* spp.) at two cold seep sites in the Mediterranean at depths of ~500–700 m. They also suggested that this relationship is an old one, egg capsules resembling those of another deepwater shark, *Apristurus* sp., have been found with bathymodiolin mussels in a fossil deposit of Eocene age. Little *et al.* (2015) report catsharks and other condrichthyan egg cases from a host of fossil seeps off New Zealand, California, Washington (the United States of America), and Europe with ages up to 100 mya. Shark egg cases have also been reported recently on basalts near the Galapagos vents (C. Fisher, personal communication).

Prime reef habitat of deep coral banks (366–783 m) off the southeast of the United States of America was found to be preferred by a small group of fish species, such as *Laemonema melanurum*, roughtip grenadier, alfonsino, and blackbelly rosefish, while deep reef habitat was frequented most commonly by a group of species including swallowtail bass, alfonsino, American conger and *Dysommina rugosa* (Ross and Quattrini, 2007). Whether these co-occurrences imply a functional relationship between the coral banks and the fish is open to question, i.e. do the fish and the coral both prefer similar habitat requirements, or is there some connection, such as availability of prey species, prevalence of hiding spaces, etc., that implies a dependence of the fish on the coral habitat (Auster, 2007; Pham *et al.*, 2015)? On the other hand, Ross and Quattrini (2007) note that some fish species showed preferential behaviour for the coral habitat. For example, American conger were always observed hiding in the coral rubble, and *L. melanurum* was mostly found moving slowly just above the coral areas, perhaps looking or waiting for prey.

Alfonsino, channelled rockfish, and wreckfish were most commonly found around or perched on the tops of the large *Lophelia* bushes, but they are also well known as species of steep terrain, rocky ledges, or other deep non-coral habitat, suggesting that the coral and the fish co-occur due to some feature of the environment preferred by both species groups (Auster, 2007). In New Zealand, orange roughy continue to be caught in areas where the coral has been mostly removed, judging by lower bycatch rates, as seamount areas are repeatedly trawled (Anderson and Clark, 2003), suggesting again that the coral, *per se*, is not a critical habitat component.

In sum, it seems that VME species may be important habitat for some species of fish, but they do not appear to be critical habitat components for most species of commercially targeted fish. Rather, both the coral and other VME suspension-feeding species on the one hand, and targeted fishery species on the other, prefer similar habitat features such as enhanced flow due to elevated topography, and the trapping of migrating zooplankton and micronekton by seamounts and offshore banks (Pham *et al.*, 2015).

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6. Vulnerabilities: invertebrate taxa (indicators for vulnerable marine ecosystems)

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Introduction

Understanding and measuring the vulnerability of species, habitats and ecosystems to climate change is a major scientific challenge, and one of utmost importance considering the rapid pace, magnitude and scale at which these changes are taking place. As currently described, VMEs encompass a wide range of ecosystems, defined by a number of intrinsic and functional characteristics (FAO, 2009). Below we summarize the current knowledge on the most prominent of these deep-sea habitats, i.e. sponge grounds/reefs, cold-water coral reefs/gardens, xenophyophore fields and chemosynthetic vents and seeps, particularly in regard to the traits that define their vulnerability and to the potential impacts that climate change may pose upon them.

Cold-water coral reefs and gardens

Cold-water corals are among the most important ecosystem engineers in the deep sea across the globe, occurring at depths ranging from about 40 m to more than 1 500 m (Roberts *et al*., 2009). They are commonly found where current flow is accelerated, often around topographic highs such as seamounts, mounds, ridges and pinnacles as well as along continental margins and canyons. The habitats formed by cold-water corals vary from coral reefs, formed mostly by Scleractinia species (stony corals), to dense mono- or multi-species coral aggregations known as coral gardens, where Alcyonacea (gorgonians and soft corals), Pennatulacea (seapens), Antipatharia (black corals) and Stylasteridae (hydrocorals) are the most conspicuous components (OSPAR, 2010). Both cold-water coral reefs and gardens provide complex three-dimensional structural habitats that support high levels of biodiversity by providing refuge, feeding opportunities, and spawning and nursery areas for a wide range of organisms, including commercially important fish and crustacean species (Buhl-Mortensen *et al*., 2010; Pham *et al*., 2015). In addition to their bioengineering role, coral gardens provide important ecosystem services such as carbon storage and nutrient remineralization (Thurber *et al*., 2014).

Sponge grounds and reefs

Sponges are a key component of benthic communities across the world's oceans. Under specific oceanographic and geological conditions, sponges form highly structured habitats known as sponge grounds, aggregations, gardens and reefs. These habitats are widely distributed both geographically and bathymetrically, and are particularly prevalent in the upper bathyal zone along continental shelves and slopes, oceanic ridges, seamounts and fjords. Sponge grounds, which are formed by species of the classes Demospongiae (demosponges) and Hexactinellida (glass sponges), are very distinct in terms of their diversity and community composition, such as: (i) highly diverse multispecific communities dominated by large tetractinellid sponges (*Geodia* spp., *Stelletta* spp., *Stryphnus* spp.) on the boreal Atlantic (Klitgaard and Tendal, 2004; Murillo *et al*., 2012); (ii) dense "monospecific" populations of glass sponges such as *Pheronema carpenteri*, *Vazella pourtalesi* and *Poliopogon amadou* found in the temperate north Atlantic (Rice, Thurston and New, 1990; Barthel, Tendal and Thiel, 1996; Fuller, 2011; Xavier, Tojeira and Van Soest, 2015); (iii) the biohermal sponge reefs built by the glass sponges *Aphrocallistes vastus*, *Heterochone calyx* and *Farrea occa*, found in the western Canadian shelf in the east Pacific (Krautter *et al*., 2001); and (iv) extremely dense hexactinellid dominated grounds of the Antarctic shelf (Barthel and Gutt, 1992), to name but a few.

Sponge grounds and reefs are increasingly recognized as providing various supporting, regulating and provisioning services, e.g. habitat and nursery, nutrient recycling and carbon sequestration, which are crucial in the functioning of the ecosystems (e.g. Kenchington, Power and Koen-Alonso, 2013; Kutti, Bannister and Fosså, 2013; Kahn *et al*., 2015).

Xenophyophore fields

Xenophyophores are large (up to 25 cm), sessile agglutinating protozoans (Foraminifera) that build complex test structures on and in the seabed (Levin, 1991). They are found in all ocean basins, often at high densities on mid-ocean ridges, continental slopes, plateaus, seamounts and the slopes of subduction trenches (Tendal, 1972; Levin and Thomas, 1988; Ashford, Davies and Jones, 2014). By providing food, habitat, and refuge for marine invertebrates, as well as entraining suspended particles and larvae, they function as biodiversity hotspots on the sedimented seafloor (Levin *et al*., 1986; Levin, 1991; Buhl Mortensen *et al*., 2010; Hori *et al*., 2013) and play key roles in carbon cycling (Levin and Gooday, 1992). Xenophyophores have been recognized as VME indicator taxa (FAO, 2009, 2016). Their fragile, easily damaged tests, structural complexity and functional significance contribute to their VME indicator designation.

Hydrothermal vents and seeps

Hydrothermal vents and seeps are regions of the ocean floor where high-biomass invertebrate communities are fuelled by the emission of fluids from below the seafloor. The energy provided as a flux of reduced inorganic chemicals (e.g. sulphide methane, and hydrogen) allows chemoautotrophic production by the fixation of carbon from CO_2 by microbes (Tunnicliffe, Juniper and Sibuet, 2003). Methane seeps generally occur in sedimented areas (Sibuet and Olu, 1998) but are also associated with carbonate pavements. Some hydrothermal vents occur on sedimented margins and volcano flanks, but vents more frequently exist on the fresh basalt and volcanic rocks produced by magmatic activity (Beaulieu *et al*., 2013). In all these environments, elevated hydrogen sulphide fluxes (and sometimes methane and hydrogen) allow the proliferation of species that attain high biomass and are structuring the communities. These chemosynthetic environments are widely and patchily distributed along ridges, back-arc basins and volcanoes, trenches and ocean margins (Beaulieu *et al*., 2013; Le Bris *et al*., 2016). When these environments are in the aphotic zone, they host

highly specialized fauna, including large invertebrates with a very high degree of endemism. Characteristic assemblages include extensive mussel and clam beds, dense aggregations of shrimps, hairy and scaly gastropods, and giant tube worms. These organisms, which dominate the environment in terms of biomass, are structuring species and/or foundation species, and they support local productivity available over much wider spatial distance than those characterizing the venting and seepage zone (Ramirez-Llodra, Shank and German, 2007; Levin *et al*., 2016a).

Biological traits underpinning the vulnerability of VME indicator taxa to climate change

In a climate change context, vulnerability is broadly defined as "the extent to which biodiversity is susceptible to or unable to cope with the adverse effects of climate change" (IPCC, 2007). However, this concept encompasses several dimensions as it "is a function of external factors that define the character, degree and rate of the climate change to which species are subjected" (i.e. their exposure), and their intrinsic biological and ecological traits (i.e. sensitivity and adaptive capacity) (IPCC, 2007, 2014). While most climate change vulnerability assessments have focused on the exposure in space and time of species and habitats to climate-derived hazards – warming, acidification, deoxygenation and changes in POC flux – far fewer have addressed species intrinsic sensitivity and adaptive capacity, which underpin their vulnerability (e.g. Jones and Cheung, 2017). This is largely due to wide gaps in our knowledge of species biological and ecological traits and on how these are influenced by both biotic and abiotic factors. Foden *et al*. (2013) developed a framework aimed at independently measuring these three dimensions of climate change vulnerability (exposure, sensitivity and adaptive capacity) and tested it at a global scale on some taxonomic groups (including shallow-water corals). From an extensive literature survey coupled with expert opinion, they identified group-specific traits associated with vulnerability, which were then consolidated in trait-sets and assigned to one of the dimensions of climate change vulnerability. Each species was then attributed a "high-low-unknown" score for each trait or exposure measure based on qualitative or threshold assessments. Using this framework, species were ultimately assigned to different classes of vulnerability (e.g. highly vulnerable, potential adapters, potential persisters, and high latent risk), each warranting particular conservation and management actions (see Figure 1 in Foden *et al*., 2013). Table 2 presents an overview of the main definitions of the various components and dimensions of vulnerability, together with a non-exhaustive list of examples of biological traits associated with each of the components or dimensions.

TABLE 2
Examples of traits within each component of climate change vulnerability identified for the main VME-indicator taxa (invertebrates only)

Trait-set	Rationale	Examples of traits
SENSITIVITY "*is the lack of potential for a species to persist* in situ" (Foden *et al*. 2013)		
a) Specialized habitat and/or microhabitat requirements	Species occurring in a very specific habitat (specialists) in one or more life-stage will be more sensitive if changes affect such habitat.	- (micro)habitat specialist
b) Environmental tolerances or thresholds (at any life stage) that are likely to be exceeded due to climate change	Species with narrow tolerance ranges or with ranges close to the thresholds that are likely to be exceeded due to climate change will be more sensitive than species with wider tolerances	- low tolerance and/or short threshold distance to expected changes (temperature, oxygen, pH, $\Omega_{Aragonite}$)
c) Dependence on environmental triggers that are likely to be disrupted by climate change	Species whose critical biological processes (e.g. reproduction, larval release/settlement) are dependent on environmental triggers (e.g. temperature, food availability) that are likely to be disrupted will be most sensitive.	- reproductive cycles dependent on thermal or nutritional triggers
d) Dependence on interspecific interactions that are likely to be disrupted by climate change	Species dependent on interspecific interactions (e.g. symbiosis) for physiological functions will be more sensitive if those interactions are likely to be disrupted by climate change.	- symbiotic microbial load [sponges and chemosynthetic invertebrates] - oxygen-requiring symbionts
e) Rarity	Species with small population sizes and/or geographically restricted will be more sensitive than species with large populations and/or widely spread	- small population sizes - restricted distribution range (latitude/longitude/depth) - small distribution extent (area)
ADAPTIVE CAPACITY "*reflects the extent to which species have the capacity to reduce the impacts of changes in their immediate environment through dispersal or adaptive change*" (Foden *et al*. 2013)		
f) Poor dispersal ability	Species with low dispersal potential are unlikely to be able to disperse to new areas in response to adverse conditions or will be more affected by change in the current regime	- sessile in adult stage - short planktonic larval duration or direct development
g) Poor ability to evolve	Species ability to adapt/acclimatize and cope largely depends on their genetic makeup and generation turnover	- slow growth and maturation - high longevity - low mutation rates - low genetic diversity

Notes: For traits that are more relevant for a specific group of VME indicators, such group is highlighted between square brackets. Generalists are more resilient as they can possibly move to other habitats. Sensitivity "is the lack of potential for a species to persist *in situ*" (Foden *et al*. 2013).

Source: Trait-sets and their rationales are adapted/modified from Foden *et al*. (2013), and Foden and Young (2016).

Perhaps the most direct measures of a species sensitivity relate to its physiological tolerance to changes in environmental conditions. Many deep-sea organisms live in relatively stable, narrow-ranged environmental conditions on daily to seasonal timescales (temperature, salinity, oxygen, pH) that may confer them less tolerance to changes in environmental conditions. Organisms that already live close to their physiological tolerances may be particularly vulnerable to climate change. For example, in a global perspective the reef-building cold-water coral *Lophelia pertusa* is typically found in waters with temperature ranges of 4–12 °C, salinity range of 34–38 ppt, dissolved oxygen concentrations of 3–5 ml litre^{-1}, and waters supersaturated with respect to aragonite (Roberts *et al*., 2009).

However, in the Mediterranean Sea and Gulf of Mexico, *Lophelia pertusa* lives close to its upper temperature physiological tolerance limit of 14 °C (Lunden *et al*., 2014; Georgian *et al*., 2016; Reynaud and Ferrier-Pagès, forthcoming), which may compromise its survival under a future warming scenario. This is particularly worrisome for the Gulf of Mexico, where in addition to increasing seawater temperature stress, corals can also experience low dissolved oxygen concentrations, low pH and low availability of carbonate ion, and may thus be especially susceptible

to combined climate-induced changes (Georgian *et al*., 2016). Although the biotic and abiotic factors influencing the distributions of sponge VMEs (or their constituent elements) are not yet fully understood, a few studies suggest that water mass characteristics, including temperature, dissolved O_2 and POC flux to the seabed, may drive such spatial patterns (e.g. Klitgaard and Tendal, 2004; Knudby, Kenchington and Murillo, 2013; Conway *et al*., 2005; Howell *et al*., 2016). These studies also show how different species (even if closely related) occur under variable and different ranges of such environmental factors.

Increased sensitivity is also positively related to the level of habitat specialization. In this regard, vent- and seep-associated taxa are probably the most specialized of all VME indicators. Their dependence on symbiotic bacteria make them rely strongly on narrow boundary layers where, both electron acceptors such as oxygen and electron donors, such as sulphide or methane, are available. Minor changes in the properties of water masses are not expected to impair the capacity of these species to grow and build high biomass communities, but the combination of the high oxygen demand of these communities and change in the oxygenation of deep waters may be detrimental to population thriving at the edge of their habitat requirements. The climate-induced rise in temperature on the bathyal margin seafloor due to direct warming or changes in circulation could lead to significant releases of methane from gas hydrates via dissociation (Phrampus and Hornbach, 2012; Berndt *et al*., 2014; Levin and Le Bris, 2015; Levin, 2018). This could either expand availability of methane that supports the primary producers at the seeps and expand seep coverage, or create added disturbance. Release of methane from melting hydrates from intermediate depth margins might enhance ocean acidification and oxygen depletion in the water column (Biastoch *et al*., 2011; Boetius and Wenzhöfer, 2013).

Other attributes, such as dependence on environmental triggers or interspecific interactions for the performance of critical biological processes and/or functions, also delineate species sensitivity. In the ground-forming sponge *Geodia barretti*, for example, the onset of the reproductive cycle in fjord populations is known to coincide with phytoplankton blooms, with gametes being released when the flux of dissolved and particulate organic matter to the seafloor is at its highest in the fjords (Spetland *et al*., 2007). At greater depths, increases in the density and average size of two hexactinellid species (*Bathydorus* sp. and *Docosaccus* sp.) corresponded to increases in food supply, suggesting that increased POC flux may prompt recruitment and growth (Kahn, Ruhl and Smith, 2012). For cold-water corals, a number of environmental factors, such as temperature, lunar cycles, tidal patterns, day length and productivity, have been identified as temporal cues for gametogenesis and/or spawning in cold-water octocorals (reviewed by Watling *et al*., 2011), although seasonal fluctuations in phytodetritus fluxes from surface waters are probably the main triggers, particularly for scleractinians (Reynaud and Ferrier-Pagès, forthcoming). The vent mussel *Bathymodiolus azoricus* spawns in late winter, allowing the planktotrophic larvae to develop in the water column during the more productive months (Colaço *et al*., 2006). Similarly, the females of the cold seep shrimp *Alvinocaris stactophila* carry their embryos until early spring in order to allow planktotrophic larvae to exploit the peak in surface productivity (Copley and Young, 2006).

Rare species, i.e. those with small population sizes and with restricted geographical and bathymetric distributions, are also presumably more vulnerable to the impacts of climate change, and potentially more prone to undergo local or regional extinction. In this regard, it is important to highlight not only a large variation in species distributions, but also the fact that these are not always coupled with the distribution of the habitats they form, which are usually considerably smaller in extent. For example, while the species *Lophelia pertusa* has a cosmopolitan distribution and can occur as individual colonies under a broad range of environmental conditions (Roberts *et al*., 2009), the

habitat it forms – *Lophelia* reefs – only occurs under much more restricted ranges of such conditions (Davies and Guinotte, 2011; Howell *et al*., 2011).

Another important component underlying species vulnerability relates to their adaptive capacity, i.e. their intrinsic potential or ability to cope with and adapt to the changes taking place, or to disperse to other areas where such changes are less pronounced. Sponges, corals and some chemosynthetic foundation species are sessile, with low motility in their adult stage, and are assumed to exhibit low dispersal capabilities, by means of short-lived larval stages, which greatly limits their levels of population connectivity. The vast majority of sponges have indirect development with production of lecithotrophic larvae with a short planktonic life, limited swimming capacity, and phylopatric behaviour (Maldonado, 2006), but knowledge on deep-sea sponge larvae is virtually non-existent. Similarly, larval stages have been poorly studied in cold-water corals. The larvae of *Lophelia pertusa* are suggested to be planktotrophic based on aquaria observations, and planktonic duration under experimental conditions can be at least 10 months (Larsson *et al*., 2014; Strömberg & Larsson, 2017), indicating potential for long-distance dispersal (Fox *et al*., 2016).

Both corals and sponges exhibit slow growth rates and high longevities. In the sponge reefs of western Canada, growth rates between 1–3 cm $year^{-1}$ (young sponges) and 7–9 cm $year^{-1}$ (for sponge projections) were estimated for the reef-forming sponge *Aphrocallistes vastus*. However, most of the sponges observed showed no apparent growth when revisited 2–3 years later (Kahn *et al*., 2016). Although age estimates for sponge species are scarce, they suggest large individuals to be multicentennial, e.g. 220 and 440 years estimated for large individuals of *Rhabdocalyptus dawsoni* and *Rossella racovitzae*, respectively (Leys and Lauzon, 1998; Fallon *et al*., 2010), whereas some sponge reefs are estimated to be up to 9 000 years old (e.g. Krautter *et al*., 2001). Similarly, cold-water corals form reefs that can reach 8 000 years, with *L. pertusa* colonies growing linearly at 6–35 mm $year^{-1}$ (Roberts *et al*., 2009). Octocorals have age spans of hundreds of years and linear growth rates of 0.44–2.32 cm per year (Watling *et al*., 2011). Deep-sea black corals are generally at the end of the spectrum of slow-growing organisms with radial growth rates of 0.002–0.066 mm per year and estimated ages in the range of from nearly hundreds to thousands of years (Roark *et al*., 2009; Carreiro-Silva *et al*., 2013). The siboglinid *Lamellibrachia luymesi* from cold seeps off Mexico is thought to live for up to 200 years (Bergquist, Williams and Fisher, 2000).

Table 3 presents a summary of a qualitative trait-based assessment of the vulnerability of the most prominent VME indicator taxa. However, this assessment should be regarded as preliminary, as it is based on very limited available data on VME indicators' biological traits and expert judgement of a small group of people (the authors).

TABLE 3

Assessment of VME-indicator taxa against FAO's VME criteria and IUCN's climate change vulnerability trait-sets

	Sponge grounds/ reefs		Coral reefs/gardens							Vents and seeps				Sloped sediments	
	Demospongiae	Hexactinellida	Scleractinia			Octocorallia		Anthipatharia	Stylasteridae	Bivalvia	Gastropoda	Decapoda	Polychaeta	Protozoa	
	demosponges	glass sponges	stony corals	cup corals	gorgonians	soft corals	seapens	black corals	lace corals	mussels/ clams	scaly/hairy gastropods	blind shrimps	tube worms	Xenophyophores	
FAO's VME criteria															
i) Uniqueness or rarity	+	++	++	+	++	+	+	+++	++	+++	+++	+++	+++	+	
ii) Functional significance	++	++	+++	+	+++	+	+++	++	+	+++	+++	+++	+++	+++	
iii) Fragility	+++	+++	+++	+	+++	+	+	+++	++	+++	+++	+++	+++	+++	
iv) Life-history traits	+++	+++	+++	++	+++	+	+	+++	++	++	++	++	++	+	
v) Structural complexity	++	++/+++ (reefs)	+++	+	+++	+	++	+++	+	++	++	++	++	+++	
IUCN's trait-sets defining vulnerability to climate change															
a) Specialized habitat and/or microhabitat requirements	+	++/+++ (reefs)	+++	+	+++	+	+	+++	+++	+++	+++	+++	+++	+	
b) Environmental tolerances or thresholds (at any life stage) that are likely to be exceeded due to climate change	+	++/+++ (reefs)	+++	+++	+++	+++	+++	+++	+++	++	++	++	++	++	
c) Dependence on environmental triggers that are likely to be disrupted by climate change	++	++	+++	++	+++	+++	+++	+++	++	++	++	++	++	++	
d) Dependence on interspecific interactions that are likely to be disrupted by climate change	++	+	+	+	+	+	+	+	+	++	++	++	++	?	
e) Rarity	+	++	++	+	++	+	+	+++	++	+++	+++	+++	+++	+	
f) Poor dispersal ability	+++	+++	++	++	++	++	++	++	++	++	++	++	++	++	
g) Poor evolvability	+++	+++	+++	++	+++	+	+	+++	++	++	++	++	++	+	

Notes: Scores (+, ++, +++) provide a semi-quantitative assessment of how well a VME indicator matches the attribute (trait). Trait-sets (a)–(e) are associated with species' heightened sensitivities, whereas (f) and (g) are associated with low adaptive capacity (see also Table 2). Cell colours represent the relative knowledge level for any given attribute – green (substantial existing knowledge); yellow (some existing knowledge); orange (poor to very poor existing knowledge).

The impacts of climate change on VME indicator taxa: summary of current knowledge and main knowledge gaps

Corals

In many regions of the world, cold-water reefs are found close to or at the carbonate saturation horizon, the natural boundary between waters promoting biocalcification (oversaturated waters) and waters corrosive to unprotected coral skeletons (undersaturated waters) (Guinotte *et al.*, 2006; Roberts, Hennige and Vierros, 2016). This makes them particularly vulnerable to predicted changes in ocean carbonate chemistry (ocean acidification) and the shoaling of the carbonate saturation horizon (see Section 5). Recent modelling efforts suggest that by the end of this century, 73 percent of cold-water coral reefs will suffer from undersaturated aragonite seawater due to the shoaling of the ASH (RCP8.5 scenario) (Zheng and Cao, 2014). These predictions are even more extreme for 2300, where only 5 percent of the cold-water coral reefs will be surrounded by seawater with aragonite supersaturation (Zheng and Cao, 2014), raising concerns about their survival. However, most experimental studies show that, despite high variability in the measured rates of calcification and respiration, scleractinian cold-water corals exhibit a high resilience to ocean acidification alone or in combination with warming (Roberts, Hennige and Vierros, 2016; Maier, Weinbauer and Gattuso, forthcoming). Scleractinians, have been shown to be able to maintain such rates constant over a large gradient in pCO_2 concentrations from present to future conditions predicted for 2100 (Maier *et al.*, 2013a, 2013b; Carreiro-Silva *et al.*, 2014; Movilla *et al.*, 2014; Hennige *et al.*, 2015; Büscher, Form and Riebesell, 2017), albeit net calcification rates (calcification + dissolution) of *L. pertusa* exposed to aragonite-undersaturated conditions or close to saturation ($\Omega_{aragonite} < 1$) often decreased to values close to zero or even became negative (Lunden *et al.*, 2014; Hennige *et al.*, 2015; Büscher, Form and Riebesell, 2017).

The resilience of cold-water corals to ocean acidification has been related to their capacity to increase pH within their internal calcifying fluid, thus inducing carbonate precipitation (McCulloch *et al.*, 2012; Wall *et al.*, 2015). The upregulation of the internal pH has been thought to require a high amount of energy and may consequently require high food availability in areas with low $\Omega_{aragonite}$ to maintain calcification constant (McCulloch *et al.*, 2012). However, studies testing the effect of increasing food availability (4- to 10-fold increase) (Maier *et al.*, 2016; Büscher, Form and Riebesell, 2017) to cold-water corals under ocean acidification conditions did not provide evidence of a mitigation effect on calcification. However, these studies have not considered the impact of ocean acidification under scarce food or starvation scenarios, which may be more relevant for predicting the impacts of future ocean changes (in particular reduction of POC fluxes) in cold-water corals. In an environment where food is permanently scarce, a shift in energy allocation might occur in favour of physiological functions other than calcification and growth (e.g. Hennige *et al.*, 2015) and compromise the survival of corals (Maier *et al.*, 2016).

Given the apparent resilience of reef-building cold-water coral growth and their survival under ocean acidification conditions, the real concern now is the impact of ocean acidification on the tissue-unprotected reef framework exposed to corrosive waters, and to both chemical dissolution and biological erosion (bioerosion) by boring micro- (bacteria, fungi) and macro-organisms (worms, sponges) (Hennige *et al.*, 2015; Schönberg *et al.*, 2017). The balance between construction and erosion processes ultimately determines whether the reef will grow or recede (Schönberg *et al.*, 2017). Shifts towards net negative balances may lead to loss of reef growth potential, reef structural collapse, and diminished ecosystem service provisioning, such as nutrient cycling, carbon storage and habitat provision.

For cold-water corals that live close to their upper temperature physiological tolerance limit (e.g. Gulf of Mexico and Mediterranean populations), calcification seems to be more affected by warming than ocean acidification stress (*D. dianthus* in the Mediterranean) (Gori *et al*., 2016), and warming can result in coral mortality (> 14 °C for *Lophelia pertusa* in Gulf of Mexico) (Lunden *et al*., 2014). In the Gulf of Mexico, where L. pertusa already lives under relatively low oxygen conditions (2.53 ± 0.05 ml l^{-1}), an exposure to hypoxic conditions (1.5 ml l^{-1}) causes coral mortality (Lunden *et al*., 2014). These results point out the need to conduct regional studies to assess sensitivity to climate change conditions. Warming may be particularly important in the Mediterranean, where deep-sea temperature lies above 12.8 °C across the full depth range, while the combination of warming and expanding hypoxic zones in the Gulf of Mexico may threaten coral survival in this region.

Studies to date have mostly focused on scleractinian corals (e.g. Form and Riebesell, 2012), while the potential impacts of climate change on coral-garden indicator taxa (e.g. gorgonians, soft corals, black corals and lace corals) has been considerably less studied. The only study to date to investigate the impact of ocean acidification on a deep-sea gorgonian species (*Dentomuricea meteor*) (Carreiro-Silva *et al*., forthcoming) showed depressed metabolism with tissue necrosis, suggesting that gorgonians may be more sensitive to ocean acidification than scleractinian corals, and highlighting the importance of increasing the range of species tested to climate change impacts.

However, the impact of a combination of stressors and their temporal dynamics are poorly studied under *in situ* conditions. Despite recent observations showing seasonal variability in the growth of *L. pertusa* and *M. oculata*, and complex and specific response to variable hydrodynamics (and related POC fluxes), very little is known about the key parameters driving growth (Lartaud *et al*., 2014).

Sponges

In contrast to other better-studied groups (i.e. of calcifying organisms), current knowledge on the impact that climate change may have across different levels of biological organization (from the individual to the ecosystem level) in sponges is very limited. The few empirical studies performed to date have almost exclusively focused on shallow tropical species, and can therefore only be tentatively transposed to the deep- and cold-water counterparts. Such studies have shown that there is considerable variability in the effects of ocean warming and acidification on different species and even communities, making large-scale generalizations unrealistic.

Regional-scale disease outbreaks and mass mortality episodes reported to affect several shallow-water sponge populations have been attributed to abnormal increases in seawater temperatures. Although some species appear resilient to such anomalies, in others these seem to cause shifts and destabilization in the associations between the host (sponge) and its symbionts (bacteria), leading to a decline in host health and performance, and ultimately death (see review in Luter and Webster, 2017).

Mass mortalities of the cold-water ground-forming sponge *Geodia barretti* observed in 2006 and 2008 in the Tisler reef (Norway) were initially attributed to a rapid 4 °C increase in bottom temperature (Guihen, White and Lundalv, 2012). However, in a subsequent *ex situ* experiment exposing the same species to acute thermal conditions (up to 5 °C above ambient temperature for 14 days), physiological and cellular effects were noted, but no tissue necrosis, mortality or changes in the associated microbial community were observed, with all parameters returning to pre-experimental levels upon a recovery phase (Strand *et al*., 2017). A more comprehensive review of the effects of increasing seawater temperature on shallow water sponge physiological and ecological processes is provided by Bell *et al*. (2017).

In comparison, even less is known about the potential effects of ocean acidification on sponge species or communities. A significant decrease in sponge abundance was

observed along a gradient of increasing pCO_2 in shallow vent sites off the island of Ischia, Italy, in the Mediterranean (Goodwin *et al*., 2013). In contrast, two sponges were 40-fold more abundant in seep versus control sites at CO_2 seeps in Papua New Guinea (Morrow *et al*., 2015), again suggesting variable effects of acidification in different communities. The potential effects of increased acidification on the biomineralization processes responsible for skeleton formation and growth in siliceous sponges (i.e. silicification) are largely unknown, but hypothesized to be less severe than those in corals or calcareous sponges (calcification).

The potential effects of ocean warming and ocean acidification on the sponge holobiont are of paramount importance given the role both the host and microbial consortia play in the wider ecosystem functions, such as nitrogen and carbon cycling (e.g. Radax *et al*., 2012; Leys *et al*., 2017). These effects will be particularly relevant for the so-called high microbial abundance sponges, several of which dominate the boreo-Arctic sponge grounds. Thus, understanding the mechanisms underlying acclimatization and adaptation to environmental changes in sponges requires an integrated holobiont approach (see the review by Pita *et al*., 2018).

The glass sponge reefs found in the continental shelf of British Columbia and coastal-adjacent fjords (western Canada) occur in areas whereby a combination of upwelling, coastal runoff and surface productivity, lead to an enrichment of the water in nutrients, including relatively high levels of dissolved silica (> 40 µM). In these areas, range of water temperatures is 5.9–7.3 °C, and that of dissolved oxygen 90–150 µM (Conway *et al*., 2005). Climate projections suggest that that decreasing oxygen levels and hypoxic events, resulting from ocean warming, stratification and upwelling intensification at the reefs' depths (in the northern part of British Columbia), and increasing surface temperatures (in the Georgian Basin and fjords) will pose the greatest risk to these habitats (Conway *et al*., 2017). The reef-building species rely largely on bacteria for nutrition (Yahel *et al*., 2007), and, therefore, changes in productivity and POC flux to the reef may impair their growth, and consequently reef development.

Xenophyophores

Relatively little is known about xenophyophore vulnerability to climate change. Levels of endemicity, dispersal ability and evolvability are poorly known. Some species appear to be widely distributed based on morphology (Ashford, Davies and Jones, 2014). However, recent work in the Clarion Clipperton Fracture Zone (tropical east Pacific) reports unexpectedly high diversity and likely endemicity, based on limited distribution, among some species (Gooday *et al*., 2017a, 2017b). Habitat suitability for the group as a whole and for several widespread taxa (*Syringammina fragilissima* and *Stannophyllum zonarum*) suggest xenophyophores exhibit thresholds associated with depth, temperature, nitrate (reflecting productivity) oxygen and carbonate chemistry (Ashford, Davies and Jones, 2014). Therefore, they are potentially vulnerable to changing climate conditions at the seafloor. Oxygen declines (< 3 mol O_2 m^{-3}) may negatively affect distributions of *S. zonarum*; rising temperatures (to conditions above 8 °C) or declining carbonate saturation (< $\Omega_{calcite}$ = 2.5) may negatively affect *Syringammina*. Some xenophyophore taxa use calcareous pelagic foraminifera tests as material for their agglutinated tests (Levin and Nittrouer, 1987). This use could be compromised by increasing carbonate undersaturation, which would make the carbonate particles less available for incorporation into tests, and potentially dissolve the particles that were incorporated into agglutinated tests.

Vents and seeps

Physical–chemical conditions in the environment of chemosynthetic fauna strongly depart from those of abyssal and bathyal waters. As a result of mixing with anoxic, sulphidic, acidic venting fluids, typical abiotic habitat ranges are naturally depleted in

oxygen, and neutral to acidic (enriched in magmatic CO_2 and sometimes in sulphur dioxide) (Van Dover, 2001; Fisher *et al*., 2007). Vent organisms are adapted to this environment as adults and sometimes as juveniles. Species adaptation to extreme and highly fluctuating conditions, including high rates of shell calcification for large *Bathymodiolus* mussels (Nedoncelle *et al*., 2015) are not expected to be sensitive to comparatively minor changes in the properties of background seawater. However, vent species exposed to temperature and to strong pH fluctuations may be specially adapted to daily extremes (i.e. Nedoncelle *et al*., 2015), but could be closer to their tolerance thresholds than other abyssal species if background deep-sea conditions change. Even for the adult stage, little is known about the minimum requirements of species that could already live at the edge of their metabolic tolerances, for example, in relation to the high oxygen demand of their symbiotic lifestyles (Childress and Girguis, 2011; Hourdez and Lallier, 2007).

Among VME species that may live at the edge of their tolerance in the depth range 200–1 500 m, there are the siboglinid tube worms and *Bathymodiolus* mussels at hydrothermal vents and seeps. These species may be particularly vulnerable to the extension of hypoxic zones (e.g. *Lamellibrachia luymesi* in the Gulf of Mexico), or within narrow oxic–anoxic interfaces at vents (e.g. *L. anaximandri* in volcanic seamounts in the Mediterranean Sea). Very little is known about the capacity of mussels from the *Bathymodiolus* genus to adapt to conditions above 15 °C, which is described as their habitat thermal boundary at hydrothermal vents.

The situation is probably more critical for seep species living in more stable abiotic conditions, where methane fuels microbial consortia, resulting in high oxygen demand. In low-oxygen areas, these processes at the basis of the ecosystem could be affected by a reduction in oxygen concentrations (Boetius and Wenzhöfer, 2013). The absence of bathymodiolin mussels and tube worms (e.g. *Lamellibrachia barhami*) at the east Pacific seeps located within the most intense (dyxoxic) oxygen minimum zones (i.e. < 10 µmol O_2 kg^{-1}) (e.g. Levin *et al*., 2010, 2016b), despite their occurrence at better-oxygenated sites, suggests potential for oxygen limitation under OMZ expansion, although this interpretation remains uncertain (Seabrook *et al*., 2017). Warming of cold waters, especially in the Arctic is expected to trigger massive escape of methane in the gaseous phase (Skarke *et al*., 2014; James *et al*., 2016), generating strong disturbance of the biogeochemical gradients, and preventing VME fauna from colonizing and accessing sulphide for their symbionts (Niemann *et al*., 2006). Little is known about the fate of authigenic carbonates formed from the oxidation of methane in these ecosystems that serve as hard substrata for scleractinian corals and habitats for numerous mobile and sessile fauna.

While tube worms have lecitotrophic larvae and short planktonic larvae duration (Hilário, Young and Tyler, 2005; Hilário *et al*., 2015), some vent and seep species have planktonic larvae and eggs spread in the water column, assuring the connectivity among these patchy and fragmented habitats. The larvae of some species, such as the mussel *Bathymodiolus* (Arellano and Young, 2011; Arellano *et al*., 2014), or the vent shrimp *Rimicaris exoculata* (Copley, Jorgensen and Sohn, 2007) migrate in the water column and can reach the surface. Effects of climate change, such as temperature increase, pH decrease and lower oxygen, will affect the physiology of the larvae (and consequently the connectivity of the species), and will also change the composition of the food available for the planktotrophic larvae, and the adults. The adults that depend on the surface production to start the gametogenesis, or to spawn, will be affected by the change of seasons, and by the decrease in the net productivity of surface waters. The vent mussel *Bathymodiolus azoricus* is a chemosynthetic species that also obtains photosynthetic nutrition from phytoplanktonic sources (Colaço *et al*., 2009).

Shifting patterns in the timing, duration and strength of deep-reaching mesoscale surface eddies that may transport propagules hundreds of kilometres from their source

(Adams *et al*., 2011) could change the dynamics of long-distance dispersal and larval retention at vents. However, the uncertainties associated with any assessment of the impact of climate change on vent ecosystems are substantial (Van Dover, 2014).

Summary

Despite considerable technological advances in recent decades that have enabled the ecosystems of the deeper parts of the oceans to be discovered and explored, large knowledge gaps still exist on the biology and ecology of such ecosystems. This is largely due to challenges related to observation and experimentation *in situ*, and to maintaining deepwater species under *ex situ* experimental conditions. Deep-sea organisms have evolved life strategies and physiological adaptations (e.g. slow metabolism and growth rates, high longevity, and late maturity) that allow them to succeed in the cold and generally food-limited deep-sea environment but that may partially impair their ability to physiologically compensate for and adapt to changes in climate. Therefore, a deeper understanding of species' biological and ecological traits, as well as their tolerance thresholds to single and cumulative climatic stressors (e.g. temperature and nutrition, pH and O_2) is much needed. Most experiments to date have been conducted under short-term (i.e. acute) conditions, thereby hindering the mechanisms potentially involved in species resilience and acclimation. Studies addressing the impact of climate change on species gametogenesis, reproductive output, or larval development and physiology are also largely lacking. While efforts continue to build a knowledge base on the impacts over the physiological and ecological processes affecting individual species, it is also necessary to start to address the impacts that climate change will have on wider ecosystem functioning.

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7. Vulnerabilities: fish and fisheries

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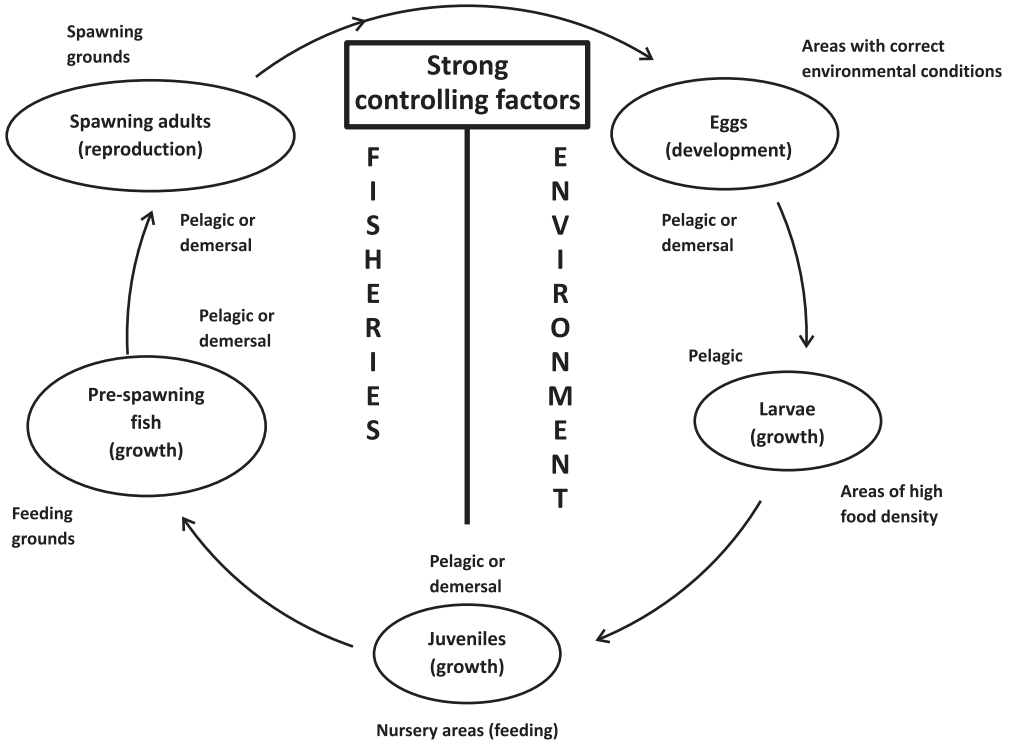
The life cycles of fish are complex, and individuals pass through several more or less distinct phases from egg to adult (Figure 4). Each phase may be further divided, as they can occur or move to various environmental regimes and interact differently with predator or prey species. Each phase is subject to different influences:

- Subject to strong environmental influence:
  - An egg phase that can be attached to the substrate or pelagic (as is more common with commercially targeted marine fish), which is strongly affected by physical conditions such as temperature and salinity.
  - A larval phase that is pelagic and highly dependent upon food availability for growth. Larvae grow quickly and their diet changes from smaller (e.g. phytoplankton and small zooplankton) to larger (zooplankton) food items. The abundance of these food items is very sensitive to environmental conditions, and larvae are, in general, unable to more sufficient distances to find food. The larvae and food items must occur in the same place at the correct time, and the production of the food items is very dependent upon environmental conditions.
  - Juveniles that may be pelagic or benthic and often migrate to food-rich areas.
- Subject to weak environmental influence (but strong predation and fisheries influence):
  - Pre-spawning fish move away from the nursery areas and are now concerned more with both growth and preparation for reproduction. This stage is less sensitive to environmental conditions, and the fish can migrate large distances to find food. Predation can still be a major source of mortality, although commercial species are subject to fishing at this stage, which can result in significant mortality. Environmental influences are probably less important, although they can affect growth rates.
  - Spawning adult fish often migrate to specific spawning areas, where they reproduce in a place and at a time to maximize the survival of their offspring. Spawning aggregations can be targeted by commercial fisheries that, if unregulated, can severely deplete populations. Environmental conditions can directly influence the spawning females' egg production and reproductive output, but the most important effect in terms of population dynamics is on the relative timing of the spawning and subsequent phyto- and zoo-plankton blooms. The timing of spawning has evolved over a long period and occurs at more or less the same time each year, although sea temperature, winds, salinity and other factors can modify this. However, the timing of the plankton blooms is highly dependent on environmental conditions and these blooms can vary greatly in their timing and extent.

FIGURE 4
Generalized life cycle for commercial marine fish



Note: Egg to larval phases are strongly influenced by abiotic environmental factors, whereas adults are more likely to be controlled by biotic factors such as predation and fisheries..

Commercial fish species are some of the most intensely studied animals in the oceans, with time series of abundance sometimes extending beyond 50 years. The fishable biomass of any commercial species consists of individuals of different ages (year-classes), and invariably just one or two strong year-classes dominate. This is known as recruitment variability, and considerable effort has gone into identifying why some years produce strong year-classes whereas as others (most) produce relatively small year-classes. This variation results from mortality processes occurring in the early life-history stages – at the egg and larval phases.

Work in the 1960s and 1970s, lead Cushing (1969, 1990) to propose his match-mismatch hypothesis, whereby the timing of spawning had to be matched to that of the phytoplankton and zooplankton blooms, so that emergent fish larvae had precisely the right type and size of food to eat (and this changes rapidly for quickly growing larvae). Other hypotheses were also proposed, for example, the larval retention hypothesis of Iles and Sinclair (1982) noted the importance of ocean currents and gyres to ensure that the patchy distribution of both larvae and zooplankton had to coincide for good survival and the development of strong year-classes. The processes generating variability in the early life-history stages include: food availability affecting growth rates and starvation; predation at all stages; and physical effects (e.g. temperature, salinity and oxygen) that alter physiological processes. Other processes are also important in regulating abundance in the adult stages, and both environmental factors and fisheries play an important role for commercial fish species.

The amount of knowledge about the factors controlling the abundance of fish populations is proportional to the commercial interest in the species. There is a lot of information on recruiting fish (those that grow to a size where they enter the fishery, which is typically a year or two prior to reaching spawning age) and adult survival for species in an active and productive fishery. It is known that adult numbers are controlled to a major extent by the number of recruits, and the number of recruits is controlled

by spawning success and early life-history survival. Typically, the relationship between the number of spawning fish and the subsequent recruitment of their offspring to the fishery is poor, with the variation believed in the main to be controlled by environmental factors. Declining fisheries, where the numbers of adult fish diminish over time, often resulting in the close of the fishery for management or commercial reasons, are often associated with successive years of poor recruitment. While this may be caused by recruitment overfishing, in many cases the poor recruitment seems to be difficult to explain and environmental factors are a more likely cause.

ICES (2017) identified the following drivers that explain distributional change:

- temperature,
- stock size,
- habitat change,
- geographical attachment,
- oceanographic features,
- species interactions,
- fishing effort distribution.

These can act on any of the life-history stages, often synergistically or antagonistically, making prediction of the final outcomes difficult. However, marine organisms have, on average, expanded the leading edges of their distributions by 72.0 ± 13.5 km per decade (generally poleward) (Poloczanska *et al*., 2013). Greenland cod is an example of distributional change for a commercial fish species that, throughout the twentieth century, showed a northward rapid range expansion under changing climatic conditions of about 50 km per year (Storr-Paulsen *et al*., 2004). Therefore, it seems most likely that the first effects of global warming will be observed in fish stocks living near the poles.

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8. Ecosystem considerations

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Model projections

In order to evaluate potential effects of climate change on seafloor habitats, VMEs, fish and fisheries, it is necessary first to project future conditions at the seafloor. To conduct this analysis, three 3-D, fully coupled earth system models were used: (i) the Geophysical Fluid Dynamics Laboratory's ESM 2G (GFDL-ESM-2G); (ii) the Institut Pierre Simon Laplace's CM6-MR (IPSL-CM5A-MR); and (iii) the Max Planck Institute's ESM-MR (MPI-ESM-MR) (Table 4). All models are part of Coupled Models Intercomparison Project Phase 5 (CMIP5) and were downloaded from Earth System Grid Federation peer-to-peer enterprise system.[7] Within each model output, the following were extracted: downward flux of particle organic carbon at 100-m depth (*epc100*), seawater potential temperature (*thetao*), dissolved oxygen concentration (O_2) and pH value (*ph*) for the historical time period 1951–2000, and RCP8.5 until 2100. The monthly data (*epc100* and *thetao*) were averaged by year before any further calculation. The bottom-most grid from each layer of *thetao*, O_2 and *ph* was retained to construct seafloor environmental condition. The *epc100* was converted to export POC flux at the seafloor (*epc*) using the Martin curve (Martin *et al*., 1987) following the equation:

$$epc = epc100\ (depth/export\ depth)^{-0.858} \quad (1)$$

The export depth was set to 100 m and water depth using the ETOPO1 Global Relief Model (Amante and Eakins, 2008). These bottom grids were then re-projected to 0.5 by 0.5-degree grids based on bilinear interpolation. Other georeferenced data were also acquired (e.g. spatial point, polyline and polygon data) representing fishable habitats, VMEs or fishery regulatory areas. These data include: (i) a global ocean basin mask from World Ocean Atlas 2013 V2 (NOAA, 2013); (ii) the high sea areas through various RFMOs, as well as the bottom-fishing and VME closed areas within these RFMO areas (Gianni *et al*., 2016); (iii) global distribution of seamounts with summits between 200 and 2 500 m (Kim and Wessel, 2011); (iv) global distribution of submarine canyons with canyon heads shallower than 1 500 m (Harris and Whiteway, 2011); and (v) global occurrence of cold-water corals between 200 and 2 500 m (Freiwald *et al*., 2017). The fishable depths in each RFMO area were masked by 200–2 500-m grids within the ETOPO1 Global Relief Model and subset other fishable habitats based on the depth information within the respective datasets.

[7] See: https://esgf-node.llnl.gov

TABLE 4
Earth system model used in this analysis

Variable	Unit	Realm	Ensemble	Frequency	Experiment	GFDL-ESM2G	IPSL-CM5A-MR	MPI-ESM-MR	Variable long name
epc100	mg m^{-2} d^{-1}	ocnBgchem	r1i1p1	Month	Historical, RCP8.5	360 × 210	182 × 149	802 × 404	Downward flux of particle organic carbon
thetao	°C	ocnBgchem	r1i1p1	Month	Historical, RCP8.5	360 × 200	182 × 149	802 × 404	Seawater potential temperature
o2	µmol kg^{-3}	ocnBgchem	r1i1p1	Year	Historical, RCP8.5	360 × 210	182 × 149	802 × 404	Dissolved oxygen concentration
ph	total scale	ocnBgchem	r1i1p1	Year	Historical, RCP8.5	360 × 210	182 × 149	802 × 404	pH

Note: Model details such as spatial grid resolutions are included.

Data analysis: The average and standard deviation of *epc*, *O2*, *thetao* and *ph* were calculated by year for 1951–2000, 2041–2060 and 2081–2100. The climate change was quantified by subtracting the historical average (1951–2000) from the future average (2041–2060 or 2081–2100). Exposure to climate change hazard is then defined as the ratio between climate change and historical standard deviation, measuring the amplitude of climate change in the unit of historical variability. By converting the climate changes of *epc*, *O2*, *thetao* and *ph* to the unit of their own historical variabilities, these standardized climate change ratios (or exposure to hazards) were added to a cumulative impact of climate change, assuming the impacts by different variable are additive (e.g. following the method described by Mora *et al.*, 2013). Two types of cumulative impacts were calculated. Exposure to hazards associated with decreasing export POC flux, deoxygenation, warming and acidification were summed to cumulative negative impact, whereas the exposure representing increased POC flux, oxygenation, cooling and basification were added up to yield positive impact. Based on the same concept, the yearly cumulative standard deviation was calculated for the future period starting from 2006. When the future cumulative standard deviation first exceeds the historical standard deviation (1951–2000), it is the time of emergence (TOE_{first}) of the climate changes. An alternative $TOE_{constant}$ was also calculated based on a condition that at least 90 percent of the cumulative standard deviations passing the TOE exceeded the historical variability. The TOE was highly correlated ($\rho > 0.97$), suggesting that once the TOE_{first} occurs, the cumulative variability does not decrease. Therefore, TOE_{first} was used throughout this analysis. Each matrix for each variable from each model was calculated (Table 4) and the ensemble average of the three models is reported throughout this paper.

Projected climate changes: The areas likely to see significant decline in export POC flux include the north and south Atlantic, north Indian and south Pacific Oceans (Figures 5 and 6). Much of the decrease will occur on the slope between 200 and 2 500 m. The Atlantic slope may experience the largest average POC flux decline of 1.67 mg C $m^{-2}d^{-1}$ by 2041–2060 (Table 5) and 2.73 mg C $m^{-2}d^{-1}$ by 2081–2100 (Table 6), whereas the slope surrounding the Antarctic might experience an average POC flux increase of 0.61 mg C $m^{-2}d^{-1}$ by 2041–2060 and 1.41 mg C $m^{-2}d^{-1}$ by 2081–2100. The north Atlantic, part of the Arctic and Southern Oceans will probably see the largest areas of intense deoxygenation to as much as 10–15 µmol kg^{-1} by 2041–2060 (Figure 5). The deoxygenation will probably spread across all the major ocean basins to as much as 40 µmol kg^{-1} decline in dissolved oxygen by 2081–2100 at high latitudes in the north Atlantic, Norwegian Sea, Greenland Sea and the continental margin of South America, Antarctica and Sea of Okhotsk (Figure 6). Almost the entire seafloor may experience reduced pH by 2041–2060 (Figure 5) and 2081–2100 (Figure 6); however, the bathyal

depths of the north Atlantic, Arctic and Southern Ocean will experience the most severe reductions in pH values with an average decline of 0.08 by 2041–2060 (Table 5) and 0.16–0.18 by 2081–2100 (Table 6). Most of seafloor may experience warming by 2041–2060 and 2081–2100, especially at higher latitudes (Figures 5 and 6). The bathyal depths of the northwest Atlantic, western Greenland Sea and Barents Sea, Red Sea and Sea of Okhotsk may see more than 2 °C warming at the seafloor by 2081–2100 (Figure 6).

FIGURE 5

Seafloor climate changes in waters deeper than 200 m by 2041–2060 (relative to 1951–2000)

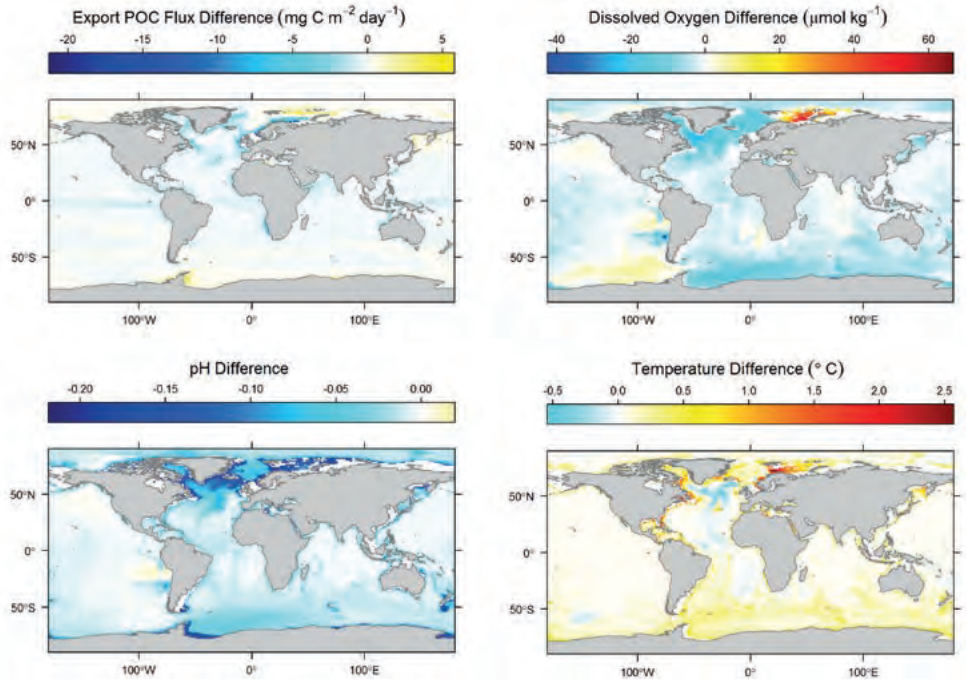


FIGURE 6

Seafloor climate changes in waters deeper than 200 m by 2081–2100 (relative to 1951–2000)

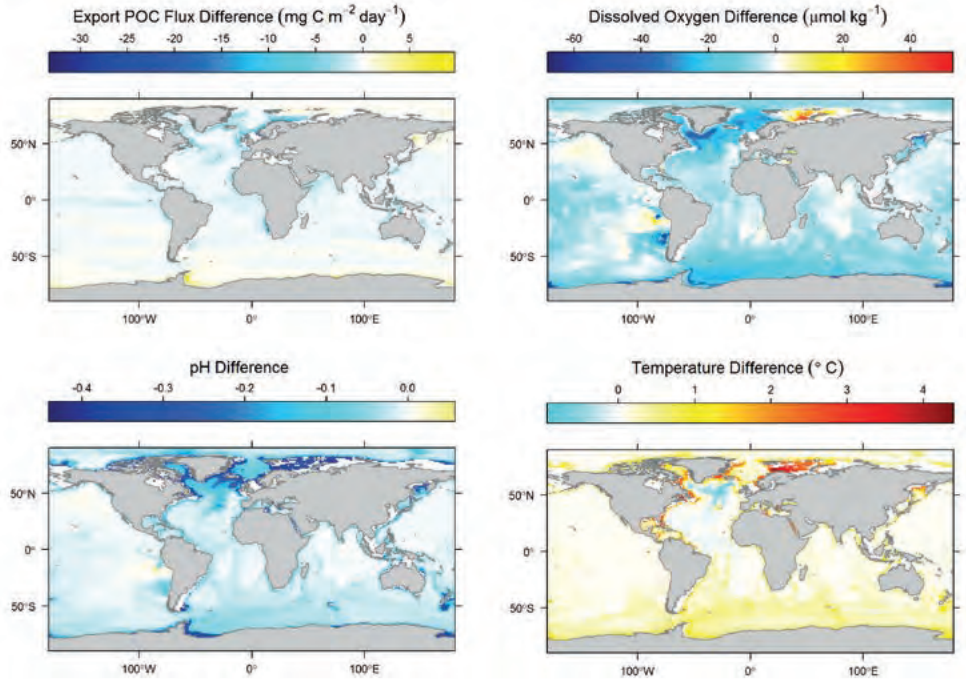


TABLE 5
Summary statistics of seafloor climate changes from 200 to 2500 m by 2041–2060

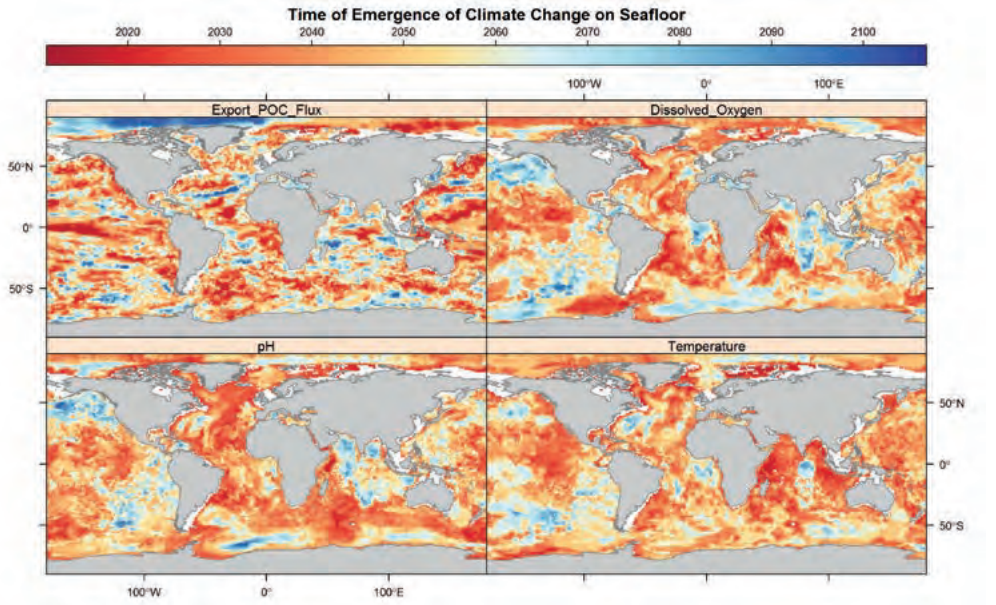
	Export POC flux			Dissolved oxygen			pH			Temperature		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Atlantic Ocean	-1.67	-21.3	2.56	-6.64	-27.5	11.28	-0.08	-0.21	0.01	0.48	-0.53	2.48
Pacific Ocean	-0.3	-7.41	6.09	-2.87	-41.2	9.63	-0.03	-0.21	0.01	0.19	-0.04	1.68
Indian Ocean	-0.65	-6.12	0.8	-1.84	-7.23	4.01	-0.03	-0.15	-0	0.17	-0.06	1.01
Southern Ocean	0.61	-2.84	4.51	-8.12	-35.8	9.13	-0.08	-0.19	-0.01	0.31	-0.1	0.85
Arctic Ocean	-0.37	-17.9	4.47	-0.06	-28.6	66.58	-0.08	-0.22	-0	0.35	-0.24	2.57

TABLE 6
Summary statistics of seafloor climate changes from 200 to 2500 m by 2081–2100

	Export POC flux			Dissolved oxygen			pH			Temperature		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Atlantic Ocean	-2.73	-33.3	2.97	-12.4	-35.5	20.89	-0.17	-0.44	-0.01	0.98	-0.84	4.4
Pacific Ocean	-0.71	-12.4	10.33	-5.67	-67.8	14.27	-0.08	-0.37	0.01	0.42	-0.04	3.14
Indian Ocean	-1.14	-10.3	2.98	-4.08	-13.1	7.74	-0.06	-0.29	-0	0.38	-0.24	1.71
Southern Ocean	1.41	-5.1	7.84	-23.5	-63.5	1.84	-0.16	-0.38	-0.02	0.71	-0.09	1.8
Arctic Ocean	-0.83	-19.9	4.43	-6.41	-37.1	53.82	-0.18	-0.4	-0.01	0.93	-0.18	4.29

Time of emergence: By 2060, the projected variability of export POC flux, dissolved oxygen, pH and temperature at the majority of world's seafloor will probably exceed historical variability (Figure 7). If only considering the bathyal depth between 200 and 2 500 m, the mean TOE may occur before 2050 in most major ocean basins for all variables except for export POC flux (Table 7).

FIGURE 7
Time of emergence of seafloor climate changes



Note: Colour ramp indicates the year when cumulative standard deviation (from 2006) exceeds the historical standard deviation during 1951–2000.

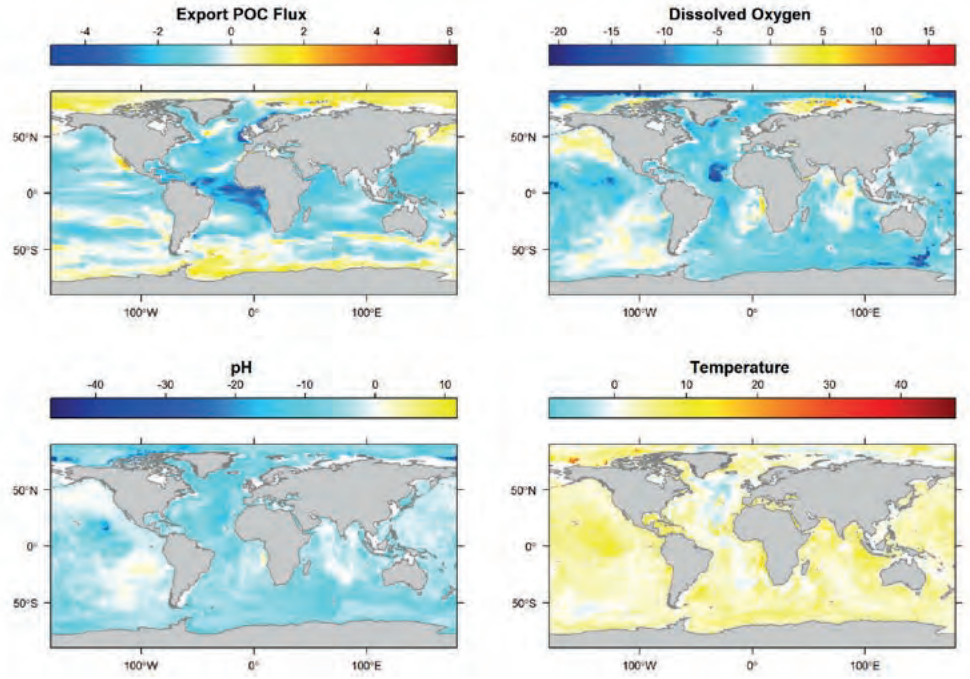
TABLE 7
Summary statistics of time of emergence of seafloor climate changes from 200 to 2 500 m

	Export POC flux			Dissolved oxygen			pH			Temperature		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
	(year)											
Atlantic Ocean	2054	2020		2042	2018	2073	2032	2022	2069	2034	2017	2066
Pacific Ocean	2049	2017	2098	2053	2025	2094	2046	2023	2091	2037	2019	2070
Indian Ocean	2057	2023		2050	2023	2080	2041	2020	2084	2033	2019	2066
Southern Ocean	2057	2017		2045	2019	2085	2037	2022	2079	2042	2017	2069
Arctic Ocean	2060	2017		2040	2019	2095	2033	2018	2070	2036	2017	2073

Exposure to climate change hazard: Except for the Arctic and Southern Oceans, most of the seafloor will probably be exposed to decline in export POC flux up to two times (by 2041–2060) and three times (by 2081–2100) of its historical variability (Figures 8 and 9). At bathyal depths (200–2 500 m), the Atlantic will probably be exposed to the largest climate change hazard in export POC flux, on average the decline is projected to be 1.34 times by 2041–2060) and 2.27 times by 2081–2100 of its historical variability, with less in the Indian and Pacific Oceans (Tables 8 and 9). Large areas of the world's seafloor will probably experience deoxygenation hazard by up to five times by 2041–2060 and ten times by 2081–2100 of their historical variability (Figures 8 and 9). The deoxygenation of regional hotspots in the Canadian high Arctic, equatorial Atlantic and Pacific and Southern Ocean may exceed ten times by 2041–2060 and 20 times by 2081–2100 of historical variability. On average, the Atlantic bathyal habitats (200–2 500 m) will probably be exposed to the most severe deoxygenation hazard by 2041–2060, followed by the Southern and Arctic Oceans (Table 8). However, by 2081–2100, the deoxygenation hazard will be most severe in the Arctic Ocean (Table 9). Large areas of the world's seafloor will simultaneously be exposed to acidification and warming hazards, which are up to ten times of their historical variability by 2041–2060 and up to 20 times by 2081–2100, respectively (Figures 8 and 9). Regional hotspots of acidification and warming hazard may occur in the Arctic Ocean, especially at bathyal depths of 200–2 500 m (Tables 8 and 9).

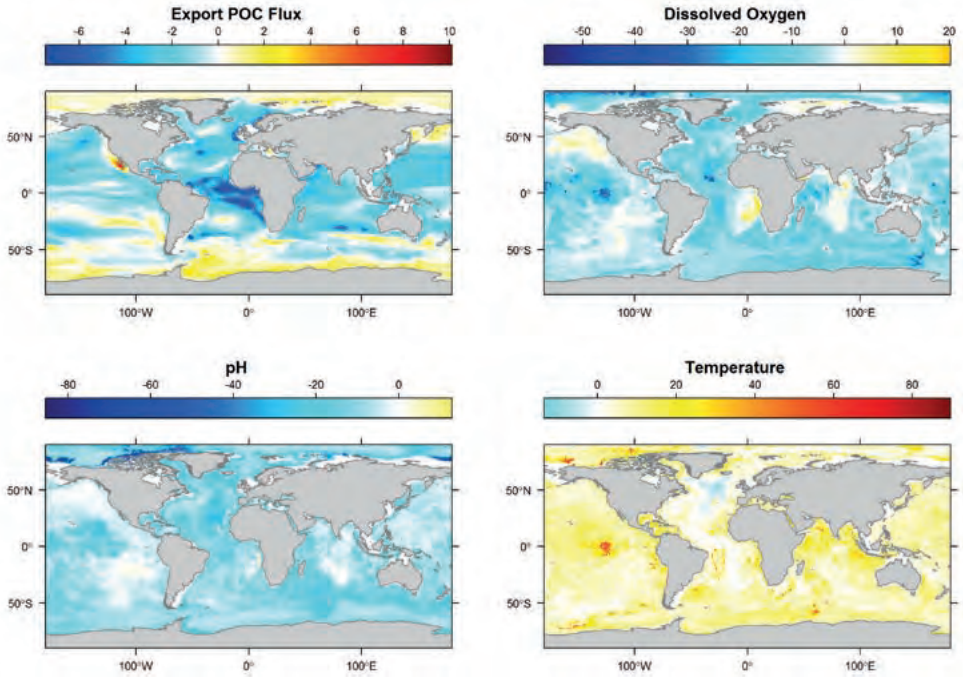
FIGURE 8

Exposure to seafloor climate change hazards in waters deeper than 200 m by 2041–2060



Note: Colour ramp indicates ratio between climate changes by 2041–2060 (relative to 1951–2000) and standard deviation during 1951–2000.

FIGURE 9
Exposure to seafloor climate change hazards beyond 200 m by 2081–2100



Note: Colour ramp indicates ratio between climate changes by 2081–2100 (relative to 1951–2000) and standard deviation during 1951–2000.

TABLE 8
Summary statistic of exposure to seafloor climate change hazards from 200 to 2 500 m by 2041-2060

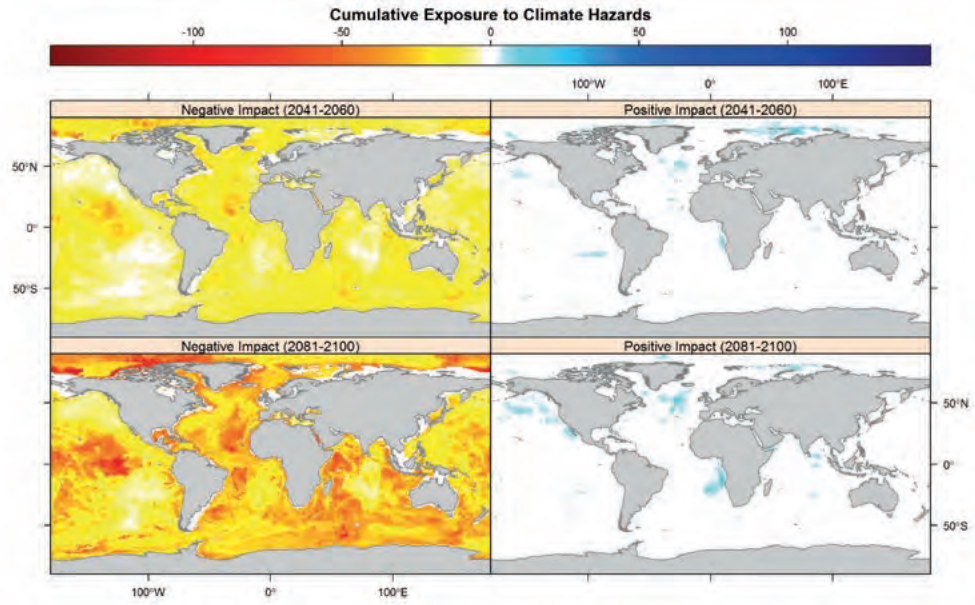
	Export POC flux			Dissolved oxygen			pH			Temperature		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Atlantic Ocean	-1.34	-4.94	0.96	-3.05	-9.34	4.9	-8.87	-14	-1.78	3.81	-4.17	13.24
Pacific Ocean	-0.49	-2.44	2.49	-1.64	-7.48	2.34	-4.8	-12.4	2.33	2.6	-1.02	9.14
Indian Ocean	-1.02	-2.24	1.05	-1.79	-7.68	4.83	-6.74	-14.4	-0.37	3.44	-1.38	15.76
Southern Ocean	0.36	-1.39	2.08	-2.48	-15.5	0.6	-7.03	-12	-1.64	2.94	-1.94	8.27
Arctic Ocean	0.2	-3.72	6.2	-2.26	-18.8	17.91	-11.2	-46.5	-1.45	3.92	-8.23	47.61

TABLE 9
Summary statistic of exposure to seafloor climate change hazards from 200 to 2 500 m by 2081-2100

	Export POC flux			Dissolved oxygen			pH			Temperature		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Atlantic Ocean	-2.27	-6.5	1.36	-5.93	-18.4	13.59	-18.4	-31.3	-4.75	7.89	-8.29	31.81
Pacific Ocean	-1.04	-4.07	7.89	-2.92	-15.9	6.16	-10.5	-28.5	3.23	6.45	-0.05	39.89
Indian Ocean	-1.91	-5.07	1.2	-3.7	-19.6	11.65	-15.2	-34.5	-1.56	7.64	-1.54	32.2
Southern Ocean	0.83	-1.83	3.21	-5.44	-23.1	0.14	-13.9	-25.8	-4.12	6.82	-1.83	48.89
Arctic Ocean	-0.05	-5.29	10.12	-6.69	-35.1	9.17	-25.5	-85.4	-6.16	12.11	-1.74	89.76

Cumulative impacts: Most of the seafloor will probably be exposed to cumulative impacts by declining export POC flux, deoxygenation, acidification and warming, whereas cumulative positive impact may occur sporadically with limited spatial extent (Figure 10). By 2081–2100, the vast abyssal plain of the Pacific will probably be exposed to more cumulative negative impact than the continental margin; both the margins and abyssal plains in the Atlantic, Indian and Southern Oceans, as well as the Arctic margin may be exposed to the highest cumulative negative impacts (> 50). At the bathyal depth between 200 and 2 500 m, the Arctic Ocean probably experiences the highest average cumulative climate change hazard (Table 10).

FIGURE 10
Cumulative impact to climate hazard by 2041–2060 and 2081–2100



Note: Summation of negative impacts including declining export POC flux, deoxygenation, acidification, and warming, or positive, impacts including increasing export POC flux, oxygenation, basification and cooling, are extracted from individual variables of exposures to climate hazards (Figures 8 and 9).

TABLE 10
Summary statistic of cumulative impact of seafloor climate change hazards from 200 to 2 500 m

	Cumulative negative impact						Cumulative positive impact					
	2041–2060			2081–2100			2041–2060			2081–2100		
	mean	min	max	mean	min	max	mean	min	max	mean	min	max
Atlantic Ocean	-17.3	-28.6	-6.5	0.22	0	4.9	-34.8	-74.8	-16.4	0.36	0	13.59
Pacific Ocean	-9.68	-19.2	-1.3	0.15	0	2.73	-21.1	-61	-4.22	0.26	0	7.89
Indian Ocean	-13.1	-32.9	-2.72	0.16	0	4.83	-28.9	-60.2	-9.24	0.44	0	11.65
Southern Ocean	-12.5	-28.1	-2.16	0.43	0	2.48	-26.2	-76.2	-10.6	0.93	0	3.21
Arctic Ocean	-18.8	-67.4	-4.57	1.67	0	23.26	-45.2	-148	-16.9	0.9	0	10.2

Regional variations: In order to assess the climate change impact to "fishable" habitats, the analysis focused on the zone of 200–2 500 m in each RFMO area (Table 11 and Figures 11–15). Detailed projected maps and summary statistics of climate change, TOE, exposure to climate change hazard and cumulative impact covering all depth range (> 200 m) can be found in the appendices to this chapter (Appendices 8.1–8.4). At bathyal depths, except for the Southern Ocean, all ocean regions are predicted to have most of their frequency distributions in the range of declining export POC flux by 2081–2100 (Figure 11). Among all regions, the northwest Atlantic area may experience the largest drop in export POC flux of 0.7–8.1 mg C $m^{-2}d^{-1}$. The northwest Atlantic

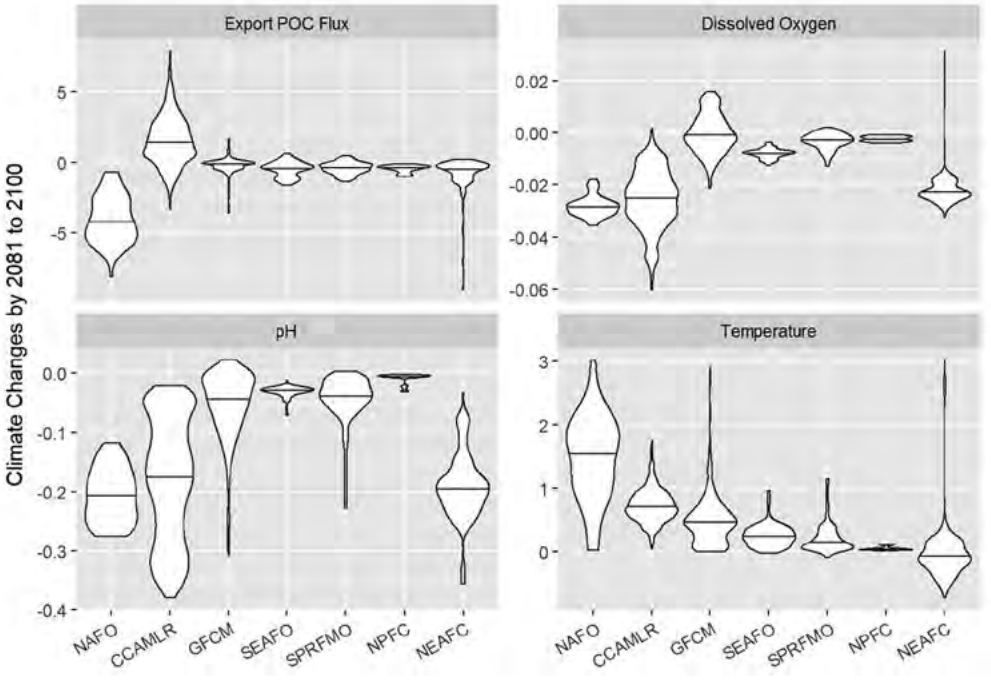
may also experience the largest decline in mean dissolved oxygen concentration of -27 µmol kg^{-1} by 2081–2100, followed by the Southern Ocean (-25 µmol kg^{-1}), northeast Atlantic (-16 µmol kg^{-1}) and southeast Atlantic (-8 µmol kg^{-1}). Almost all regions will exhibit ocean acidification by 2081–2100. The northwest and northeast Atlantic will probably have the highest mean acidification (~-0.2 in pH total scale) but the Southern Ocean may have the largest spatial variability in ocean acidification. The northwest Atlantic again may experience the most extreme warming of up to 3 °C by 2018–2100, followed by the Southern Ocean, Mediterranean, southeast Atlantic and south Pacific (Figure 11).

TABLE 11
Deep-sea ocean regions and associated fisheries management bodies

Ocean region	Management body
Northwest Atlantic	NAFO
Northeast Atlantic	NEAFC (Regulatory Area 1)
Southeast Atlantic	SEAFO
Mediterranean Sea	GFCM
Indian Ocean	SIOFA
North Pacific	NPFC
South Pacific	SPRFMO
Southern Ocean	CCAMLR

Note: See also Figure 1 for global map.

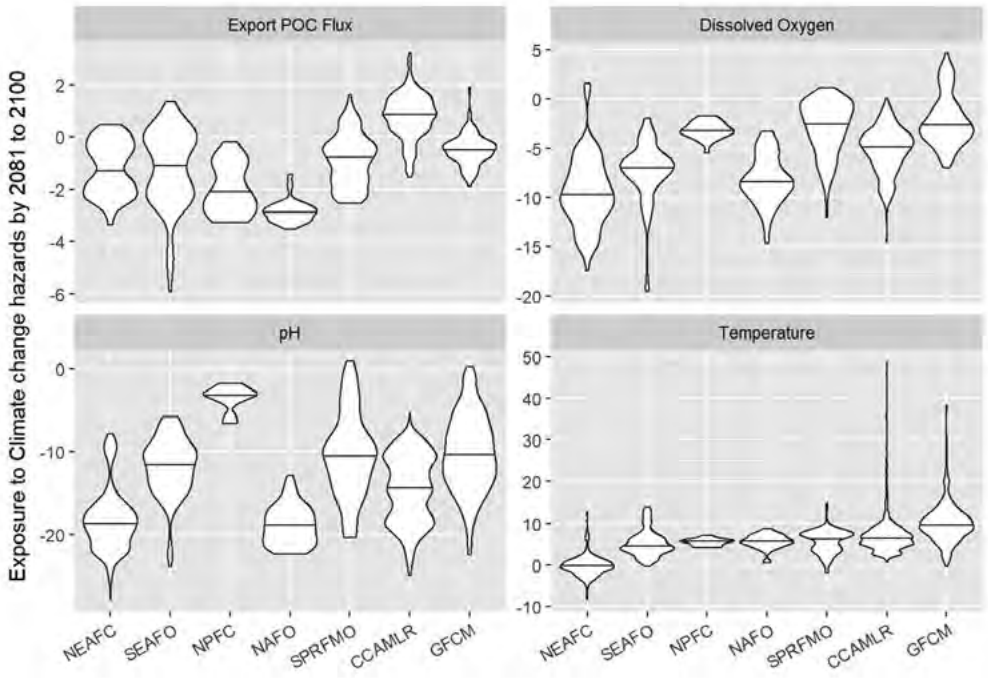
FIGURE 11
Relative frequency distribution of seafloor climate changes in RFMO areas (200–2 500 m) by 2081–2100



Note: Horizontal line indicates the median values.

The highest mean exposure to hazards in declining export POC flux is expected to occur in the northwest Atlantic and north Pacific with declines 2.9 and 2 times of their historical variability, respectively (Figure 12). The northeast Atlantic, northwest Atlantic and southeast Atlantic areas may be exposed to the most severe deoxygenation hazards with an average of about 7.4–9.4 times historical variability. The northwest and northeast Atlantic will probably experience the highest degree of mean acidification hazard at a level of 18.2–18.8 times of their historical variability. The Mediterranean and Southern Ocean may see the highest degree of warming hazard, of 7.2–9.9 times historical variability.

FIGURE 12
Relative frequency distribution of exposure to seafloor climate change hazards in RFMO areas (200–2 500 m) by 2081–2100

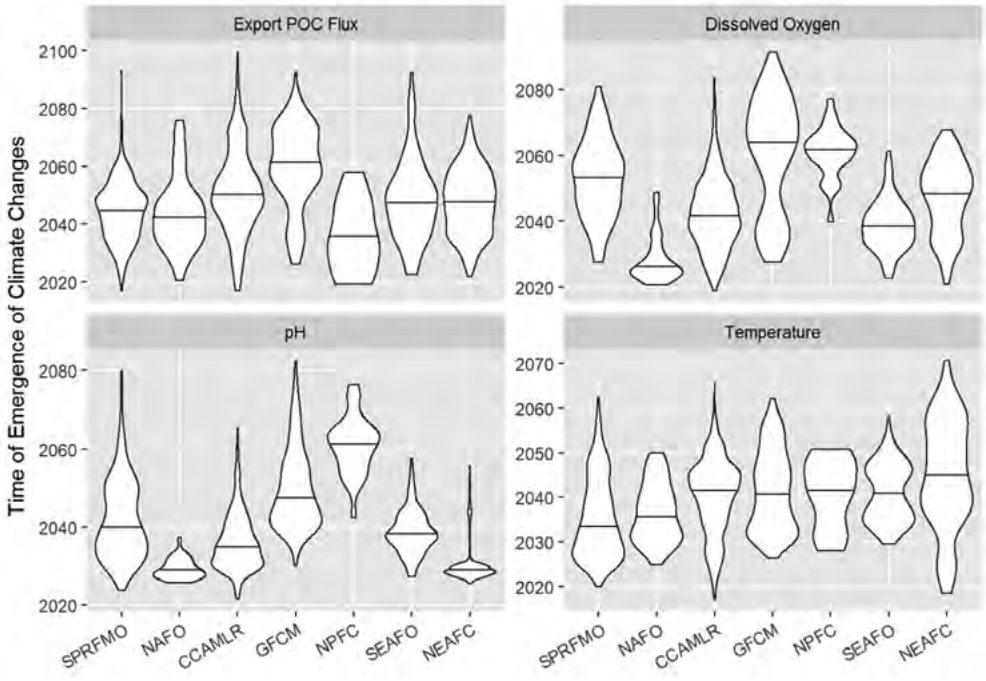


Note: Horizontal line indicates the median values.

In terms of timing of the climate change emergence, almost all regions will probably exhibit emergence (TOE) before about 2060; however, the TOE of acidification and warming are likely to occur ~10 years earlier in most regions (Figure 13).

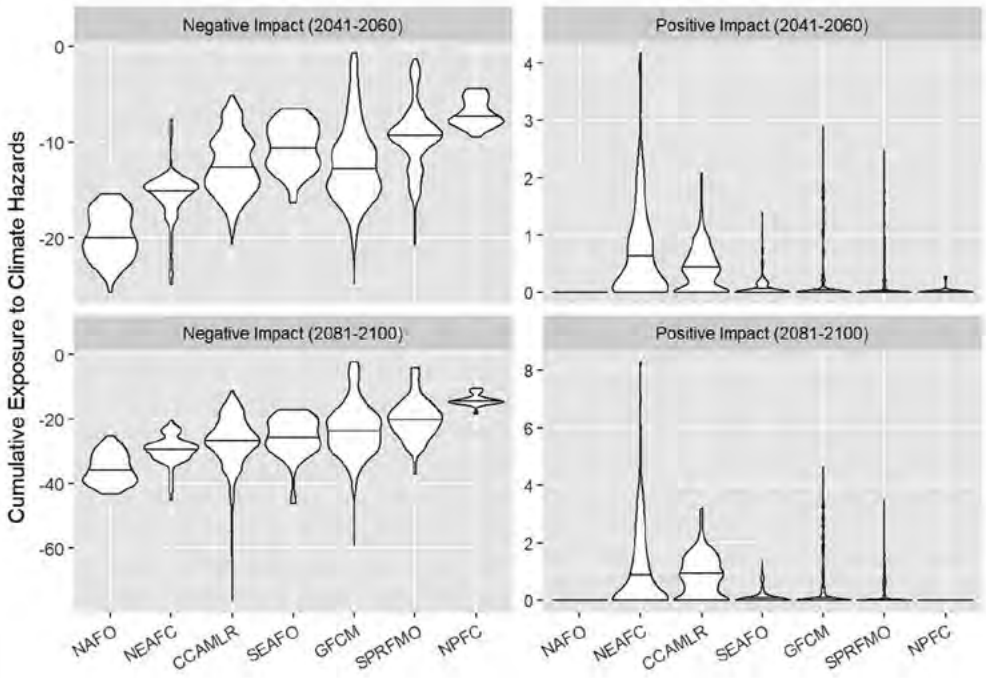
By combining the hazard in declining export POC flux, deoxygenation, acidification and warming, the northwest Atlantic will probably be exposed to the highest cumulative negative impact among all regions (Figure 14). The mean cumulative score of negative impact in northwest Atlantic is 35.4, or equivalent to 8.85 times of its historical variability if averaging across all four variables. The northeast Atlantic and Southern Ocean are also likely to be highly affected by climate changes with a mean cumulative negative impact score of 26.9–29.7, or equivalent to 6.73–7.43 times of their historical variabilities.

FIGURE 13
Relative frequency distribution of time of emergence of seafloor climate changes in RFMO areas (200–2 500 m)



Note: Horizontal line indicates the median values.

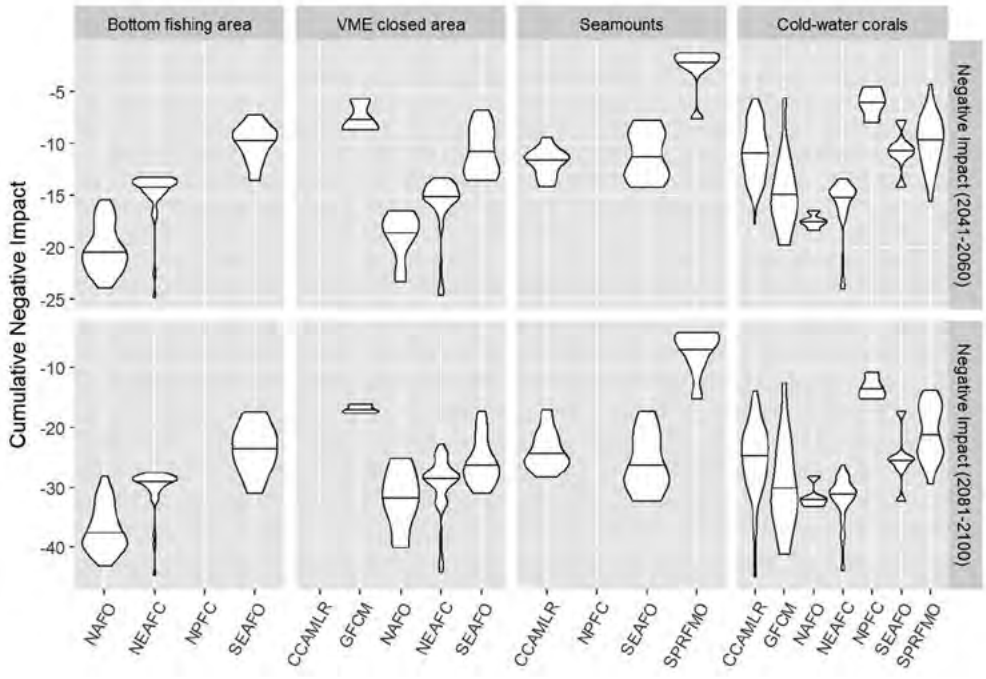
FIGURE 14
Relative frequency distribution of cumulative impact to climate hazard by 2041–2060 and 2081–2100 in RFMO areas



Note: Horizontal line indicates the median values.

Among all habitats and regulatory areas in the RFMOs, the bottom-fishing area, VME closed area and cold-water corals in the northwest Atlantic area of the Northwest Atlantic Fisheries Organization (NAFO), as well as the cold-water corals in the Mediterranean GFCM area and northeast Atlantic NEAFC area, are expected to experience the highest cumulative negative impact by 2081–2100. Their mean cumulative negative impact scores are over 30, or about 7.5 times over their historical average across the four variables (Figure 15). Although some of the RFMO areas may experience cumulative positive impact (e.g. in the NEAFC and CCAMLR regulatory areas, Figure 14), the mean cumulative scores are all less than 1, suggesting the minimum positive effects are unlikely to compensate for the negative impact caused by climate change. According to this assessment, the northwest Atlantic NAFO region and its regulatory area are potentially at greater risk under the RCP8.5 climate change scenario.

FIGURE 15
Relative frequency distribution of cumulative negative impact to climate hazard by 2041–2060 and 2081–2100 in selected RFMO habitats



Note: Horizontal line indicates the median values.

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APPENDIX A8.1

Climate change between model-averaging future and historical projections in each RFMO area

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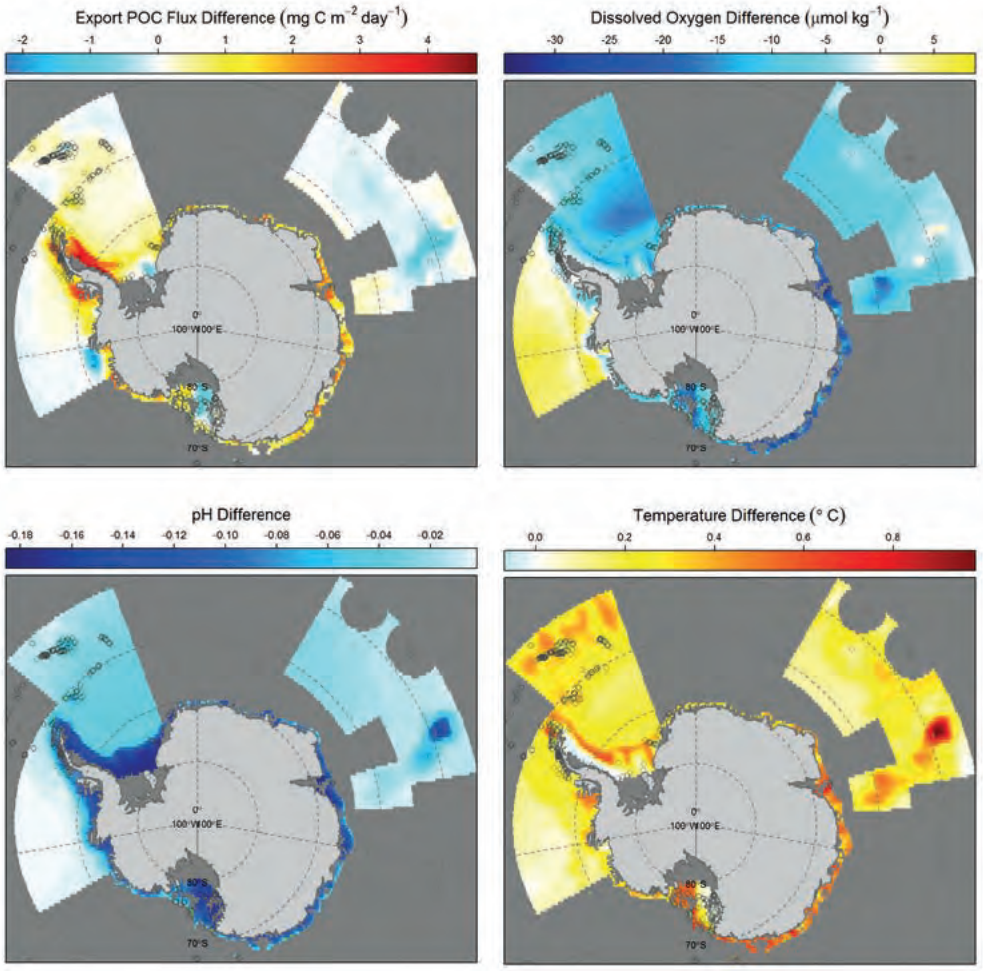
TABLE A8.1.1
Summary statistics of seafloor climate changes in RFMO areas by 2041–2060

RFMO	Habitat	Export POC flux			Dissolved oxygen			pH			Temperature		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
CCAMLR	>200 m	0.27	-2.35	4.51	-5.72	-35.5	9.13	-0.04	-0.18	0	0.22	-0.06	0.94
	200–2 500 m	0.68	-2.35	4.51	-7.78	-35.5	9.13	-0.09	-0.18	-0.01	0.3	-0.06	0.94
	VME closed area	1.02	0.37	1.73	-15.58	-20.21	-8.22	-0.07	-0.09	-0.05	0.43	0.3	0.49
	Seamounts	-0.04	-0.5	0.39	-4.16	-9.48	5.42	-0.02	-0.03	-0.001	0.21	0.06	0.39
	Cold-water corals	0.65	-1.24	3.1	-7.31	-19.8	2.81	-0.08	-0.18	-0.01	0.28	0.01	0.62
	Canyons	0.68	-1.93	3.63	-7.27	-23.96	7.84	-0.05	-0.14	-0.01	0.34	0.08	0.8
GFCM	>200 m	-0.1	-2.89	1.82	-0.82	-16.22	9.62	-0.02	-0.14	0.02	0.16	-0.02	1.42
	200–2 500 m	-0.13	-2.89	1.82	-0.36	-16.22	9.62	-0.02	-0.14	0.02	0.24	-0.02	1.42
	VME closed area	-0.44	-0.61	-0.39	0.98	-5.93	3.18	-0.03	-0.09	-0.002	0.29	-0.01	0.94
	Cold-water corals	0.08	-0.66	1.59	-4.22	-13.06	1.95	-0.05	-0.13	0.001	0.36	-0.01	0.98
	Canyons	-0.16	-2.62	1.59	-0.68	-9.73	9.62	-0.03	-0.13	0.01	0.28	-0.02	1.41
NAFO	>200 m	-0.47	-5.63	0.39	-11.14	-25.88	-3.58	-0.04	-0.14	-0.01	0.09	-0.38	1.75
	200–2 500 m	-2.47	-5.63	-0.28	-16.36	-22.68	-7.28	-0.11	-0.14	-0.07	0.81	0.1	1.75
	Bottom-fishing area	-2.93	-5.63	-0.77	-16.87	-22.68	-9.69	-0.12	-0.16	-0.08	1.03	0.54	2.03
	VME closed area	-0.33	-3.64	-0.09	-7.81	-19.92	-4.08	-0.02	-0.12	-0.01	0.12	0.02	1.1
	Cold-water corals	-0.41	-1.93	0.39	-8.37	-18.65	-3.99	-0.04	-0.12	-0.01	0.25	-0.36	1.31
	Canyons	-1.86	-3.8	-0.5	-13.02	-21.24	-5.92	-0.08	-0.13	-0.03	0.79	0.07	2.01
NEAFC	>200 m	-0.22	-9.03	1.2	-7.11	-25.2	45.4	-0.04	-0.15	-0.003	-0.01	-0.46	1.28
	200–2 500 m	-0.62	-9.03	1.09	-4.42	-20.25	45.4	-0.11	-0.15	-0.02	0.11	-0.43	1.28
	Bottom-fishing area	-2.2	-9.03	0.91	13.9	-20.56	44.52	-0.12	-0.15	-0.02	0.56	-0.25	1.28
	VME closed area	-0.27	-1.73	0.29	-13.51	-20.25	-6.52	-0.09	-0.14	-0.03	-0.14	-0.35	0.56
	Cold-water corals	-0.44	-3.14	0.41	-10.23	-20.56	-0.4	-0.1	-0.14	-0.01	0.01	-0.36	0.73
	Canyons	-0.58	-3.14	-0.002	-8.74	-13.1	-1.72	-0.09	-0.13	-0.04	-0.05	-0.35	0.3
NPFC	>200 m	-0.11	-0.38	0.26	-0.55	-4.75	2.8	-0.001	-0.01	0.002	0.01	0.002	0.05
	200–2 500 m	-0.19	-0.34	0.17	-0.93	-1.77	-0.28	-0.004	-0.01	-0.001	0.02	0.004	0.05
	Bottom-fishing area	-0.13	-0.3	0.03	-1.04	-1.77	-0.32	-0.01	-0.01	-0.001	0.03	0.01	0.05
	Seamounts	-0.16	-0.33	0.07	-1.21	-2.95	0.84	-0.002	-0.005	0.001	0.02	0.01	0.03
	Cold-water corals	-0.14	-0.34	0.11	-0.77	-3.5	0.97	-0.002	-0.01	0.001	0.01	0.004	0.05
	Canyons	-0.21	-0.22	-0.2	-0.79	-0.87	-0.71	-0.01	-0.01	-0.01	0.03	0.03	0.03
SEAFO	>200 m	-0.2	-2.46	0.42	-1.64	-7.81	7.3	-0.01	-0.03	0.001	0.07	-0.12	0.52
	200–2 500 m	-0.3	-2.46	0.25	-3.11	-6.45	-1.12	-0.01	-0.03	-0.01	0.1	-0.06	0.36
	Bottom-fishing area	-0.17	-2.46	0.29	-2.35	-6.45	2.36	-0.01	-0.03	-0.002	0.09	-0.02	0.32
	VME closed area	-0.14	-0.85	0.29	-1.57	-6.18	7.15	-0.01	-0.03	-0.001	0.06	-0.1	0.36
	Seamounts	-0.18	-1.84	0.24	-2.15	-4.88	1.98	-0.01	-0.03	-0.001	0.07	-0.06	0.36
	Cold-water corals	-0.52	-0.71	-0.25	-3.38	-4.96	-0.97	-0.01	-0.02	-0.01	0.06	-0.05	0.15
	Canyons	-0.29	-0.71	0.09	-3.13	-6.45	-0.01	-0.01	-0.03	-0.002	0.1	0.001	0.36
SPRFMO	>200 m	-0.15	-1.52	0.58	-1.23	-41.13	9.08	-0.005	-0.11	0.02	0.05	-0.21	0.52
	200–2 500 m	-0.18	-1.52	0.58	-2.36	-7.76	1.76	-0.02	-0.11	0.005	0.11	-0.1	0.52
	Seamounts	-0.04	-0.29	0.21	-0.64	-5.12	3.14	-0.003	-0.01	0.01	0.03	0.01	0.09
	Cold-water corals	-0.16	-0.72	0.55	-2.45	-6.65	0.7	-0.02	-0.08	-0.004	0.09	-0.05	0.42
	Canyons	-0.1	-0.48	0.08	-2.91	-4.73	-1.07	-0.03	-0.09	-0.01	0.16	0.02	0.46

TABLE A8.1.2
Summary statistics of seafloor climate changes in RFMO areas by 2081–2100

RFMO	Habitat	Export POC flux			Dissolved oxygen			pH			Temperature		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
CCAMLR	>200 m	0.59	-3.32	7.84	-17.2	-60.28	1.84	-0.08	-0.38	-0.01	0.5	0.05	1.76
	200–2 500 m	1.57	-3.32	7.84	-25.39	-60.28	1.84	-0.18	-0.38	-0.02	0.73	0.05	1.76
	VME closed area	2.72	1.89	4.56	-29	-33.51	-25.28	-0.13	-0.17	-0.09	0.81	0.73	1.06
	Seamounts	-0.1	-0.73	0.98	-12.27	-21.06	-2.87	-0.04	-0.06	-0.01	0.45	0.29	0.74
	Cold-water corals	1.26	-1.38	6.24	-23.04	-59.19	-7.25	-0.16	-0.38	-0.02	0.67	0.29	1.69
	Canyons	1.37	-2.11	6.93	-22.09	-46.26	-4.1	-0.11	-0.28	-0.02	0.72	0.29	1.55
GFCM	>200 m	-0.14	-3.59	1.67	-0.71	-21.44	15.69	-0.04	-0.31	0.02	0.35	0.01	2.9
	200–2 500 m	-0.2	-3.59	1.67	-0.19	-21.44	15.69	-0.05	-0.31	0.02	0.51	0.01	2.9
	VME closed area	-0.51	-0.73	-0.45	4.04	-4.14	8.5	-0.07	-0.19	-0.003	0.6	0.03	1.86
	Cold-water corals	-0.06	-0.94	1.66	-5.72	-19.74	8.5	-0.1	-0.27	0.002	0.72	0.03	2.04
	Canyons	-0.27	-3.52	1.67	-1.74	-19.74	15.1	-0.07	-0.3	0.02	0.57	0.02	2.83
NAFO	>200 m	-0.8	-8.08	0.18	-16.99	-38.51	-7.44	-0.05	-0.28	-0.01	0.12	-0.5	3.01
	200–2 500 m	-3.8	-8.08	-0.67	-27.15	-35.46	-14.84	-0.2	-0.28	-0.12	1.48	0.03	3.01
	Bottom-fishing area	-4.51	-8.08	-1.43	-27.78	-35.46	-17.88	-0.23	-0.31	-0.16	1.92	0.83	3.61
	VME closed area	-0.52	-5.29	-0.07	-12.09	-32.4	-7.58	-0.04	-0.23	-0.02	0.15	-0.04	2.02
	Cold-water corals	-0.71	-2.69	0.16	-13.9	-29.84	-7.67	-0.07	-0.24	-0.02	0.43	-0.46	2.5
	Canyons	-2.78	-5.71	-0.72	-22.26	-33.49	-11.03	-0.16	-0.27	-0.05	1.39	0	3.58
NEAFC	>200 m	-0.48	-9.04	0.22	-13.03	-39.29	31.24	-0.07	-0.36	-0.01	0.01	-0.82	3.02
	200–2 500 m	-1.18	-9.04	0.19	-16	-32.38	31.24	-0.21	-0.36	-0.03	0.36	-0.72	3.02
	Bottom-fishing area	-3.02	-8.98	0.1	1.45	-30.37	29.77	-0.29	-0.36	-0.03	1.53	-0.32	3.05
	VME closed area	-0.6	-4	0.15	-23.05	-31.13	-11.17	-0.15	-0.28	-0.06	-0.33	-0.72	1.35
	Cold-water corals	-1.15	-4.5	0.17	-19.61	-30.58	-2.36	-0.18	-0.28	-0.01	0.17	-0.75	1.41
	Canyons	-1.4	-3.89	-0.63	-18	-24.91	-3.93	-0.17	-0.25	-0.07	-0.01	-0.41	0.77
NPFC	>200 m	-0.3	-1.03	0.33	-1.95	-11.81	3.81	-0.003	-0.03	0.003	0.03	0.01	0.11
	200–2 500 m	-0.45	-1.03	-0.1	-2.31	-4.03	-0.81	-0.01	-0.03	-0.002	0.05	0.02	0.11
	Bottom-fishing area	-0.69	-1.03	-0.35	-3.03	-4.03	-2.03	-0.02	-0.03	-0.004	0.07	0.02	0.11
	Seamounts	-0.38	-0.73	-0.19	-3.27	-8.51	1.01	-0.01	-0.01	0	0.04	0.02	0.09
	Cold-water corals	-0.31	-0.96	0.25	-2.31	-11.37	1.33	-0.004	-0.03	0.002	0.03	0.01	0.11
	Canyons	-0.6	-0.64	-0.56	-1.95	-2.07	-1.83	-0.02	-0.02	-0.02	0.07	0.07	0.08
SEAFO	>200 m	-0.34	-4.49	0.73	-4.91	-13.87	5.51	-0.02	-0.07	-0.002	0.16	-0.12	0.97
	200–2 500 m	-0.61	-4.49	0.63	-7.97	-12.48	-3.77	-0.03	-0.07	-0.01	0.25	-0.02	0.97
	Bottom-fishing area	-0.32	-4.49	0.73	-7.04	-12.48	1.1	-0.02	-0.07	-0.01	0.27	0.01	0.86
	VME closed area	-0.25	-1.38	0.59	-5.83	-13.13	4.88	-0.02	-0.07	-0.01	0.21	-0.07	0.97
	Seamounts	-0.39	-3.03	0.25	-5.93	-10.49	0.83	-0.02	-0.07	-0.01	0.21	-0.03	0.97
	Cold-water corals	-1.05	-1.64	-0.46	-7.22	-10.86	-1.92	-0.02	-0.03	-0.01	0.16	0.002	0.36
	Canyons	-0.72	-1.64	0.15	-7.1	-12.48	-1.96	-0.03	-0.07	-0.01	0.28	0.03	0.97
SPRFMO	>200 m	-0.21	-2.35	0.54	-4.83	-59.36	22.88	-0.01	-0.23	0.06	0.12	-0.11	1.16
	200–2 500 m	-0.42	-1.38	0.48	-3.26	-12.73	1.96	-0.05	-0.23	0.003	0.22	-0.09	1.16
	Seamounts	0.01	-0.8	0.37	-2.05	-8.21	4.01	-0.01	-0.03	0.01	0.09	0.03	0.3
	Cold-water corals	-0.41	-1.38	0.48	-4.09	-10.95	1.58	-0.04	-0.18	-0.01	0.2	-0.04	0.88
	Canyons	-0.34	-1.38	0.02	-3.22	-8.12	-0.48	-0.07	-0.19	-0.02	0.33	0.1	0.97

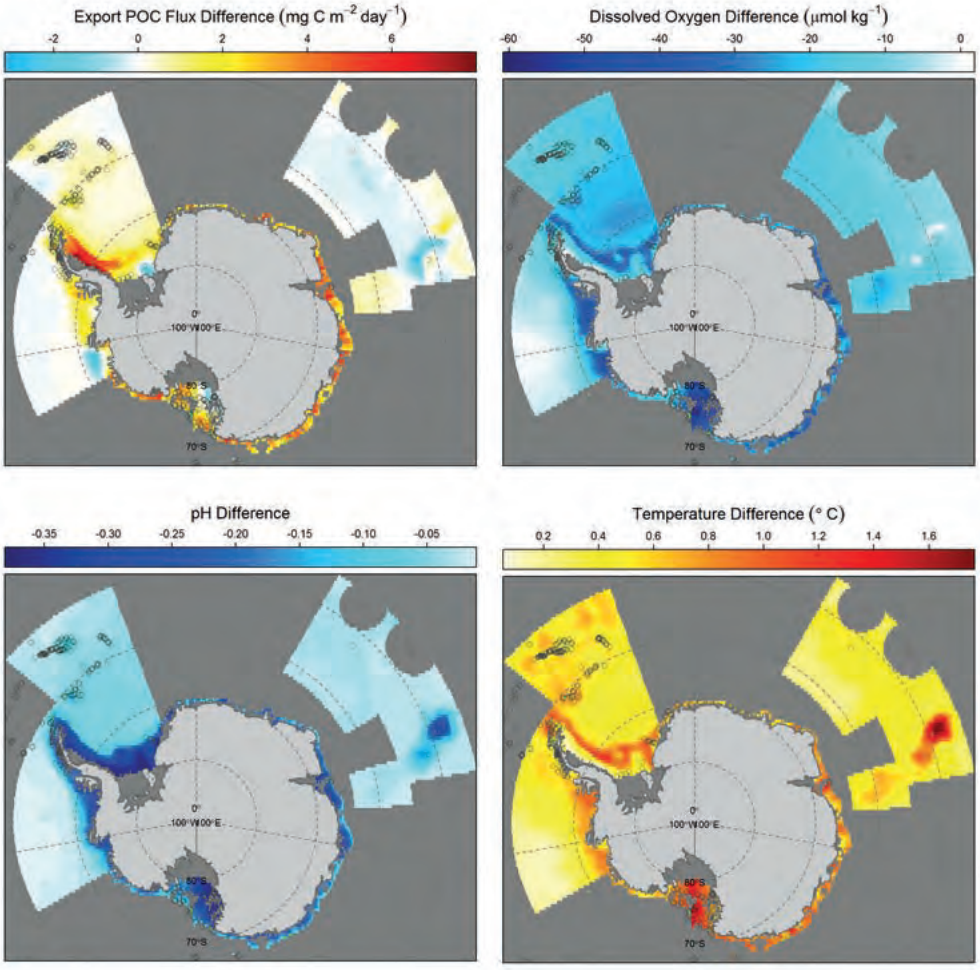
FIGURE A8.1.1
Seafloor climate changes in CCAMLR by 2041-2060 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.2

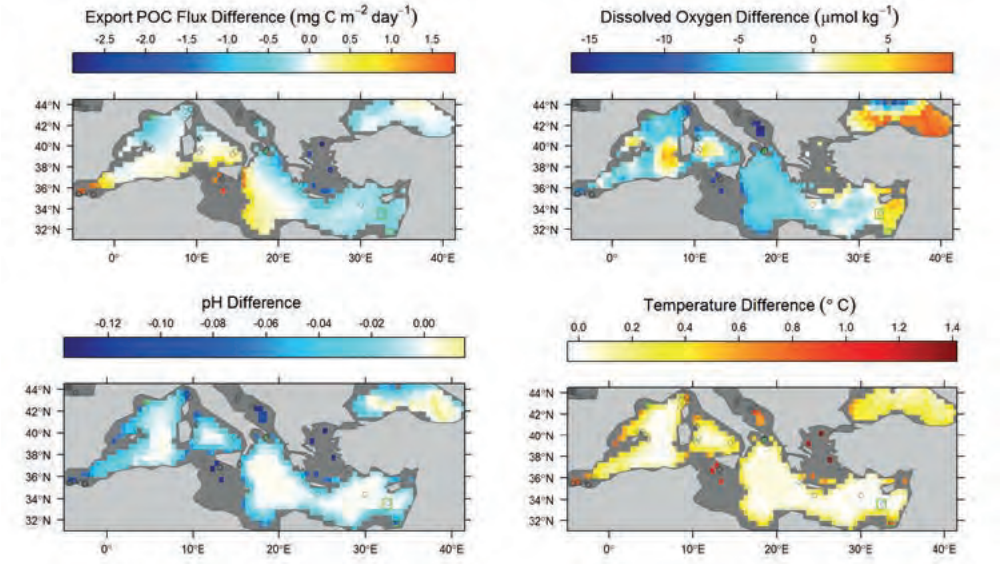
Seafloor climate changes in CCAMLR by 2081–2100 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.3

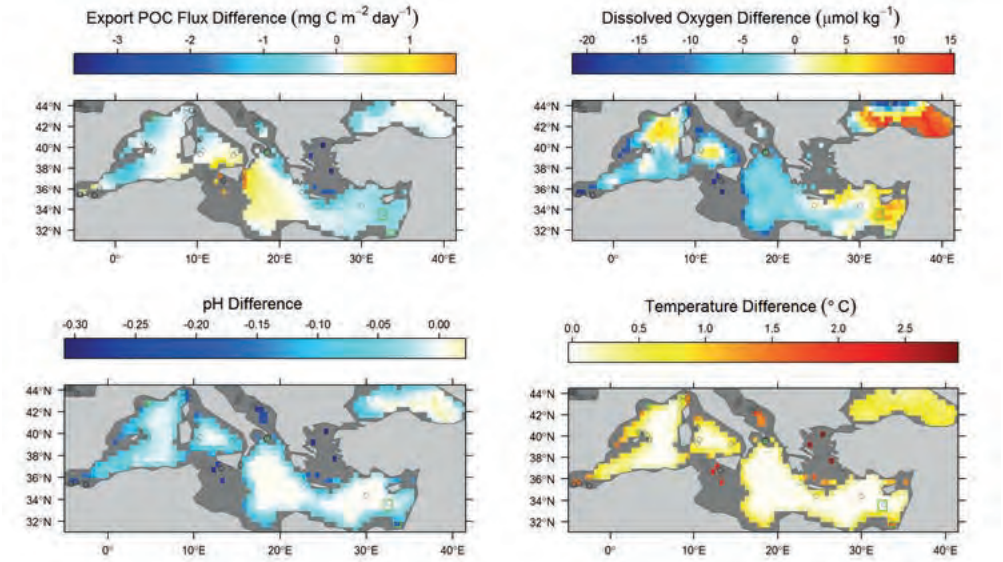
Seafloor climate changes in GFCM by 2041–2060 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

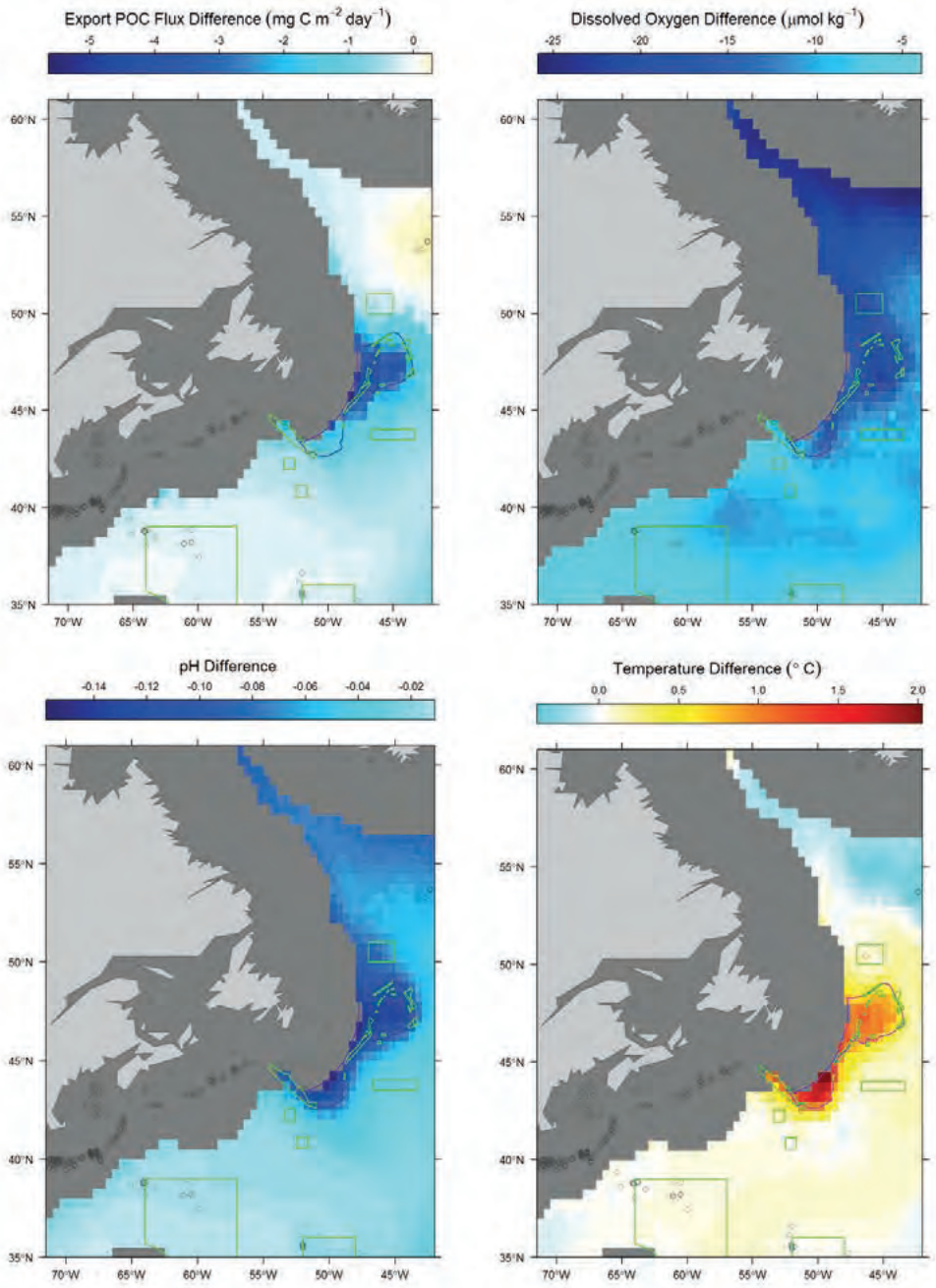
FIGURE A8.1.4

Seafloor climate changes in GFCM by 2081–2100 (relative to 1951–2000)



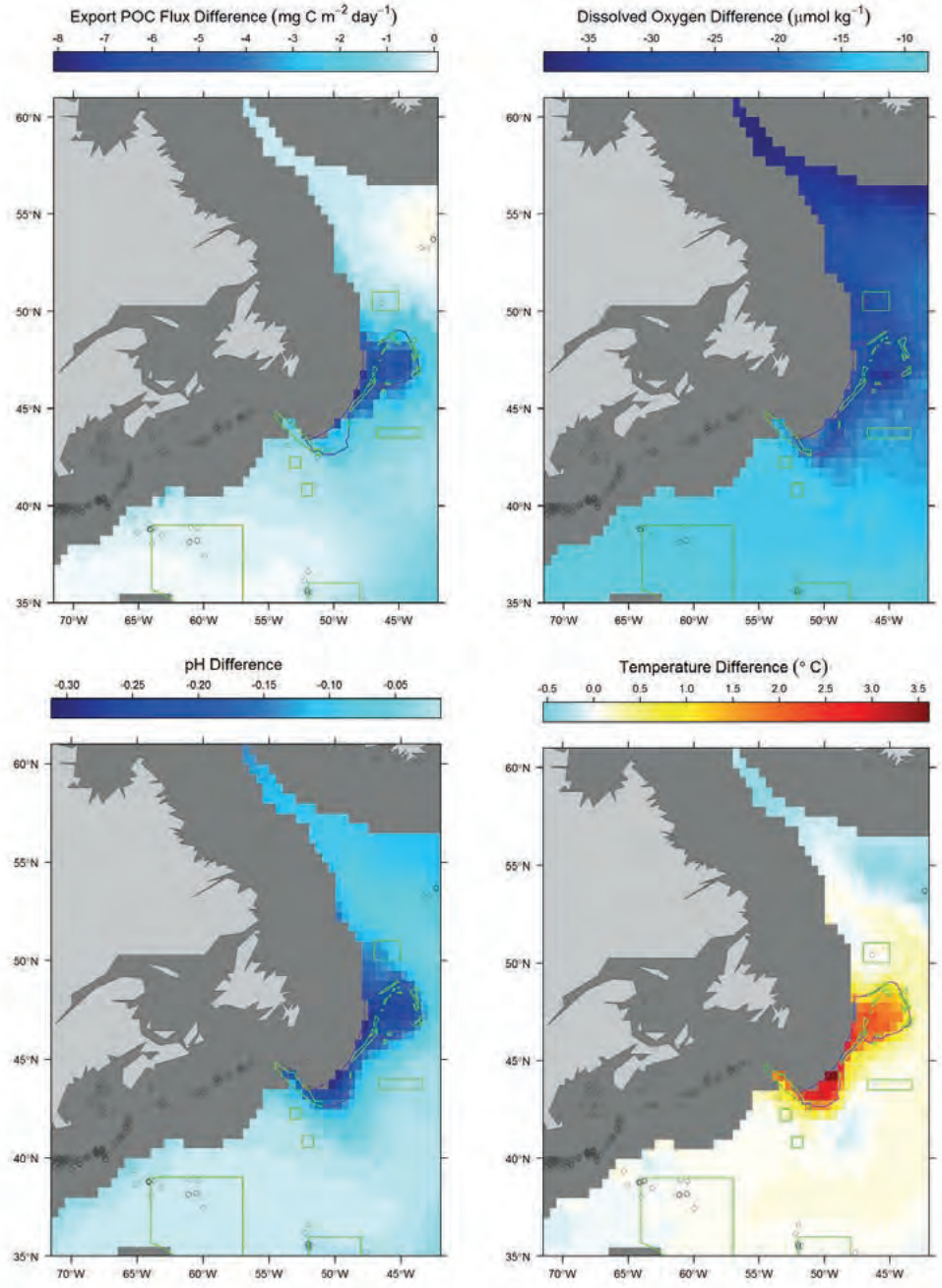
Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.5
Seafloor climate changes in NAFO by 2041–2060 (relative to 1951–2000)



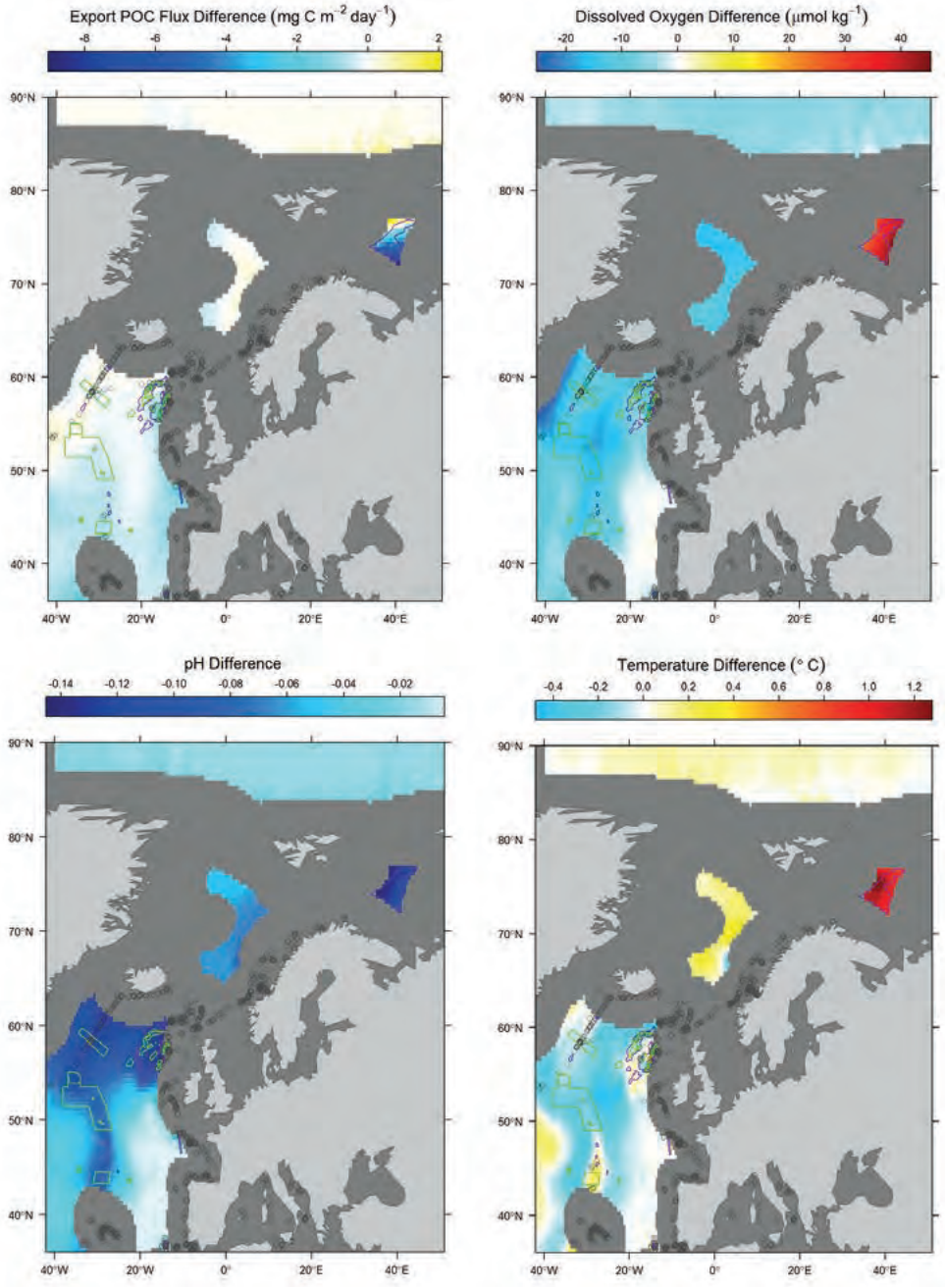
Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.6
Seafloor climate changes in NAFO by 2081–2100 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

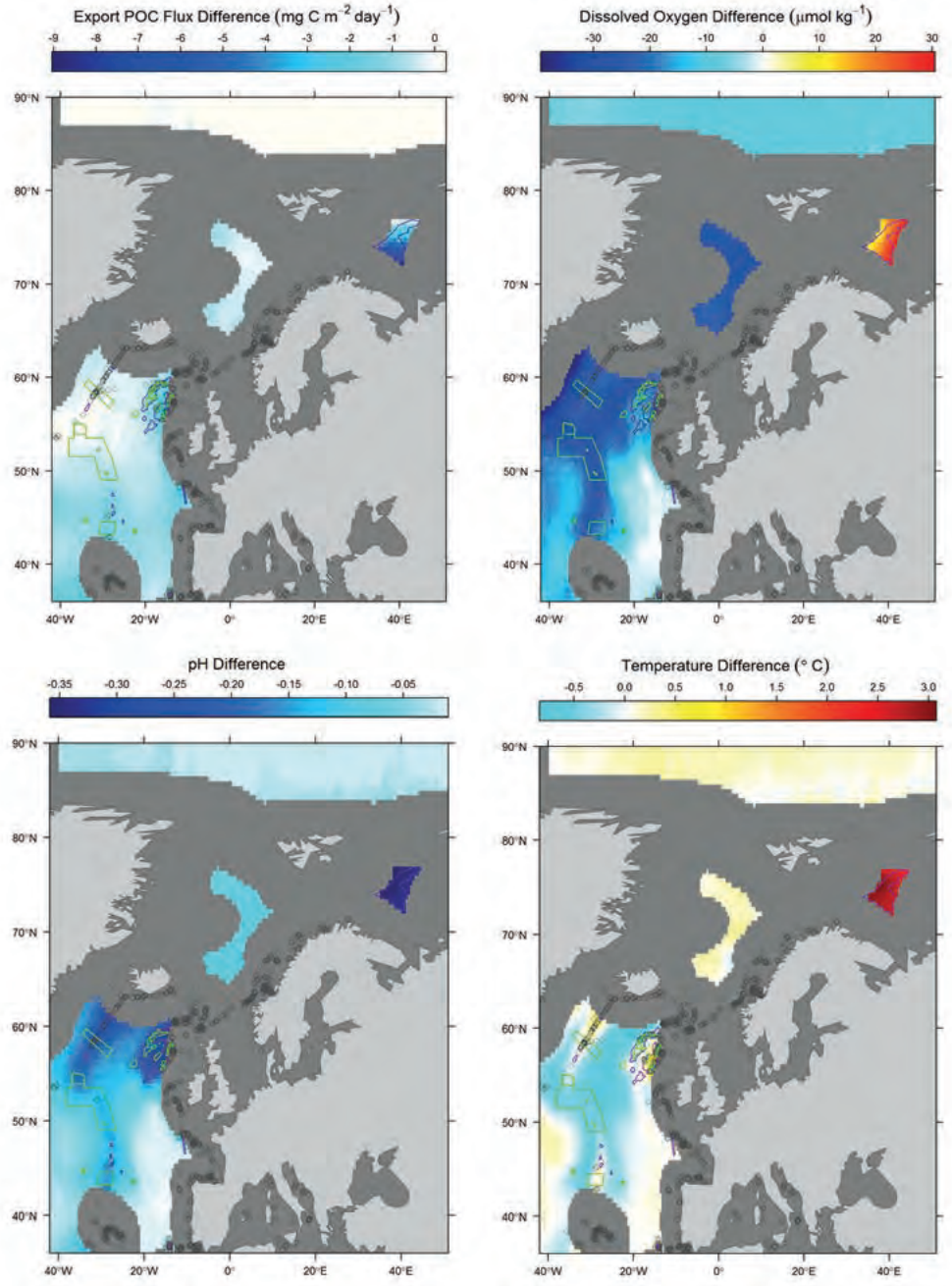
FIGURE A8.1.7
Seafloor climate changes in NEAFC by 2041–2060 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.8

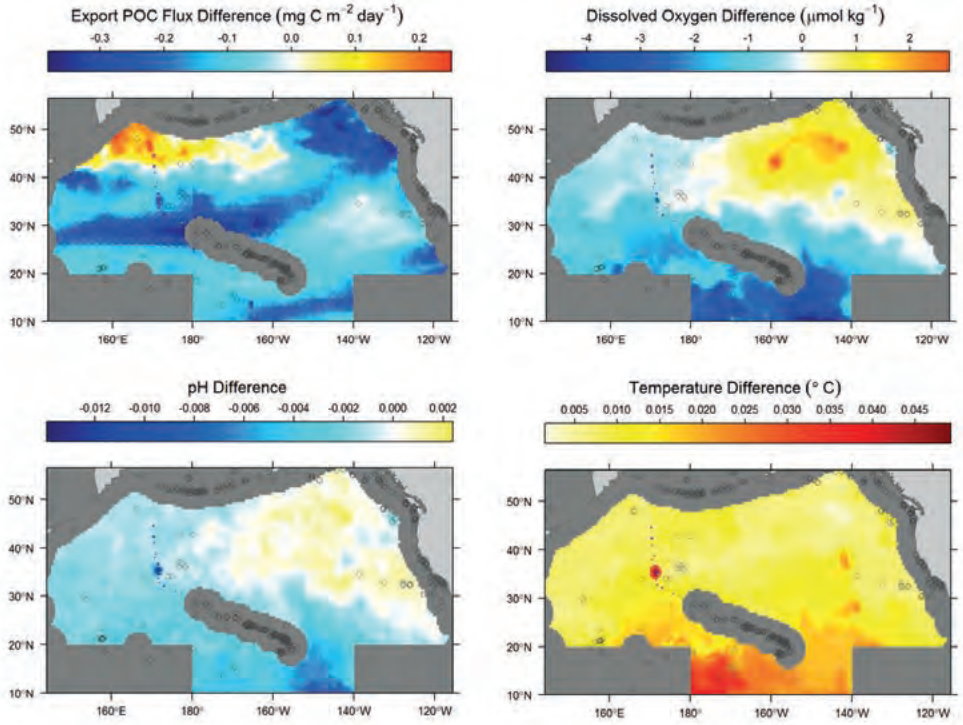
Seafloor climate changes in NEAFC by 2081–2100 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.9

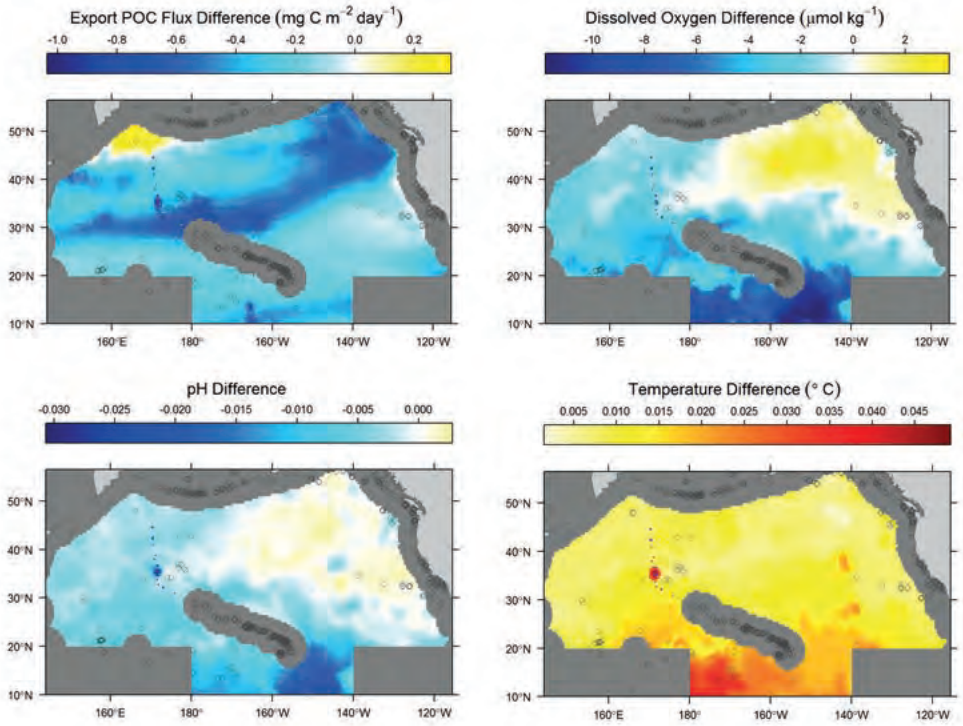
Seafloor climate changes in NPFC by 2041–2060 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

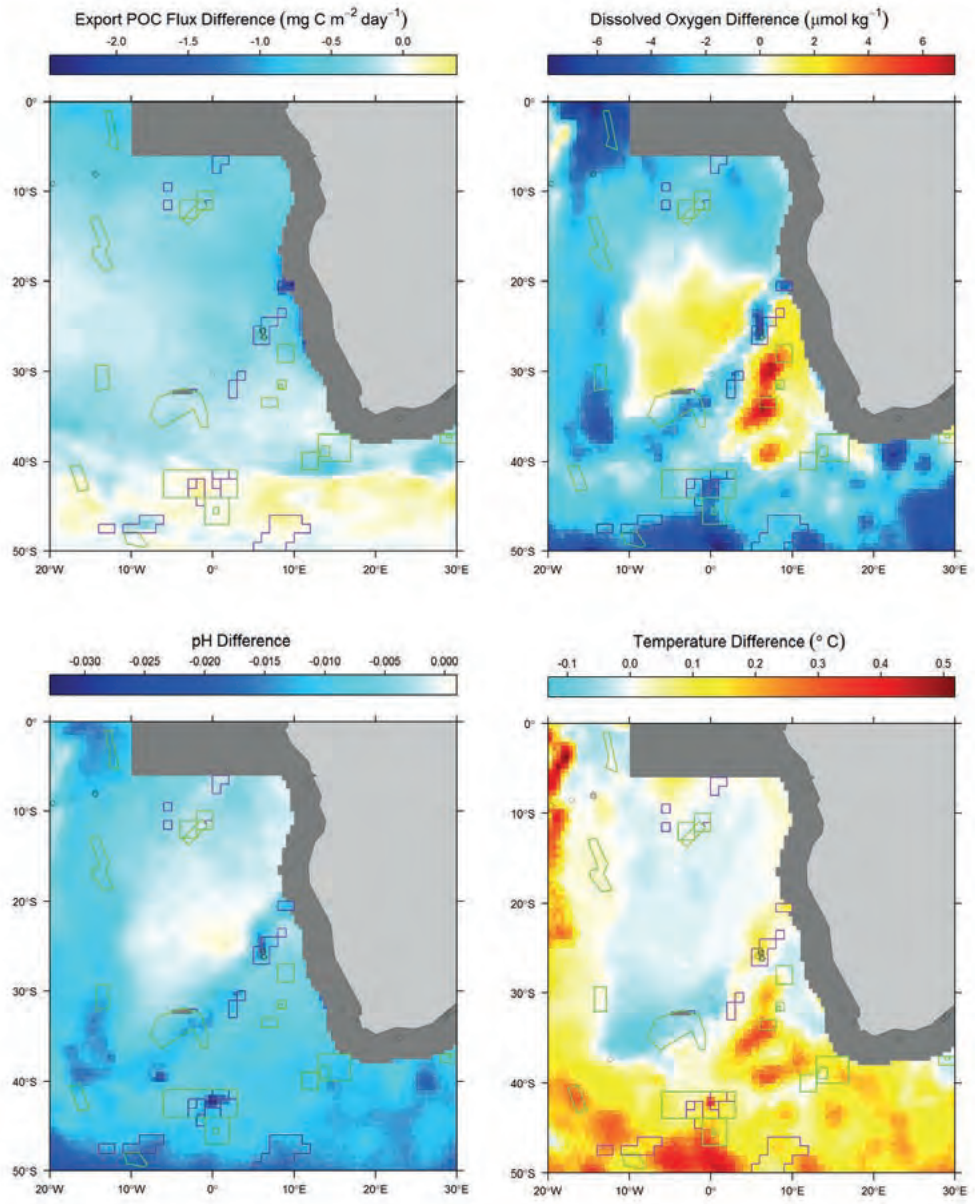
FIGURE A8.1.10

Seafloor climate changes in NPFC by 2081–2100 (relative to 1951–2000)



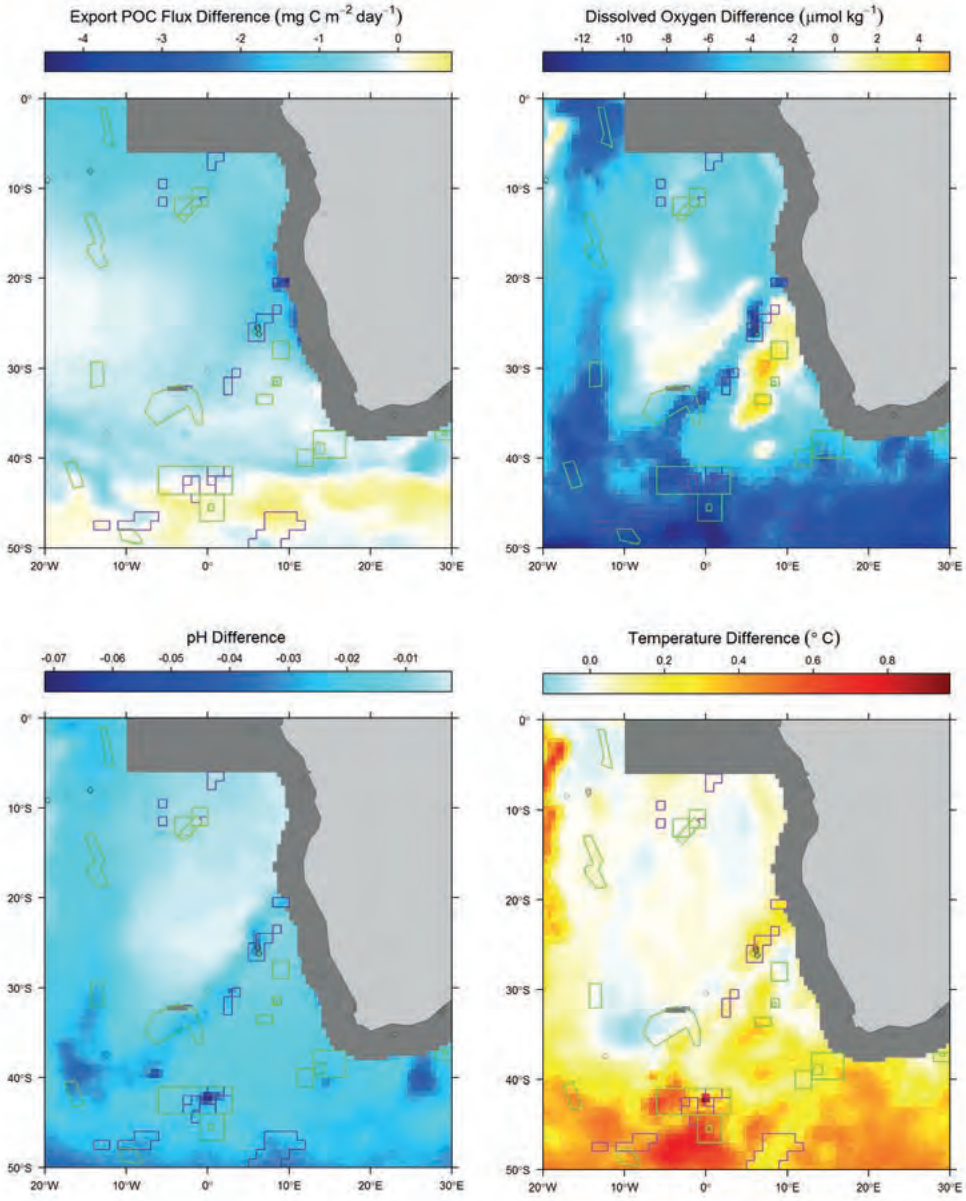
Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.11
Seafloor climate changes in SEAFO by 2041–2060 (relative to 1951–2000)



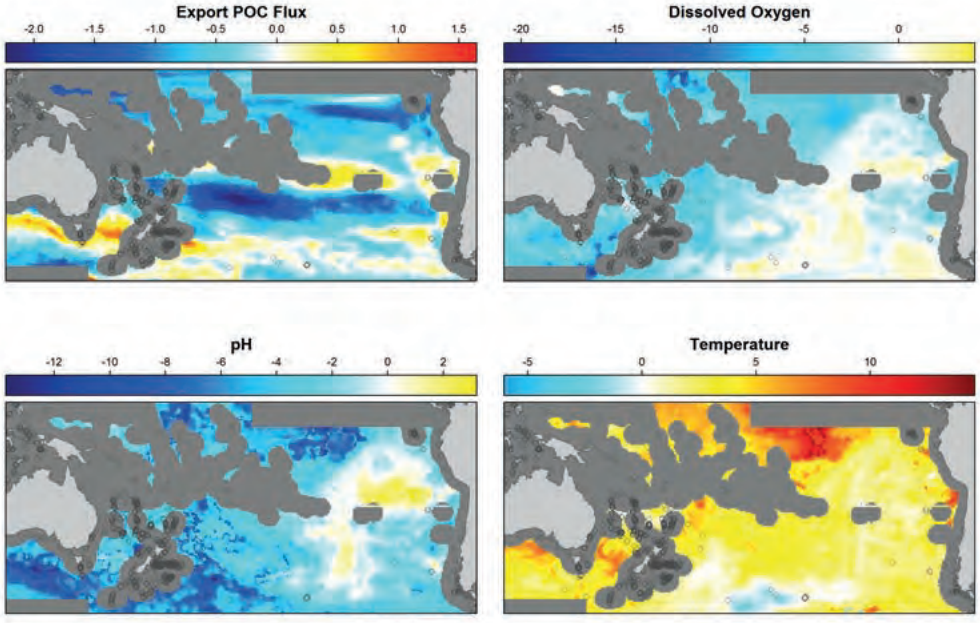
Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.12
Seafloor climate changes in SEAFO by 2081–2100 (relative to 1951–2000)



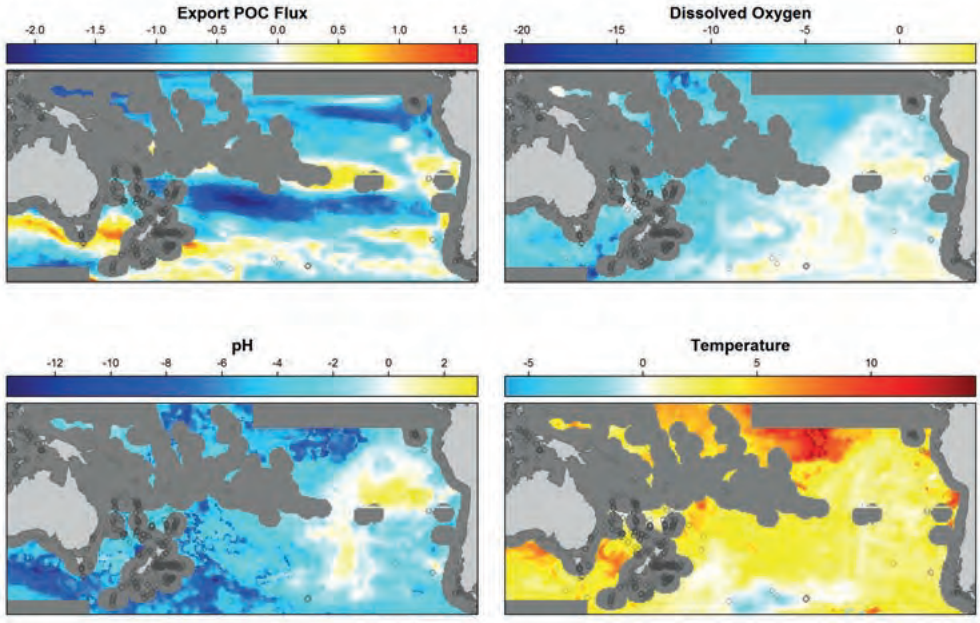
Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.13
Seafloor climate changes in SPRFMO by 2041–2060 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.1.14
Seafloor climate changes in SPRFMO by 2081–2100 (relative to 1951–2000)



Notes: Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

APPENDIX A8.2

Model-averaging exposure to seafloor climate change hazards in each RFMO area

Contributors: **William Cheung** and **Lisa Levin**

TABLE A8.2.1
Summary statistics of exposure to seafloor climate change hazards in RFMO areas by 2041–2060

RFMO	Habitat	Export POC flux			Dissolved oxygen			pH			Temperature		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
CCAMLR	>200 m	0.26	-1.49	2.17	-2.48	-11.59	1.77	-5.95	-13.55	-2.04	3.51	-5.43	11.4
	200–2 500 m	0.34	-1.39	2.08	-2.22	-6.68	0.6	-7.18	-11.25	-2.96	2.88	-0.47	8.27
	VME closed area	0.44	0.16	0.55	-2.92	-3.96	-2.03	-6.84	-7.4	-5.73	2.84	2.21	3.29
	Seamounts	-0.12	-0.72	0.98	-2.73	-4.66	-0.35	-6.06	-8.73	-2.68	3.06	2.1	4.67
	Cold-water corals	0.48	-1.12	1.38	-1.51	-3.92	0.09	-7.08	-11.05	-3.86	1.99	0.24	7.12
	Canyons	0.48	-1.39	2.07	-2.47	-5.6	-0.11	-6.86	-10.88	-3.18	3.25	0.27	6.52
GFCM	>200 m	-0.39	-1.38	1.08	-0.94	-4.29	2.9	-3.68	-10.56	0.48	4.07	-2.44	18.67
	200–2 500 m	-0.51	-1.38	1.08	-1.22	-4.29	2.9	-5.22	-10.56	0.2	4.91	-1.52	18.67
	VME closed area	-1.08	-1.37	-0.56	-1.54	-2.93	-0.61	-4.78	-7.95	-2.29	3.59	1.54	5.86
	Cold-water corals	-0.14	-1.37	1.03	-1.68	-3.26	0.43	-5.96	-9.75	0.04	4.95	2.07	7.84
	Canyons	-0.44	-1.38	1.07	-1.48	-3.66	2.9	-5.96	-9.75	-1.11	5.01	1.31	9.49
NAFO	>200 m	-1.23	-2.67	1.49	-5.57	-9.65	-1.84	-5.75	-11.12	-2.67	0.96	-4.87	5.09
	200–2 500 m	-1.82	-2.18	-0.58	-4.78	-9.34	-1.84	-9.96	-11.12	-8.49	3.1	0.92	5.09
	Bottom-fishing area	-1.89	-2.15	-1.6	-4.27	-7.09	-1.49	-10.29	-11.12	-9.36	3.12	2.18	4.61
	VME closed area	-1.14	-2.58	-0.56	-5.52	-7.77	-1.88	-5.24	-10.51	-3.54	1.72	-1.7	4.61
	Cold-water corals	-1.19	-2.18	1.49	-4.7	-7.32	-1.84	-6.64	-10.06	-3.54	1.3	-2.97	4.07
	Canyons	-1.95	-2.24	-1.73	-4.14	-7.38	-1.79	-9.1	-10.06	-7.41	2.79	1.01	5.09
NEAFC	>200 m	-0.42	-4.29	1.5	-4.19	-11.6	3.82	-6.82	-13.7	-2.11	0.07	-7.02	9.11
	200–2 500 m	-0.43	-2.13	0.7	-3.73	-8.62	3.82	-9.59	-12.79	-5.38	0.2	-4.17	9.11
	Bottom-fishing area	-0.8	-4.27	0.34	-0.05	-8.24	3.59	-8.37	-12.3	-5.38	0.99	-1.35	3.43
	VME closed area	-0.59	-1.7	0.7	-4.44	-8.38	-1.72	-9.98	-13.31	-8.01	-1.62	-6.32	3.66
	Cold-water corals	-0.63	-4.29	1.5	-3.99	-8.32	-0.56	-9.96	-12.58	-5.87	0.12	-3.01	4.64
	Canyons	-1.25	-4.29	-0.28	-3.33	-6.25	-1.27	-9.92	-11.25	-6.72	-0.17	-1.78	1.17
NPFC	>200 m	-0.68	-2.15	1.1	-1.62	-10.51	5.29	-2.4	-21.42	2.3	3.85	-1.02	11.17
	200–2 500 m	-0.84	-1.61	0.27	-1.61	-2.87	-0.73	-1.86	-3.41	-0.86	2.64	1.87	3.28
	Bottom-fishing area	-0.36	-0.72	-0.001	-1.2	-1.49	-0.92	-2.34	-3.39	-1.29	2.23	2.12	2.33
	Seamounts	-0.99	-1.93	0.19	-2.48	-5.53	0.7	-2.15	-4.13	0.14	3.75	1.91	5.92
	Cold-water corals	-0.83	-1.94	1.01	-1.64	-6.41	1.32	-1.88	-7.79	0.16	3.25	0.75	6.89
	Canyons	-0.75	-0.76	-0.74	-1.35	-1.36	-1.34	-2.99	-3.02	-2.97	2.25	2.25	2.26
SEAFO	>200 m	-0.95	-3.4	2.15	-1.93	-6.46	7.97	-4.28	-11.2	12.13	2.62	-4.6	22.46
	200–2 500 m	-0.61	-2.98	0.35	-2.51	-5.84	1.56	-5.15	-9.2	-2.57	2.33	-1.4	7.96
	Bottom-fishing area	-0.56	-3.25	0.33	-2.42	-4.09	1.56	-4.58	-8.27	-1.26	2.59	0.23	7.96
	VME closed area	-0.63	-3.4	0.44	-2.68	-6.46	0.68	-4.79	-10.49	-0.16	2.13	-1.68	7.31
	Seamounts	-0.88	-3.26	0.33	-2.38	-4.79	0.65	-4.67	-8.01	-0.36	2.19	-0.35	5.77
	Cold-water corals	-1.49	-2.79	-0.48	-2.46	-3.48	-0.1	-5.73	-9.42	-4.02	1.99	-0.2	4.22
	Canyons	-0.57	-3.15	0.17	-2.18	-4.09	-0.84	-4.99	-7.67	-3.24	2.95	0.07	5.73
SPRFMO	>200 m	-0.43	-2.23	1.65	-2.11	-20.92	4.4	-3.34	-13.74	3.37	3.02	-5.86	14.58
	200–2 500 m	-0.42	-1.38	0.86	-1.8	-7.68	0.93	-4.69	-9.99	0.87	2.51	-1.94	5.69
	Seamounts	-0.2	-1.14	0.37	-0.58	-3.57	0.93	-1.15	-6.34	0.87	1.92	0.64	6.82
	Cold-water corals	-0.48	-1.4	0.86	-1.99	-7.7	0.32	-4.73	-9.54	-0.37	2.24	-0.93	5.34
	Canyons	-0.32	-0.77	0.06	-2.02	-5.81	-0.7	-6.59	-9.8	-2.88	3.34	0.47	4.82

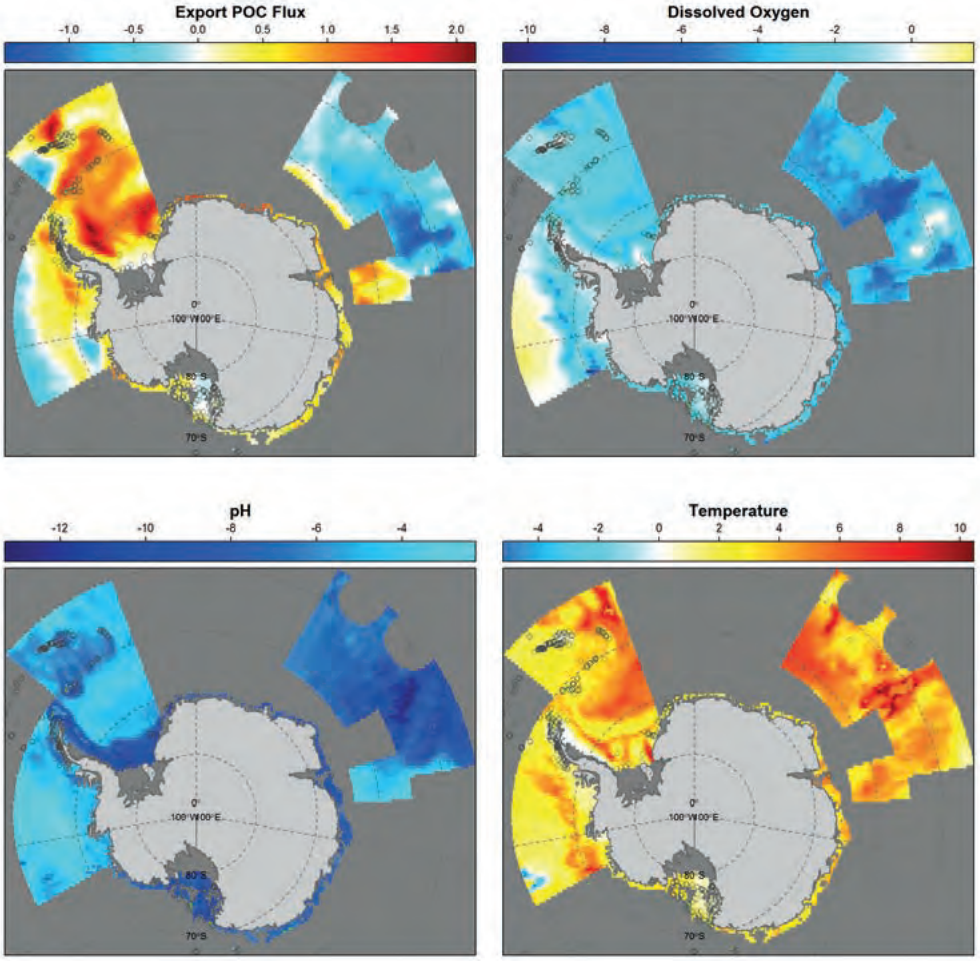
TABLE A8.2.2

Summary statistics of exposure to seafloor climate change hazards in RFMO areas by 2081–2100

RFMO	Habitat	Export POC flux			Dissolved oxygen			pH			Temperature		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
CCAMLR	>200 m	0.47	-2.02	3.21	-6.25	-23.02	0.14	-10.96	-29.41	-3.03	8.35	0.65	54.27
	200–2 500 m	0.79	-1.56	3.21	-5.2	-14.52	0.14	-14.48	-24.9	-5.2	7.16	0.65	48.89
	VME closed area	1.16	0.75	1.5	-5.6	-6.96	-4.95	-13.61	-18.77	-11.38	5.45	4.82	6.32
	Seamounts	-0.4	-1.47	1.67	-6.52	-9.78	-4.63	-11.47	-17.77	-5.2	6.28	5.02	8.35
	Cold-water corals	0.83	-1.22	2.32	-4.34	-8.46	-0.57	-14.18	-22.95	-6.03	5.76	1.42	23.06
	Canyons	0.9	-1.56	3.2	-5.86	-12.31	-0.82	-13.58	-24.45	-5.22	6.83	1.63	12.55
GFCM	>200 m	-0.3	-1.89	2.71	-1.61	-7	4.66	-7.27	-22.39	0.51	7.99	-3.17	38.37
	200–2 500 m	-0.51	-1.89	1.92	-2.14	-7	4.66	-10.15	-22.39	0.35	9.94	-0.35	38.37
	VME closed area	-1.25	-1.64	-0.35	-2.44	-6.06	0.03	-10.36	-16.97	-5.33	8.75	6.3	12.11
	Cold-water corals	-0.16	-1.64	0.57	-3.27	-6.71	0.63	-12.37	-21.06	0.19	10.11	3.17	14.94
	Canyons	-0.49	-1.89	1.68	-2.79	-6.56	4.66	-11.84	-20.77	-2.82	9.82	3.7	20.52
NAFO	>200 m	-2.24	-5.77	0.66	-9.21	-15.55	-3.31	-8.93	-22.35	-4.89	0.9	-7.95	8.76
	200–2 500 m	-2.88	-3.54	-1.44	-7.97	-14.67	-3.31	-18.76	-22.35	-12.79	5.66	0.48	8.76
	Bottom-fishing area	-2.95	-3.54	-2.48	-7.13	-11.17	-2.69	-19.96	-22.35	-16.61	5.98	3.87	8.76
	VME closed area	-1.93	-3.97	-0.77	-9.42	-12.29	-3.58	-9.05	-19.95	-5.51	1.4	-5.7	8.76
	Cold-water corals	-2.13	-3.64	0.66	-8.25	-12.61	-3.43	-11.53	-20.14	-6.18	1.55	-5.7	7.24
	Canyons	-3	-3.53	-2.54	-7.19	-12.61	-3.06	-16.71	-20.14	-12.27	4.85	0.12	8.76
NEAFC	>200 m	-1.02	-5.56	1.04	-7.86	-20.52	1.63	-11.16	-27.81	-4.58	0.86	-12.94	14.86
	200–2 500 m	-1.23	-3.37	0.47	-8.08	-17.43	1.63	-18.05	-27.81	-7.85	0.8	-8.29	12.72
	Bottom-fishing area	-1.51	-5.56	0.19	-2.43	-15.55	1.65	-18.24	-24.1	-13.52	3.87	-4.07	7.51
	VME closed area	-1.32	-3.14	0.39	-8.07	-16.18	-4.5	-17.19	-25.81	-12.32	-4.16	-12.5	3.72
	Cold-water corals	-1.66	-5.46	0.61	-8.36	-15.46	-2.92	-19.19	-25.07	-11.24	0.95	-7.25	7.76
	Canyons	-2.7	-5.46	-1.66	-6.93	-10.72	-2.92	-18.59	-22.95	-9.62	-0.03	-2.53	3.46
NPFC	>200 m	-1.81	-4.42	2.5	-3.82	-35.89	8.82	-5.05	-29.48	1.66	7.66	1.27	23.13
	200–2 500 m	-2.02	-3.28	-0.2	-3.15	-5.49	-1.75	-3.48	-6.57	-1.79	5.49	4.22	7.11
	Bottom-fishing area	-1.44	-2.02	-0.86	-3.13	-3.91	-2.35	-5.28	-6.5	-4.06	4.93	4.24	5.62
	Seamounts	-2.2	-3.74	-0.45	-5.23	-14.52	1.25	-4.75	-15.22	-0.16	7.37	4.29	11.38
	Cold-water corals	-1.78	-3.24	2.11	-3.62	-18.22	2.09	-4.18	-25.11	-0.14	6.62	3	13.64
	Canyons	-2.03	-2.07	-2	-2.35	-2.48	-2.22	-5.92	-6.11	-5.73	4.15	4.13	4.16
SEAFO	>200 m	-1.57	-7.31	4.18	-5.11	-20.21	14.81	-9.51	-24.64	12.98	5.61	-3.26	50.77
	200–2 500 m	-1.36	-5.92	1.36	-7.25	-19.56	2.72	-11.67	-23.82	-5.79	5.55	-0.33	17.21
	Bottom-fishing area	-1.15	-6.98	1.04	-6.96	-14.94	2.72	-10	-19.32	-4.35	6.14	1.99	17.21
	VME closed area	-1.14	-7.23	1.53	-8.41	-17.05	2.09	-11.11	-24.64	-3.08	5.38	-3.21	16.85
	Seamounts	-1.79	-6.57	0.58	-6.77	-12.5	1.67	-11.22	-17.86	-3.08	4.99	-0.51	12.19
	Cold-water corals	-3.39	-5.92	-2.16	-5.43	-8.03	-2.15	-12.32	-19.14	-8.23	5.09	0.5	11.01
	Canyons	-1.62	-5.31	0.42	-5.17	-9.08	0.22	-11.21	-16.13	-8.23	7.26	1.01	13.57
SPRFMO	>200 m	-0.54	-4	3	-5.69	-43.53	3.95	-8.16	-34.18	3.02	7.49	-2.25	60.62
	200–2 500 m	-0.91	-2.54	1.63	-2.95	-12.07	1.13	-10.54	-20.33	0.94	5.65	-1.83	14.9
	Seamounts	0.14	-2.42	1.37	-2.06	-7.89	0.6	-3.46	-12.71	-0.07	5.01	2.72	14.34
	Cold-water corals	-1.14	-3.27	1.32	-3.58	-13.77	1.13	-10.8	-20.3	-1.51	5.13	-0.47	13.48
	Canyons	-0.76	-2.34	0.08	-3	-10.22	-0.27	-14.51	-21.48	-6.13	6.96	2.05	10.4

FIGURE A8.2.1

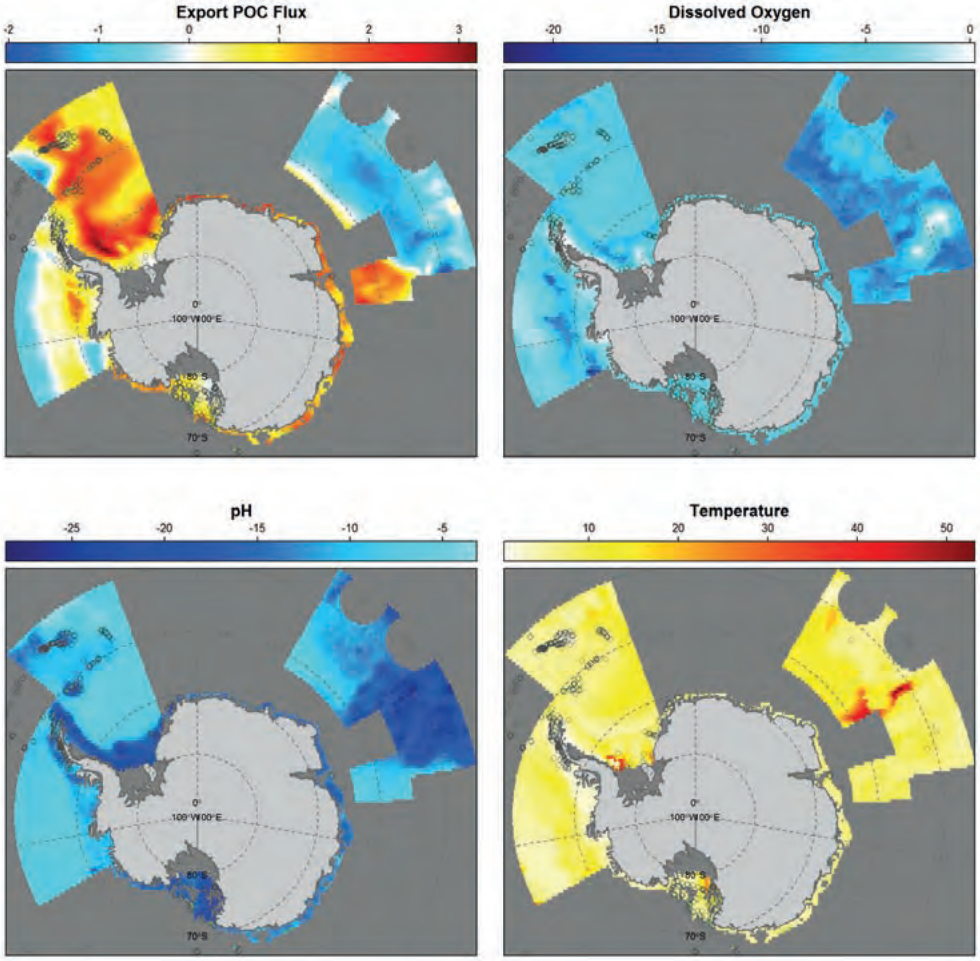
Exposure to seafloor climate change hazards in CCAMLR by 2041–2060



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.2

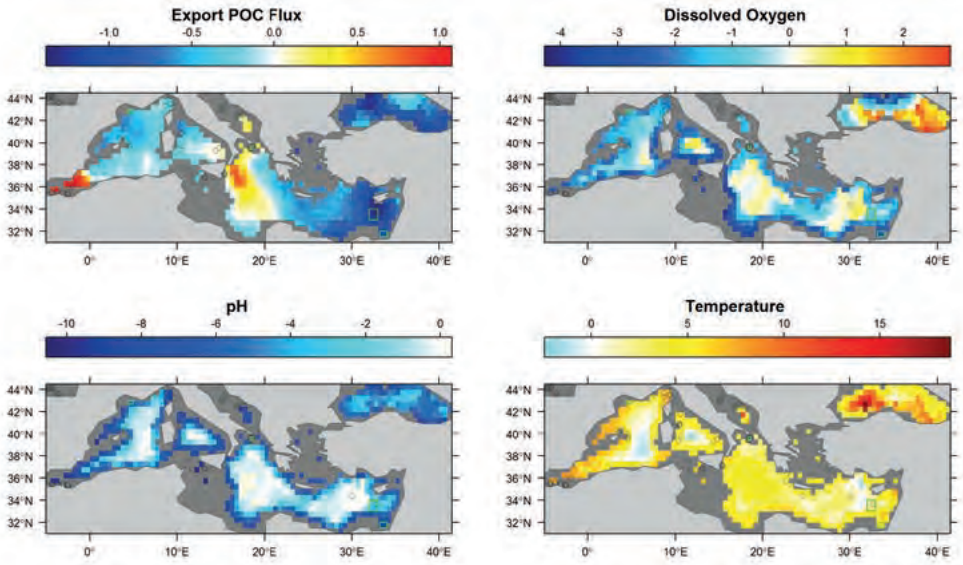
Exposure to seafloor climate change hazards in CCAMLR by 2081–2100



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.3

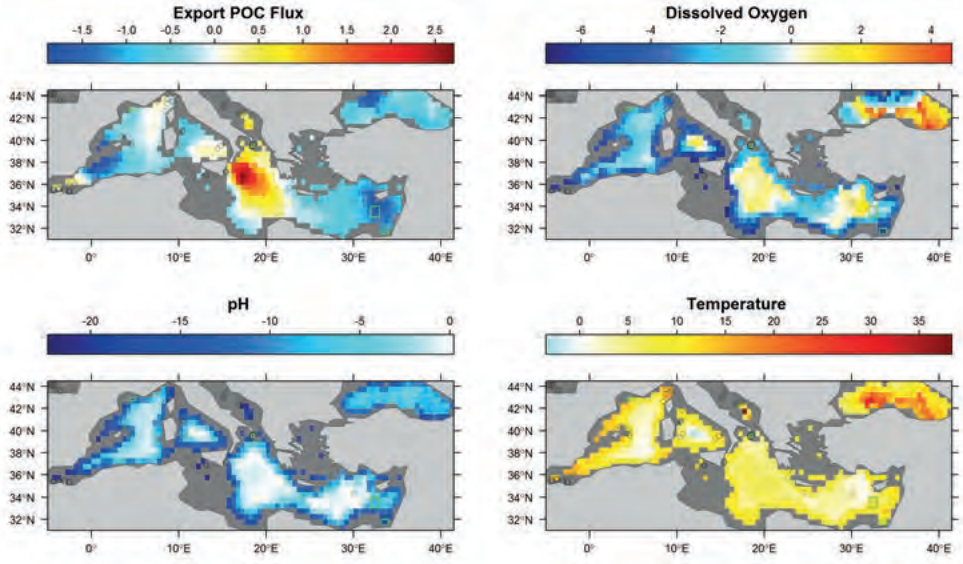
Exposure to seafloor climate change hazards in GFCM by 2041–2060



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.4

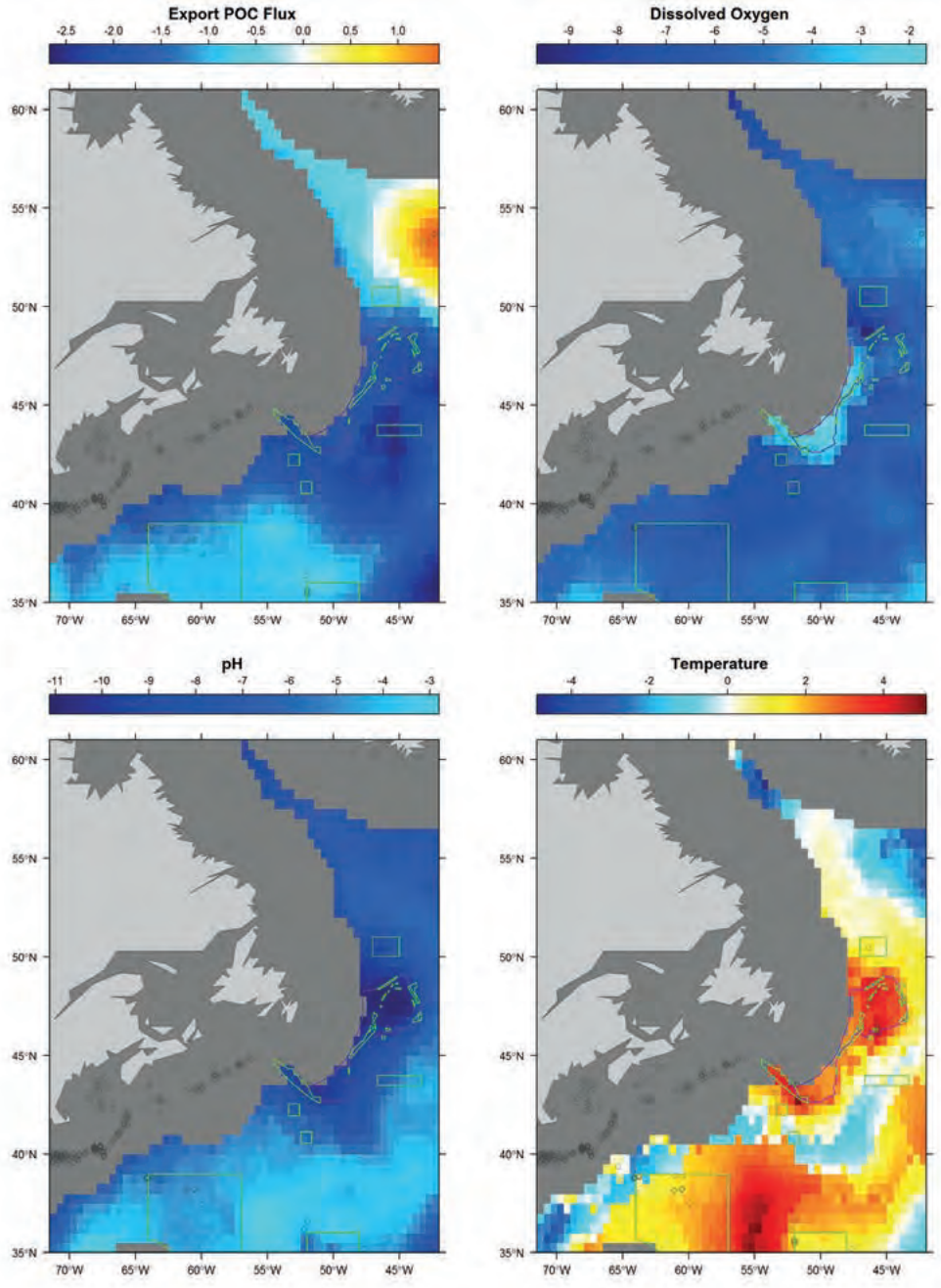
Exposure to seafloor climate change hazards in GFCM by 2081–2100



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

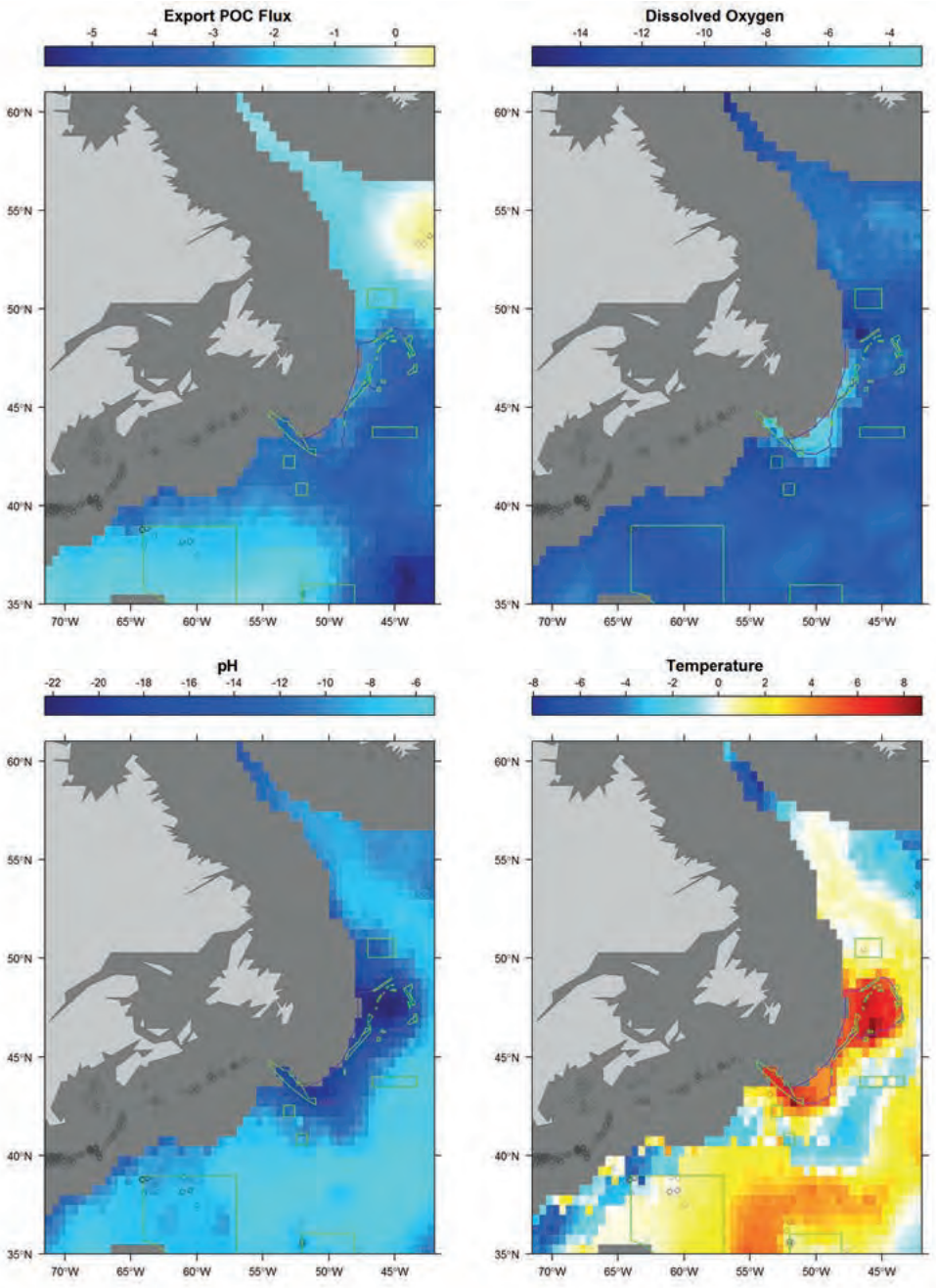
FIGURE A8.2.5

Exposure to seafloor climate change hazards in NAFO by 2041–2060



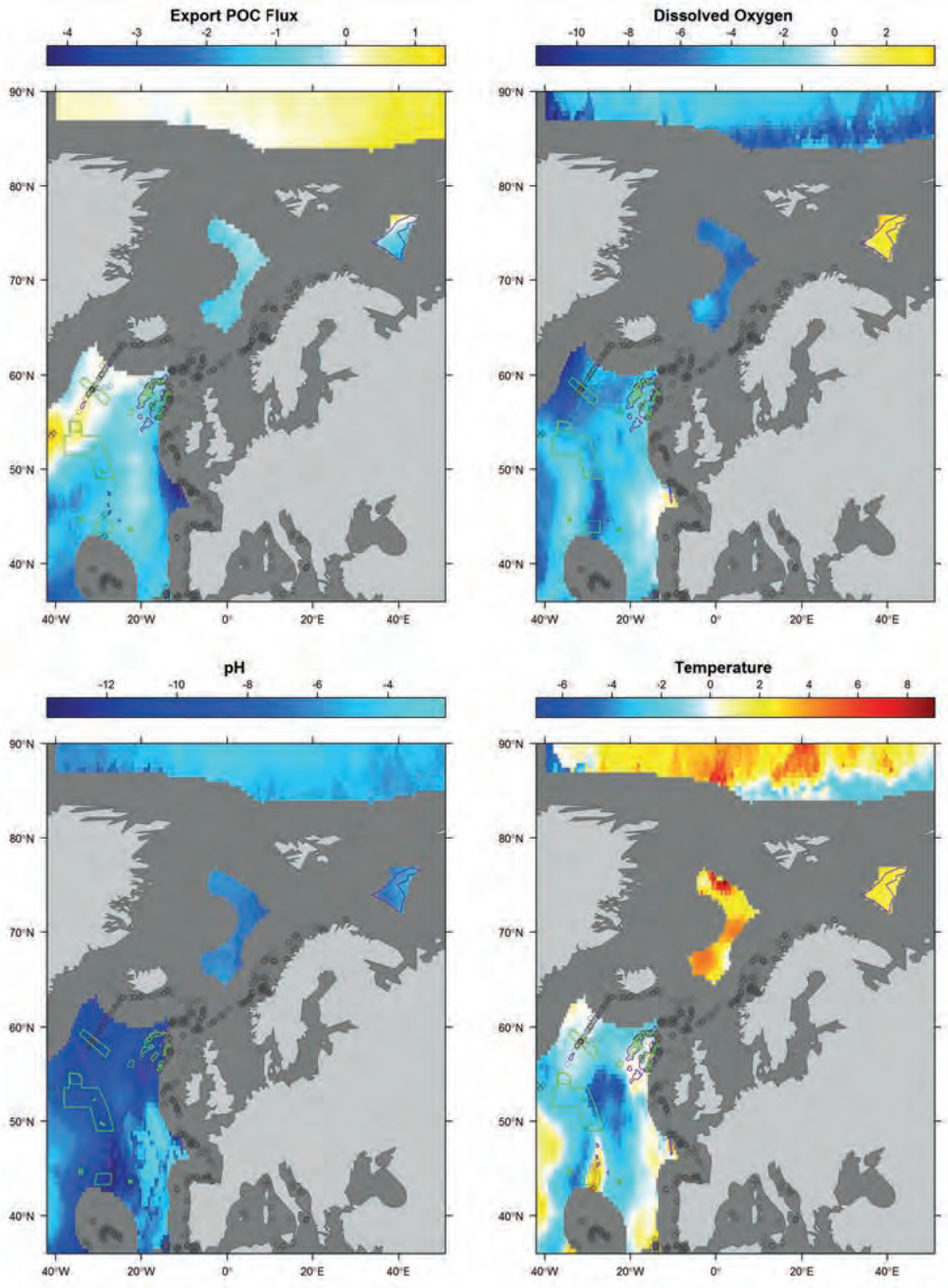
Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.6
Exposure to seafloor climate change hazards in NAFO by 2081–2100



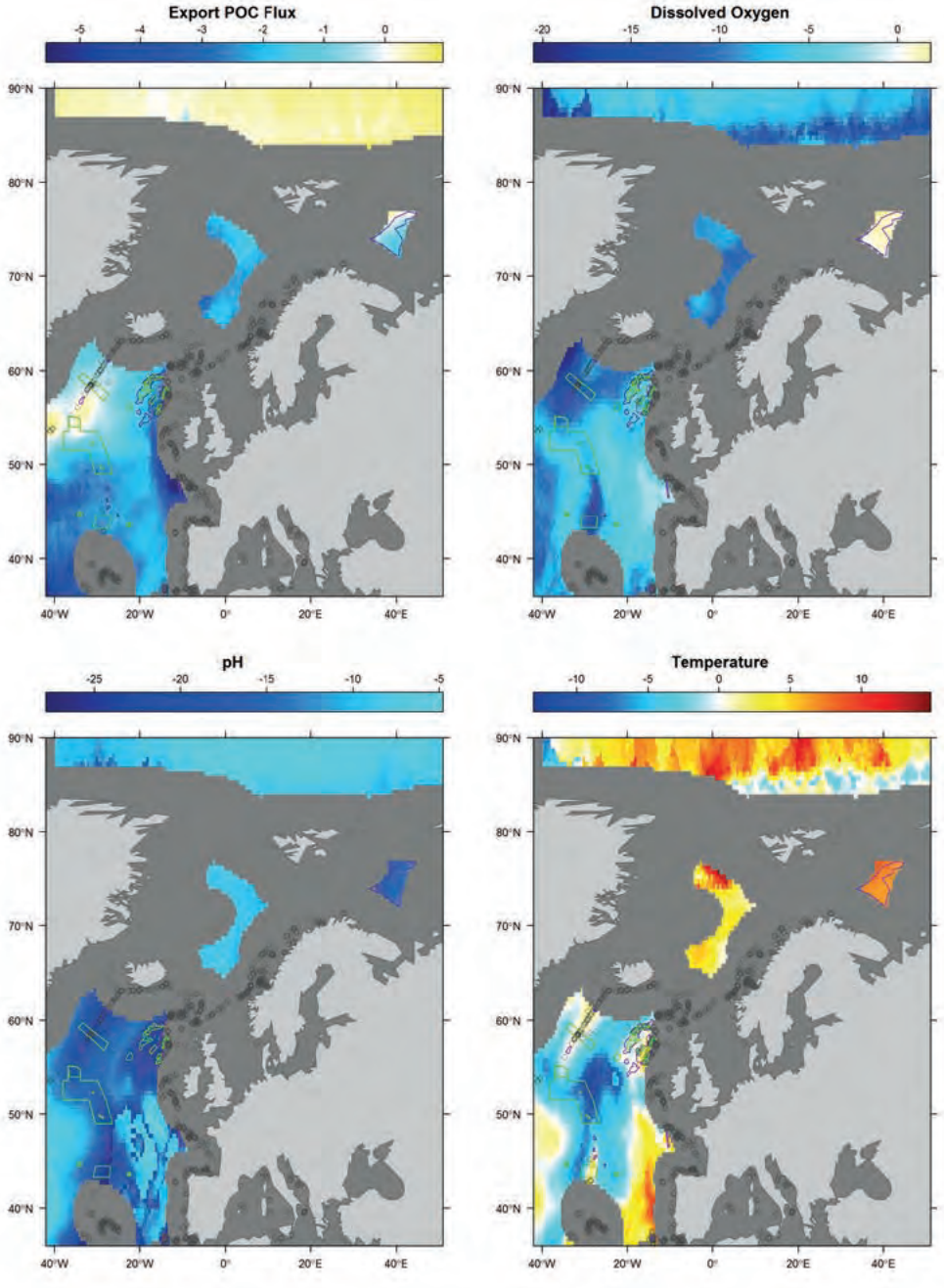
Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.7
Exposure to seafloor climate change hazards in NEAFC by 2041–2060



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

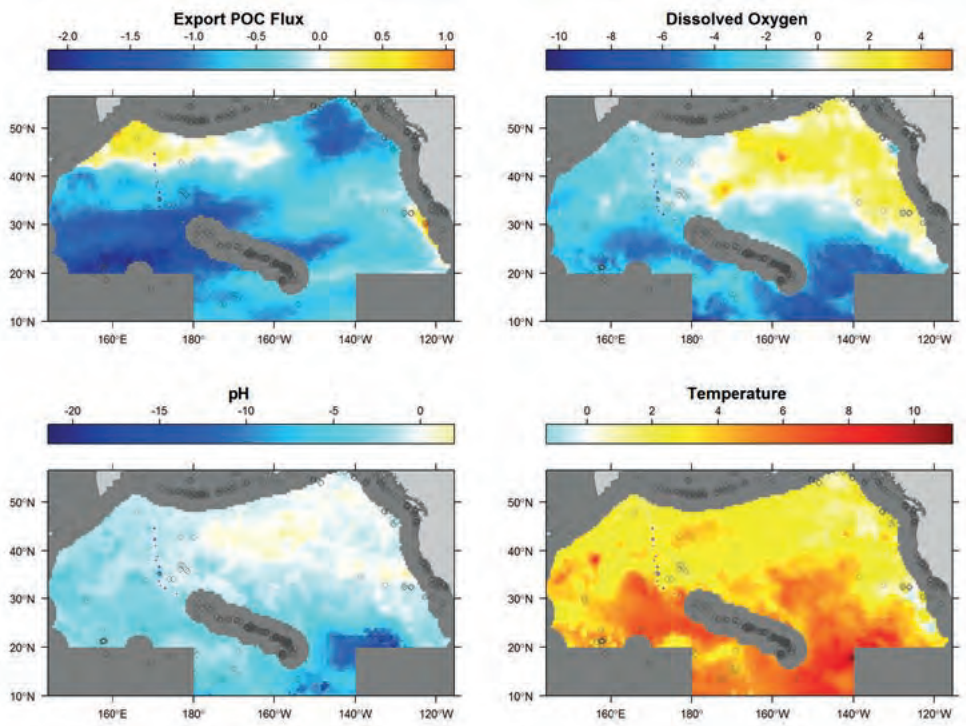
FIGURE A8.2.8
Exposure to seafloor climate change hazards in NEAFC by 2081–2100



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.9

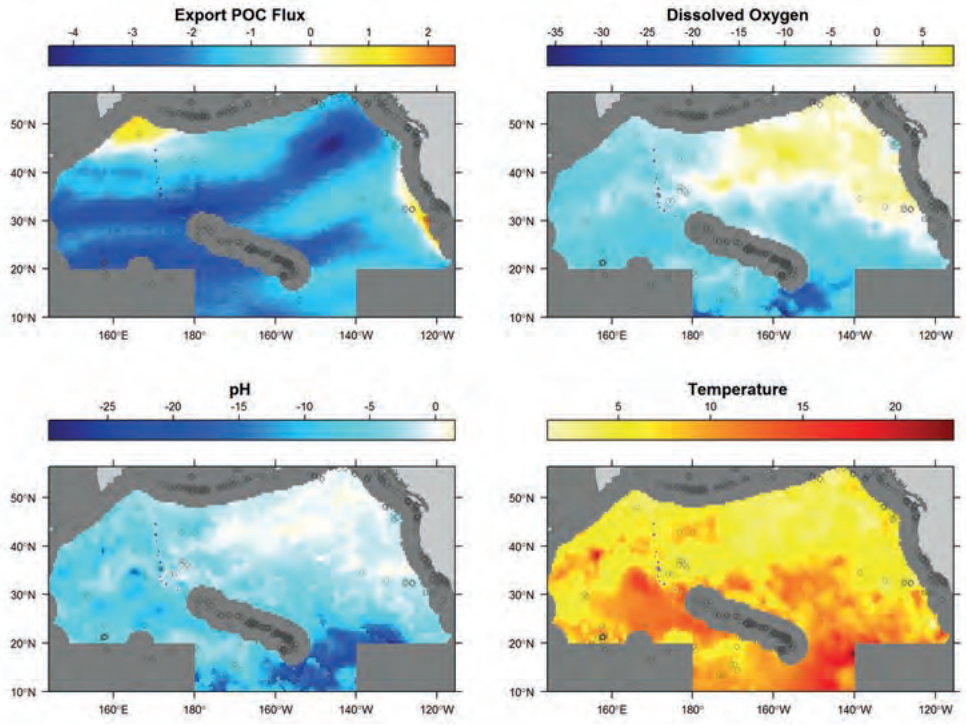
Exposure to seafloor climate change hazards in NPFC by 2041–2060



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

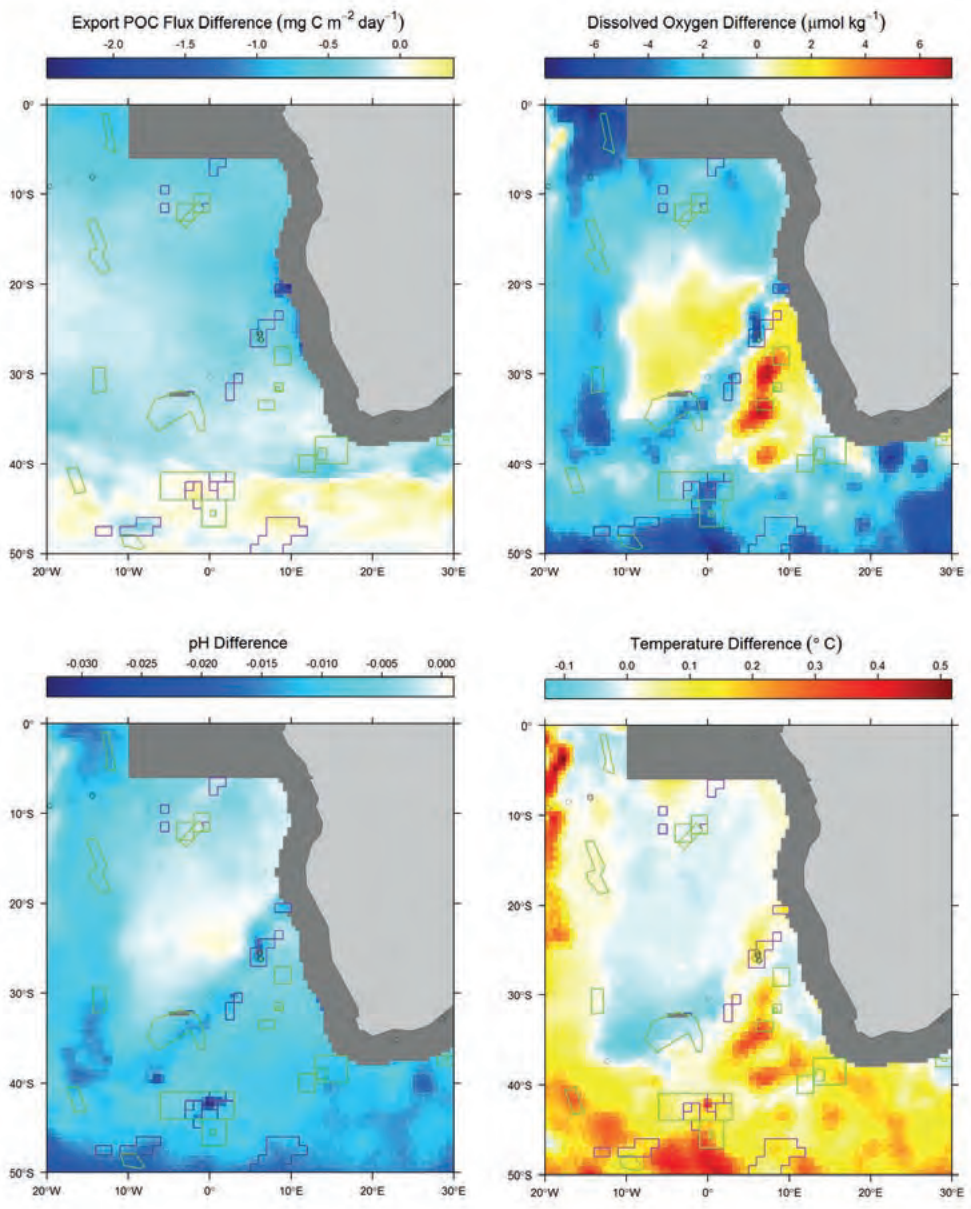
FIGURE A8.2.10

Exposure to seafloor climate change hazards in NPFC by 2081–2100



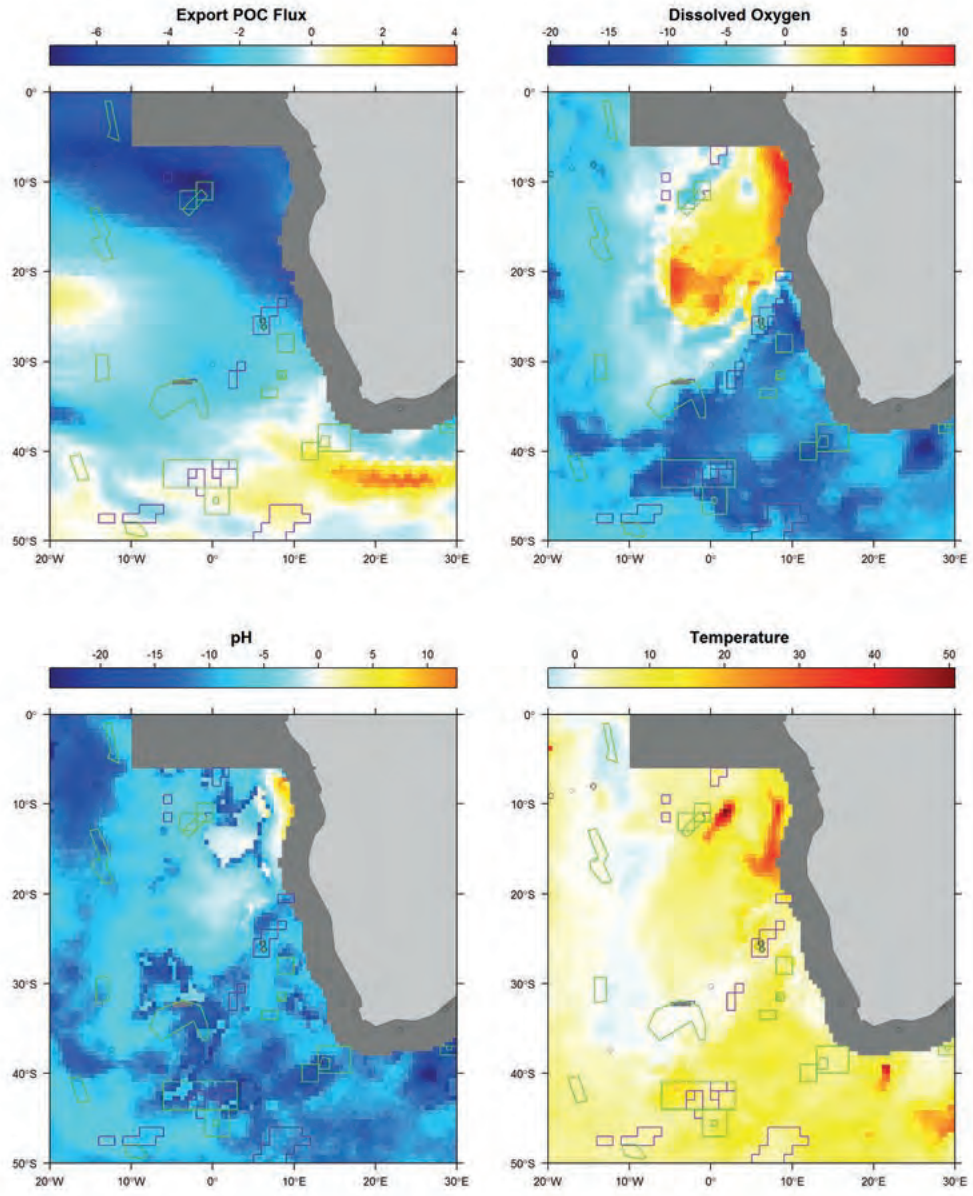
Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.11
Exposure to seafloor climate change hazards in SEAFO by 2041–2060



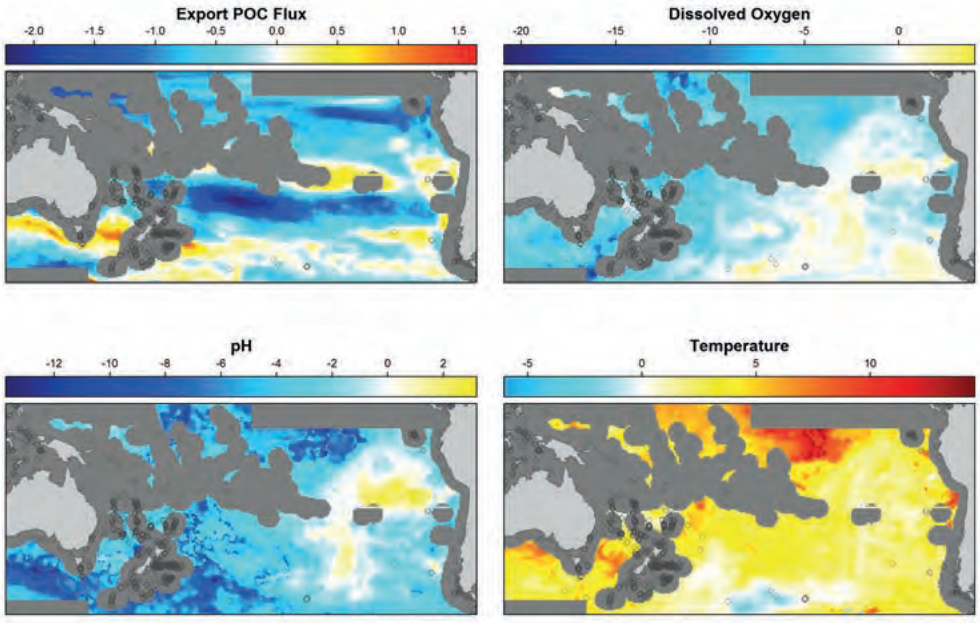
Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.12
Exposure to seafloor climate change hazards in SEAFO by 2081–2100



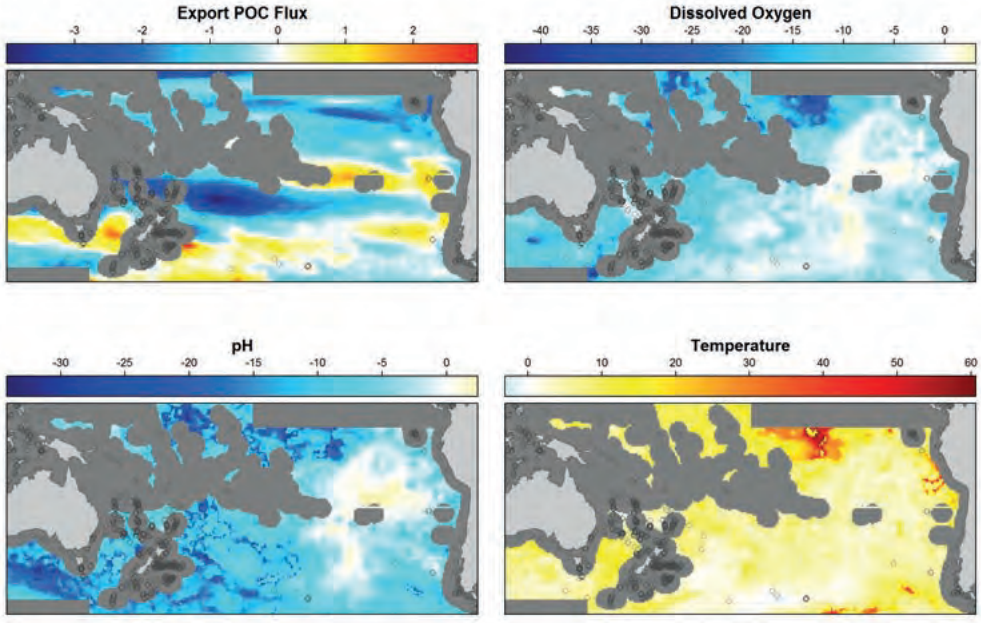
Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.13
Exposure to seafloor climate change hazards in SPRFMO by 2041–2060



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.2.14
Exposure to seafloor climate change hazards in SPRFMO by 2081–2100



Notes: The exposure to hazard is estimated by climate change between future and historical projections divided by the standard deviation of historical projection. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

APPENDIX A8.3

Model-averaging time of emergence of climate change in each RFMO area

Contributors: **William Cheung** and **Lisa Levin**

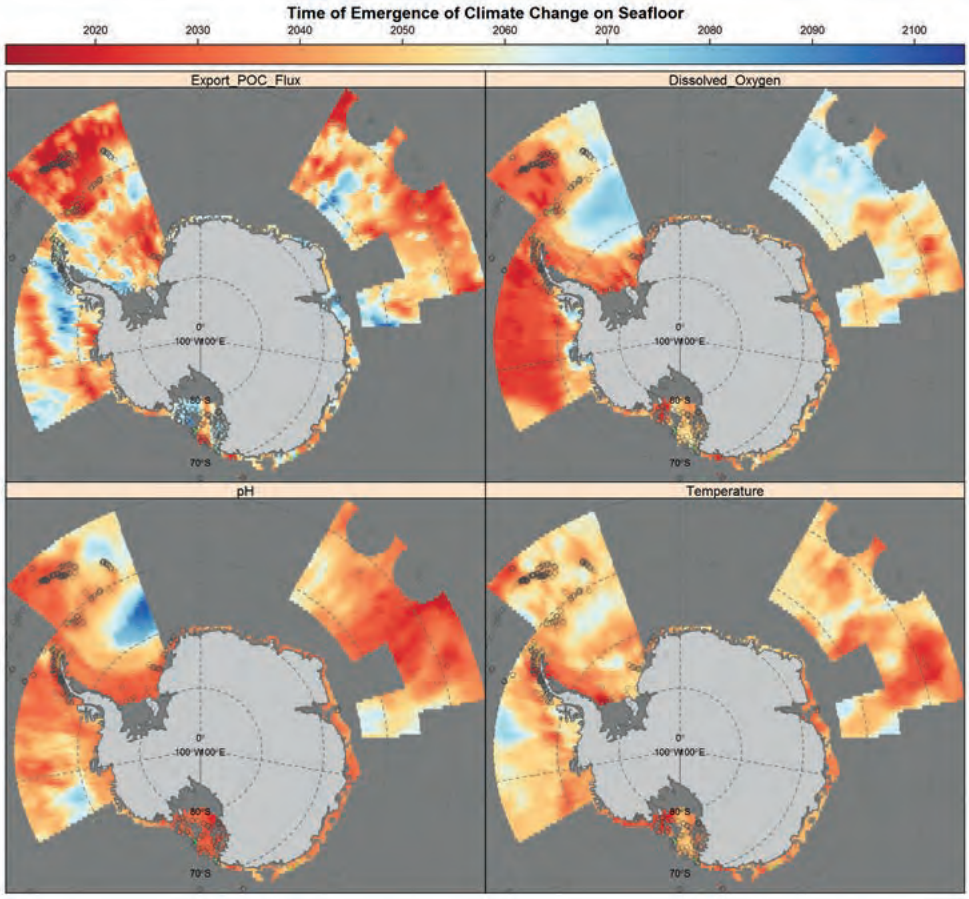
TABLE A8.3.1

Summary statistics of time of emergence of seafloor climate changes in RFMO areas

RFMO	Habitat	Export POC flux			Dissolved oxygen			pH			Temperature		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
CCAMLR	>200 m	2048	2017	2099	2047	2017	2084	2043	2018	2099	2047	2017	2075
	200–2 500 m	2051	2017	2099	2042	2019	2084	2036	2022	2065	2040	2017	2066
	VME closed area	2060	2052	2069	2046	2037	2055	2040	2034	2044	2044	2038	2048
	Seamounts	2049	2028	2074	2059	2026	2076	2040	2026	2065	2044	2033	2058
	Cold-water corals	2046	2017	2090	2038	2020	2071	2033	2022	2058	2040	2018	2053
	Canyons	2048	2017	2093	2041	2021	2075	2038	2024	2065	2039	2023	2057
GFCM	>200 m	2062	2026	2093	2066	2028	2095	2054	2030	2084	2045	2026	2069
	200–2 500 m	2060	2026	2093	2060	2028	2091	2050	2030	2083	2041	2026	2062
	VME closed area	2064	2056	2070	2067	2055	2077	2053	2040	2060	2044	2036	2050
	Cold-water corals	2060	2035	2077	2068	2051	2092	2051	2035	2076	2041	2026	2060
	Canyons	2059	2026	2083	2064	2028	2092	2051	2030	2083	2041	2027	2062
NAFO	>200 m	2044	2017	2085	2041	2020	2061	2049	2026	2083	2056	2020	2091
	200–2 500 m	2045	2021	2076	2030	2021	2052	2030	2026	2040	2036	2025	2050
	Bottom-fishing area	2045	2023	2073	2029	2021	2049	2028	2025	2033	2035	2025	2048
	VME closed area	2039	2022	2075	2040	2022	2054	2053	2028	2076	2070	2026	2091
	Cold-water corals	2041	2022	2065	2044	2032	2060	2047	2029	2074	2052	2025	2078
	Canyons	2055	2021	2076	2037	2024	2052	2032	2028	2049	2032	2025	2046
NEAFC	>200 m	2057	2021		2044	2019	2081	2044	2021	2074	2050	2018	2082
	200–2 500 m	2048	2022	2078	2045	2019	2068	2030	2024	2056	2041	2018	2071
	Bottom-fishing area	2051	2027	2075	2037	2019	2066	2028	2023	2040	2027	2019	2059
	VME closed area	2048	2025	2076	2043	2021	2067	2029	2022	2036	2037	2023	2062
	Cold-water corals	2052	2028	2078	2049	2022	2065	2032	2024	2051	2041	2024	2063
	Canyons	2043	2029	2067	2043	2030	2059	2031	2027	2050	2040	2025	2059
NPFC	>200 m	2049	2017	2100	2054	2020	2099	2054	2019		2047	2021	2086
	200–2 500 m	2036	2019	2058	2061	2040	2077	2061	2042	2076	2041	2028	2051
	Bottom-fishing area	2040	2033	2048	2065	2057	2072	2056	2054	2059	2047	2046	2048
	Seamounts	2045	2018	2077	2048	2032	2085	2053	2033	2083	2041	2028	2051
	Cold-water corals	2045	2023	2076	2052	2025	2085	2053	2028	2085	2041	2028	2062
	Canyons	2030	2029	2031	2066	2064	2068	2059	2059	2060	2051	2049	2052
SEAFO	>200 m	2047	2017		2046	2021	2096	2042	2023	2079	2050	2021	2093
	200–2 500 m	2048	2021	2092	2039	2023	2061	2039	2027	2058	2041	2029	2058
	Bottom-fishing area	2042	2020	2069	2040	2024	2084	2039	2029	2063	2048	2029	2076
	VME closed area	2044	2017	2084	2044	2026	2085	2041	2026	2064	2053	2029	2073
	Seamounts	2040	2020	2063	2040	2025	2076	2042	2029	2062	2053	2041	2072
	Cold-water corals	2046	2025	2058	2048	2034	2059	2044	2027	2058	2042	2032	2053
	Canyons	2046	2025	2069	2040	2027	2058	2037	2032	2047	2044	2033	2060
SPRFMO	>200 m	2049	2017		2053	2020	2100	2049	2019	2098	2054	2020	2094
	200–2 500 m	2045	2022	2093	2053	2028	2081	2042	2024	2080	2035	2020	2060
	Seamounts	2048	2023	2097	2057	2044	2076	2057	2039	2073	2056	2039	2069
	Cold-water corals	2048	2023	2093	2057	2039	2090	2044	2029	2064	2043	2023	2075
	Canyons	2046	2031	2067	2053	2027	2070	2039	2021	2060	2035	2027	2049

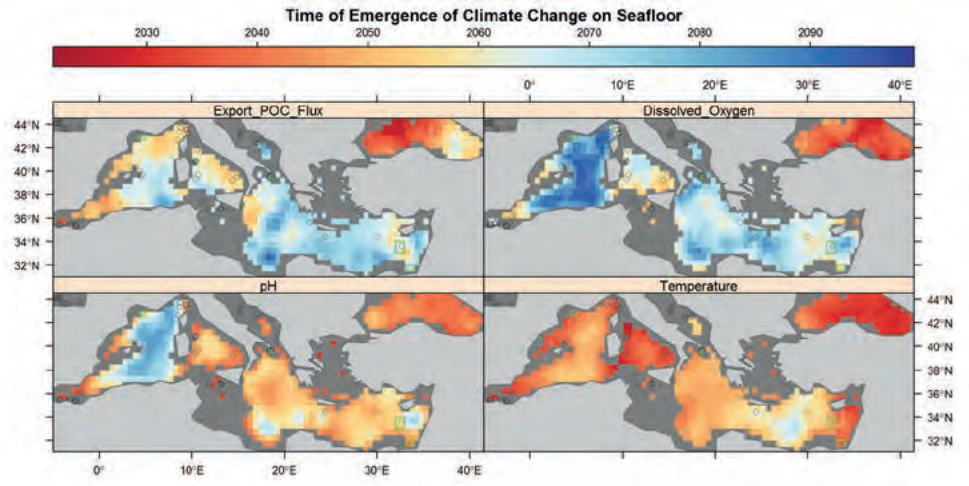
Note: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000.

FIGURE A8.3.1
Time of emergence in CCAMLR



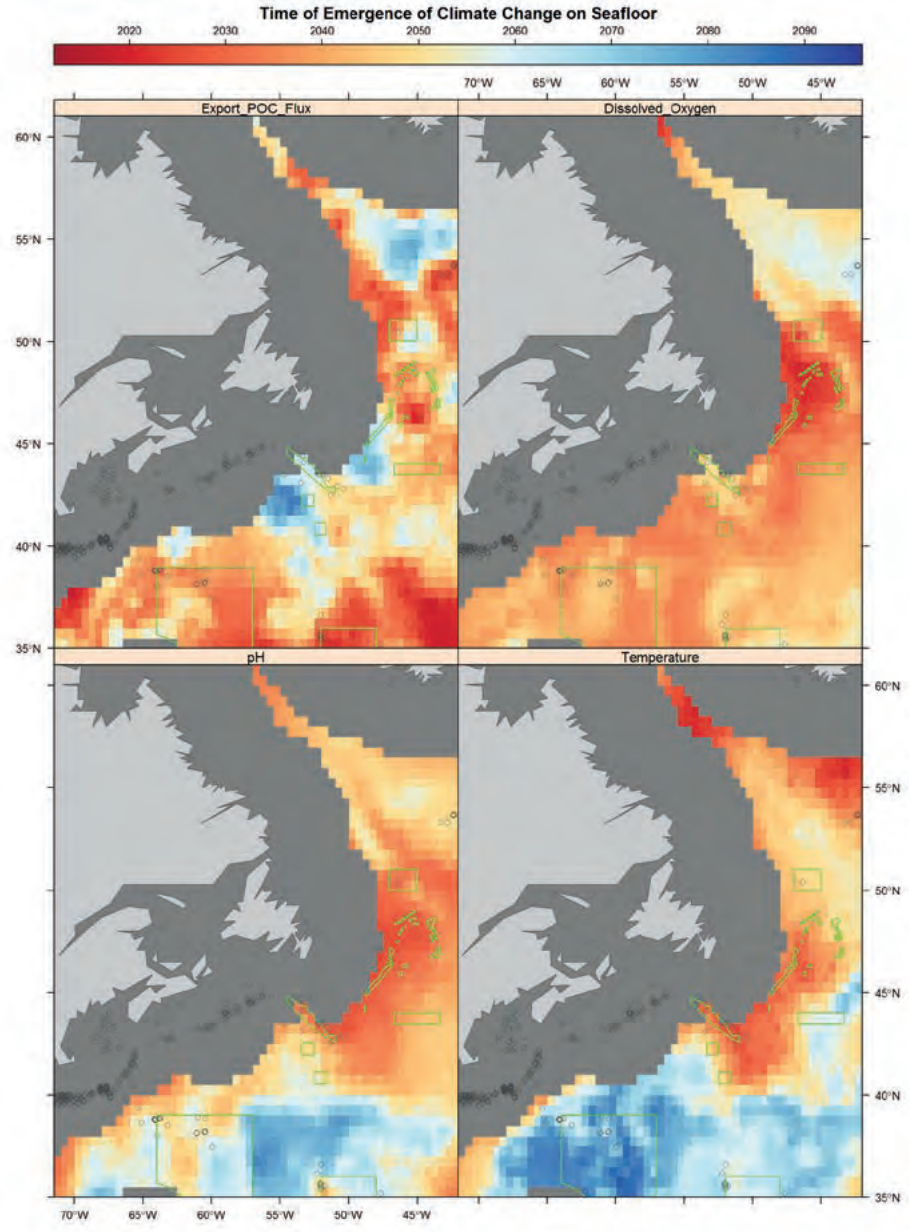
Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.3.2
Time of emergence in GFCM



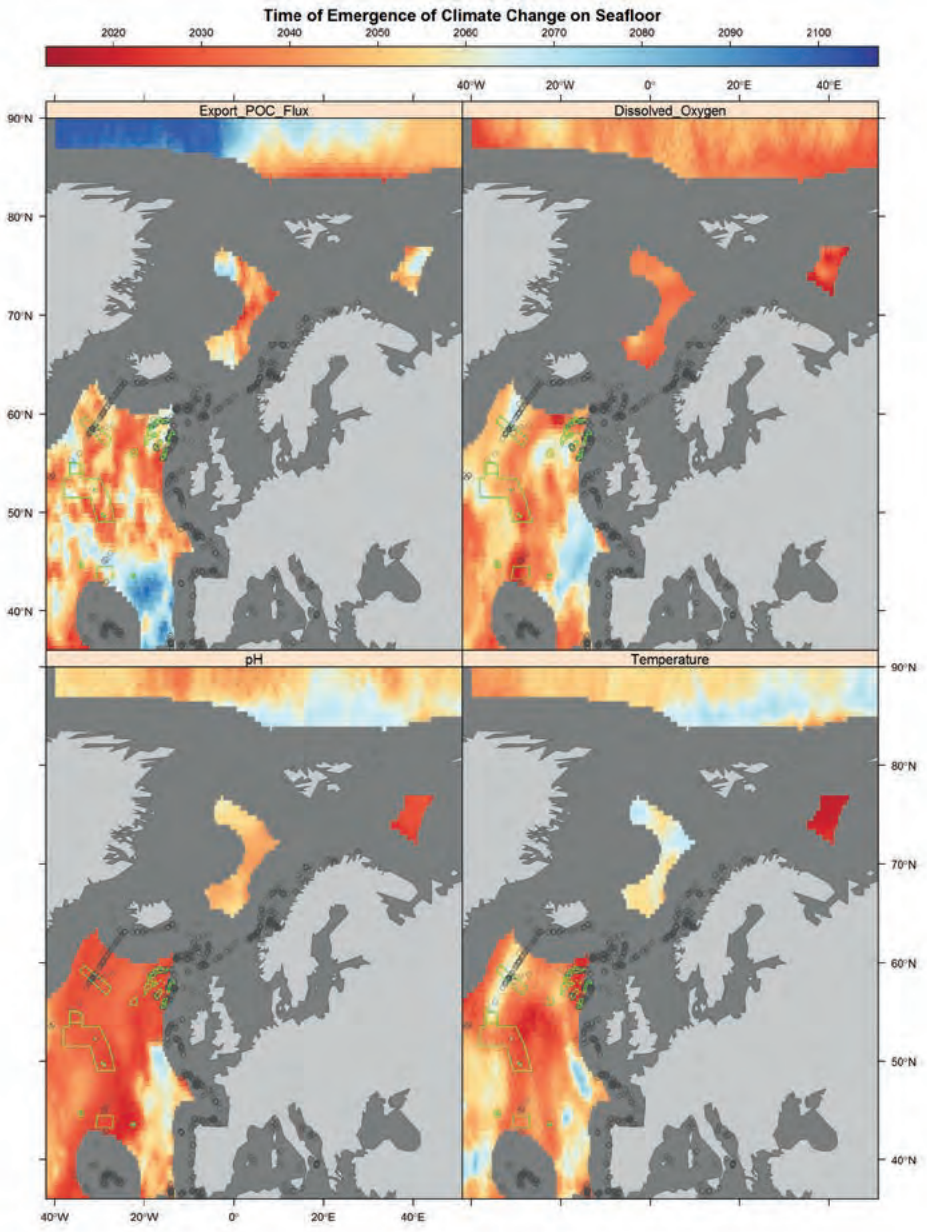
Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.3.3
Time of emergence in NAFO



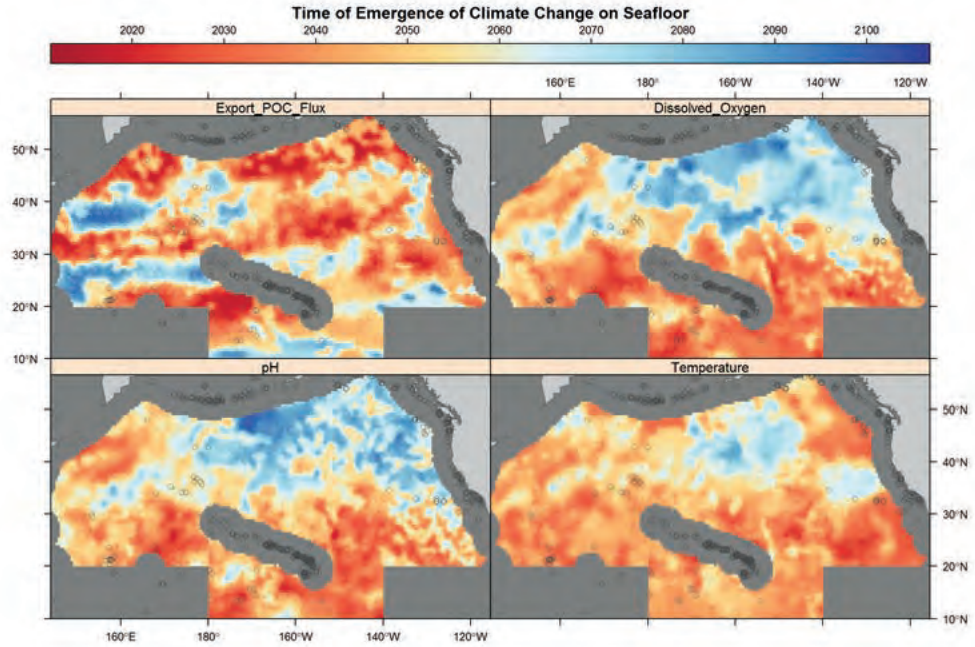
Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.3.4
Time of emergence in NEAFC



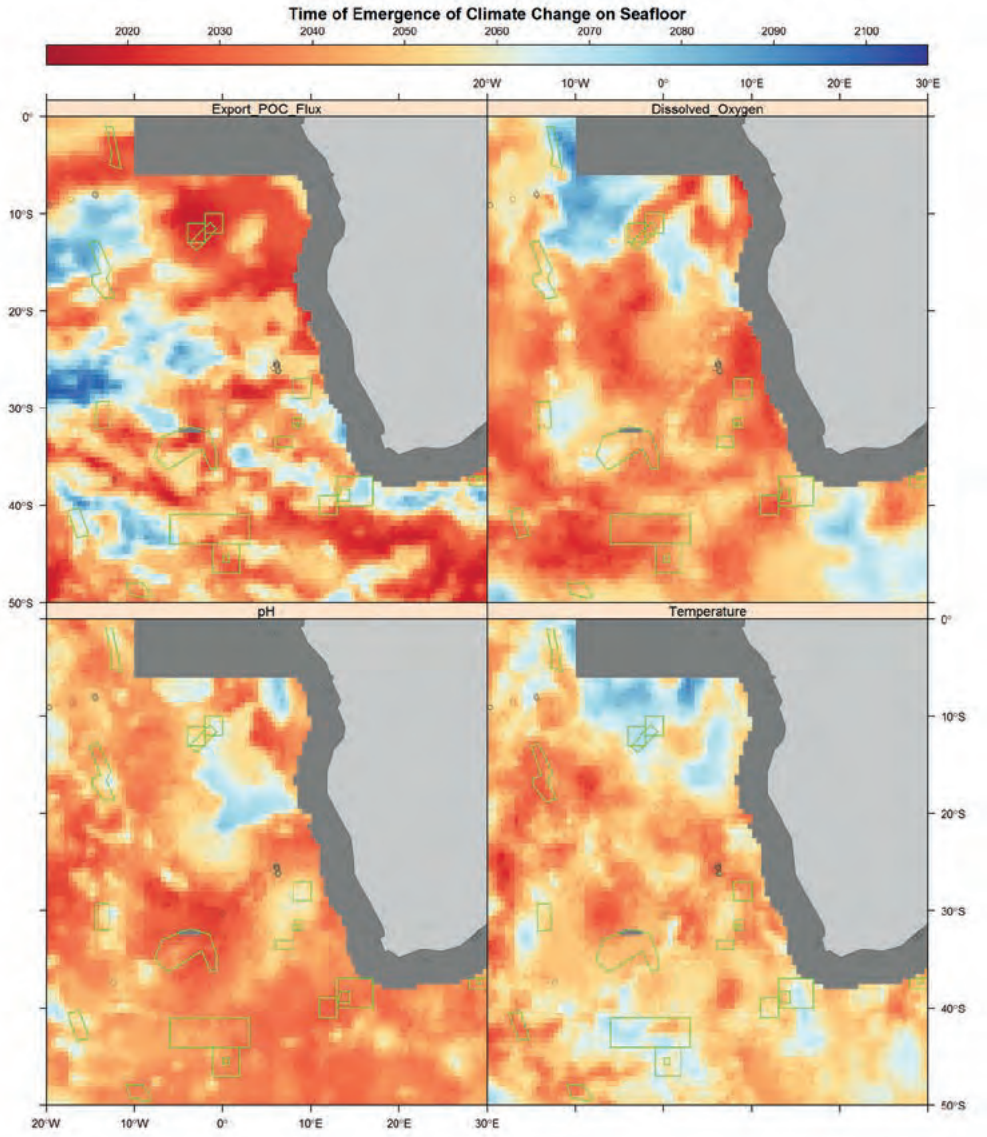
Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.3.5
Time of emergence in NPFC



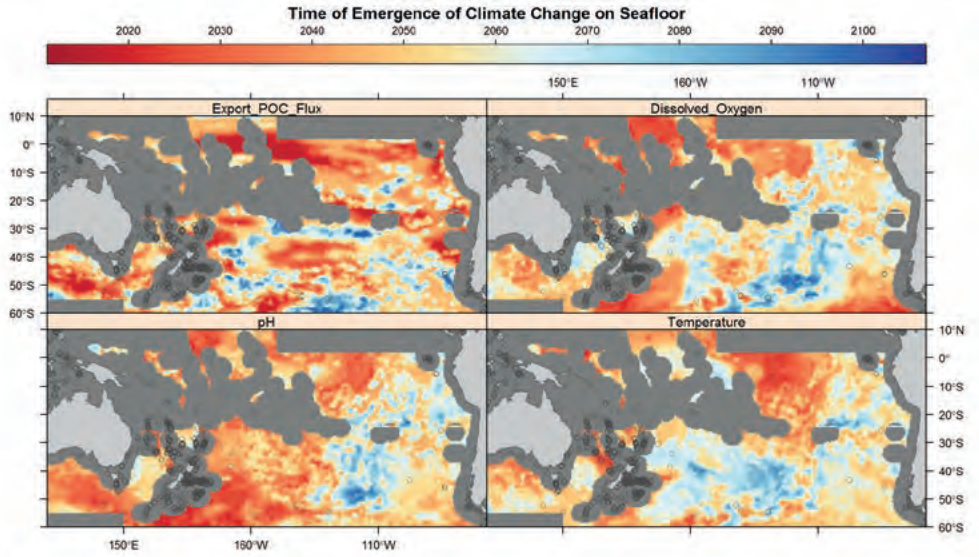
Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.3.6
Time of emergence in SEAFO



Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.3.7
Time of emergence in SPRFMO



Notes: The year when accumulated standard deviation of future projection (accumulating since 2006) exceeds historical standard deviation from 1951–2000. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

APPENDIX A8.4

Model-averaging cumulative impact of climate changes in each RFMO area

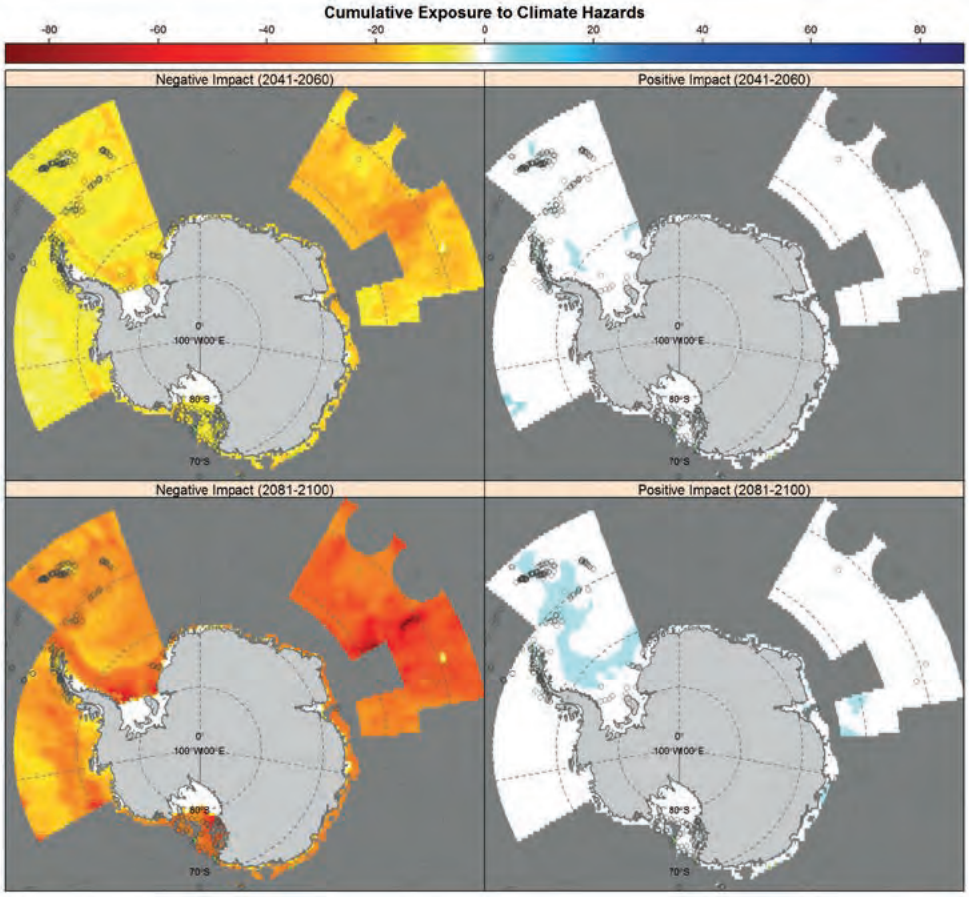
Contributors: **William Cheung** and **Lisa Levin**

TABLE A8.41
Summary statistic of cumulative impact of climate changes in RFMO areas

RFMO	Habitat	Export POC flux			Dissolved oxygen			pH			Temperature		
		mean	min	max	mean	min	max	mean	min	max	mean	min	max
CCAMLR	>200 m	-12.17	-30.75	-3.94	0.49	0	6.61	-25.8	-89.25	-11.38	0.72	0	3.21
	200–2 500 m	-12.37	-20.69	-5.11	0.44	0	2.08	-26.94	-76.18	-11.38	0.89	0	3.21
	VME closed area	-12.6	-14.26	-10.15	0.44	0.16	0.55	-24.66	-30.56	-22.61	1.16	0.75	1.5
	Seamounts	-12.18	-18.62	-5.33	0.21	0	0.98	-25.02	-35.21	-17.06	0.36	0	1.67
	Cold-water corals	-10.06	-17.83	0	0.47	0	1.38	-23.07	-45	0	0.8	0	2.32
	Canyons	-12.53	-18.29	0	0.61	0	2.07	-26.07	-40.33	0	1.05	0	3.2
GFCM	>200 m	-9.37	-24.77	-0.01	0.29	0	3.39	-17.7	-59.05	0	0.53	0	4.66
	200–2 500 m	-12.17	-24.77	-0.75	0.3	0	2.9	-23.2	-59.05	-2.35	0.48	0	4.66
	VME closed area	-10.98	-16.99	-5.7	0	0	0	-22.81	-34.36	-14.14	0	0	0.03
	Cold-water corals	-12.91	-19.78	-3.53	0.17	0	1.03	-26.05	-41.19	-3.89	0.14	0	0.82
	Canyons	-13.14	-20.06	-3.51	0.25	0	2.9	-25.29	-42.58	-8.1	0.35	0	4.66
NAFO	>200 m	-13.89	-25.69	-8.15	0.38	0	4.87	-21.88	-43.13	-14.65	0.6	0	7.95
	200–2 500 m	-19.66	-25.69	-15.44	0	0	0	-35.26	-43.13	-25.27	0	0	0
	Bottom-fishing area	-19.57	-23.92	-15.32	0	0	0	-36.02	-43.13	-28.16	0	0	0
	VME closed area	-13.64	-23.36	-10.71	0.03	0	1.7	-21.89	-40.13	-17.42	0.09	0	5.7
	Cold-water corals	-14.29	-19.35	-10.71	0.46	0	4.45	-24.08	-36	-16.55	0.62	0	5.7
	Canyons	-17.99	-22.29	-15.32	0	0	0	-31.76	-40.13	-25.53	0	0	0
NEAFC	>200 m	-12.69	-24.91	-4.72	1.18	0	7.02	-22.55	-45.23	-11.6	1.65	0	12.94
	200–2 500 m	-14.79	-24.91	-7.08	0.84	0	4.17	-29.09	-45.23	-20.35	0.93	0	8.29
	Bottom-fishing area	-11.68	-24.83	-7.08	1.46	0	3.59	-26.76	-44.71	-20.35	0.7	0	4.07
	VME closed area	-15.33	-24.65	-10.92	1.94	0	6.32	-26.81	-44.2	-18.77	4.39	0	12.5
	Cold-water corals	-15.34	-24.01	-10.4	0.64	0	4.49	-30.95	-43.88	-17.84	0.78	0	7.25
	Canyons	-14.75	-17.28	-13.4	0.42	0	1.78	-28.81	-34.43	-23.37	0.62	0	2.53
NPFC	>200 m	-9.06	-35.45	-0.66	0.51	0	7.59	-19.05	-64.61	-4.01	0.7	0	10.48
	200–2 500 m	-6.96	-9.45	-4.4	0.01	0	0.27	-14.14	-18.37	-10.58	0	0	0
	Bottom-fishing area	-6.13	-7.93	-4.33	0	0	0	-14.78	-15.12	-14.45	0	0	0
	Seamounts	-9.48	-15.9	-2.51	0.1	0	0.74	-19.65	-42.41	-6.07	0.12	0	1.25
	Cold-water corals	-7.85	-21.88	-1.99	0.26	0	1.66	-16.56	-56.92	-5.44	0.36	0	2.11
	Canyons	-7.34	-7.36	-7.32	0	0	0	-14.44	-14.75	-14.14	0	0	0
SEAFO	>200 m	-10.11	-28.3	-1.19	0.34	0	18.72	-22.8	-70.85	-7.27	1	0	24.7
	200–2 500 m	-10.71	-18.6	-6.5	0.12	0	1.56	-25.96	-46.28	-17.37	0.12	0	2.72
	Bottom-fishing area	-10.23	-18.6	-4.18	0.08	0	1.56	-24.46	-41.29	-14.14	0.21	0	2.72
	VME closed area	-10.42	-17.17	-1.61	0.19	0	2.16	-26.24	-49.07	-10.61	0.2	0	3.21
	Seamounts	-10.22	-15.18	-3.4	0.09	0	0.65	-24.93	-39.66	-9.48	0.15	0	1.67
	Cold-water corals	-11.69	-16.08	-7.14	0.02	0	0.2	-26.23	-33.05	-16.09	0	0	0
	Canyons	-10.72	-14.48	-6.83	0.04	0	0.17	-25.32	-34.29	-17.37	0.06	0	0.42
SPRFMO	>200 m	-9.23	-32.61	0	0.33	0	6.36	-22.14	-106.53	-1.47	0.26	0	5.68
	200–2 500 m	-9.58	-20.75	-1.3	0.16	0	2.48	-20.21	-36.96	-4.24	0.17	0	3.48
	Seamounts	-4.19	-14.96	-0.87	0.34	0	1.77	-11.06	-33.2	-3.64	0.66	0	1.85
	Cold-water corals	-9.58	-19.71	-2.41	0.13	0	0.97	-20.84	-39.59	-7.55	0.2	0	1.32
	Canyons	-12.28	-18.13	-5.78	0.01	0	0.06	-25.24	-35.48	-12.8	0.01	0	0.08

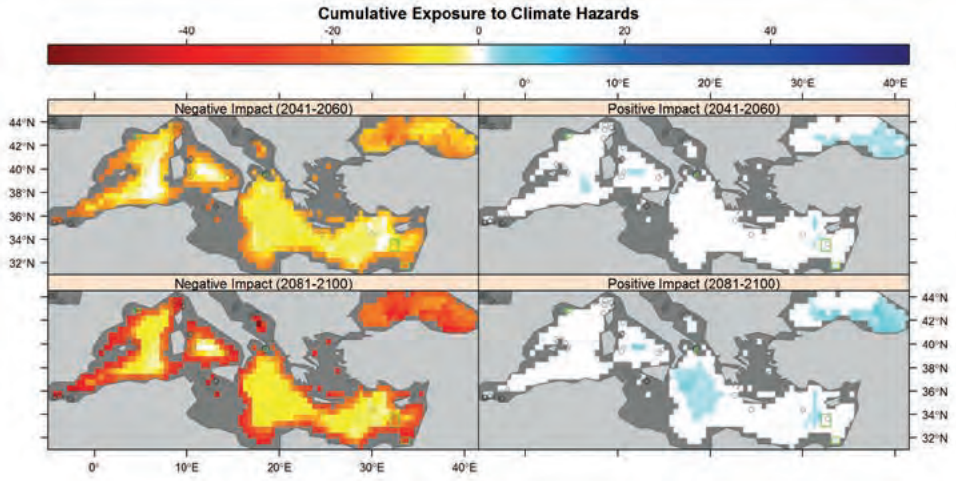
Note: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts.

FIGURE A8.4.1
Cumulative impact of climate changes in CCAMLR



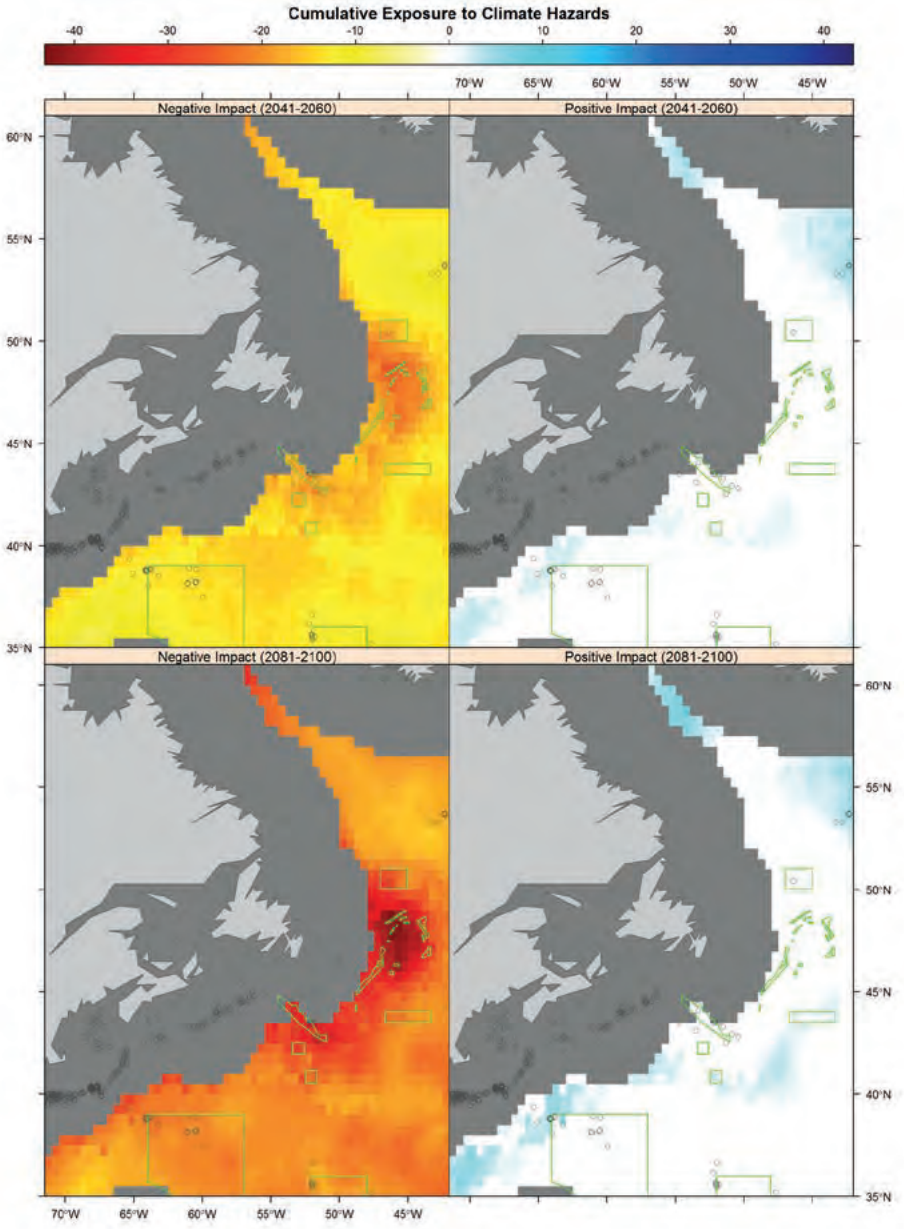
Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.4.2
Cumulative impact of climate changes in GFCM



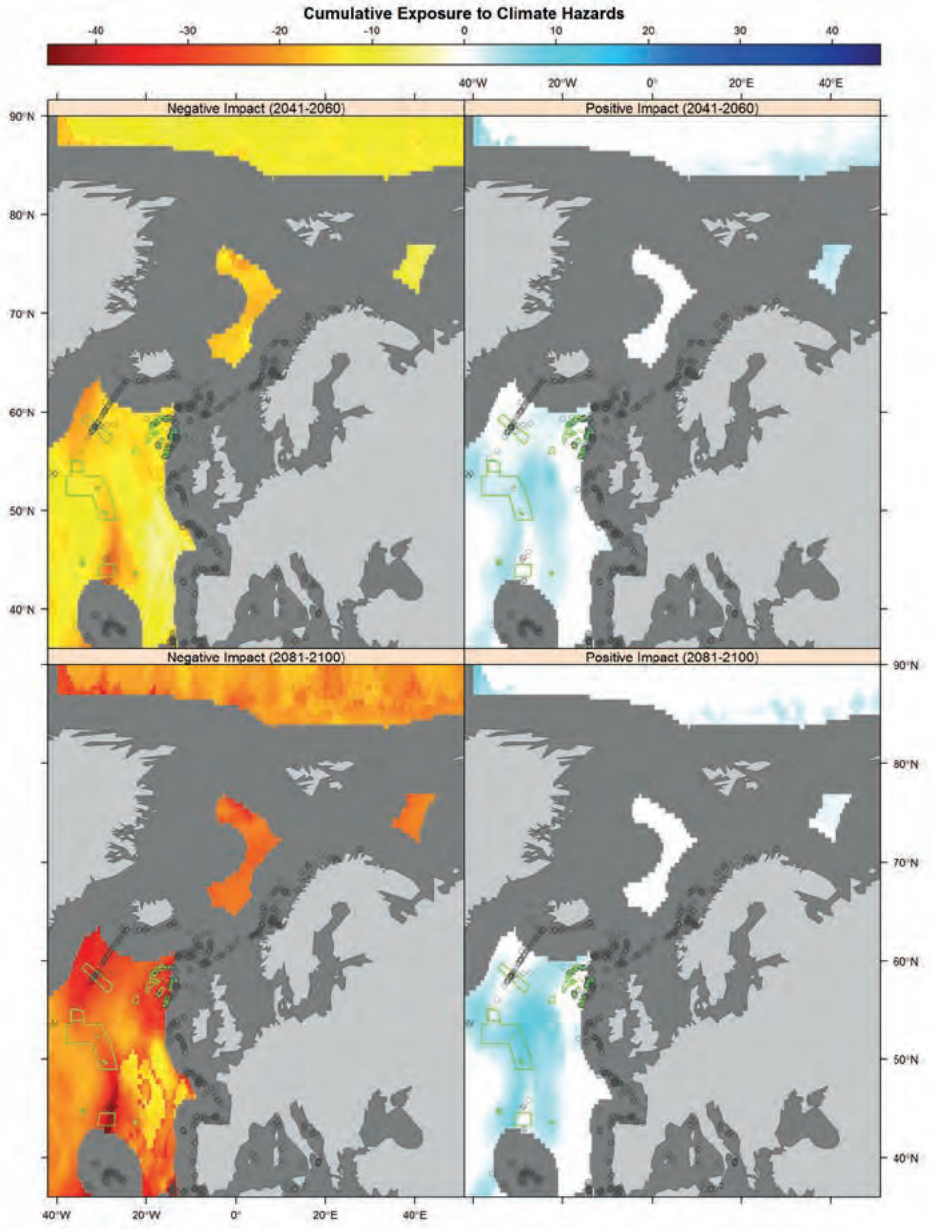
Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.4.3
Cumulative impact of climate changes in NAFO



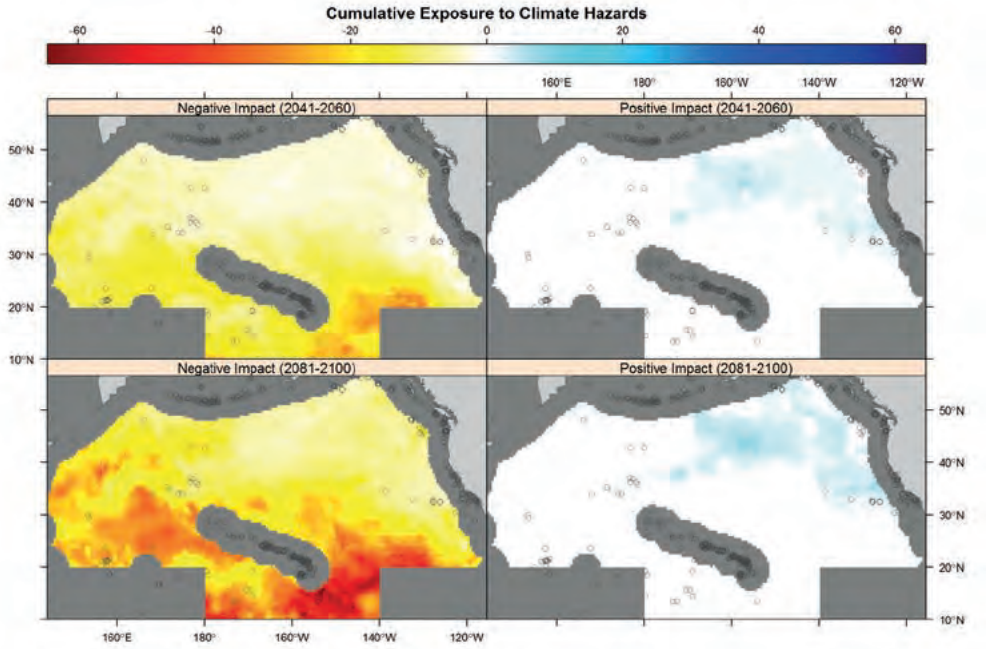
Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.4.4
Cumulative impact of climate changes in NEAFC



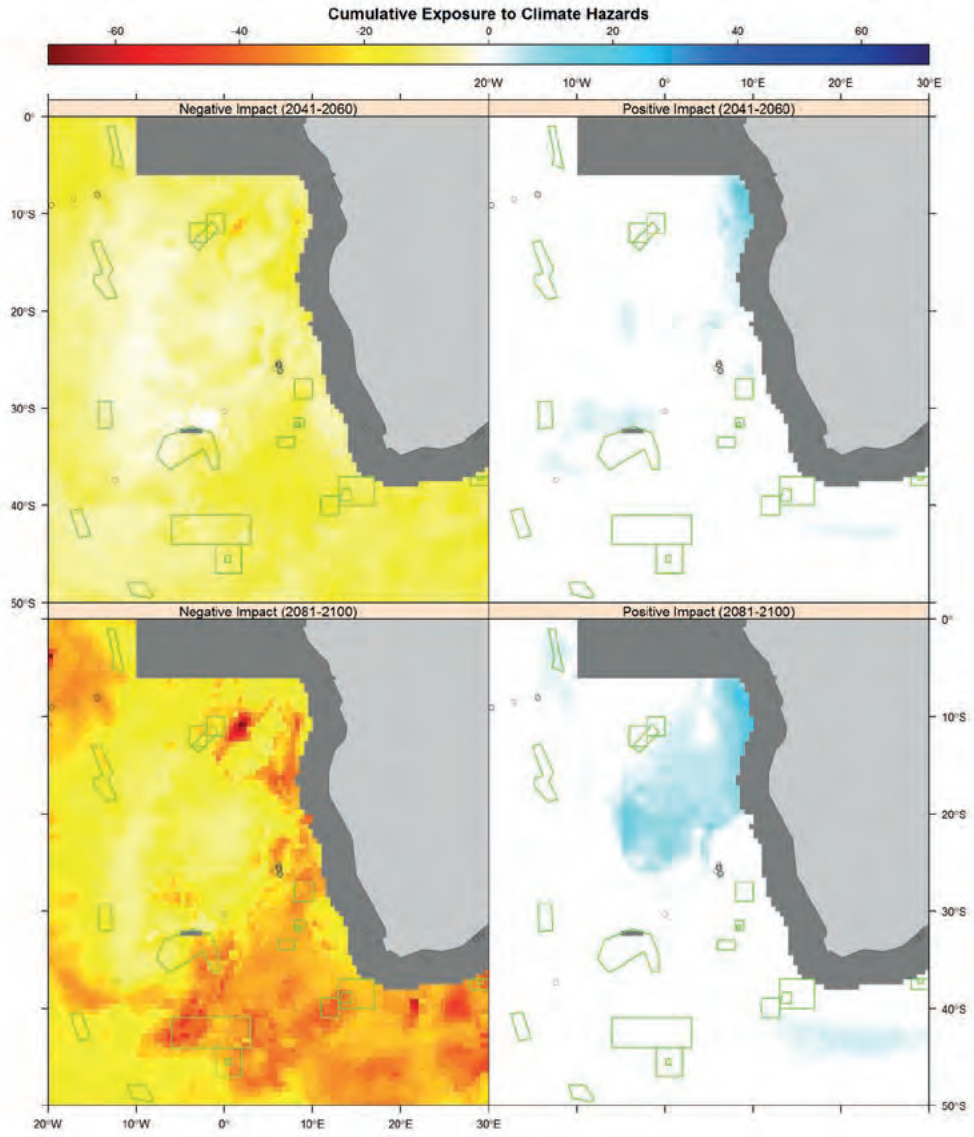
Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.4.5
Cumulative impact of climate changes in NPFC



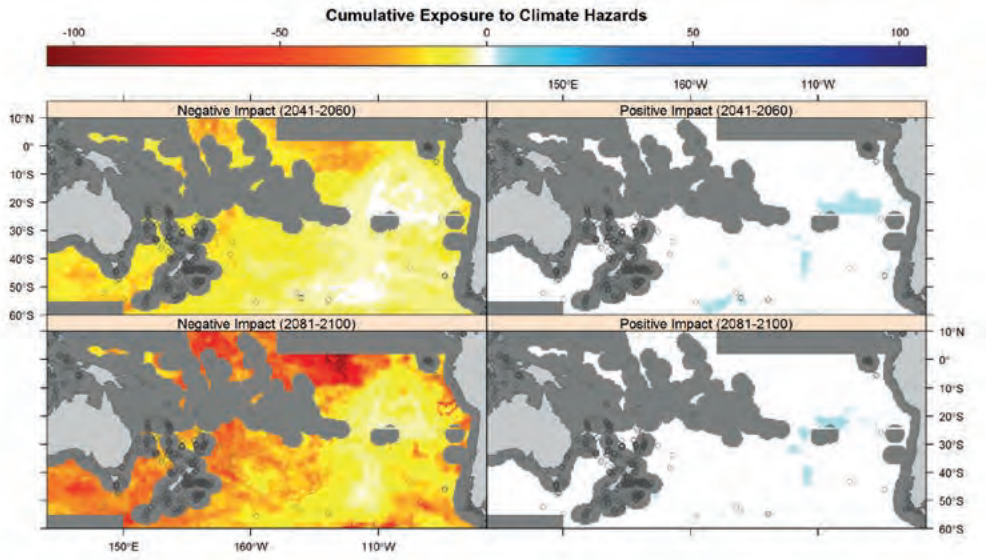
Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.4.6
Cumulative impact of climate changes in SEAFO



Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

FIGURE A8.4.7
Cumulative impact of climate changes in SPRFMO



Notes: Cumulative impact is calculated by summing exposure to climate change hazards. Negative impacts include declining export POC flux, deoxygenation, acidification and warming, and vice versa for positive impacts. Green and purple polylines indicate the VME closed and bottom-fishing areas, respectively (when applicable). Open circles indicate the occurrence of cold-water corals.

9. Exposure to hazard

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Introduction

The risk of deep-sea species to climate change is dependent on their exposure to hazardous habitat conditions. Deep-sea species that are important for fisheries (mainly fishes and invertebrates) are sensitive to temperature, oxygen level, acidity level and food availability. Climate change is expected to alter these conditions, with regional differences (Pörtner *et al*., 2014; Gattuso *et al*., 2015). However, the extent to which commercial deep-sea species would be exposed to these changes is not clear.

If long-term changes in environmental conditions exceed the limit to which marine species can adapt, the long-term viability of the population or community may be threatened by these changes. Marine species have evolved with the characteristics of the environment and, thus, they are expected to have adapted to the natural fluctuation in environmental conditions. However, when carbon dioxide and other greenhouse gases emitted from human activities drive long-term changes in habitat environmental conditions to a level beyond the natural fluctuation that the species are adapted to, their biological and ecological performances such as growth and reproduction may be impacted. Thus, exposure of deep-sea species to climate change hazards should also consider the natural vaToriability of environmental conditions that the species inhabit.

In this section, exposure to climate hazard is calculated for 41 commercial deep-sea species. Climate hazards relate to the main habitat characteristics that may affect the long-term viability of these species. Outputs from earth system models are used to calculate indices of exposure to climate hazard for each species. These species are then compared to identify those exposed to the highest level of climate hazards.

Calculating exposure to hazard

Exposure to hazard describes the extent to which species would be subjected to climate hazards (predicted changes in physical environment) (Jones and Cheung, 2017). Climate hazards for fisheries species (fishes and invertebrates) are indicated by the physical and chemical ocean variables, including: sea bottom temperature, oxygen concentration, pH and export production (see Section 8). The index of exposure to climate change hazard (*ExV*O) is based on the analysis of global earth system model outputs in Section 8, i.e. mean changes in each variable relative to its historical variability (defined by the standard deviation in the historical time period). An exposure to hazard metric (*ExV*) for each variable (*V*) is:

$$ExV_i = \frac{|\overline{V}_{future,i} - \overline{V}_{historical,i}|}{\delta V_{historical,i}} \qquad (2)$$

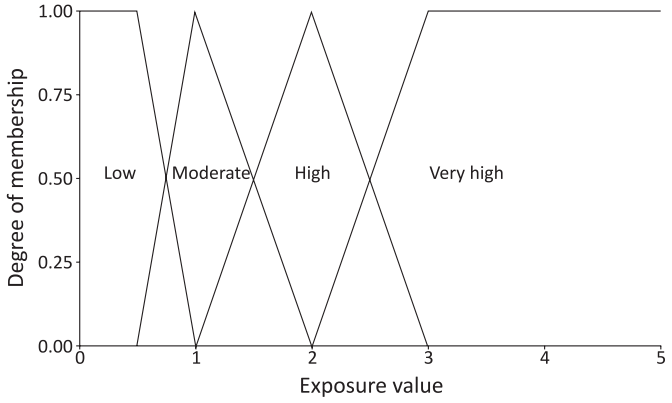
where $\overline{V}_{future}$ and $\overline{V}_{historical}$ are the mean annual value of an ocean variable for the future and past, respectively. Two future periods are considered: 2050 (annual average of 2041–2060); and 2090 (annual average of 2081–2100). *ExV* was calculated for each 0.5° latitude × 0.5° longitude cell *i* of the global ocean where a species is predicted to occur.

To determine the species' current distribution range, current range boundaries were obtained for each species as predicted using the Sea Around Us method (for details,

see Jones *et al.*, 2012). The range boundary was defined based on latitudinal and depth ranges, as well as expert-delineated range boundaries such as those published in FAO species catalogues. The range boundary was then subsequently rasterized on a 0.5° latitude × 0.5° longitude grid.

The level of exposure to climate hazards is classified as low, medium, high or very high using a fuzzy logic algorithm (Figure 16). Fuzzy logic allows for the classification of multiple categories of exposure concurrently, with different level of degree of membership (for details, see Jones and Cheung, 2018). Specifically, for each *ExV* estimate in a 0.5° latitude × 0.5° longitude grid cell of the four ocean variables considered here, the degree of membership to the four categories of exposure to climate hazard was calculated using pre-specified fuzzy membership functions. For the low and very high categories, trapezoid functions were used, while triangular functions were used for medium and high categories. For example, if the *ExV* for temperature is 2.5 times the historical variability, the species is exposed to both high and very high hazards with degree of membership of 0.5 for both categories.

FIGURE 16
Fuzzy membership functions for the four categories of exposure to climate hazards



The fuzzy logic algorithm accumulated the degree of membership associated with each level of exposure to hazards concluded for each of the four ocean variables and the three earth system models from the rules using an algorithm called MYCIN (Cheung, Pitcher and Pauly, 2005), where:

$$AccMem_{(i+1)} = AccMem_{(i)} + (Membership_{(i+1)})(1 - AccMem_{(i)}) \quad (3)$$

where *AccMem* is the accumulated membership of a particular conclusion (e.g. high exposure to hazard), and *i* denotes one of the rules that has led to this conclusion.

The index of exposure to climate hazard was expressed on a scale from 1 to 100, 100 being the most vulnerable. Index values (*Indval*) corresponding to each linguistic vulnerability category (x) were: low = 1, medium = 25, high = 75, and very high = 100. The final index (*FlnInd*) of risk of impacts or vulnerability was calculated from the average of the index values weighted by their accumulated membership (Cheung *et al.*, 2005):

$$FlnInd = \frac{\sum_{x=1}^{4} AccMem_x \cdot Indval_x}{\sum_{x=1}^{4} AccMem_x} \quad (4)$$

For the exposure to hazard index (for both the 2050 and 2090 periods), *FlnInd* was calculated for each spatial grid cell. The exposure to hazard of each species was then calculated as the average *FlnInd* across grid cells weighted by the cell's water area.

Comparing exposure to hazard among species

The median values of the index of exposure to climate hazard are 66 (lower and upper limits are 55 and 77) and 74 (limits are 61 and 89), respectively, projected for 2050 and 2090 periods under the RCP8.5 scenario (100 being the highest level of exposure to climate hazard) (Table 12).

TABLE 12
Calculated exposure to hazard index.

Common name	Scientific name	2050	2090
Black scabbardfish	*Aphanopus carbo*	77	89
White hake	*Urophycis tenuis*	74	87
Beaked redfish	*Sebastes mentella*	73	85
Roundnose grenadier	*Coryphaenoides rupestris*	72	84
Tusk	*Brosme brosme*	72	82
Ling	*Molva molva*	72	81
Roughhead grenadier	*Macrourus berglax*	71	82
Greater argentine	*Argentina silus*	71	81
Atlantic cod	*Gadus morhua*	70	79
Yellowtail flounder	*Limanda ferruginea*	70	85
Haddock	*Melanogrammus aeglefinus*	70	80
Golden redfish	*Sebastes norvegicus*	69	79
Blackbelly rosefish	*Helicolenus dactylopterus*	69	78
Argentine	*Argentina sphyraena*	68	75
Portuguese dogfish	*Centroscymnus coelolepis*	67	79
Blue ling	*Molva dypterygia*	67	74
Orange roughy	*Hoplostethus atlanticus*	67	78
European hake	*Merluccius merluccius*	66	73
Northern shrimp	*Pandalus borealis*	66	74
Greenland halibut	*Reinhardtius hippoglossoides*	66	75
Deepwater rose shrimp	*Parapenaeus longirostris*	65	71
Wreckfish	*Polyprion americanus*	65	73
Pelagic red crab	*Pleuroncodes planipes*	65	76
Black cardinal fish	*Epigonus telescopus*	64	73
Argentine shortfin squid	*Illex argentinus*	64	70
European conger	*Conger conger*	64	73
Atlantic halibut	*Hippoglossus hippoglossus*	63	72
Baird's slickhead	*Alepocephalus bairdii*	63	73
Patagonian scallop	*Zygochlamys patagonica*	63	70
Silver scabbardfish	*Lepidopus caudatus*	63	73
Alfonsino	*Beryx decadactylus*	63	76
Rabbit fish	*Chimaera monstrosa*	62	70
Alfonsino	*Beryx splendens*	62	76
Argentine hake	*Merluccius hubbsi*	61	66
Snow crab	*Chionoecetes opilio*	61	70
Forkbeard	*Phycis phycis*	59	63
Longtail southern cod	*Patagonotothen ramsayi*	59	65
Giant red shrimp	*Aristaeomorpha foliacea*	59	63
Patagonian toothfish	*Dissostichus eleginoides*	57	61
Sablefish	*Anoplopoma fimbria*	57	64
Antarctic toothfish	*Dissostichus mawsoni*	55	61

Species that are among the most exposed to climate hazards are black scabbardfish, white hake, and beaked redfish. The least exposed species are Patagonian toothfish, sablefish, and Antarctic toothfish; however, exposure to hazard is still considered high to very high even for these relatively less exposed species.

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10. Habitat suitability model utility

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The spatial distribution of many VME indicator taxa and commercially important deep-sea fish species is largely driven by localized terrain characteristics and environmental settings. These organisms are likely to respond to future changes in climate conditions (Sections 8 and 11). Therefore, understanding how species distribution may shift in response to climate change over the course of this century is of paramount importance for developing management measure capable of taking climate change into consideration. Climate envelope models, habitat suitability models, and species distribution models (SDMs) have been frequently used to predict changes in distribution of species under past and future climate conditions (e.g. Pearson and Dawson, 2003; Hijmans and Graham, 2006; Coro *et al.*, 2016). However, due to the lack of reliable prediction of the future environmental conditions close to the seabed, SDMs have not been widely applied in the context of deep-sea species.

With the recent development of scenarios of future seabed environmental conditions (Sweetman *et al.*, 2017), SDMs can now be a useful tool to evaluate shifts in the distribution of deep-sea VME indicator taxa and fish. Making use of species occurrence data from the Ocean Biodiversity Information System (OBIS) and a set of projections for POC flux, dissolved oxygen, seawater pH and potential temperature at seafloor in 2100 (Sweetman *et al.*, 2017), the habitat suitability for six cold-water coral species and six fish species was modelled under current and future climate conditions, using Maxent, for the northwest and northeast Atlantic. This work is a preliminary attempt to determine whether SDMs are useful tools for predicting potential future changes in the distribution of deepwater species in the north Atlantic.

Modelling approach

Study area

Habitat suitability models of VME indicator taxa and commercially important deep-sea fish species were developed for the deeper waters of the northwest and northeast Atlantic, under the management of NAFO and NEAFC, respectively. The northeast Atlantic study area was limited to approximate to the NEAFC Regulatory Area 1 in the northwest Atlantic west of Europe. For the purpose of extracting environmental and occurrence data, the spatial extent considered was ca. 64.5°N, 77°W to 35°N 42°W for

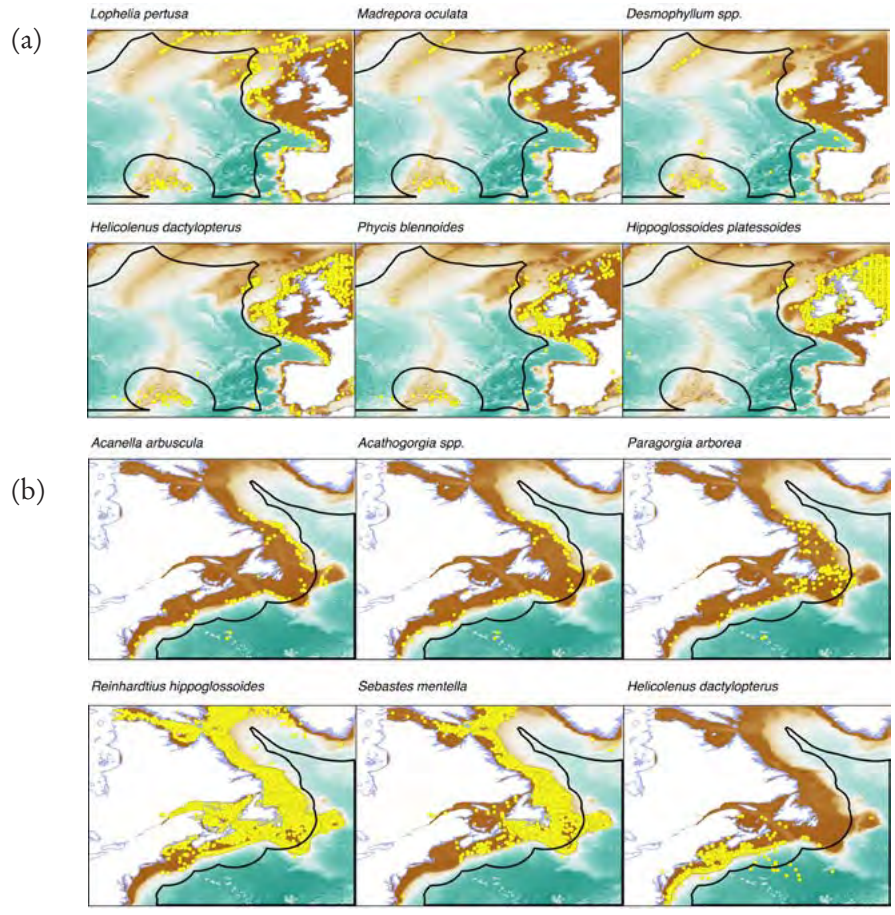
the northwest Atlantic, and ca. 64.5°N, 42°W to 35°N, 2.5°E for the northeast Atlantic. These two north Atlantic regions are among the best-surveyed high-seas deepwater marine areas in the world, with extensive data sets and well established RFMOs.

Selection of species

Three VME indicator taxa and three commercially important deep-sea fish species were selected for each ocean region based on their ecological and fisheries catch relevance, and on the availability and spatial coverage of existing occurrence records (Figure 17) in the OBIS portal.[8] The VME indicator taxa selected for the northeast Atlantic area were *Lophelia pertusa* (n = 1 626), *Madrepora oculata* (n = 778), and *Desmophyllum* spp. (n = 272), while for the northwest Atlantic area they were *Acanella arbuscula* (n = 411), *Acanthogorgia* spp. (n = 201), and *Paragorgia arborea* (n = 233). The commercially important deep-sea fish species selected for the northeast Atlantic were blackbelly rosefish (n = 2 637), greater forkbeard (n = 1 387), and American plaice (n = 8 867), while for the northwest Atlantic they were Greenland halibut (n = 40 205), beaked redfish (n = 14 976), and blackbelly rosefish (n = 4 110). Species occurrences were retrieved using their aphiaID code from the OBIS database using the package "robis" version 0.2.1 in the R environment.

FIGURE 17

Records used in the predictive modelling (yellow dots) for the species selected and extracted from the OBIS portal



Note: Black line corresponds to the limits of the regulatory area of (a) NEAFC, and (b) NAFO.

[8] See: www.iobis.org

Terrain and environmental variables

Predictions of suitable habitat for different species were based on a set of terrain variables (static in time) and environmental variables of both present day and predicted future conditions. The terrain variables used were extracted or derived from GEBCO_2014 (Weatherall *et al*., 2015), which provides a 30 arc-second global grid of elevations (cell size of 0.0083º). Derived variables were computed from the bathymetric grid based on a 3 × 3 pixel size window using the function "terrain" included in the package "raster" of the R environment (Hijmans, 2016), and included slope, aspect, terrain ruggedness index (TRI), topographic position index, and roughness (Appendix A10.1).

The set of environmental variables under current and future conditions was developed by Sweetman *et al*. (2017) and adapted from Section 8. These variables include: POC flux to seafloor (mg C $m^{-2}d^{-1}$); dissolved oxygen concentration at seafloor (mol m^{-3}); pH concentration at seafloor (M); and potential temperature at seafloor (K). Yearly means of these parameters were calculated for the periods 1951–2000, 2041–2060 and 2081–2100 (see Section 8 for more details) using the average values obtained from the GFDL-ESM-2G, IPSL-CM5A-MR and MPI-ESM-MR models within CMIP5. Standard deviation, coefficient variation of the mean and linear detrended standard deviation were also calculated for all three periods for each of the variables (see Section 8). Grid size of all environmental variables was 0.5º, so all layers were re-scaled to match the grid size of the bathymetric data using the function "resample" of the package "raster" in the R environment. Maps of the variables used in the predictive modelling are shown in Appendix A10.2.

Model development

The maximum entropy model (Maxent version 3.4.0; Phillips *et al*., 2017) was used to predict the presence/absence of all species in the three different scenarios: 1951–2000, 2041–2060, and 2081–2100. Maxent was selected as the modelling technique due to the nature of the data obtained from OBIS, which provides presence-only records. Maxent has been shown to be a reliable modelling tool for predicting changes in species distribution under climate change scenarios (Ashford, Davies and Jones, 2014; Beaumont *et al*., 2016; Morán-Ordóñez *et al*., 2017). At the present stage, only one run per species and scenario was performed, but future developments will incorporate the use of more replicates to obtain the final outputs. Past-to-present environmental data (1951–2000) was used to train the model, which was then projected on the set of environmental layers of future scenarios (2041–2060 and 2081–2100). Model outputs provided an estimate of probability of presence of each species of between 0 and 1, which was converted to presence/absence using the 10 percentile training presence logistic threshold. Response curves for each predictor variable were generated together with jack-knife estimates of the relative contribution of each of the environmental predictors to the model output.

Model outputs

The outputs of this modelling exercise aim to illustrate the approach to be taken to evaluate changes in the potential distribution of VMEs in future climatic scenarios, and caution should be taken when drawing conclusions about the particular changes predicted for future environmental conditions. This is mainly because this work still lacks a comprehensive model validation by measuring both model performance and accuracy, and estimates of model error or uncertainty in modelled distributions. Nevertheless, all models performed reasonable well and were able to define suitable habitats better than random (area under the curve, AUC > 0.5) (Table 13). However, it is acknowledged that AUC values are generally high for species with narrow ranges relative to the study area, and that high AUC does not necessarily mean a good model performance.

In general, terrain variables provided some of the highest contributions to the predictive models, but POC flux, dissolved oxygen concentration, and bottom seawater temperature were also important variables for many species (Table 13, Figures A10.3.1–A10.3.12). In particular, depth played a key role in determining the distribution of all species, with TRI also observed as an important terrain variable for VME indicator taxa in the northeast Atlantic, and roughness for VME in the northwest Atlantic. In terms of the environmental variables, POC flux played an important role for most VME and fish species especially for *Paragorgia arborea*, *Acanella arbuscula*, American plaice, Greenland halibut, beaked redfish (average values) and also for *Lophelia pertusa*, *Desmophyllum* spp., and greater forkbeard (linear detrended standard deviation). Average values of dissolved oxygen concentration were also important in determining the distribution of *Lophelia pertusa*, *Madrepora oculat*a, blackbelly rosefish (northeast Atlantic), and American plaice, while temperature was important mostly for deep-sea fish and *Acanella arbuscula* in the northwest Atlantic. For many species in the northwest Atlantic, pH (linear detrended standard deviation) and temperature were important driving parameters.

TABLE 13
Model validation statistics generated using the maximum entropy model (Maxent); heuristic estimates of the relative contribution of the explanatory variables to the maximum entropy model (Maxent)

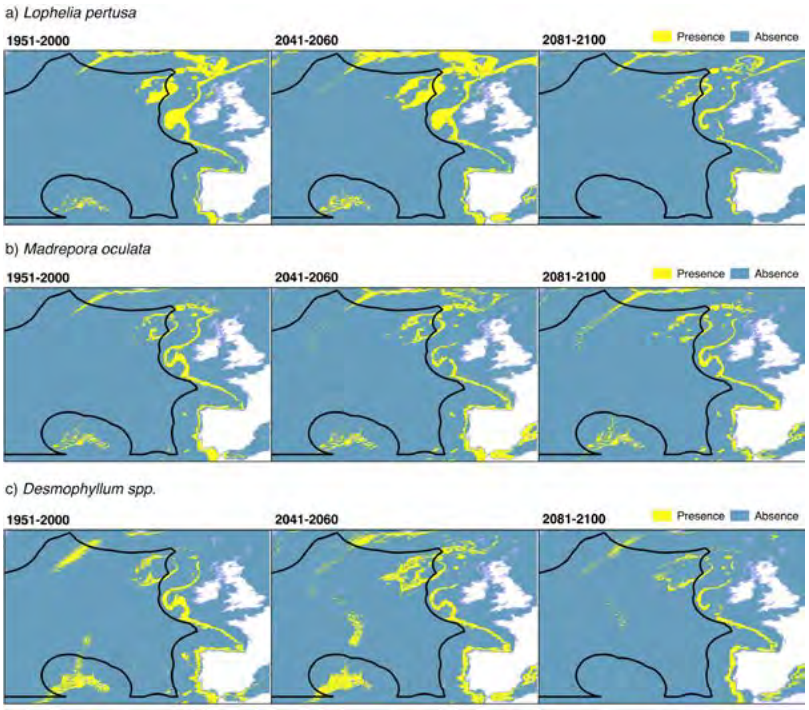
Common name		n	Test AUC	10% min. threshold	Omission rate %	Relative contribution of the explanatory variables						
						Depth	TRI	Rough.	EPC	O_2	Temp.	pH
Northeast Atlantic												
VME	*Lophelia pertusa*	1 626	0.944	0.310	9.9	44.3			23.5[1] 5.3[2]	7.0[3]		
VME	*Madrepora oculata*	778	0.967	0.219	9.8	40.2	21.0		6.5[1]	8.1[3]		
VME	*Desmophyllum* spp.	272	0.950	0.218	9.6	19.2	24.7	10.7	21.1[1]			
Deep-sea fish	Blackbelly rosefish	2 637	0.909	0.440	10.0	77.1			3.2[1]	8.4[3]	2.4[3]	
Deep-sea fish	Greater forkbeard	1 387	0.940	0.400	10.0	33.6			32.7[1]	16.1[3]		3.4[1]
Deep-sea fish	American plaice	8 867	0.808	0.568	10.0	5.9			69.8[3] 8.9[1]		5.2[3]	
Northwest Atlantic												
VME	*Acanella arbuscula*	411	0.967	0.232	9.7	25.2		39.5	11.4[3]		7.9[3]	
VME	*Acanthogorgia* spp.	201	0.937	0.188	9.3	40.4	29.6	5.0				4.5[1]
VME	*Paragorgia arborea*	233	0.956	0.323	10.0	17.1		10.7	34.5[3]			5.7[1]
Deep-sea fish	Greenland halibut	40 205	0.619	0.572	10.0	66.8			29.2[3]		1.2[3]	0.9[3]
Deep-sea fish	Beaked redfish	14 976	0.727	0.538	10.0	70.3			14.9[3]		4.8[3]	4.0[3]
Deep-sea fish	Blackbelly rosefish	4 110	0.895	0.559	10.0	7.2				6.7[1]	62.8[3] 15.3[4]	

[1] Linear detrended standard deviation.
[2] Standard deviation.
[3] Average.
[4] Coefficient variation of the mean.

Changes in the distribution of the suitable habitat under future climate conditions show contrasting patterns for the different VME and deep-sea fish species evaluated. On the one hand, the model outputs in the northeast Atlantic for *Desmophyllum* spp. and *Lophelia pertusa* (Figure 18), and all three fish species (blackbelly rosefish, greater forkbeard, and American plaice) (Figure 19), showed that a decrease in the potential suitable habitat might occur towards the last period modelled (2081–2100), but with an increase for the intermediate period (2041–2060) for *Desmophyllum* spp. and *Lophelia pertusa*. On the other hand, the model outputs for *Madrepora oculata* showed an increase in the suitable habitat for both future periods (Figure 18). No marked latitudinal or depth shifts were predicted for most taxa modelled in the northeast Atlantic, although model predictions for American plaice showed a slight shift towards higher latitudes, and a shift towards deeper waters for the three fish species (Figures A10.3.13–A10.3.24).

FIGURE 18

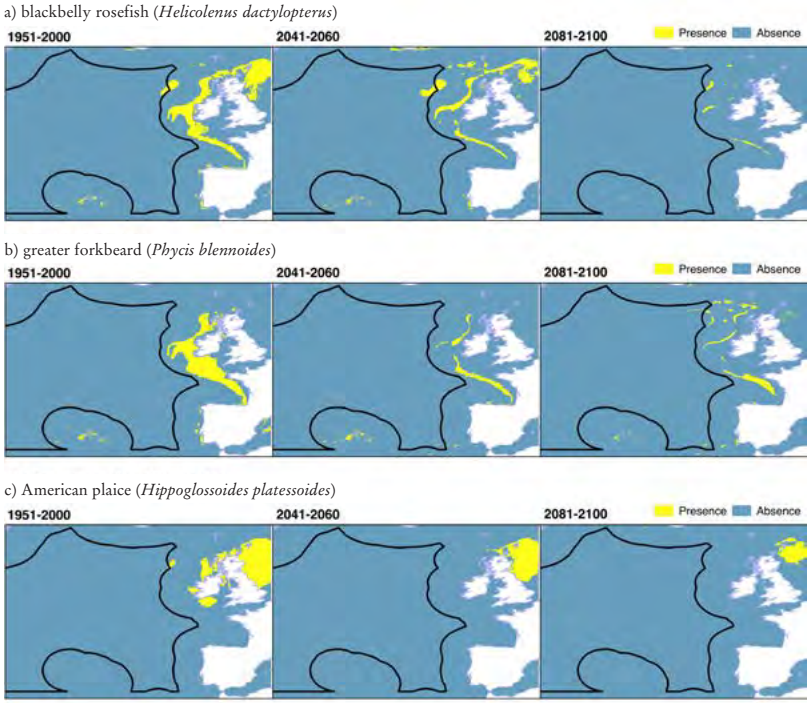
Habitat suitability maps using the 10 percent minimum threshold for VME indicator taxa in the northeast Atlantic



Notes: Generated using the maximum entropy model (Maxent) for the current climatic conditions (1951–2000). Showing differences in the area occupied by the species according to the predictions for future scenarios (2041–2060 and 2081–2100).

FIGURE 19

Habitat suitability maps using the 10 percent minimum threshold for commercially important deep-sea fish in the northeast Atlantic

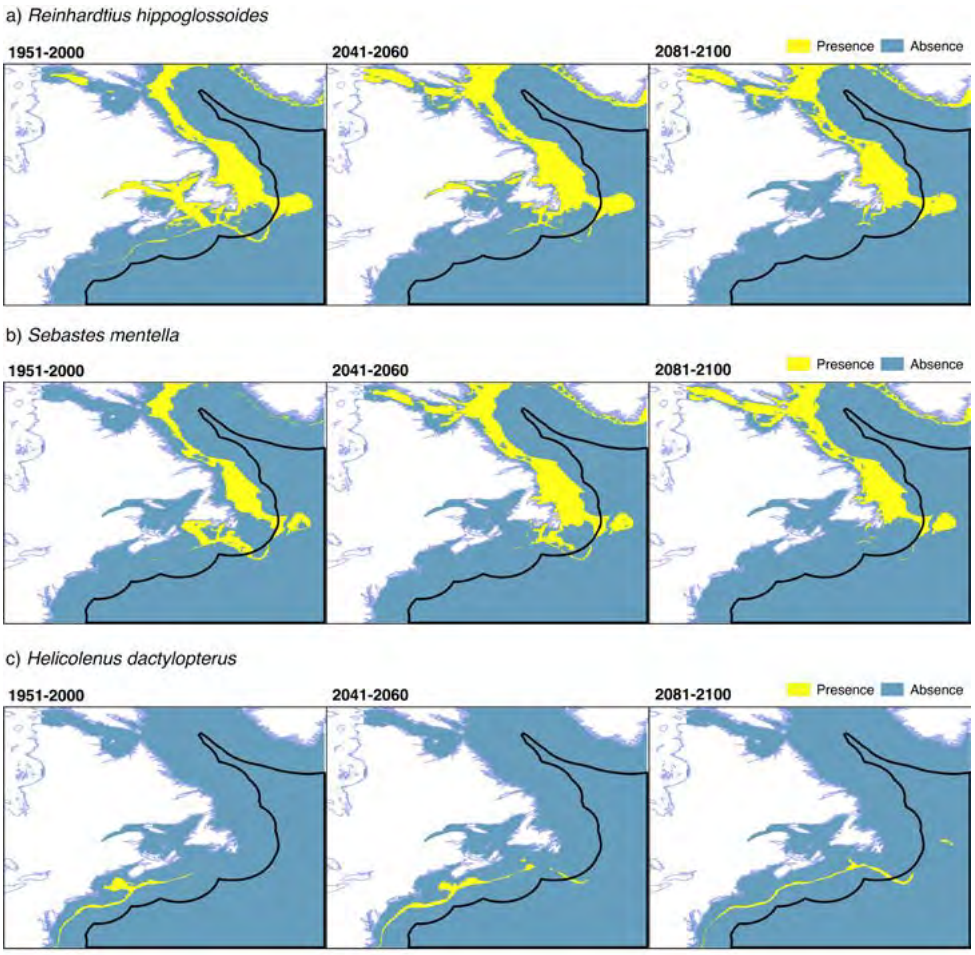


Notes: Generated using the maximum entropy model (Maxent) for the current climatic conditions (1951–2000). Showing differences in the area occupied by the species according to the predictions for future scenarios (2041–2060 and 2081–2100).

In the northwest Atlantic, the model outputs revealed the possibility of a decrease in the suitable habitat for all VME species evaluated (*Acanella arbuscula*, *Acanthogorgia* spp., and *Paragorgia arborea*) across all modelled periods (Figure 20), with the exception of a predicted increase of the suitable habitat for *Paragorgia arborea* during the intermediate period (2041–2060). The model outputs for the commercially important fish species showed very contrasting results (Figure 21), with a decrease in the potential suitable habitat towards the last modelled period (2081–2100) for Greenland halibut and blackbelly rosefish, but an increase for the intermediate period (2041–2060), and an increase in the suitable habitat for both future periods for *Sebastes mentella*. For five out of the six species modelled, outputs predict a shift in the occurrence towards higher latitudes but no marked depth related shifts (Figures A10.3.13–A10.3.24).

FIGURE 20

Habitat suitability maps using the 10 percent minimum threshold for VME indicator taxa in the northwest Atlantic

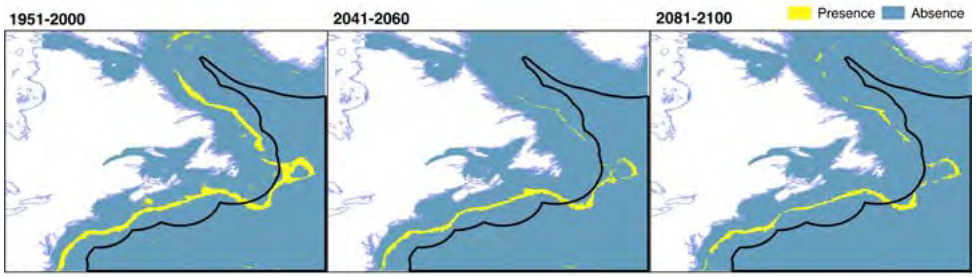


Notes: Generated using the maximum entropy model (Maxent) for the current climatic conditions (1951–2000). Showing differences in the area occupied by the species according to the predictions for future scenarios (2041–2060 and 2081–2100).

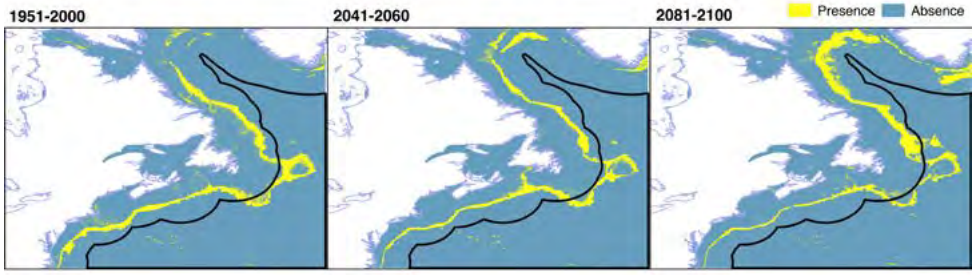
FIGURE 21

Habitat suitability maps using the 10 percent minimum threshold for commercially important deep-sea fish in the northeast Atlantic

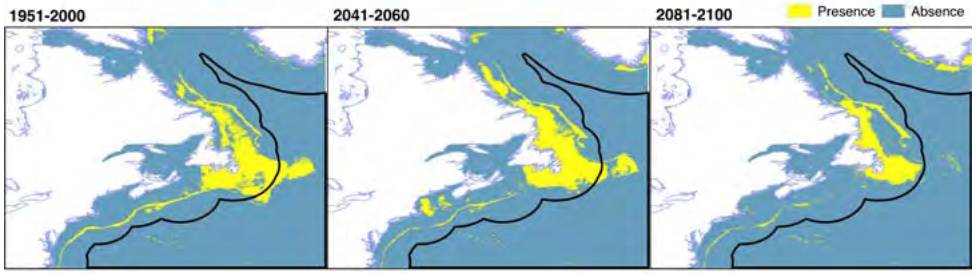
a) Greenland halibut (*Reinhardtius hippoglossoides*)



b) beaked redfish (*Sebastes mentella*)



c) blackbelly rosefish (*Helicolenus dactylopterus*)



Notes: Generated using the maximum entropy model (Maxent) for the current climatic conditions (1951–2000). Showing differences in the area occupied by the species according to the predictions for future scenarios (2041–2060 and 2081–2100).

Detailed results on the predicted probability of the suitable habitat, presence/absence maps using 10 percent minimum threshold and relative contribution of the environmental variables to the Maxent model are shown as Figures A10.3.1–A10.3.24. With the exception of *Madrepora oculata* in the northeast Atlantic, all VME indicator taxa were predicted to have their suitable habitat reduced inside the NAFO and NEAFC regulatory areas by 2100.

Model interpretation, caveats and future directions

This pilot study highlights the appropriateness of SDMs in evaluating changes in the habitat suitability for key deep-sea species under future climate scenarios and at large spatial scales. The model predictions showed that most species could be facing a reduction in suitable habitat towards 2100. In some cases, predictions indicated that this reduction could become more than 50 percent of the area currently considered as a suitable habitat (see the examples of *Lophelia pertusa* and *Desmophyllum* spp., and blackbelly rosefish, greater forkbeard and American plaice in the northeast Atlantic, or *Acanella arbuscula* and Greenland halibut in the northwest Atlantic). The predictions also showed a northward shift in the distribution of many deep-sea fish species, which corroborates the hypothesis of a poleward shift in response to climate change (Perry *et al.*, 2005; Jones *et al.*, 2013; Poloczanska *et al.*, 2013).

However, the reliability of such models and their usefulness for management purposes depend on many aspects (Robinson *et al*., 2017). These include: the spatial resolution and quality of the terrain and environmental data; the volume, quality and spatial coverage of the occurrence data; the availability of absence records; model selection; assumptions and parametrization.

The models suffer from some common and well-known limitations that may be more pronounced when modelling deep-sea taxa. It is known that cold-water coral distributions respond to small-scale fluctuations of different terrain attributes, such as substrate type and seabed rugosity (De Clippele *et al*., 2017), and oceanographic conditions (Bennecke and Metaxas, 2017). However, both terrain and environmental information was derived from the global datasets and not from detailed deep-sea *in situ* measurements, which does not allow for discriminating within areas with high small-scale heterogeneity. Moreover, predictions of future climate conditions may not capture localized effects that are most important for benthic organisms. As the aim is to evaluate the potential effect of climate change using species distribution or habitat suitability modelling at large spatial scales, the data and grid size used in the habitat suitability models performed in this study can be considered adequate.

There are other sources of uncertainty including the quantity and the spatial distribution of available occurrence data, to some degree of uncertainty on deep-sea species identification (mostly for VME indicator taxa) and geolocation of data obtained from OBIS. Moreover, the use of presence-only records (as opposed to abundance data) with no true absence data generates increased uncertainty. The deep sea is still one of the least studied and sampled areas on the planet (see Section 12) and, therefore, many species are still unknown or the taxonomy still has to be resolved, and the real spatial distribution is also undetermined (mostly for VME indicator taxa). Therefore, this source of uncertainty will only be reduced through extensive exploration of the deep-sea environment. Finally, this work still lacks a comprehensive model validation through measurement of both model performance and accuracy, and estimates of model error or uncertainty in modelled distributions. Such limitations should be considered when drawing conclusions from the outputs generated.

The results showed that depth was identified as the most important predictor variable in determining habitat suitability for most species. This is consistent with similar studies that have evaluated the distribution of other deep-sea corals (e.g. Davies and Guinotte, 2011; Guinotte and Davies, 2014; Buhl-Mortensen *et al*., 2015; Lauria *et al*., 2017) and deep-sea fish (Gomez *et al*., 2015; Parra *et al*., 2017). However, depth is highly correlated with other environmental (e.g. temperature, and oxygen concentration) and biological factors (e.g. availability of food) and, therefore, it is difficult to specify which of these environmental parameters are primarily responsible for the observed patterns. The importance of other terrain variables such as roughness and slope some coral and fish species could be linked to seafloor hydrodynamics and provides indirect information related to current regimes, with implications for species distributions (Parra *et al*., 2017).

In addition to terrain variables, POC flux, dissolved oxygen concentration, bottom seawater temperature, and pH were also important variables for many species. The north Atlantic is expected to experience some of the greatest projected changes in temperature, pH and oxygen concentrations at bathyal depths (Gehlen *et al*., 2014; Sweetman *et al*., 2017; Section 8). Low food availability in these areas will exacerbate the likely negative effects of these environmental conditions on corals and deep-sea fish. This is because not enough energy will be available to sustain the costs of key physiological processes of corals (e.g. Maier *et al*., 2016; Büscher, Form and Riebesell, 2017) and key deep-sea fish prey taxa (Ruhl and Smith, 2004; Bailey, Ruhl and Smith, 2006).

The availability of food (POC flux) has been linked with the physiological performance of corals (e.g. calcification and respiratory metabolism) (Naumann *et al*., 2011; Larsson, Lundälv and van Oevelen, 2013) and their potential ability to cope with ocean change (see Section 9, Maier *et al*., 2016; Büscher, Form and Riebesell, 2017). However, in an environment where food is permanently scarce, a shift in energy allocation might occur in favour of physiological functions other than calcification and growth, and compromise the survival of corals (Hennige *et al*., 2015; Maier *et al*., 2016). These important physiological aspects are not currently taken into account in the modelling exercises.

Although pH showed little explanatory power on the occurrence of cold-water coral species, other variables related to seawater carbonate chemistry, such as aragonite and calcite saturation state, have been shown to be important factors determining cold-water coral habitat suitability (e.g. Davies and Guinotte, 2011; Yesson *et al*., 2012; Thresher *et al*., 2015). Some regions of the world ocean are projected to become undersaturated with respect to aragonite and calcite by 2100, particularly in deep waters and higher latitudes (Orr *et al*., 2005). As a result, large areas of cold-water coral habitat that are currently located in saturated waters will experience undersaturated conditions within this century (Orr *et al*., 2005; Guinotte *et al*., 2006). Corals in these areas may not have enough carbonate ion for the construction and growth of their skeletal elements, constraining the occurrence of cold-water corals there. To take this into consideration, future modelling efforts should include these variables as they are likely to change the predicted distribution ranges of the cold-water corals studied.

It is very difficult to infer the capacity of deep-sea species to overcome changes in the water chemistry forecasted by climatic models. Recent work suggests that interspecific genetic variability could be sufficient for certain populations to support an adaptive response to climate change conditions, with certain individuals being more resilient than others (Kurman *et al*., 2017). It is also likely that some species may colonize or occupy new areas in which conditions become more favourable due to climate change, if their dispersal capacity can cope with the rate of change. In fact, Maxent results predict that many coral and fish species could expand their distribution range to higher latitudes towards 2100. At the same time, there also exists the possibility that future changes in the properties of the bottom seawater could modify the depth range at which species are currently found. This scenario was only predicted for *Paragorgia arborea*, for which Maxent predicts an increase in the area suitable for this species towards the coastline, in shallower areas than those where it is found now.

In summary, although improvements in the modelling approach may be required, species distribution or habitat suitability models are useful tools for predicting potential future changes in the distribution of deepwater species in the north Atlantic, and may inform management decisions within RFMOs.

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APPENDIX A10.1

Terrain and environmental data for the northeast Atlantic area

FIGURE A10.1.1
Terrain variables used in the habitat suitability modelling in the northeast Atlantic area

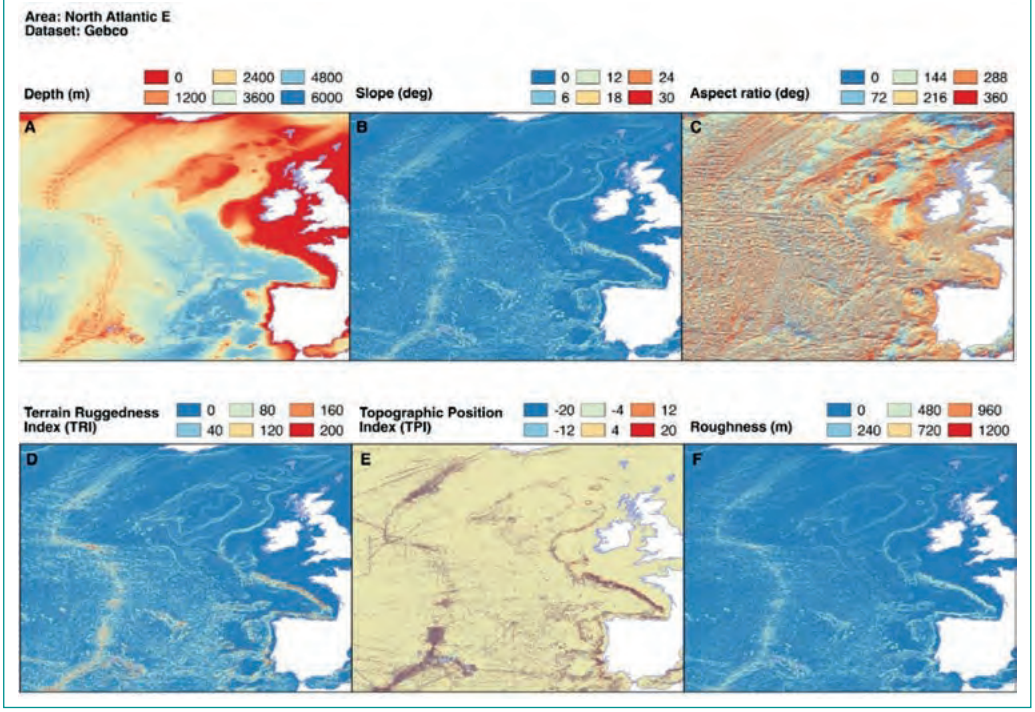


FIGURE A10.1.2
Mean values of the seafloor environmental data in the northeast Atlantic area

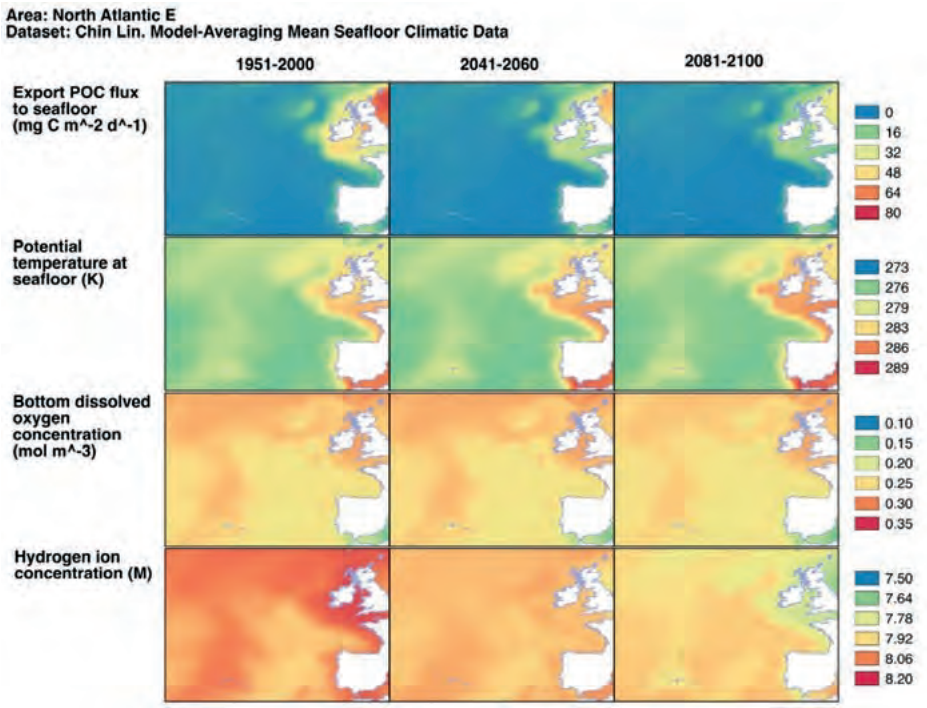


FIGURE A10.1.3
Coefficient of variance of the seafloor environmental data in the northeast Atlantic area

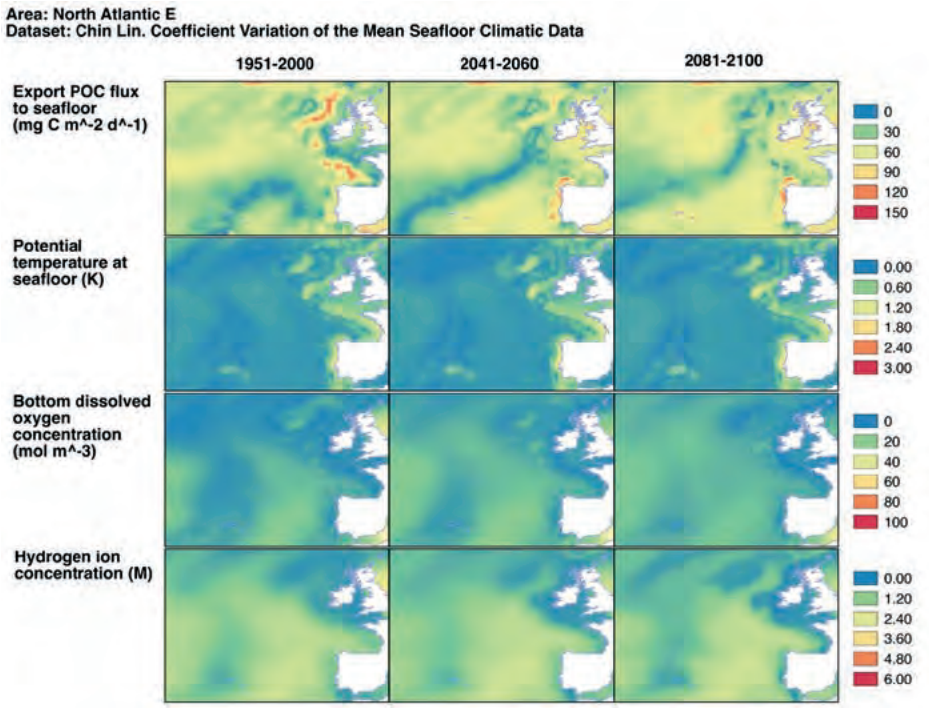


FIGURE A10.1.4
Detrended standard deviation of the seafloor environmental data in the northeast Atlantic area

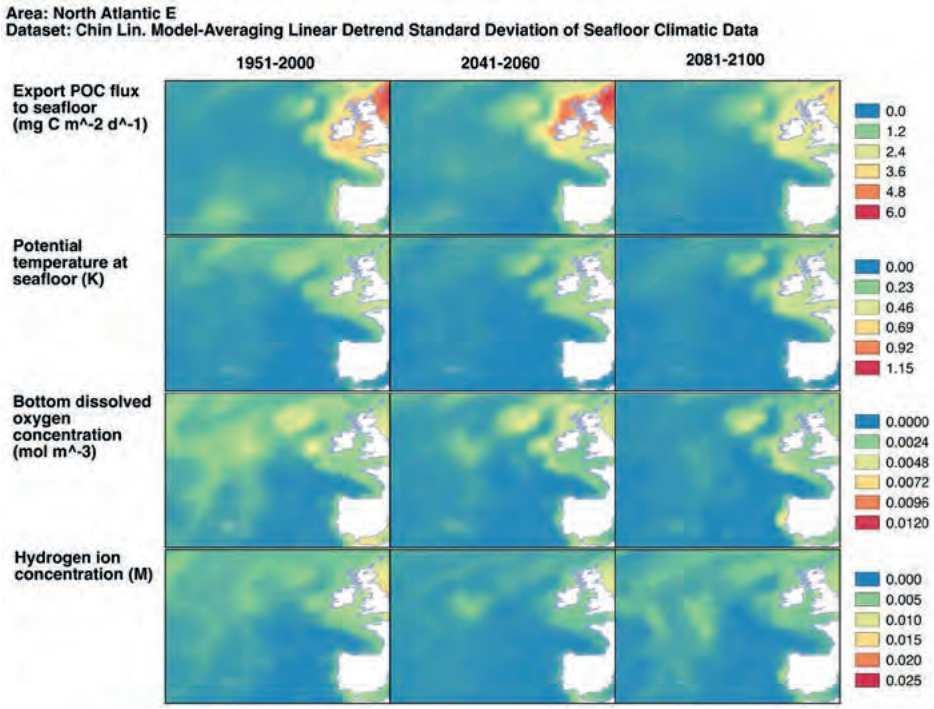
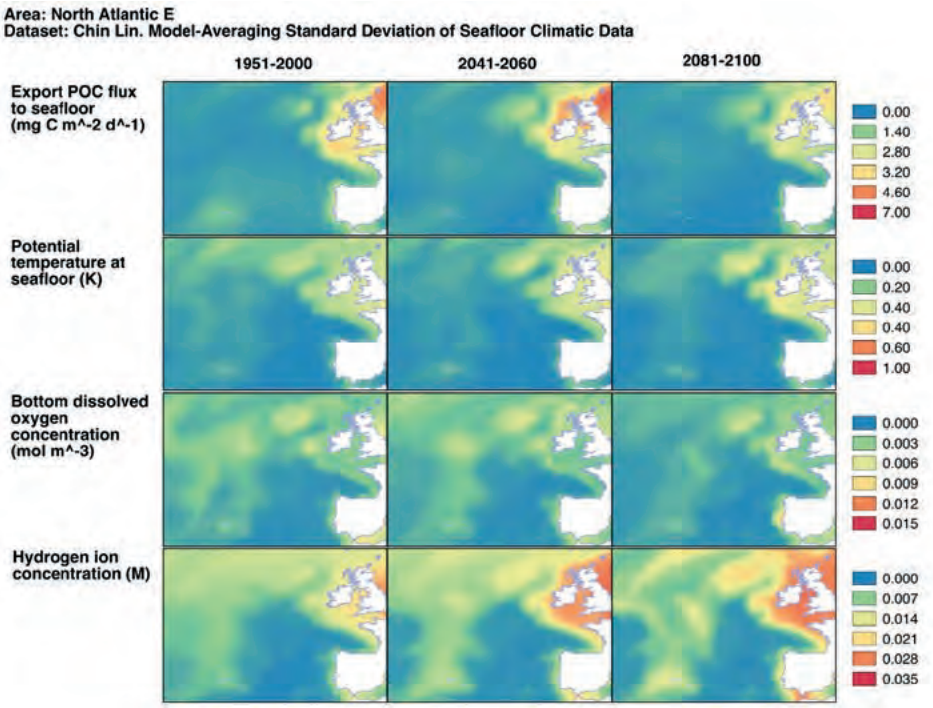


FIGURE A10.1.5
Standard deviation of the seafloor environmental data in the northeast Atlantic area



APPENDIX A10.2

Terrain and environmental data for the northwest Atlantic area

FIGURE A10.2.1
Terrain variables used in the habitat suitability modelling in the northwest Atlantic area

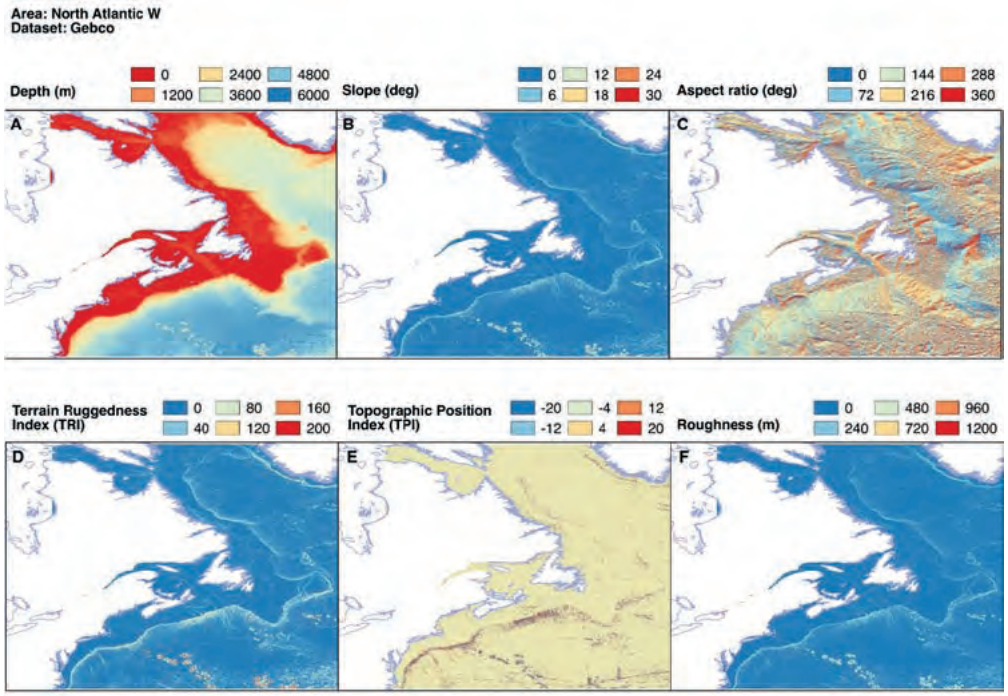


FIGURE A10.2.2
Mean values of the seafloor environmental data in the northwest Atlantic area

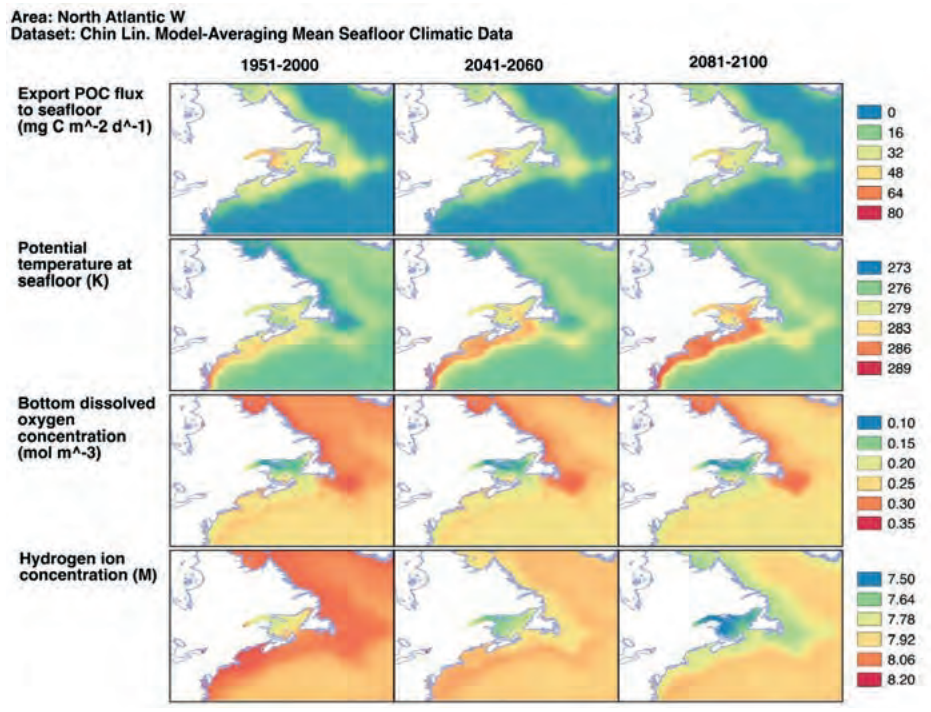


FIGURE A10.2.3
Coefficient of variance of the seafloor environmental data in the northwest Atlantic area

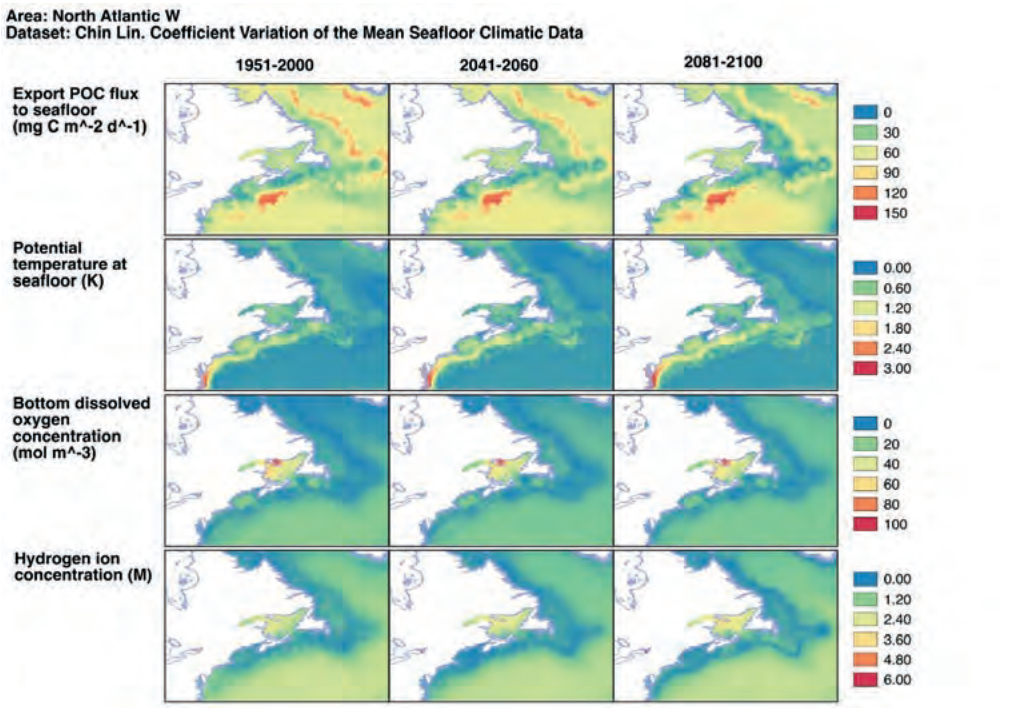


FIGURE A10.2.4
Detrended standard deviation of the seafloor environmental data in the northwest Atlantic area

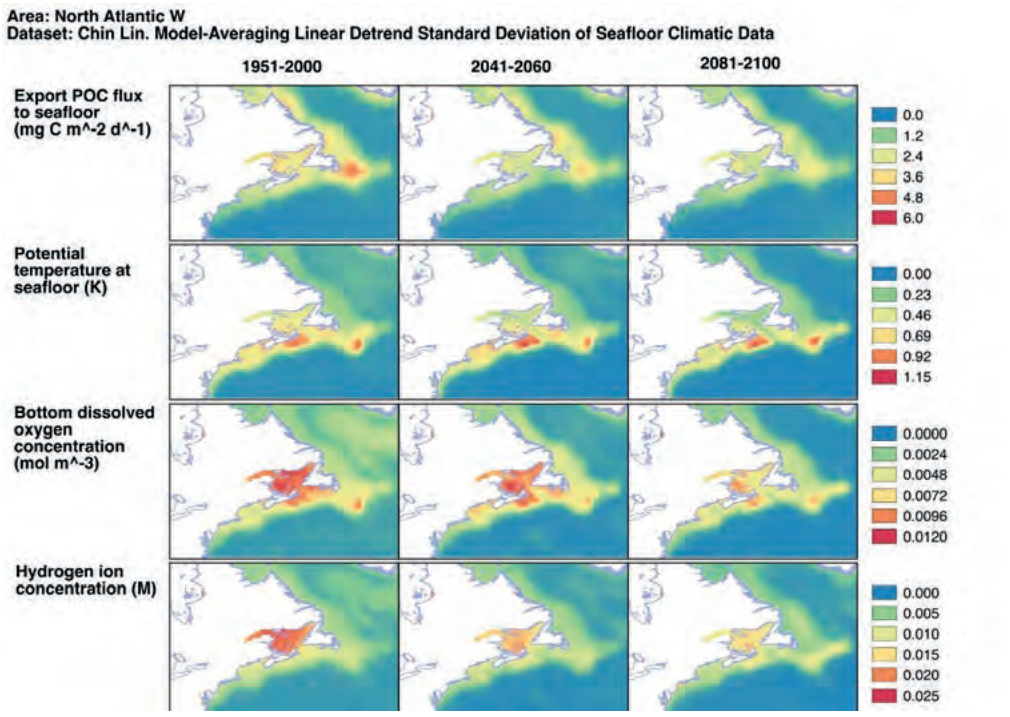
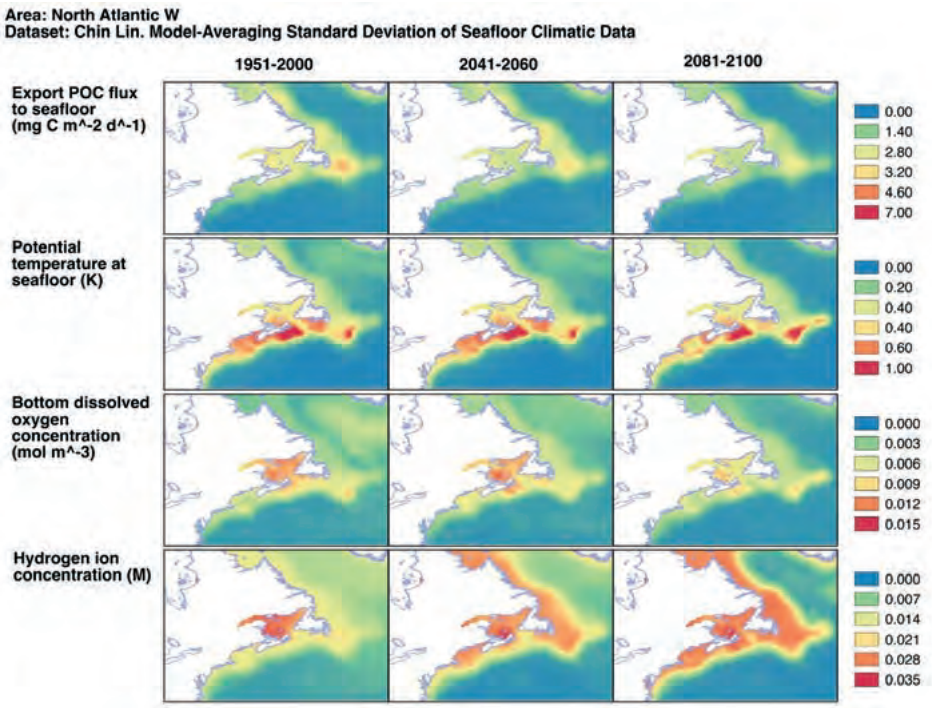


FIGURE A10.2.5

Standard deviation of the seafloor environmental data in the northwest Atlantic area



APPENDIX A10.3.1

Supplementary figures: predicted probability of the suitable habitat

FIGURE A10.3.1

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for *Lophelia pertusa* in the northeast Atlantic area for the current and future climate scenarios

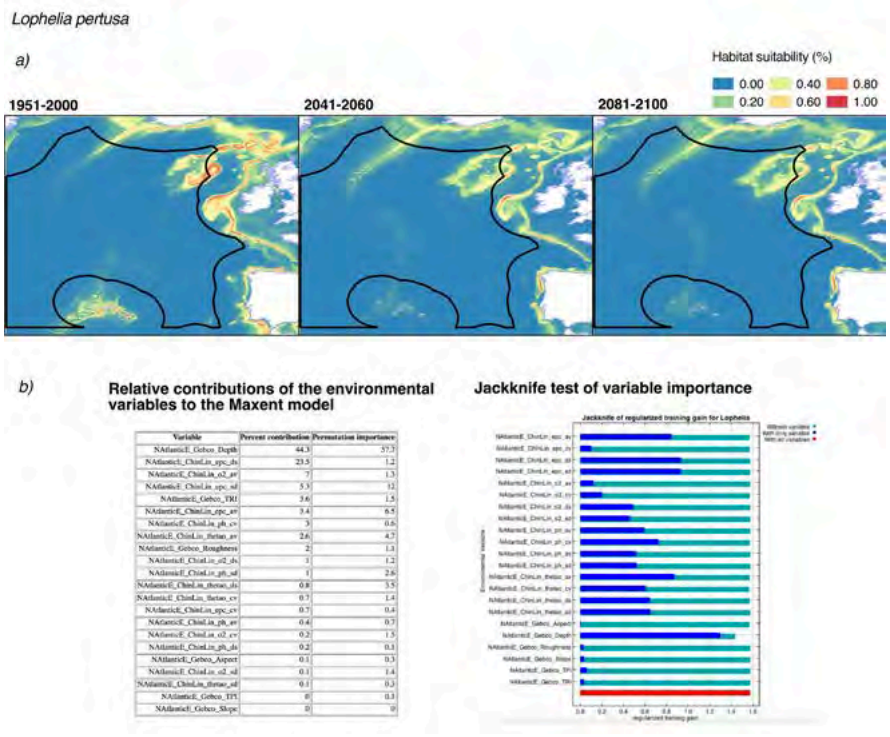


FIGURE A10.3.2

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for *Madrepora oculata* in the northeast Atlantic area for the current and future climate scenarios

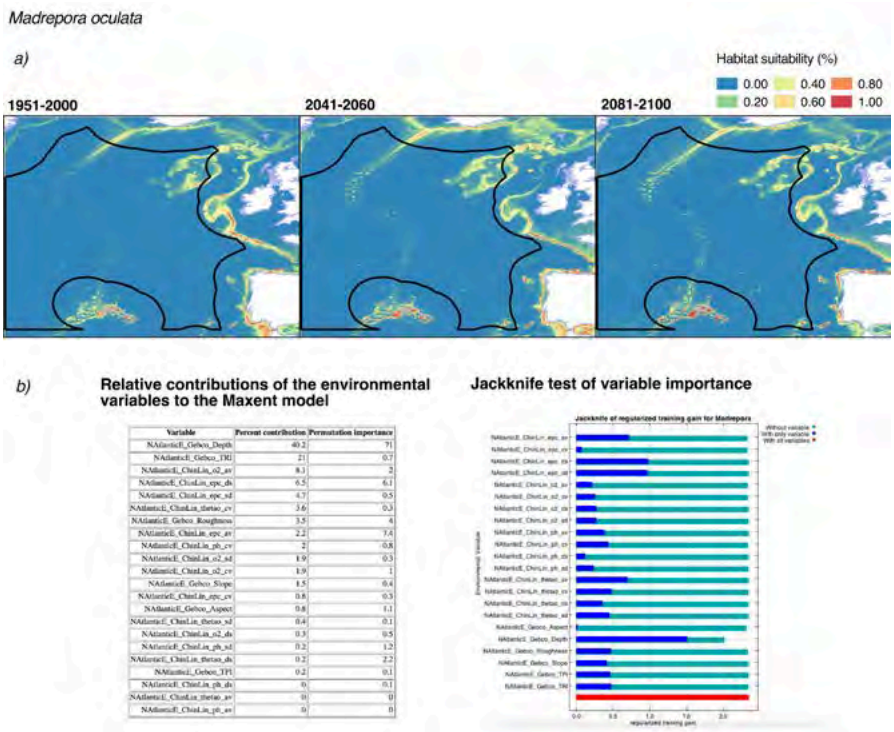


FIGURE A10.3.3

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for *Desmophyllum* spp. in the northeast Atlantic area for the current and future climate scenarios

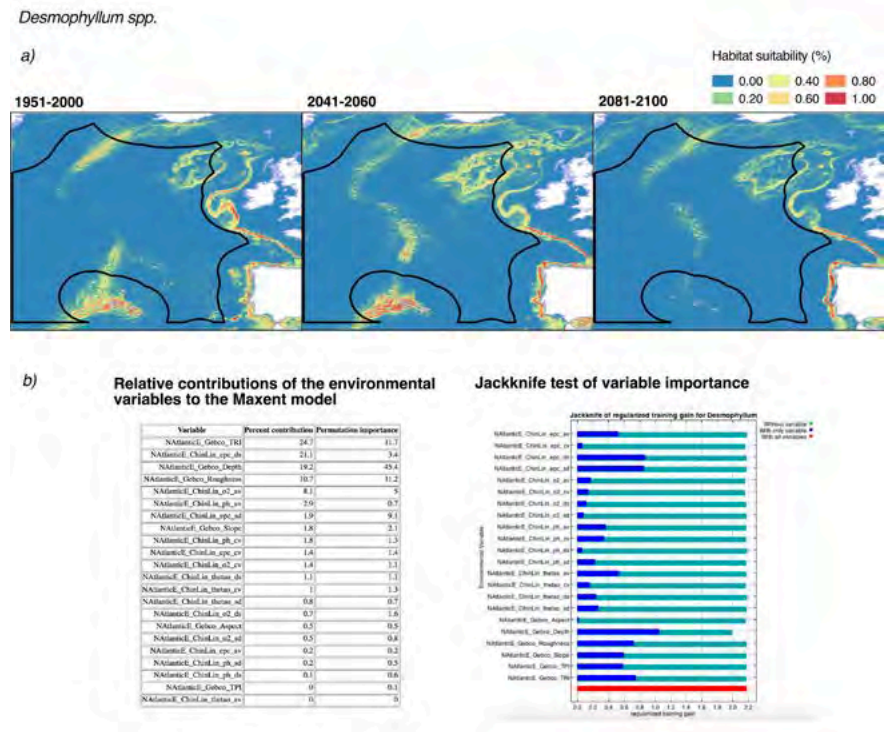


FIGURE A10.3.4

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for blackbelly rosefish in the northeast Atlantic area for the current and future climate scenarios

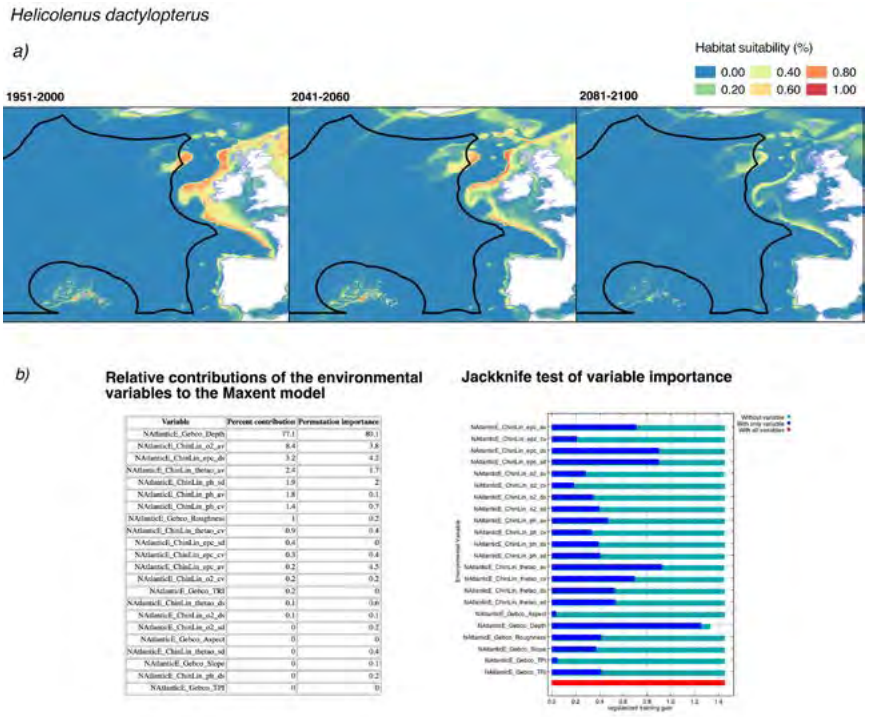


FIGURE A10.3.5

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for greater forkbeard in the northeast Atlantic area for the current and future climate scenarios

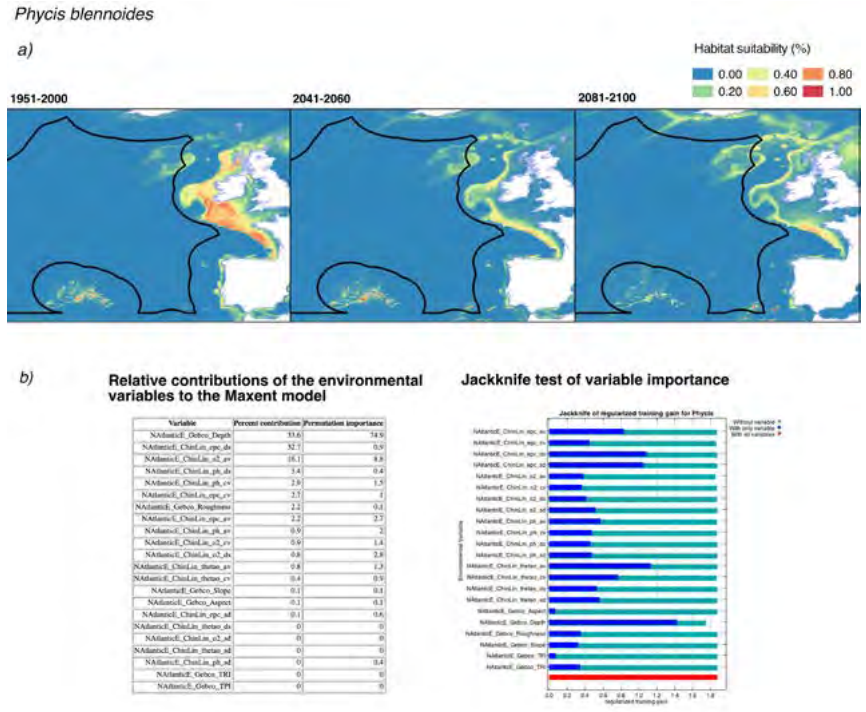
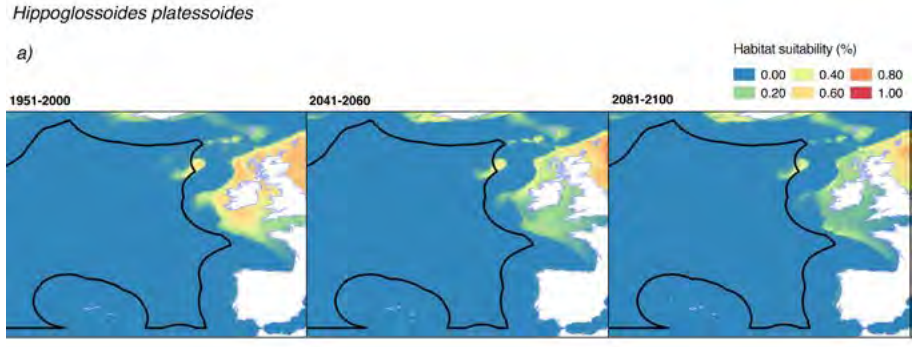


FIGURE A10.3.6

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for American plaice in the northeast Atlantic area for the current and future climate scenarios



b)

Relative contributions of the environmental variables to the Maxent model

Variable	Percent contribution	Permutation importance
NAtlanticE_ChinLin_epc_av	69.8	14.3
NAtlanticE_ChinLin_epc_ds	8.9	7
NAtlanticE_Gebco_Depth	5.9	22.7
NAtlanticE_ChinLin_thetao_av	5.2	17.3
NAtlanticE_ChinLin_thetao_ds	3.5	18.4
NAtlanticE_ChinLin_ph_cv	2.2	2.7
NAtlanticE_ChinLin_epc_sd	2	0
NAtlanticE_ChinLin_ph_av	0.7	0.1
NAtlanticE_ChinLin_o2_av	0.5	6
NAtlanticE_ChinLin_ph_sd	0.4	0.2
NAtlanticE_ChinLin_o2_cv	0.3	0.4
NAtlanticE_Gebco_TRI	0.3	2.6
NAtlanticE_ChinLin_o2_ds	0	2.7
NAtlanticE_Gebco_Slope	0	0.1
NAtlanticE_ChinLin_epc_cv	0	0
NAtlanticE_ChinLin_ph_ds	0	0
NAtlanticE_ChinLin_thetao_sd	0	4.9
NAtlanticE_ChinLin_thetao_cv	0	0.7
NAtlanticE_ChinLin_o2_sd	0	0
NAtlanticE_Gebco_Aspect	0	0
NAtlanticE_Gebco_Roughness	0	0

Jackknife test of variable importance

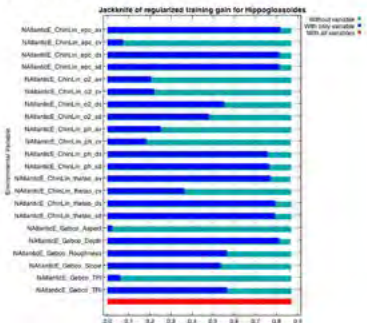
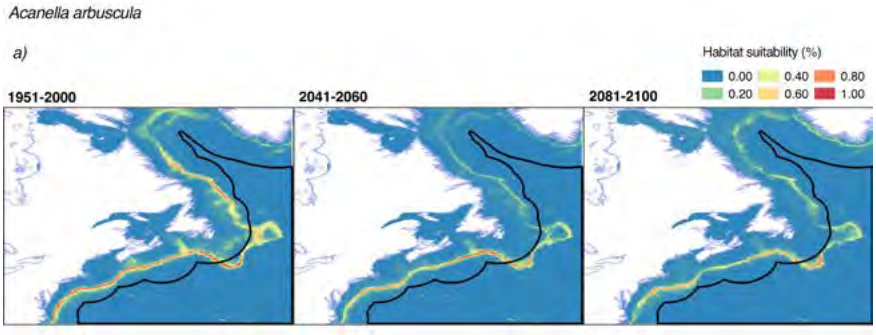


FIGURE A10.3.7

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for *Acanella arbuscula* in the northwest Atlantic area for the current and future climate scenarios



b)

Relative contributions of the environmental variables to the Maxent model

Variable	Percent contribution	Permutation importance
NAtlanticW_Gebco_Roughness	39.5	0.3
NAtlanticW_Gebco_Depth	25.2	66.3
NAtlanticW_ChinLin_epc_av	11.4	4.5
NAtlanticW_ChinLin_thetao_av	7.9	8
NAtlanticW_ChinLin_ph_sd	3.9	6.4
NAtlanticW_ChinLin_o2_cv	2.6	1.6
NAtlanticW_ChinLin_ph_av	2.1	1.2
NAtlanticW_ChinLin_thetao_cv	1.5	0.2
NAtlanticW_ChinLin_ph_cv	1.2	0.8
NAtlanticW_ChinLin_epc_sd	0.9	4.7
NAtlanticW_Gebco_Slope	0.7	0
NAtlanticW_ChinLin_o2_ds	0.7	0.2
NAtlanticW_ChinLin_o2_sd	0.5	1.9
NAtlanticW_ChinLin_epc_ds	0.5	0.5
NAtlanticW_ChinLin_epc_cv	0.4	0.9
NAtlanticW_Gebco_Aspect	0.4	0.4
NAtlanticW_Gebco_TRI	0.3	0.1
NAtlanticW_ChinLin_thetao_ds	0.2	0.8
NAtlanticW_ChinLin_o2_av	0.1	0.4
NAtlanticW_ChinLin_ph_ds	0.1	0.6
NAtlanticW_ChinLin_thetao_sd	0.1	0.2
NAtlanticW_Gebco_TPI	0	0

Jackknife test of variable importance

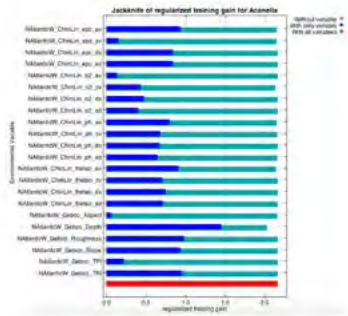


FIGURE A10.3.8

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for *Acanthogorgia* spp. in the northwest Atlantic area for the current and future climate scenarios

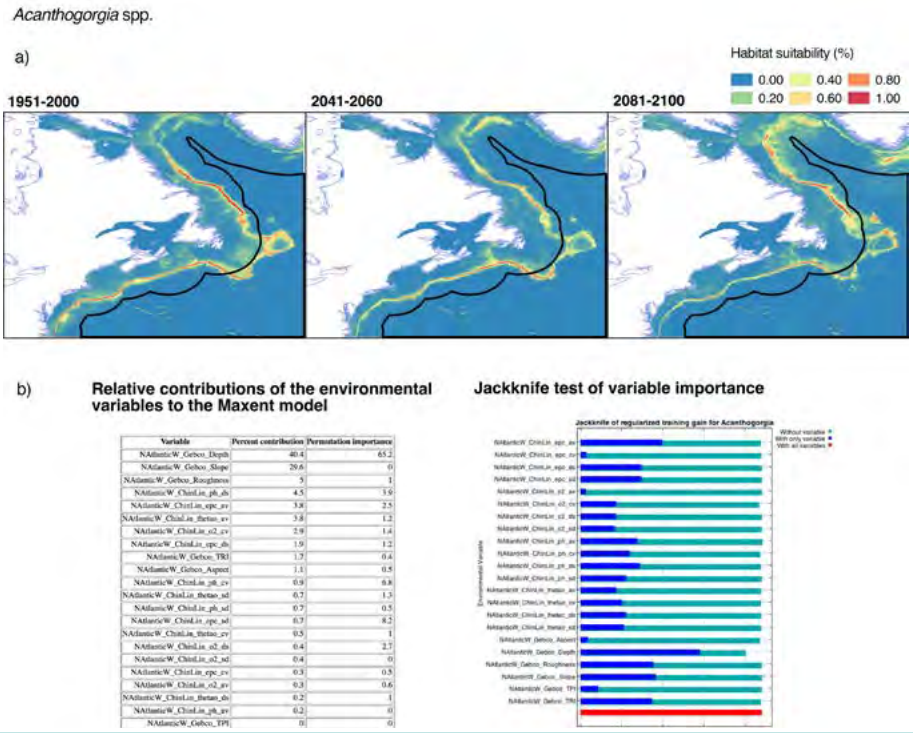


FIGURE A10.3.9

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for *Paragorgia arborea* in the northwest Atlantic area for the current and future climate scenarios

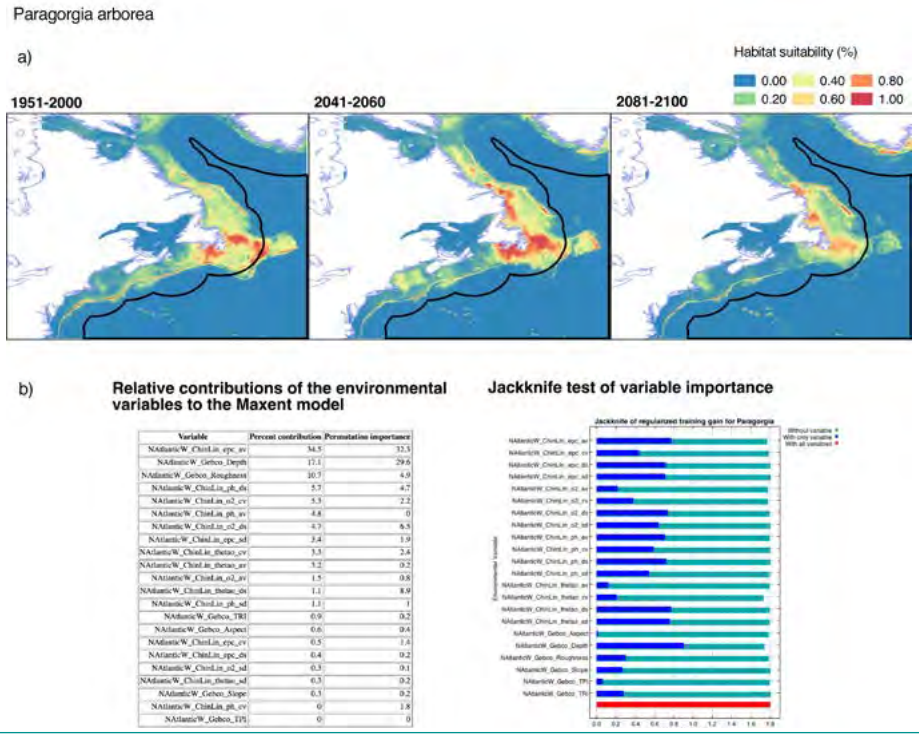


FIGURE A10.3.10

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for Greenland halibut in the northwest Atlantic area for the current and future climate scenarios

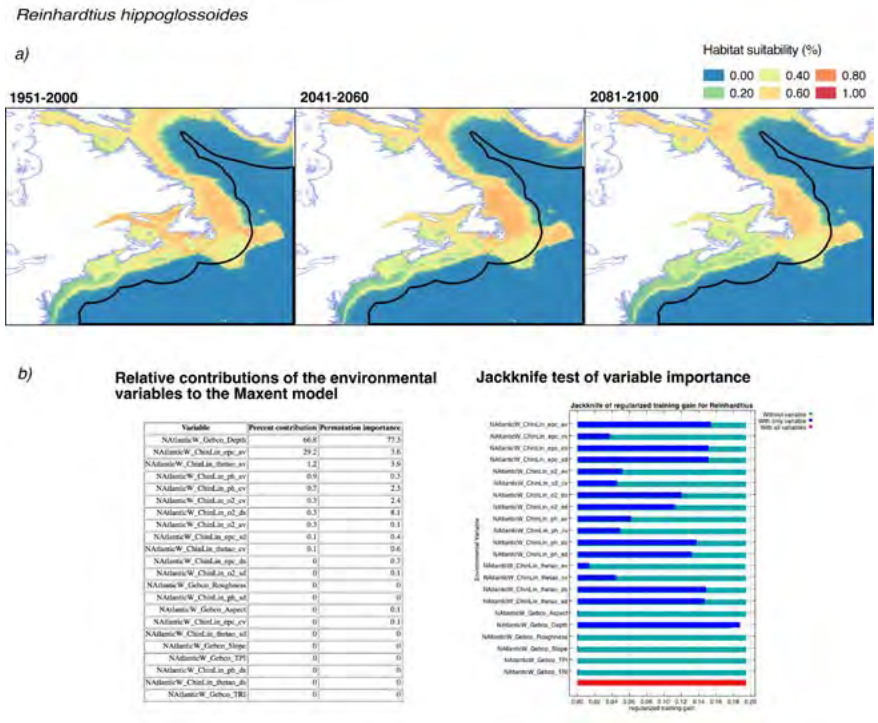


FIGURE A10.3.11

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for beaked redfish in the northwest Atlantic area for the current and future climate scenarios

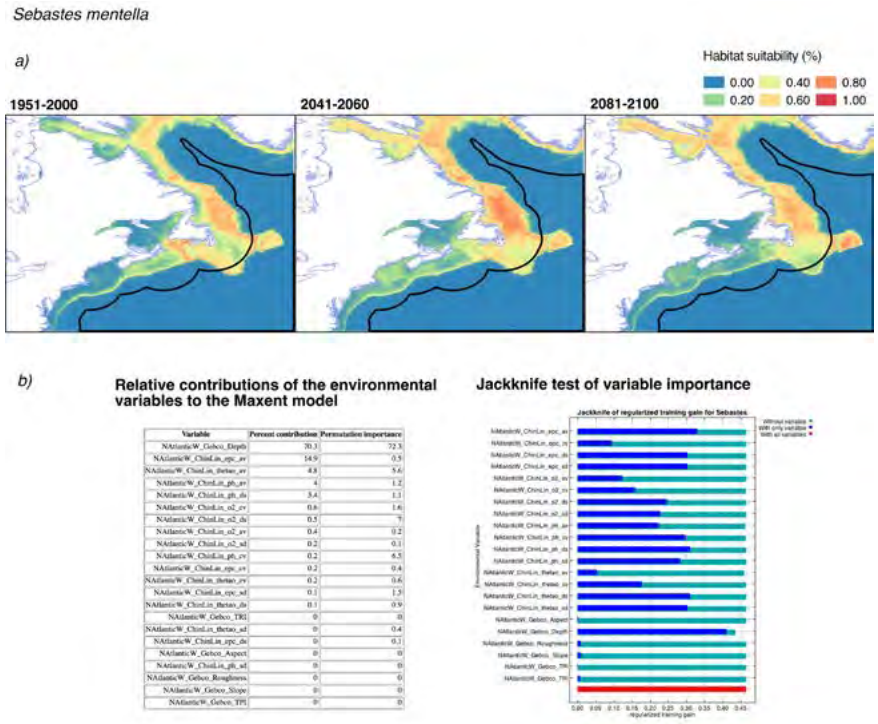


FIGURE A10.3.12

Predicted probability of the suitable habitat, (a) presence/absence maps using the 10% minimum threshold, and (b) relative contribution and jackknife test of the environmental variables to the Maxent model for blackbelly rosefish in the northwest Atlantic area for the current and future climate scenarios

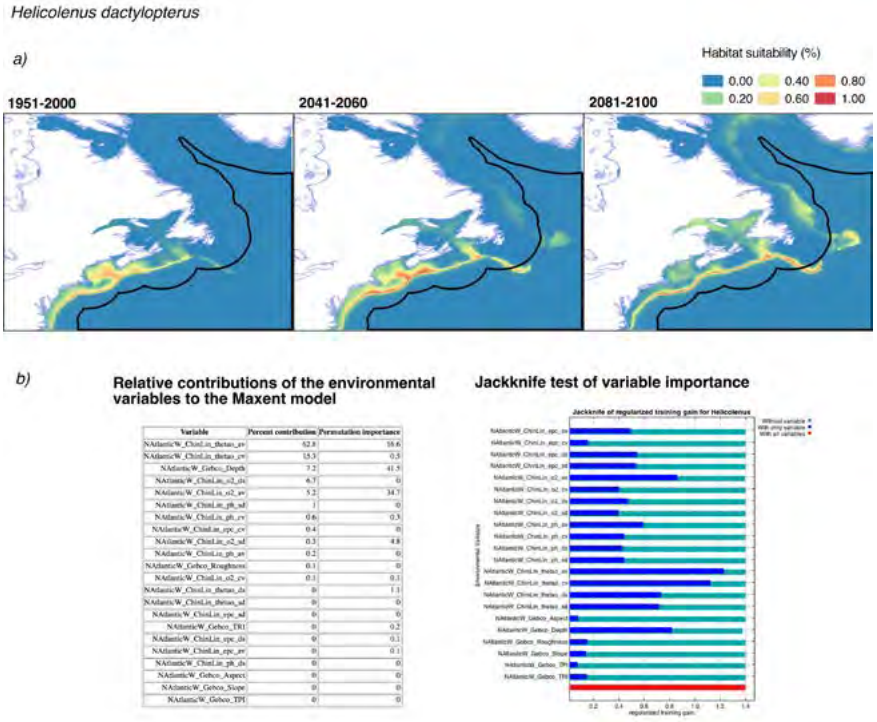
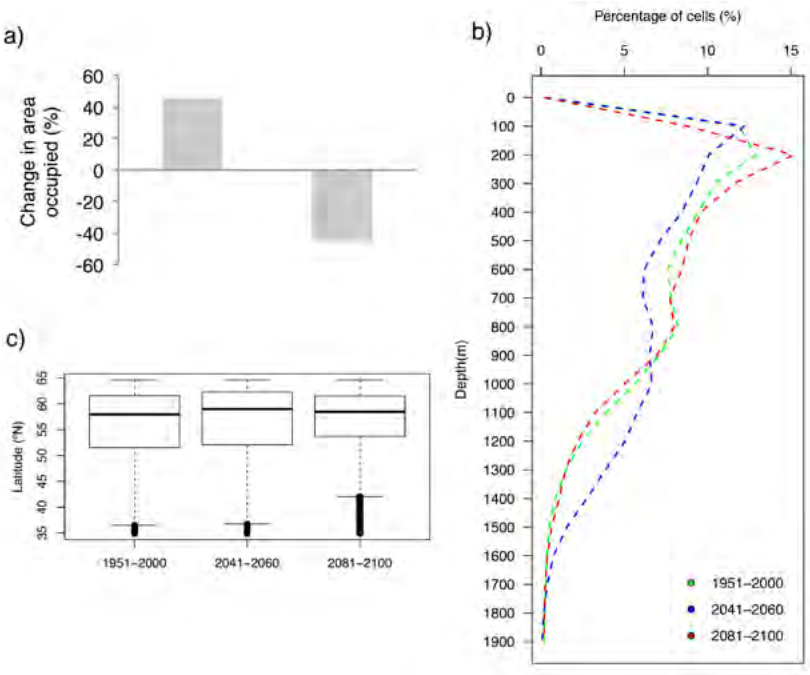


FIGURE A10.3.13

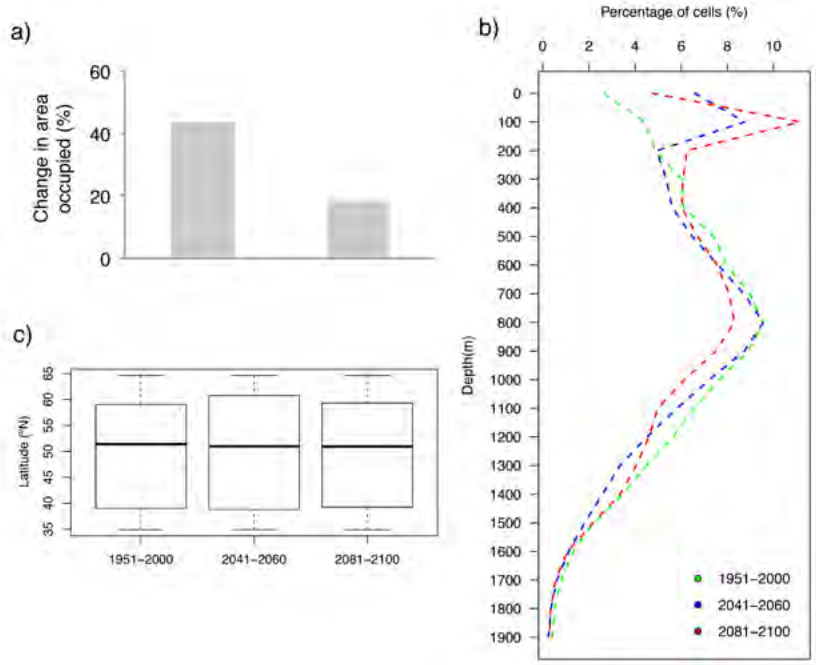
Changes in the predicted habitat suitable for *Lophelia pertusa* in the northeast Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.1b, and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.14

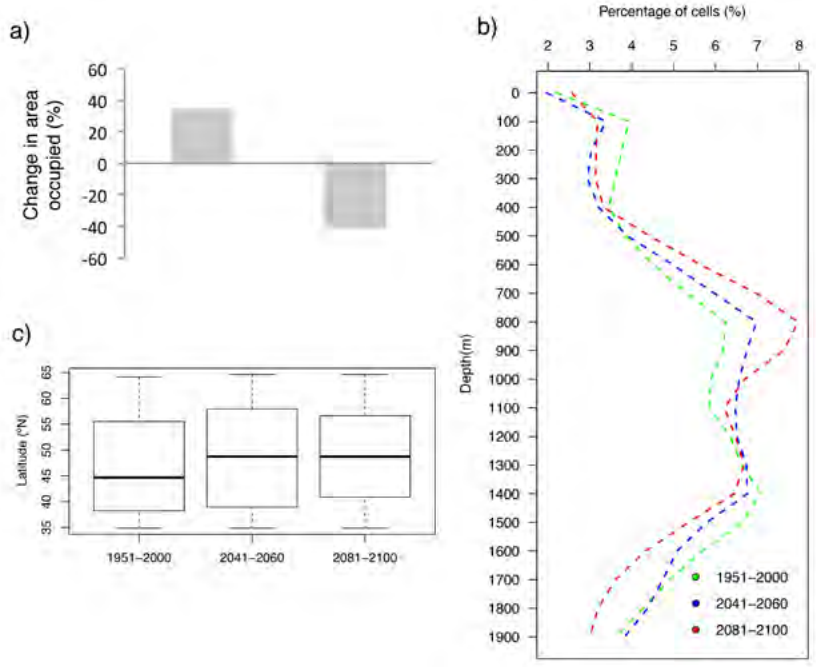
Changes in the predicted habitat suitable for *Madrepora oculata* in the northeast Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.2b, and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.15

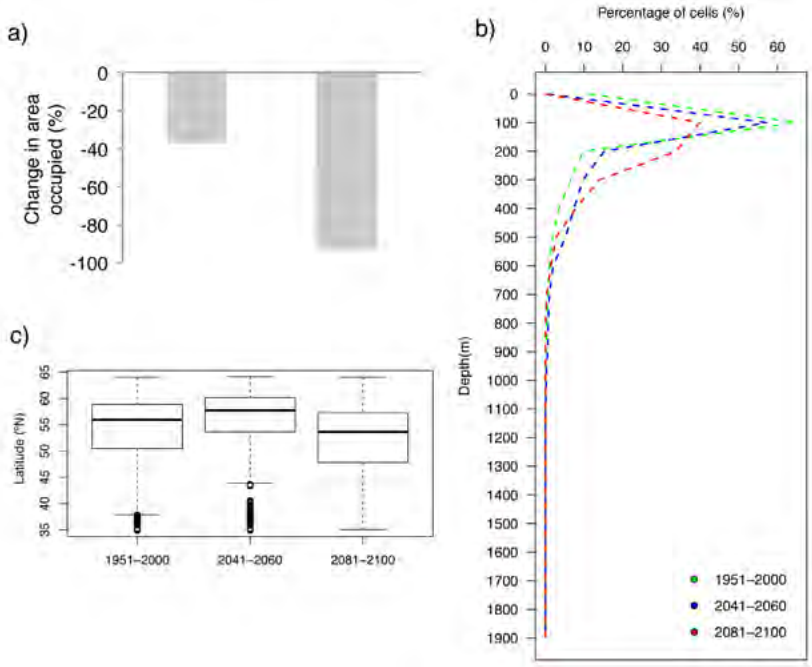
Changes in the predicted habitat suitable for *Desmophyllum* spp. in the northeast Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.3b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.16

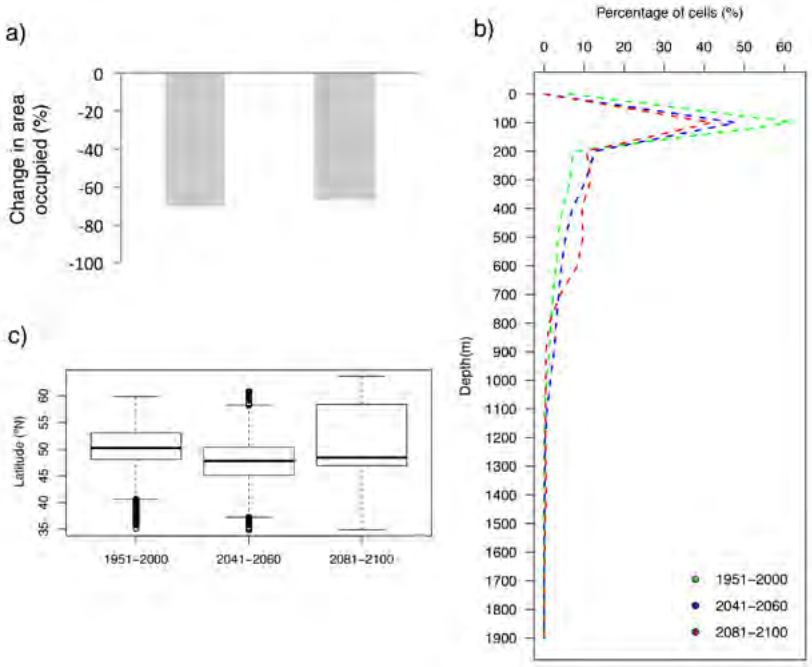
Changes in the predicted habitat suitable for blackbelly rosefish in the northeast Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.4b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

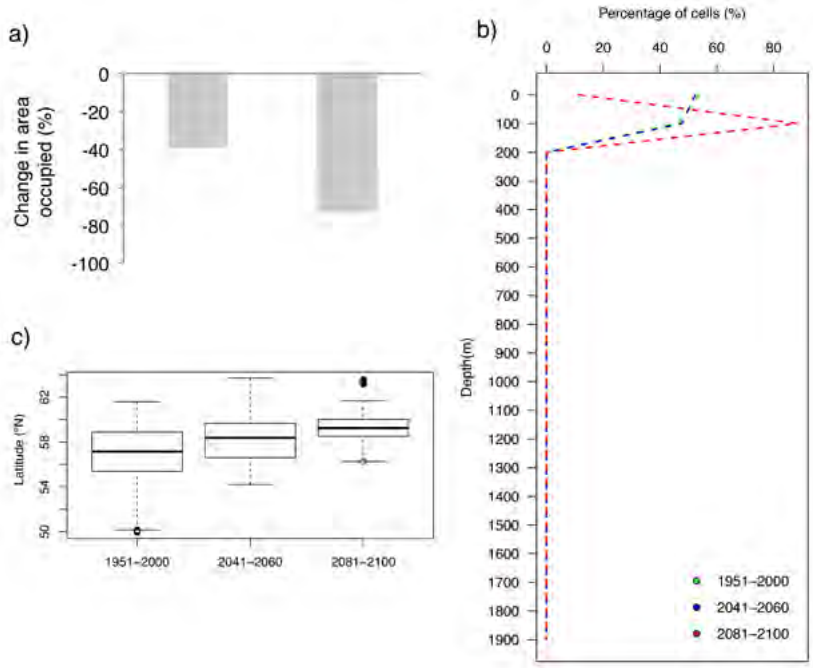
FIGURE A10.3.17

Changes in the predicted habitat suitable for greater forkbeard in the northeast Atlantic under future climatic scenarios



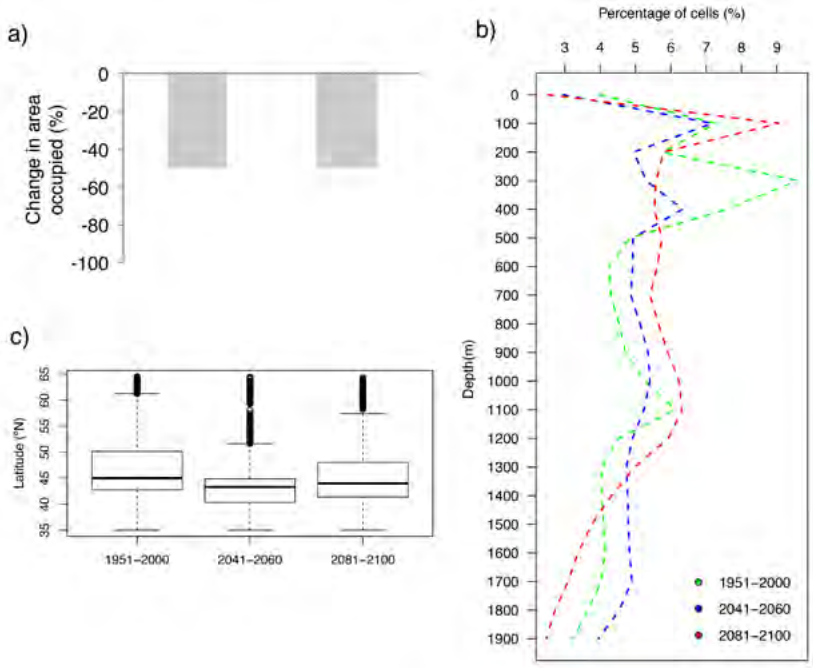
Notes: Based on the presence/absence maps shown in Figure A10.3.5b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.18
Changes in the predicted habitat suitable for American plaice in the northeast Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.6b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

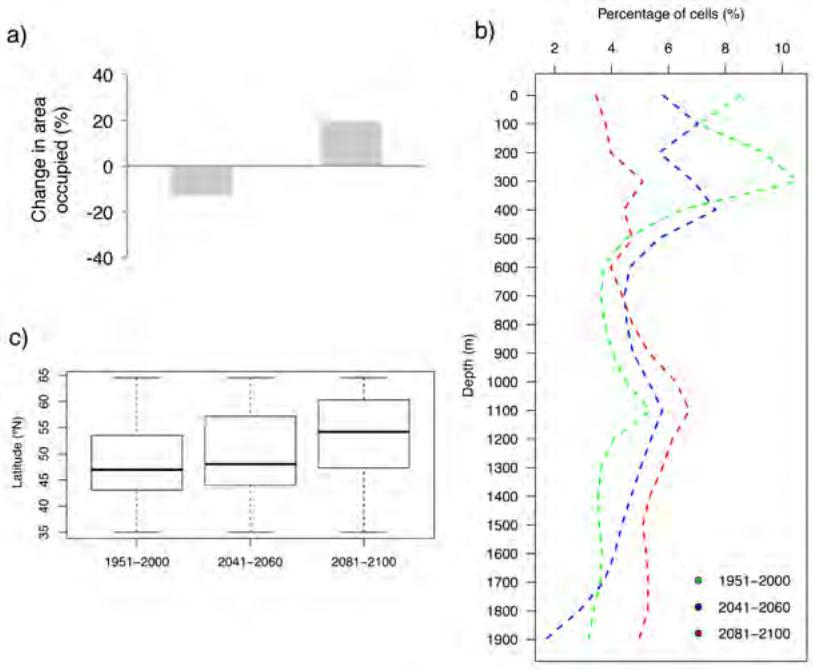
FIGURE A10.3.19
Changes in the predicted habitat suitable for *Acanella arbuscula* in the northwest Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.7b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.20

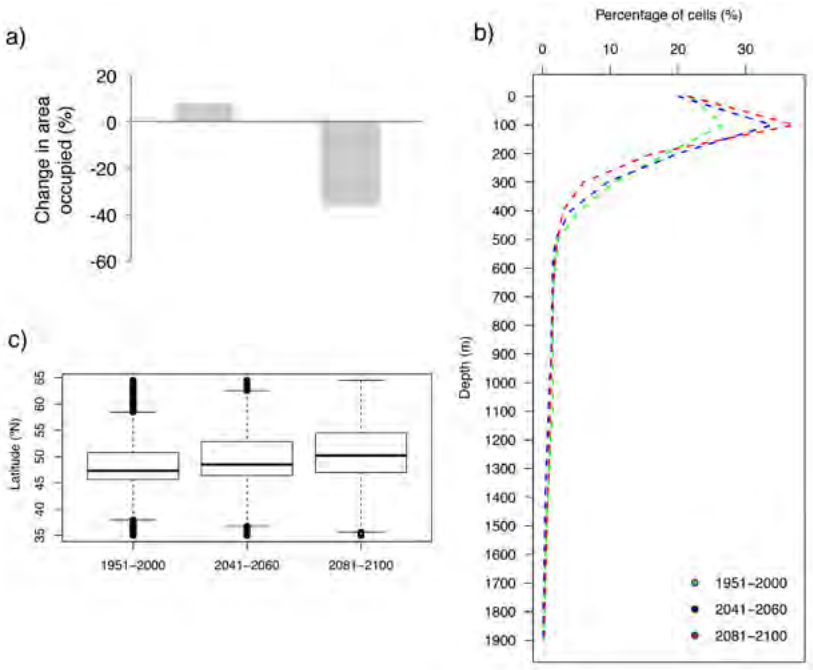
Changes in the predicted habitat suitable for *Acanthogorgia* spp. in the northwest Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.8b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.21

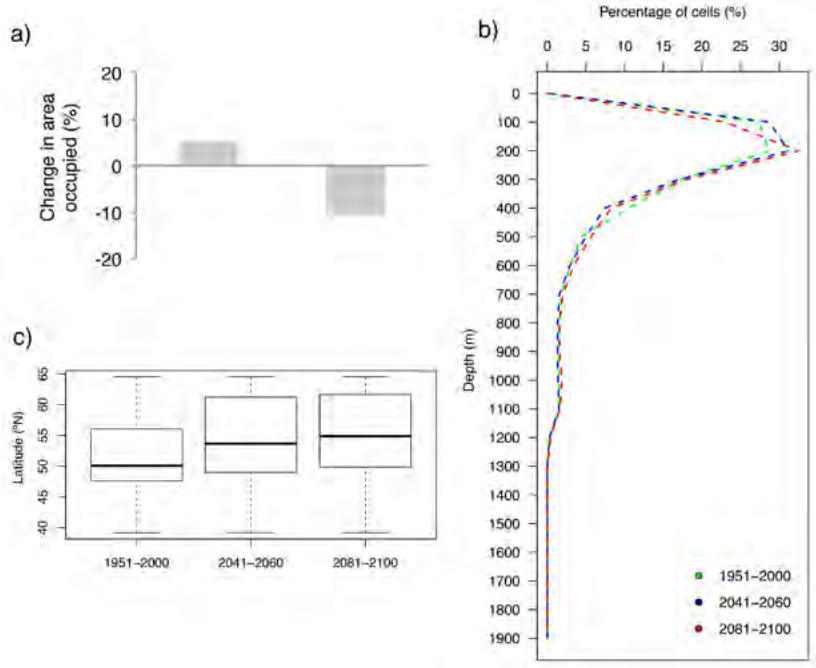
Changes in the predicted habitat suitable for *Paragorgia arborea* in the northwest Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.9b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.22

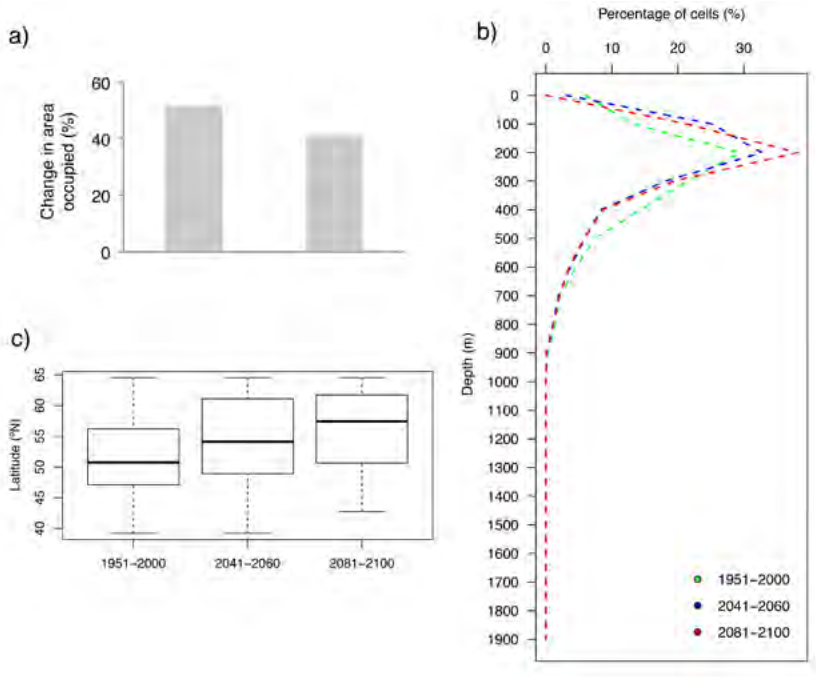
Changes in the predicted habitat suitable for Greenland halibut in the northwest Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.10b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.23

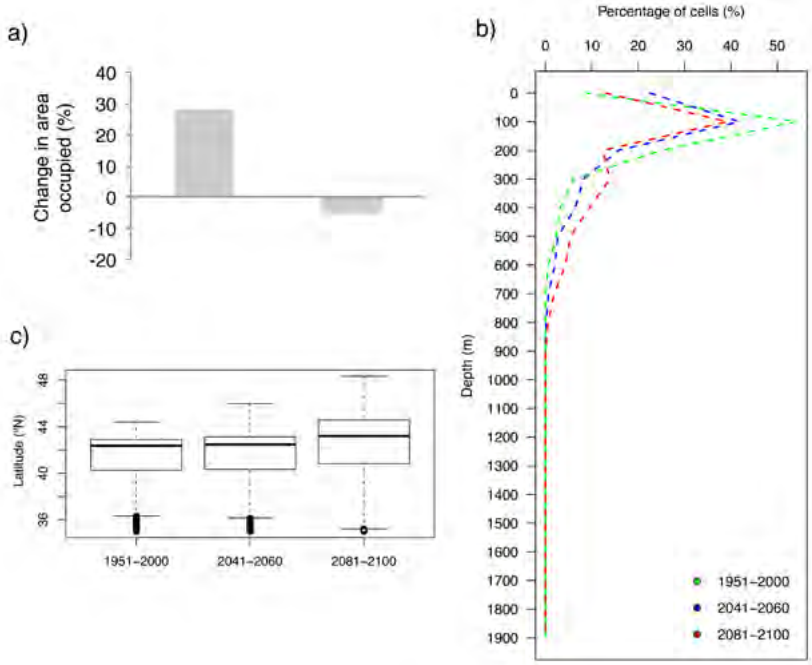
Changes in the predicted habitat suitable for beaked redfish in the northwest Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.11b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

FIGURE A10.3.24

Changes in the predicted habitat suitable for blackbelly rosefish in the northwest Atlantic under future climatic scenarios



Notes: Based on the presence/absence maps shown in Figure A10.3.12b and modelled using Maxent. (a) Percentage of cells with suitable habitat with respect to the area occupied in the present situation. (b) Number of cells considered suitable in each depth for the three climatic scenarios. (c) Box plot of the number of cells considered suitable in each latitude for the three climatic scenarios.

11. Vulnerability and risk of impact analysis

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Calculating vulnerability and risk of impacts

Based on pre-defined heuristic rules, the levels of climate change as well as categories of species' biological and ecological traits are classified into levels of exposure to hazards, sensitivity, adaptive capacity and, consequently, their vulnerability and risk of impacts. These rules describe the empirical and/or theoretical relationship between the traits (temperature tolerance range, habitat specificity, latitudinal range, depth range, fecundity and maximum body length) and the expected levels of sensitivity, adaptive capacity and vulnerability of marine fishes. Table 14 shows the trait values for each studied species, which are obtained from FishBase[9] and SeaLifeBase.[10] Published heuristic rules described in Jones and Cheung (2018) (for climate change) were used. Actions defined by each rule are operated when a threshold value of membership is exceeded, thereby defining the minimum required membership of the premise that an expert would expect for a particular rule to be fired. The algorithm accumulated the degree of membership associated with each level of conclusions from the rules using an algorithm called MYCIN (Cheung, Pitcher and Pauly, 2005):

$$AccMem_{(i+1)} = AccMem_{(i)} + (Membership_{(i+1)})(1 - AccMem_{(i)}) \quad (5)$$

where *AccMem* is the accumulated membership of a particular conclusion (e.g. high vulnerability), and *i* denotes one of the rules that has led to this conclusion.

Vulnerability and risk of impacts were expressed on a scale from 1 to 100, 100 being the most vulnerable. Index values (*Indval*) corresponding to each linguistic vulnerability category (x) were: Low = 1, Medium = 25, High = 75 and Very high = 100. The final index (*FlnInd*) of risk of impacts or vulnerability was calculated from the average of the index values weighted by their accumulated membership (Cheung, Pitcher and Pauly, 2015):

$$FlnInd = \frac{\sum_{x=1}^{4} AccMem_x \cdot Indval_x}{\sum_{x=1}^{4} AccMem_x} \quad (6)$$

For the risk of impact index (for both the 2050 and 2090 periods), *FlnInd* was calculated for each spatial grid cell. The risk of impact of each species was then calculated as the average *FlnInd* across grid cells weighted by the cell's water area.

[9] See: www.fishbase.org
[10] See: www.sealifebase.org

TABLE 14
Trait values of deep-sea commercial species used for vulnerability modelling

Common name	Scientific name	Temperature tolerance range	Habitat specificity	Latitudinal range	Depth range (m)	Fecundity	Maximum length (cm)
Alfonsino	*Beryx decadactylus*	22	0.75	136	890	NA	100
Antarctic toothfish	*Dissostichus mawsoni*	2	NA	20	1 599	796 204	175
Argentine	*Argentina sphyraena*	15	NA	45	650	NA	43
Argentine hake	*Merluccius hubbsi*	18	NA	35	750	NA	95
Argentine shortfin squid	*Illex argentinus*	10	NA	25	799	NA	23
Atlantic cod	*Gadus morhua*	12	NA	54	599	1 610 435	200
Atlantic halibut	*Hippoglossus hippoglossus*	16	NA	37	1 950	2 133 073	267
Baird's slickhead	*Alepocephalus bairdii*	23	NA	36	1 335	1 797	122
Beaked redfish	*Sebastes mentella*	11	NA	31	1 141	11 632	55
Black cardinalfish	*Epigonus telescopus*	10	NA	108	1 125	NA	75
Black scabbardfish	*Aphanopus carbo*	18	NA	36	1 500	NA	134
Blackbelly rosefish	*Helicolenus dactylopterus*	22	0.1	116	1 050	NA	47
Blue ling	*Molva dypterygia*	23	0.5	50	850	NA	155
Deepwater rose shrimp	*Parapenaeus longirostris*	12	NA	75	680	NA	4
European conger	*Conger conger*	26	NA	54	1 170	4 898 979	300
European hake	*Merluccius merluccius*	12	NA	54	1 045	811 172	140
Forkbeard	*Phycis phycis*	4	NA	32	601	NA	65
Giant red shrimp	*Aristaeomorpha foliacea*	2	NA	110	1 239	NA	6
Golden redfish	*Sebastes norvegicus*	8	NA	34	900	81 653	100
Greater argentine	*Argentina silus*	15	NA	30	1 300	NA	85
Greenland halibut	*Reinhardtius hippoglossoides*	12	NA	46	1 999	45 166	80
Haddock	*Melanogrammus aeglefinus*	13	NA	43	440	429 756	100
Ling	*Molva molva*	15	NA	45	900	NA	200
Longtail southern cod	*Patagonotothen ramsayi*	8	NA	19	450	NA	44
Northern shrimp	*Pandalus borealis*	12	NA	50	1 441	NA	14
Orange roughy	*Hoplostethus atlanticus*	15	0.8	121	1 629	59 161	75
Patagonian scallop	*Zygochlamys patagonica*	6	NA	23	150	NA	10
Patagonian toothfish	*Dissostichus eleginoides*	14	0.5	51	3 800	360 610	215
Pelagic red crab	*Pleuroncodes planipes*	9	NA	21	299	NA	5
Portuguese dogfish	*Centroscymnus coelolepis*	17	NA	112	3 550	NA	120
Rabbit fish	*Chimaera monstrosa*	22	NA	38	960	NA	150
Roughhead grenadier	*Macrourus berglax*	13	NA	45	900	NA	110
Roundnose grenadier	*Coryphaenoides rupestris*	17	NA	46	2 420	23 467	110
Sablefish	*Anoplopoma fimbria*	16	0.75	32	2 739	316 228	120
Silver scabbardfish	*Lepidopus caudatus*	16	NA	113	578	NA	210
Slender armourhead	*Pseudopentaceros wheeleri*	NA	0.75	NA	654	NA	53
Snow crab	*Chionoecetes opilio*	10	NA	55	1 180	NA	20
Splendid alfonsino	*Beryx splendens*	11	0.75	88	1 275	426 907	70
Tusk	*Brosme brosme*	11	NA	40	982	2 449 490	120
White hake	*Urophycis tenuis*	11	NA	37	820	3 872 983	133
Wreckfish	*Polyprion americanus*	18	0.5	125	560	5 974 948	210
Yellowtail flounder	*Limanda ferruginea*	7	NA	17	337	NA	64

Vulnerability and risk of impacts of commercially fished deep-sea species

A subset of 41 deep-sea fishes and invertebrates were identified that were targeted by commercial fisheries in the 2000s (Table 15). Catches of these species were reported in the fisheries statistics of FAO.

Deep-sea commercial species that are predicted to be most vulnerable to climate change include Antarctic toothfish, yellowtail flounder and golden redfish. Their high vulnerability is generally conferred by large body size and narrow thermal tolerance, rendering them particularly sensitive to changes in ocean conditions. Their high vulnerabilities and the high exposure to hazards result in high levels of risk of impacts by the mid- and late twenty-first century (Table 15). In contrast, some deep-sea species are predicted to be less vulnerable e.g. argentine shortfin squid, argentine and blackbelly rosefish.

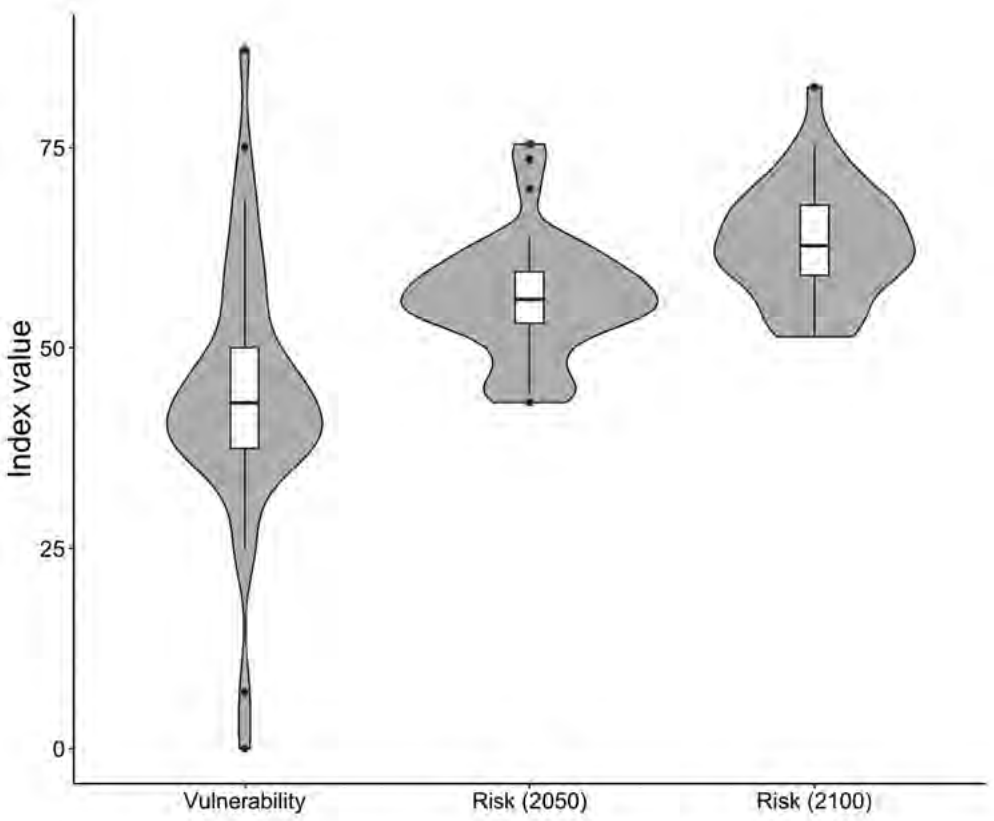
TABLE 15
Vulnerability and risk of impacts for 41 deep-sea commercial fish and invertebrate species.

Common name	Scientific name	Vulnerability	Risk of impacts	
			2041–2060	2081–2100
Antarctic toothfish	*Dissostichus mawsoni*	87	74	75
Yellowtail flounder	*Limanda ferruginea*	75	75	83
Golden redfish	*Sebastes norvegicus*	69	70	75
Forkbeard	*Phycis phycis*	68	64	65
Alfonsino	*Beryx decadactylus*	62	62	71
Patagonian scallop	*Zygochlamys patagonica*	62	55	62
Splendid alfonsino	*Beryx splendens*	58	59	68
Sablefish	*Anoplopoma fimbria*	58	57	61
Orange roughy	*Hoplostethus atlanticus*	54	62	70
White hake	*Urophycis tenuis*	53	63	72
Wreckfish	*Polyprion americanus*	50	58	64
Giant red shrimp	*Aristaeomorpha foliacea*	48	55	59
Blue ling	*Molva dypterygia*	47	58	63
Baird's slickhead	*Alepocephalus bairdii*	47	56	63
Greater argentine	*Argentina silus*	47	60	67
Patagonian toothfish	*Dissostichus eleginoides*	47	51	55
Black scabbardfish	*Aphanopus carbo*	44	63	72
Cusk	*Brosme brosme*	44	59	68
Argentine hake	*Merluccius hubbsi*	44	54	58
Longtail southern cod	*Patagonotothen ramsayi*	44	50	56
Atlantic halibut	*Hippoglossus hippoglossus*	43	55	61
Beaked redfish	*Sebastes mentella*	42	58	67
Roughhead grenadier	*Macrourus berglax*	41	60	68
Haddock	*Melanogrammus aeglefinus*	40	57	66
Pelagic red crab	*Pleuroncodes planipes*	40	49	59
Atlantic cod	*Gadus morhua*	39	56	64
Greenland halibut	*Reinhardtius hippoglossoides*	39	54	61
European hake	*Merluccius merluccius*	39	55	61
Snow crab	*Chionoecetes opilio*	38	44	51
Ling	*Molva molva*	38	60	68
Roundnose grenadier	*Coryphaenoides rupestris*	38	59	68
European conger	*Conger conger*	38	53	61
Rabbit fish	*Chimaera monstrosa*	38	53	59
Silver scabbardfish	*Lepidopus caudatus*	38	54	61
Portuguese dogfish	*Centroscymnus coelolepis*	38	56	65
Black cardinal fish	*Epigonus telescopus*	32	54	60
Deepwater rose shrimp	*Parapenaeus longirostris*	32	47	55
Northern shrimp	*Pandalus borealis*	25	44	53
Argentine shortfin squid	*Illex argentinus*	25	46	52
Argentine	*Argentina sphyraena*	7	43	52
Blackbelly rosefish	*Helicolenus dactylopterus*	1	44	53

Overall, across the 41 deep-sea species, the median vulnerability and risk of impacts (2050 and 2100) are predicted to be 43, 56 and 63, respectively, with 100 being most vulnerable or at risk (Figure 22). The ranges of predicted risk of impacts between species are much smaller relative to the vulnerability because all the species are predicted to exposure to high level of climate hazards. The risk of impacts by 2100 is on average 13 percent higher than the risk by 2050.

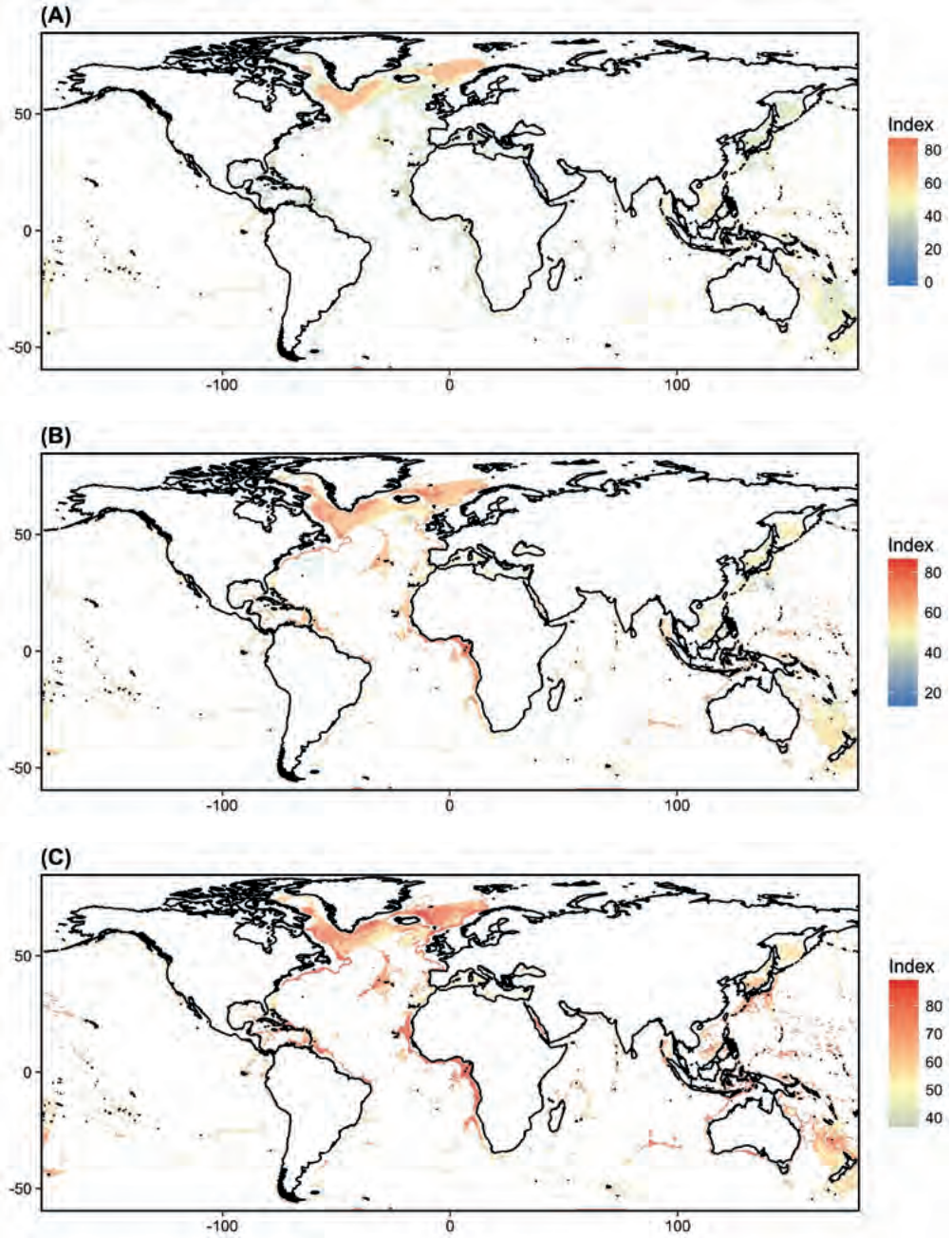
Spatially, high concentrations of highly vulnerable deep-sea commercial species were predicted in the north Atlantic and the Indo-Pacific regions (Figure 23A). The high vulnerability in the Antarctic region is due to the presence of the highly vulnerable Antarctic toothfish. Deep-sea areas with high risk of impacts were more widespread than low-risk areas. In addition to the north Atlantic and Indo-Pacific regions, areas with high risk of impacts were predicted in offshore West Africa and in the south Pacific (Figure 23B and 23C).

FIGURE 22
Indices of vulnerability and risk of impacts by 2050 (2041–2060) and 2100 (2081–2100) of the subset of deep-sea commercial species (N = 41)



Notes: The box plot represents the maximum/minimum limits (upper/lower end of the vertical line), the 75th and 25th percentiles (upper and lower boundaries of the box) and the median value (horizontal line in the box). The shaded area represents the relative frequency distribution of the predicted index values of the species.

FIGURE 23
Predicted indices of vulnerability and risk of impacts of deep-sea commercial species (N = 41 spp.)



Notes: (a) vulnerability index, (b) risk of impacts by 2050 (2041–2060), and (c) risk of impacts by 2090 (2091–2100). The maps only show predicted values in waters that are deeper than 500 m.

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12. Data gaps, observing needs and data transfer

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Current climate-change scenarios are framing decisions for the next decades to the end of the century. These models are based on the thermohaline ocean circulation across basins. However, they still hold large uncertainties when extrapolated to depths greater than 200 m. At the seafloor, Mora *et al*. (2013) have identified significant limitations in accuracy (i.e. the difference between multimodel average projections and current data) and precision (standard deviation among the projections of all CMIP5 models). In the depth range (200–2 500 m) considered in this publication, better parametrization of models is available to reduce these uncertainties, but mismatches still exist between predictions and observations for some critical boundaries (e.g. oxygen below 40 µM at 200–600 m) (Bopp *et al*., 2013; 2017; Oschlies *et al*., 2017). Main causes of these uncertainties are: (i) the limited observational data to fit the models at depth; and (ii) the relatively poor knowledge of ecosystem processes below 400–600 m depth and the biogeochemical functions they drive (e.g. organic matter degradation). Furthermore, the 1° grid of the model does not account for strong gradients over short distances on margins and mesoscale oceanographic features such as those generated by atmospheric (deep eddies and internal waves) (Simmons and Alford, 2012) and geomorphic forcing (seamounts, ridge, canyons) (Turnewitsch *et al*., 2013).

These features play prominent roles in the distribution of VME species through their influence on habitat properties and connectivity. Finally, the models do not account for the non-linear response of ecosystems resulting from the combination of stressors and species interactions (e.g. trophic cascades and invasive species). Recent attempts to assess these vulnerabilities suggest that environmental conditions and ecosystem health status may be locally more sensitive to climate change than is defined by regional model predictions, raising the issue of scale in VME designation. Evidence of rapid changes in fish migration combined with the observation of even faster changes in deoxygenation than predicted (Schmidtko, Stramma and Visbeck, 2017) strongly indicate a need to better document environmental changes at bathyal and mesopelagic depth and develop process studies to accurately monitor vulnerabilities to climate change at the metapopulation and ecosystem (VME) levels.

Times-series observations are still rare and relatively recent on the deep-sea floor. Most observing systems on the ocean floor have barely reached the required 15–20 year minimum duration to start distinguishing trends from climate fluctuations (Glover *et al*., 2010). For example, the Hausgarten observatory in the Arctic has revealed 15-year-long

warming trends at its 2 500 m central site and documented associated benthic community changes, but the contribution of the natural climatic decadal fluctuations to these changes is still not fully assessed (Soltwedel *et al*., 2016). The station M observatory on the abyssal Pacific revealed that POC fluxes are increasing with extremes in the most recent years of a 27-year series, but it is not known whether this is indicating a significant shift or an extreme event (Smith *et al*., 2016). Continuous long-term observations at the seafloor are even scarcer at bathyal depths (e.g. < 2 000 m) than at abyssal depths. Apart from the shallower nodes of deep-sea observatories such as the ONC-node in Barkley canyon (NEPTUNE Canada, 2012), the Cable Continental Margin Array in the northwest Pacific (OOI, 2018), and the hydrothermal Tour Eiffel node of the MOMAR observatory (Sarrazin *et al*., 2014), integrated monitoring of ecosystem processes and oceanographic data are generally limited to short-term, cruise-based operations. Today, most continuous observations on the ocean floor are being acquired at a few benthic observatories (Glover *et al*., 2010). Most of these large infrastructures have not been designed or located for climate change studies, although they may be located in areas with representative VMEs (e.g. on ridge crests with vents, seamounts or canyon systems, or on margins with seeps). Due to operational and funding limitations, continuous times-series and regular sampling on the seafloor are difficult to maintain on a multiannual/multidecadal basis using mooring and regular sampling cruises.

The situation is different for the pelagic realm at bathyal depths, where a larger number of areas close to the continental shelves are benefiting from long-term monitoring surveys that include measurements of deep-sea oceanographic conditions (e.g. CALCOFI off California, MOOSE Western Mediterranean Gulf of Lion and more general GO-SHIP surveys (Talley *et al*., 2016) and ocean-sites moorings.[11] Moreover, hydrological and hydrodynamic conditions at those depths are much better constrained, thanks to the Argo programme, which has almost 4 000 floats deployed globally since 2000 to provide a broad geographical coverage of temperature, salinity and, increasingly, of O_2 (although only 7 percent of floats sense O_2).Optical methods that provide details on the flux of organic particles and their composition (at least for the fresh phytoplankton components), and newly available pH sensors, have been successfully tested for long-term deployments on biogeochemical Argo floats, which exist mainly in the Southern Ocean but should become increasingly available in the near future (Williams *et al*., 2017). To date, pH is only monitored using autonomous systems in the surface ocean. Recurrent observations are complemented by regular ship surveys, which have a much more limited spatial coverage but provide access to a much wider range of parameters (e.g. pH-pCO_2, POC, alkalinity, dissolved inorganic carbon, nutrients and photosynthetic pigments).

Major gaps still exist in available observation data to accurately constrain climate change impacts on relevant scales for deep-sea VMEs. There is a very important lack of systematic observations on and immediately above the seabed at local and regional scales on representative features of typical deep-sea VME habitats (e.g. on seamount chains, ridge crests, canyon systems, and slopes). Moreover, VMEs on the seafloor (coral reefs and sponge gardens) are generally associated with mesoscale or submesoscale hydrodynamic features generated by winds and tides, and enhanced by topographic heterogeneity (canyon, seamounts and ridge crests) (Turnewitsch *et al*., 2013). Similarly, there is also a lack of observation data for deep pelagic areas with permanent or seasonal ice cover, as they remain inaccessible to conventional floats. Beyond changes in the properties of ocean water masses, the dynamics of these features can profoundly influence ecosystems (see Section 2 Climate overview), by favouring the vertical mixing of deep and surface waters. There are very few examples of continuous observations spanning at least a decade that capture the periodicity and

[11] For an inventory of sustained deep-ocean observations, see www.deepoceanobserving.org

intensity of short-term events and characterize their impacts on species and habitats (Company *et al*., 2008). The capacity to monitor these short-term phenomena is crucial in order to anticipate their synergistic or antagonistic effects with long-term climate stressors, and to establish baselines in specific areas of interest for VME designation. Owing to the episodic and patchy nature of these features, changes in their intensity and frequency should be documented by local and regional observations in order to predict potentially rapid effects on deep-sea ecosystems; such events are poorly constrained in current climate scenarios.

Beyond changes in commercial species stocks that are regularly documented, changes in associated vertebrate and invertebrate species abundance are largely lacking in the risk assessment of abrupt ecological changes. Very little is known about diversity changes in microbe to megafauna communities in response to climate stressors (temperature, O_2, pH and POC) in the deep-sea; in the best case, regular surveys of zooplankton have been obtained for the last 50 years on an annual basis using continuous plankton recorders deployed from oceanographic regular transects or ships of opportunity (e.g. ferries) (Reid *et al*., 2003). Moreover, changes in trophic behaviour, migrations, trophic interactions, growth, and rates of organic matter remineralization are also very poorly documented, as they have large seasonal and interannual variability (Smith *et al*., 2008), which could impede the early detection of abrupt changes in ecosystem structure and function. For example, when the invasive species king crab started to colonize new habitats on the Antarctic shelf, as a result of warming, it announced a rapid decline in the benthic communities so far protected from predation.

Moreover, most deep-sea monitoring is generally performed with goals other than ecosystem vulnerability assessment (mostly understanding heat and carbon transfer to depth through water mass transport or seismic risk assessment), and it does not consider the full range of parameters with potential major impacts (e.g. high-frequency records able to capture high temperature, low pH or low O_2 fluctuations combined with quantitative observations of the quantity and quality of resources). The dynamics of the benthic interface are the least-well described, although the seabed and overlying benthic boundary layer are one of the most important compartments for deep-sea VME designation (i.e. where enhanced organic matter remineralization and energy transfer to trophic networks occur, ecosystem engineering species settle and grow, forming nursery and feeding grounds for numerous species of fish and crustaceans).

An integrated oceanographic–ecological approach is essential in order to understand what may be occurring for ecosystems at intermediate bathyal depths, where mesoscale features interact with long-term trends and result in a complex combination of factors generating instabilities. It is necessary to both understand the taxon response mechanisms and predict future ecosystem responses to the changes occurring (Ramirez-Llodra *et al*., 2011). To do this, it is necessary to know not only the exposures to climate change stressors, but also the critical roles taxa play in ecosystems (i.e. key primary or secondary producers, those creating or modifying habitat such as deep-sea corals and sponges, providing substrate or refuge, serving as prey or predators), and how they will respond to multiple climate drivers. Alterations in physiological state, energy acquisition, growth, reproduction, behaviour, and species interactions of these critical taxa will all affect the distribution of species, ecosystem functions and, ultimately, the services they provide. Most of this information is currently lacking for deep ocean species and ecosystems (Ramirez-Llodra *et al*., 2010; Levin and Le Bris, 2015). Some of the newer tools available to develop this knowledge include: (i) *in situ* examination of gene expression under different climate exposures (using variation in space or time); (ii) use of geochemical proxies to assess exposure (e.g. in carbonate) combined with measures of condition, growth or fitness; (iii) *in situ* manipulation of experimental conditions in mesocosm or controlled settings; (iv) transplanting organisms to manipulate exposures combined with marking or labelling to track growth, evaluate

diet, etc.; (v) time-series imaging to document species interactions in association with (i)–(iv) above; and (vi) widespread observatory facilities for benthic ecological studies (e.g. Danovaro *et al*., 2017). Additional tools – acoustics to monitor fish and mammals, environmental deoxyribonucleic acid to monitor the microbial realm (prokaryotes and eukaryotes), and novel animal tags – may also inform the questions discussed above.

Efforts to develop cost-effective, low-energy devices (chemical sensors, cameras, and onboard robotics/data treatment systems) are increasing their capacity to integrate them in "mini-observatories" and "microlabs", building on the expertise of deep-sea physical oceanographers, biogeochemists and ecologists. Innovative integrated approaches have started to shed light on environmental variability at spatial and temporal scales more relevant to ecosystems and fisheries. Original observing strategies involving new technologies are becoming available, such as using long-range under-ice autonomous underwater vehicles and crawlers (Thomsen *et al*., 2017), and miniaturized sensors to equip marine mammals used as oceanographic mobile platforms informing on ecological features (e.g. prey concentration) in conjunction with oceanographic data (temperature, sulfur and more recently oxygen) (up to a maximum of 2 000 m depth for elephant seals in the Southern Ocean) (Bailleul, Vacquie-Garcia and Guinet, 2015). In addition, there is a particularly crucial gap in instrument systems able to document changes in the sediment–water interface conditions, and related changes in biological rates. New devices have been implemented for behavioural monitoring through direct observation (Aguzzi *et al*., 2012; Doya *et al*., 2017) or indirect optical or acoustical measurements (Tamburini *et al*., 2013; Van Haren and Compton, 2013), *in situ* biodiversity assessments, biogeochemical rates, and associated physical and chemical conditions. To date, these instruments have generally been associated with large infrastructure to overcome power-supply limitation and allow regular maintenance. There is a crucial need for mobile arrays of instrumented platforms that could be distributed over a much wider range of seafloor habitats (including those potentially set as VMEs).

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13. Relevant observation and research programme linkages

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The investigation of climate change in the deep ocean is in its infancy and is largely studied from a physical perspective via the Argo, GO-SHIP and Ocean Sites programmes mentioned above. BGC Argo and Deep Argo will expand biogeochemical capabilities and depth of study, respectively, but these programmes generally receive limited biological input. The issues addressed and the questions raised in this technical paper could allow RFMOs to provide information to the large deep-observing programmes about priority geographical areas, depths and features for observation. The number of biological observatories (Glover *et al*., 2010) is growing, as is the number of eyes on the seafloor, advanced through telepresence advocated by the NOAA Office of Ocean Exploration and Research, the Ocean Exploration Trust and the Schmidt Ocean Institute, as well as expanded use of remotely operated (underwater) vehicles, autonomous underwater vehicles, and observatory imaging. Although each programme is managed independently, all have opportunities to direct activities towards specific societal needs. The FAO priorities reported here can and should provide relevant input.

Several new international networks have emerged that focus on observation and research in the high seas and deep water. Within the Global Ocean Observing System there is a new programme, the Deep Ocean Observing Strategy (DOOS)[12] that brings scientists together to promote observations in the deep ocean to address the grand societal issues, including climate change prediction and adaptation, conservation and sustainability. DOOS is eager for input from management organizations, such as RFMOs, about location-specific observational needs and motivations. DOSI is a multisectoral, interdisciplinary network comprised largely of deep-sea practitioners with expertise in biology, law and policy, economics, and technology.[13] DOSI provides guidance on sustainable management and conservation of the deep-sea. A sister network to DOSI is the International Network for Scientific Investigations of Deep-sea Ecosystems (INDEEP), focused on deep-sea science (biogeography, evolution, connectivity and function). These three organizations have banded together to strengthen their climate impact. They have provided a voluntary commitment to Sustainable Development Goal 14 entitled "Science for Deep-Ocean Sustainability", have become part of the Ocean and Climate Initiatives Alliance, with a presence at the Conference of the Parties of the United Nations Framework Convention on Climate Change, and plan input to UN treaty development for Biodiversity Beyond National Jurisdiction as well as the UN Decade of Ocean Science for Sustainable Development.

[12] See: www.deepoceanobserving.org
[13] See: www.dosi-project.org

The findings as well as the observing and research needs identified here can stimulate recommendations to these programmes.

The IPCC is hosting a special report on oceans and the cryosphere, to be completed in 2019. Several of the authors of this technical paper are involved in that effort, and climate impacts on the deep ocean ecosystems will be addressed. Region-specific research programmes have been ramping up in recent years to address climate change issues. Table 16 lists examples from Europe.

TABLE 16
European programmes that address climate change

Acronym	Title (years active)	Home page
ATLAS	*A Trans-AtLantic Assessment and deep-water ecosystem-based Spatial management plan for Europe (H2020 2016–2020)*	http://eu-atlas.org/
AORAC-CSA	*Atlantic Ocean Research Alliance Coordination and Support Action (H2020 2015–2020)*	https://www.atlanticresource.org/aora/
BIOACID	*German programme Biological Impacts of Ocean Acidification (national 2009–present)*	https://www.oceanacidification.de/
Blue-Action	*Arctic Impact on Weather and Climate (H2020 2016–2021)*	http://www.blue-action.eu/
CERES	*Climate change and European aquatic RESources (H2020 2016–2020)*	https://ceresproject.eu/
ClimeFish	*Co-creating a decision support framework to ensure sustainable fish production in Europe under climate change (H2020 2016–2020)*	http://climefish.eu/
EPOCA	*European Project on Ocean Acidification (FP7 2008–2012)*	http://epoca-project.eu/
HERMIONE	*Hotspot Ecosystem Research and Man's Impact on European seas (FP7 2009–2012)*	http://www.eu-hermione.net/
MARmaED	*MARine MAnagement and Ecosystem Dynamics under climate change (Training Network H2020 2015–19*	http://www.marmaed.uio.no/
MedSeA	*Mediterranean Sea Acidification in a Changing Climate (FP7 2011–14)*	http://medsea-project.eu/
PRIMAVERA	*PRocess-based climate sIMulation: AdVances in high resolution modelling and European climate Risk Assessment (H2020 2015–19)*	https://www.primavera-h2020.eu/
SponGES	*Deep-sea Sponge Grounds Ecosystems of the North Atlantic: an integrated approach towards their preservation and sustainable exploitation (H2020 2016–2020)*	http://www.deepseasponges.org/
UKOA	*UK Ocean Acidification Research Programme (national 2010–16)*	http://www.oceanacidification.org.uk/

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14. Implications for management

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Fisheries management and climate change in the high seas

The RFMOs have a key role in managing international fisheries and their impact on affected ecosystems. They have been developed to ensure long-term conservation and optimum utilization of the fishery resources, and thereby to safeguard the marine ecosystems and to address international obligations such as given in UNCLOS and the Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks (1995) (UNFSA). With varying geographical area and biological regime (the nature of the fish stocks, habitat coverage, etc.) each RFMO has its specific tasks to address.

Along with changes in fish migrations and stock distributions induced by climate change, fisheries managers must adapt to maintain their objective of optimum utilization of the fishery resources and safeguarding the marine ecosystems. This will unavoidably require more adaptive decision-making procedures in RFMOs than those mostly in place now. The incentive to be adaptive among the major consolidated states sharing a total allowable catch (TAC) is by nature low when entering a negotiating process. This could be solved partly by introducing other "currencies" or side-payments in the negotiation process, e.g. to introduce other bargaining solutions (Diekert and Nieminen, 2017). Other means of making management more efficient in decision-making could be to aim for majority solutions instead of consensus (Pentz and Klenk, 2017). More direct involvement of stakeholders from the social and economic segments may also contribute to a higher flexibility within the management negotiation process (Pentz and Klenk, 2017).

From the science side, the challenges are to deliver proper and adequate information on the ecosystem changes well in advance of the foreseen changes. Rules for flow of scientific information to managers and aims for science–policy communication are important prerequisites for successful digestion and treatment by managers (Soomai, 2017). In the mutual dialogue between science and management, it is important that clear management objectives be formulated in order for the scientific community to operate and have available information for reference in its analyses and advice to managers. This often happens in a science–management–policy dialogue, where science examines a range of plausible management objectives that thereafter is narrowed to fewer and more relevant scenarios as considered by the managers. This will enable RFMOs to act in time and prepare the fishing industry for the upcoming changes.

An analysis of how RFMOs in general respond to climate change issues claims that it may lead to ignorance on catch limits by focusing on the new threat of climate

change (Axelrod, 2011). In this context, the science community has a responsibility to deliver timely and proper advice that provides the management with an operational perspective to facilitate management effectiveness to adapt to climate changes.

Climate-induced changes in the deep oceans lead to changes in deep-sea environment and ecosystems (Levin and Le Bris, 2015; Sweetman *et al.*, 2017). This will affect pelagic and deep-sea fish stocks, as well as the primary and secondary production processes upon which they depend. Therefore, fisheries management will face challenges as a consequence of shifts in fish stock distribution and changes in migratory behaviour. The shifting of fish distributions will affect the spatial distributions of the fisheries, and this, in turn, results in new challenges for managing the sustainability of the fishery and impacts that fishery may have on components of ecosystems, such as VMEs.

Changes due to climate change, and other factors, are difficult to predict, and often difficult to understand. However, what is certain is that there will be distributional changes in fish stocks, and these will result in changes to the location of the fisheries, and this will lead to new impacts that require mitigation. However, the 2017 ICES advice summary on distributional shifts in fish stocks in the northeast Atlantic, states "ICES cannot predict these changes at present" (ICES, 2017a).

Examples of fish stock distributional changes and selected consequences for management

Northeast Atlantic

ICES (2017b) analysed fish distribution shifts in the northeast Atlantic for 19 fish stocks (commercial species), of which about half could be considered benthic and occurring in deep water, using information from national bottom-trawl surveys and the literature. There was convincing evidence for distributional changes in nine species that were regarded as "big movers" (Table 17). Most of the other species showed some signs of movement, but this was considered as being within the normal fluctuations caused by environmental or fishing patterns. There was no evidence, based on the information available, that Greenland halibut showed distribution changes in the northeast Atlantic. Distributional changes of commercial fish stocks have both ecological and management implications.

TABLE 17
Fish distributional changes in the northeast Atlantic

"Big mover" species	Response
European anchovy	*Northward shift in the North Sea from 1990 onwards*
Anglerfish (blackbellied and white)	*Regional changes in the North Sea*
Blue whiting	*Increase in the North Sea and west of Scotland (United Kingdom)*
Atlantic cod	*Northward shift*
European hake	*Expansion in the North Sea*
Atlantic herring	*Changes seen in North Sea and Baltic*
Atlantic mackerel	*Major changes across northeast Atlantic*
Megrims	*Regional changes in the North Sea, Bay of Biscay and Celtic Sea*
European plaice	*Increase in North Sea and Baltic Sea*

Note: For details, see ICES (2017b, Section 4.1).

Of all the parameters considered, temperature was found to be an important controlling factor for the species considered. For example, this has been well studied for cod that have tended to move northwards when conditions are warmer, owing to increased survival at the northern end of the range and decreased survival at the southern end of the range (Drinkwater, 2005; Planque and Fredou, 1999). Changes consistent with a northward shift driven by global warming occurred to a greater or lesser extent for stocks of eight species (European anchovy, white anglerfish, Atlantic cod, common

sole, megrim, haddock, European hake and European plaice), whereas observed distributional changes for stocks of five species were not consistent with a northward shift due to global warming (white anglerfish, blackbellied anglerfish, Atlantic cod [Porcupine Bank], megrim and haddock) (for details, see Table 4.2.1 of ICES, 2017b). Similar examples can be found in other regions of the world that have sufficient annual distributional information over an extended period to be able to identify changes.

An example of the management consequences of distributional change is provided by mackerel, which for one straddling stock has changed its relative abundance in international and national waters (ICES, 2017a, 2017b). Through agreement among its members, the NEAFC manages the TAC for mackerel in the northeast Atlantic (NEAFC, 2009, 2010). Under the UNFSA, straddling stocks are to be managed jointly, and through consultation a scientifically based TAC is (ideally) agreed upon for the entire stock, and quotas apportioned to the fishing nations. Atlantic mackerel has changed its migratory pattern considerably within the last decade, leading to fisheries in previously unfished national zones. This change in fishery and stock abundance has given rise to new TAC claims from states that experience the stock within their national zones. Due to these TAC claims from "new" fishing nations, and to an overall relocation of the Atlantic mackerel stock within both national and international zones, the contracting parties under the NEAFC have not been able to reach agreement on a mackerel TAC since 2008. The dispute relates to allocation criteria and on the permanence of the shift in stock distribution. This lack of agreement has led each state to set and claim an autonomous quota. The combined quotas have exceeded the biological advice provided by ICES (ICES, 2017b, p. 100). Similar cases with lack of joint management have occurred for some of the other larger pelagic stocks that have undergone migratory changes in the northeast Atlantic along with a changing climate; blue whiting and Norwegian spring-spawning Atlantic herring are examples.

The climate-induced changes in fish stock shifts illustrate a potential future problem for joint management; as fixed TAC allocations do not work in a variable environment. Parties already established within an agreement have little incentive to invite more parties to share the resource as this will inevitably reduce their own share. Therefore, the changing migratory routes and distribution of many fish stocks illustrates the need for more adaptive decision-making procedures among the contracting parties within the high seas and national management bodies to ensure joint management. As climate-change-induced alterations in the deep sea are likely to amplify the shifts in stock distribution, fisheries management will face further similar challenges in the future.

Arctic and Barents Sea

The last decade has been the warmest on record, and has generally resulted in decreased ice coverage, particularly in the summer months. However, there is still great variation, and the North Atlantic Oscillation (NAO), a result of pressure differences between the Icelandic low and Azores high, greatly influences events in the Barents Sea. Variations in the NAO resulted in 2012 being the lowest summer ice coverage ever observed, whereas in 2014 the NAO resulted in the widest ice coverage observed in 20 years. Such changes in marine environmental conditions have resulted in changes to species compositions affecting animal communities from zooplankton to fish (ICES, 2016).

The principal concern here is that new fisheries could rapidly develop in areas not previously subject to fishing, and this could have uncontrolled effects on both fish stocks and the biotic environment. Whereas partial mitigation exists in the Barents Sea for demersal stocks under NEAFC control, through the exploratory bottom-fishing protocol, the area is mostly within an existing bottom-fishing footprint, and rapid expansion could still occur, particularly for pelagic stocks. For demersal stocks under NEAFC control, the exploratory fishing protocol applies to "all commercial bottom fishing activities outside area closures and existing bottom fishing areas, **or**

if there are significant changes to the conduct and technology of bottom fishing activities within existing bottom fishing areas" [bold added] (NEAFC, 2014). Many of the fishable stocks in the Barents Sea are shellfish and under state control, so responsibilities for controlling expansion on these stocks rest with the flag states.

The high seas portion of the Arctic Ocean is currently ice covered and has no commercial fisheries. However, it is not currently under the management of any RFMO (except for a small part that lies within the NEAFC regulatory area), and retreating ice coverage means that new fisheries could develop. This prompted nine nations and the European Union (Member Organization) to conclude negotiations in 2016 on the draft Agreement to Prevent Unregulated High Seas Fisheries in the Central Arctic Ocean. This will prohibit commercial fishing in the high seas of the Artic, known as the "Arctic donut hole" for at least 16 years, and allow for research programmes to develop and establish sustainable fisheries potential, should any exist. The agreement itself still needs to go through a final process of drafting, adoption and ratification before it enters into force.

Southern Ocean

Fisheries in the Southern Ocean target primarily krill, icefish and toothfish. All are under the management of the CCAMLR, which has a remit that focuses on the marine ecosystem of which fisheries is a part. An overview of climate change in the Antarctic is provided by the Scientific Committee on Antarctic Research (SCAR, 2013). Model predictions are uncertain and the confidence for prediction is low. An average prediction, based on current trends, is for a reduction in sea ice of 33 percent by the end of the century. One member's address to the CCAMLR (CCAMLR, 2017a), drew attention to the collapse of the Larsen C ice shelf into the Weddell Sea on 12 July 2017 opening 5 800 km2 of ocean. Similar but smaller collapses occurred in 1992 and 2002. The CCAMLR and its scientific committee (CCAMLR, 2017b) are concerned about possible rapid expansion of the krill fisheries, and have proposed a number of mitigation measures to avoid uncontrolled impacts on the ecosystem. Discussions are currently underway to introduce networks of "priority areas for conservation" along latitudinal gradients to both safeguard the ecosystem and provide area for scientific study.

The CCAMLR, owing to the more immediate threat of impacts from global warming and climate change compared with other regions, formed the Climate Change Intersessional Correspondence Group in 2015, and is holding discussions on the need to develop a specific climate change response work programme. The current five-year plan for the scientific committee already contains many elements relating to climate change.

The CCAMLR already has resolutions and conservation measures that consider climate change (CCAMLR, 2017c). Some examples are:

- Resolution 30/XXVIII (2009). Climate Change. Increased consideration of climate change impacts in the Southern Ocean to better inform CCAMLR management decisions.
- Conservation Measure 91-04(2011). General framework for the establishment of CCAMLR Marine Protected Area. The underlying objectives of this conservation measure include: (i) maintaining the ability to adapt in the face of climate change; and (ii) protection of areas to maintain resilience or the ability to adapt to the effects of climate change.
- Conservation Measure 24-04 (2016). Establishes time-limited special areas for scientific study in newly exposed marine areas following ice-shelf retreat or collapse in Statistical Subareas 48.1, 48.5 and 88.3.
- Conservation Measure 91-05 (2016). Ross Sea region marine protected area. The underlying objectives of this conservation measure include: (i) opportunities for the study of climate change effects in the region; and (ii) understanding ecosystem impacts of climate change separate from those of fishing.

The CCAMLR, partly due to its wider ecosystem approach and partly due to the more immediate impacts of climate change, has adopted a three-pronged approach to climate change: (i) establish mechanisms to increase scientific understanding; (ii) set up representative managed areas; and (iii) ensure that fisheries in new areas develop slowly, consistent with the scientific knowledge needed to manage these fisheries.

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15. Considerations for management of deep-sea fisheries

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This technical paper has covered many aspects of climate change and the deep-seas. Many aspects have very wide implications, and many are outside of the control of those who rely on the provisioning power of the oceans. Major obvious stakeholders include shipping, mineral and mining extraction, cable and pipe laying, fisheries, recreation, and issues relating to the military and national jurisdiction – most of this being covered by UNCLOS and other international agreements. Below is a summary of selected points that relate to the scope of this technical paper, and more directly to the consequences of climate change on deep-sea fisheries and their management by states and RFMOs:

- Focus is on bottom fisheries at 200–2 500 m depth in the high seas.
- Model predictions include physical (atmospheric warming on ocean temperature and oxygen availability, and the effects of ocean acidification) and biological (particulate organic matter flux to the seafloor, VME species, and fish species) climate-induced changes in deep pelagic and benthic zones.
- Climate-induced changes are region-specific in extent and timing. Often more severe towards the poles. Fisheries at all depths will be affected.
- Species will react differently. Changes in distribution are difficult to predict but are expected (and have already been observed).
- Effects on ecosystems could have positive and negative aspects. New fisheries could develop and existing ones disappear. Productivity could go up or down.
- Species affected may or may not be able to colonize new areas. It is difficult to predict whether individual species will show distributional shifts or suffer local extinctions.
- Although climate change predictions tend to be at the 20–50-year time frame, some changes can occur rapidly and need to be considered in fisheries management, which typically works on a 2–5-year time frame.
- Adaptive and dynamic fisheries management, and cooperation across jurisdictional boundaries, are important.

The eight deep-seas RFMOs with the competence to manage bottom fisheries have largely similar processes to carry out their responsibilities to monitor fish stocks and protect VMEs. These RFMOs all have their management responsibilities tied to the high seas, and many have advisory roles in the EEZs of coastal states especially when straddling stocks are considered; all have contracting parties from coastal states; all have access to scientific advice to guide the management process; and all support (thought their contracting parties) the necessary research needs to provide that advice. Given the above bullet points, what measures are currently in place to provide for sustainable fisheries, and how could these be strengthened to help mitigate against the negative effects of climate change? The following points contain quotations, set in italics, from UNCLOS (1982), UNFSA (UN, 1995) and the FAO DSF Guidelines (FAO, 2009), that have served to guide the RFMOs in the formulation of their measures.

Support for RFMOs by states

It is a requirement for States to cooperate with each other in the conservation and management of living resources in the high seas (UNCLOS, Article 117).

States should strengthen existing RFMO/As which have the competence to manage and regulate DSFs and their impacts on VMEs, including through incorporating established principles of relevant international law and related instruments into the mandates of such organizations or arrangements (FAO DSF Guidelines, paragraph 27).

Cooperation among fishing nations, including the sharing of information and adoption of unified management plans, for both long-term sustainable fisheries and the prevention of significant impacts to the environment, is essential. Although it is not an absolute requirement to do this through RFMOs, and bilateral and/or multilateral agreements are important, the establishment and support of RFMOs is codified in UNCLOS and serves to unite many nations under a common umbrella. UNCLOS and the UNFSA also provide RFMOs with the legal backing necessary to carry out their duties in the high seas.

Application of the precautionary approach

States shall apply the precautionary approach widely to conservation, management and exploitation of straddling fish stocks and highly migratory fish stocks in order to protect the living marine resources and preserve the marine environment (UNFSA, Article 6, paragraph 1).

Climate change models suggest that fish stocks and the marine environment will probably undergo changes, although the details of the changes are difficult to predict. These changes could happen rapidly. Thus, climate change generates additional uncertainties, and a more cautious approach should be adopted to ensure long-term sustainability.

New and developing fisheries

A functioning regulatory framework should include an appropriate set of rules and regulations for the management of existing fisheries, as well as for the opening of new areas to exploratory fishing, … Such a framework should also include regulations to protect vulnerable populations, communities and habitats. (FAO DSF Guidelines, paragraph 61).

Precautionary conservation and management measures, including catch and effort controls, are essential during the exploratory phase of a DSF, and should be a major component of the management of an established DSF. They should include measures to manage the impact of the fishery on low productivity species, non-target species and sensitive habitat features. Implementation of a precautionary approach to sustainable exploitation of DSFs should include the following measures:

i. *precautionary effort limits, particularly where reliable assessments of sustainable exploitation rates of target and main by-catch species are not available;*
ii. *precautionary measures, including precautionary spatial catch limits where appropriate, to prevent serial depletion of low-productivity stocks;*
iii. *regular review of appropriate indices of stock status and revision downwards of the limits listed above when significant declines are detected;*
iv. *measures to prevent significant adverse impacts on vulnerable marine ecosystems; and*
v. *comprehensive monitoring of all fishing effort, capture of all species and interactions with VMEs.* (FAO DSF Guidelines, paragraph 65).

New fishing opportunities are predicted to occur as climate change affects the environment. NAFO defines such opportunities as "exploratory bottom-fishing activities", meaning bottom-fishing activities conducted outside the footprint, or within the footprint with significant changes to the conduct or in the technology used in the fishery (NAFO CEM 2018 Article 15, paragraph 2). Such new fisheries are subject to protocols that typically include impact assessments to ensure that the fishery does not develop faster than the knowledge acquired to manage that fishery, and to protect VMEs. Under climate change scenarios, it is suggested that the application of these protocols, both inside and outside of the existing bottom-fishing areas (footprint), be strengthened and subject to increased review prior to allowing the fishery to develop.

Fishing within existing fishing areas

Comprehensive maps showing the spatial extent of existing fisheries should be compiled by RFMO/As. For areas not covered by RFMO/As, each flag State should develop such maps and cooperate with other States concerned and FAO in developing joint maps for relevant areas (FAO DSF Guidelines, paragraph 64).

Most RFMOs have produced a map of existing bottom-fishing areas based on historical fishing patterns over some previous period, which maybe up to 20 years. When this was undertaken, vessel monitoring systems (VMS) were in their infancy, and logbooks provided much of the supporting information. These maps are typically for all bottom gear types combined and cover all fishing intensities from very heavy to very lightly fished. With the advent of VMS and other improved monitoring techniques, it is strongly recommended that these maps of existing bottom-fishing areas be reviewed regularly and cover a more recent historic period, and be disaggregated by fishing gear and previous fishing effort. Although this is increasingly undertaken by scientific bodies to better understand the fishery and make assessments, consideration should also be given to adopting suitable measures to support sustainable fisheries and monitor impacts on the environment.

Improved monitoring of benthic habitats

States and RFMO/As should have an appropriate protocol identified in advance for how fishing vessels in DSFs should respond to encounters in the course of fishing operations with a VME, including defining what constitutes evidence of an encounter. … (FAO DSF Guidelines, paragraph 67 part).

The RFMOs have typically linked thresholds to the response to an encounter with a VME indicator species. The management response is usually to report the encounter to the flag states and the RFMO, and to take some form of action to avoid further encounters. The use of a threshold, although necessary for a management response, limits the amount of information gained on the distribution of VME type species (or VME indicator species) to include only those area that have high concentrations (and would be considered VMEs). Information on subthreshold encounters and no encounters can be recorded by observers and scientists onboard but are not formally reported. Under a climate change scenario, where new VMEs are likely to become established in new areas, it is important to widen the reporting requirements to gain a better indication of overall distributions of VMEs, including where they do not occur and where they are developing. To this end, it is important to encourage the use of camera systems attached to fishing gear, especially trawls that can be used to monitor seafloor habitats. The technology exists, and is being used in some regions by industry.

Scientific research

In determining the allowable catch and establishing other conservation measures for the living resources in the high seas, States shall: (b) take into consideration the effects on species associated with or dependent upon harvested species with a view to

maintaining or restoring populations of such associated or dependent species above levels at which their reproduction may become seriously threatened. (UNCLOS, Article 119 paragraph 1b)

In order to conserve and manage straddling fish stocks and highly migratory fish stocks, coastal States and States fishing on the high seas shall, in giving effect to their duty to cooperate in accordance with the Convention: (k) promote and conduct scientific research and develop appropriate technologies in support of fishery conservation and management (UNFSA, Article 5k).

There is a great need for a better scientific understanding of the processes affecting the oceans under climate change scenarios. Most RFMOs have coordinated scientific programmes to gather information that support better decision-making. This can include the identification of specific study areas. Of interest is the monitoring of the health of existing closures designed to protect VMEs from any SAIs caused by bottom fisheries, and to monitor closely appropriate areas that may form suitable habitats for newly emerging VMEs (or any other vulnerable species or species group).

Conservation of biodiversity

The RFMOs' conventions and agreements provide the boundaries within which the RFMOs operate. For the most part, this is confined to fisheries and impacts from fisheries. The CCAMLR, operating in the Southern Ocean, has a wider remit covering the marine ecosystem in more general terms, of which fish stocks and fisheries are a part. Whereas the management of fisheries does help conserve biodiversity by mitigating against impacts caused by the fisheries, there are also many other threats to biodiversity of which global warming, ocean acidification and ocean deoxygenation are perhaps the most significant. Partnerships must be developed and supported that allow for these wider issues to be regulated in order to protect the health and productivity of the oceans.

Novel methods of management

States and RFMO/As should develop and adopt fishery management plans for specific DSFs, including a set of measures with defined long-term/multi-annual management objectives. Such plans should be tailored on a case-by-case basis to the characteristics of each fishery, making use of relevant management tools … (FAO DSF Guidelines, paragraph 75 part).

Fisheries management typically works by monitoring catch, undertaking an assessment, determining the proportion of the stock harvested, comparing this with references points for sustainable utilization, and finally setting catch (or effort) limits to ensure sustainability. The information exists for this to work well with the majority of fished stocks, and this is made easier when the stock is productive and the catch is relatively high (productive stocks can sustain higher catch rates). Although there is nothing unique about deep-sea fishing, it is often the case that stocks are less productive, resulting in a lower sustainable catch and much less information on which to base assessments. Coupled with this, deep-sea stocks tend to be highly aggregated, and this makes assessment challenging. Many of these stocks are regarded as data-limited, and assessment methods have improved substantially in the last decade. Although it is difficult to move away from the traditional ways in which fisheries are managed, especially in the high seas, scientists and managers should continue to work with industry to explore new techniques in assessment, management and technologies, especially when climate change is likely to affect the abundance and distribution of many fish stocks.

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16. Key conclusions and recommendations

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The deep ocean is increasingly subject to changing environmental conditions as a result of rising carbon dioxide in the earth's atmosphere, with likely effects on deep pelagic and benthic ecosystems. Rising temperatures and declining oxygen levels have already been documented at the 200–2 500 m depths where deep-sea bottom fisheries take place in the high seas and EEZs. Climate projections generated by earth system models project that seafloor warming, acidification, deoxygenation and decline in particulate organic matter flux to the seafloor will exceed natural variability over many areas in the coming 20–50 years.

The largest changes for multiple climate variables are predicted in the north Atlantic and Southern Oceans, where areas close to the polar ice are particularly vulnerable. These changes are anticipated to modify the distributions and fitness of demersal fish and vulnerable marine indicator species such as cold-water corals and sponges that often form critical habitat supporting fish and other species important for the maintenance of ecosystem services and biodiversity. Changes in distributions have already occurred, and modelling suggests many more are predicted, with taxa such as Antarctic toothfish, yellowtail flounder, golden redfish, and a variety of cold-water corals being particularly sensitive. Redistribution of species in response to environmental change may lead some areas to experience increased fish biomass and an influx of new species, while other areas may experience losses. However, redistribution will not happen with taxa that do not have the ability to colonize new suitable areas, leading to local extinctions in both fish and invertebrate populations. There are threshold values (e.g. for temperature, oxygen or pH) that if exceeded, may yield rapid change (over 2–10 years) and may require immediate management attention.

Climate change can be incorporated into RFMO management actions in several ways. Protocols for impact assessment of new fisheries can be implemented more rigorously, and strengthened if needed, to include cumulative impacts from climate change, and a more thorough review process prior to allowing new fisheries to develop. The monitoring and mapping of bottom-fishing areas by gear and species associated with VMEs should be strengthened to provide an early warning of the impacts of climate change. Corresponding maps should be reviewed for projected climate impacts, and areas identified for intensified monitoring of fishing impacts on the environment as part of the RFMO's research responsibilities. The reporting of VME indicator species should be broadened to include all encounters supported by enhanced observer programmes. This should be accompanied by increased monitoring of other bycatch species, such as deepwater sharks and seabirds, with the objective of preventing further significant impacts and monitoring the effects of climate change.

Increases in deep-ocean observing platforms are required in order to ground-truth models, verify projections, and identify areas near critical-point thresholds, particularly around existing and exploratory RFMO fishing areas and VME closures. Additional

scientific research is also needed to better understand the vulnerability and adaptability of key habitat-forming species and fisheries species to changing conditions. State and RFMO collaboration with scientific networks such as DOOS, DOSI and INDEEP can guide the development of new observatories and platforms, and mobilize scientific information quickly. Scientists and managers should continue to work with industry to explore new techniques for data assessment and sustainable management. Development of new climate-relevant sensors (and application of existing instruments) for use on fishing vessels and gear (as platforms) may provide real-time information needed for adaptive management. Ultimately, sustainable management will require cooperation across jurisdictional boundaries (EEZs and high seas), sectors (science, industry and regulators), and disciplines, and a forward-looking commitment to sustaining deep-sea ecosystem services.

Appendix 1

Workshop summary

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Climate Change Impacts on Deep-Sea Habitats, Fish and Fisheries, 26–27 August 2017, Woods Hole Oceanographic Institution, Woods Hole, United States of America

A group of scientific experts and RFMO representatives with expertise in the fields of climate change and deep-sea environmental science and modelling, marine benthic ecology, fish biology, fisheries management and biodiversity conservation met at the Woods Hole Oceanographic Institution to discuss climate change impacts on deep-sea habitats, fish and fisheries. The meeting was a collaborative effort between the FAO ABNJ Deep Seas and Biodiversity project and the Deep Ocean Stewardship Initiative (DOSI) Climate Change and Fisheries Working groups. There were 19 participants present from 12 countries and territories.

The overarching objective of the project is the analysis of potential impacts of climate change on deep-sea ecosystems and the implications for the management of deep-sea fisheries. Key goals were to:

- Establish spatio-temporal scenarios for major climate change stressors on the deep-sea floor and its biodiversity.
- Examine the impacts on the functioning of deep ocean ecosystems.
- Assess how climate impacts might affect deep-sea fish and fisheries.
- Identify regions and fisheries that might be most vulnerable.
- Identify which vulnerable marine ecosystem (VME) indicator species are most vulnerable (and locations, depths) and anticipate spatial planning to ensure efficient protection.
- Determine what essential ocean variables (EOVs) are important to monitor those changes in order to assess the risks to deep-sea species and communities due to climate change.

The workshop began on Day 1 with a brief introduction to the project objectives, deliverables and approaches by L. Levin. This was followed by participant introductions with a description of expertise, and a discussion of FAO needs and goals relevant to the project by A. Thompson. M. Gianni then gave a report on the UN General Assembly Resolutions and international guidelines relevant to deep-sea fisheries, VMEs, and climate change. The workshop discussions then moved to the projection of climate change stressors at depths ranging from 200 m to 2 000 m (including warming, ocean acidification, ocean deoxygenation, and POC flux). C.L. Wei compiled a series of future climate projections in the form of kmz files, including average, standard deviation, hazard exposure to thetao, O_2, pH, and POC flux, and presented examples

including regional and habitat assessments. There was group discussion of projection scale and methods for extrapolating POC flux. W. Cheung presented a framework for assessing vulnerability to climate change based on IPCC SREX and AR5 approaches that combine hazard and exposure to evaluate risk of climate impacts.

He presented a fuzzy logic approach to evaluating species-level and community vulnerability, and the group discussed issues and challenges. N. Le Bris presented on how climate-change disturbances propagate rapidly to the deep-sea via seasonal and short-term oceanographic features on regional- and meso-scales, including upwelling and downwelling, deep convection, eddies, and dense shelf-water cascading. The need to consider how such processes, driven by the wind and sea-ice regime, will change the mixed layer depth climatology and influence DOM and POM export fluxes, both in quantity and quality, was discussed.

Turning to benthic habitats, L. Levin, with input from A. Colaco and M. Silva, gave an overview of VME criteria, indicators and functions, as well as examples of warming, acidification and deoxygenation reaching the deep ocean. Biodiversity tipping points, modes of climate influence, and vulnerabilities of corals and sponges were discussed. L. Watling presented the interaction of fish and benthic habitats, particularly VMEs. Following a group lunch on site, T. Morato presented on species distribution and habitat suitability modelling, the environmental variables that are most closely associated with deep-sea species distributions, and the challenges arising. W. Cheung then focused on the application of fuzzy logic modelling to assess vulnerability via sensitivity and adaptive capacity assessment, and then the combination of vulnerability with exposure to hazard metrics to arrive at risk of impact. The group discussed how best to apply this approach (to whom and where).

The final portions of Day 1 were spent outlining the elements of the report presented above and engaging authors in specific components. There was agreement that the report should focus on what is known now, provide examples of modelling approaches, and provide a platform for future work on the subject. Leads were selected to coordinate writing of each section. At the end of the day, some time was spent addressing the question: Are existing RFMO measures appropriate under climate change scenarios? The discussion including issues related to VME guidance, feedback management, marine protected areas, timescales, and non-VME organisms and systems.

The first half of Day 2 was spent in a plenary session of the DOSI, which reviewed past activities of DOSI including the progress of 11 working groups. The DOSI–FAO project was introduced, and participants met in an expanded Climate Change working group in the afternoon, engaging working-group members and young scientists that attended the DOSI meeting. There was further discussion of the report outline, and addition of new expertise not present the previous day, to yield an expanded co-author list. The discussions also led to several other working-group projects relevant to this report, including a proposed technical paper on mechanisms underlying climate change in the deep-sea, to be led by N. Le Bris, and expansion of a Zotero-based deep-ocean climate change bibliography, which will be open- access. These were reported on in a final DOSI plenary at the end of the day.

DOSI–FAO Climate Change and Fisheries Meeting

Location: **WHOI Clark Lab No. 507**
Date: **Saturday 26 August 2017**

Agenda

09:00	Introduction: brief backgrounds & key issues of concern from each participant
09:30	FAO Goals, VME rationale/target Fisheries (Tony Thompson)
09:50	VME Report 2016 (MCI) & habitat suitability modelling (Matt Gianni)
10:10	Deep ocean climate change projections: I: (Chih–Lin Wei)
10:40	Coffee break
11:00	Deep ocean climate change projections: II: (William Cheung)
11:30	Climate-relevant oceanographic features in the deep-sea (Nadine Le Bris)
12:00	VMEs: influence of climate change and benthic–pelagic linkages (Lisa Levin / Ana Colaço)
12:15	Fish use of VME habitats and benthic–pelagic coupling (Les Watling)
12:30	Lunch
13:30	Habitat suitability models / species distribution model (Telmo Morato)
14:00	Vulnerability modelling – needed input (William Cheung)
14:30	Additional FAO participant contributions
15:00	Group Discussion I: Are existing deep-sea fisheries measures appropriate under climate change scenarios? Do closures cover areas and species vulnerable to climate change? How should RFMOs factor in climate change impacts when expanding fishing footprint?
15:30	Coffee break
16:00	Group Discussion II: Species-specific vulnerability to warming, acidification, deoxygenation or changes in POC flux
16:30	Project road-map development, Day 2 planning

DOSI DEEP-OCEAN STEWARDSHIP INITIATIVE
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This publication presents the outcome of a meeting between the FAO/UNEP ABNJ Deep-seas and Biodiversity project and the Deep Ocean Stewardship Initiative. It focuses on the impacts of climatic changes on demersal fisheries, and the interactions of these fisheries with other species and vulnerable marine ecosystems. Regional fisheries management organizations rely on scientific information to develop advice to managers. In recent decades, climate change has been a focus largely as a unidirectional forcing over decadal timescales. However, changes can occur abruptly when critical thresholds are crossed. Moreover, distribution changes are expected as populations shift from existing to new areas. Hence, there is a need for new monitoring programmes to help scientists understand how these changes affect productivity and biodiversity.

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