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Vulnerability of exploited deep-sea demersal species to ocean warming, deoxygenation, and acidification

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Abstract Vulnerability of marine species to climate change (including ocean acidification, deoxygenation, and associated changes in food supply) depends on species' ecological and biological characteristics. Most existing assessments focus on coastal species but systematic analysis of climate vulnerability for the deep sea is lacking. Here, we combine a fuzzy logic expert system with species biogeographical data to assess the risks of climate impacts to the population viability of 32 species of exploited demersal deep-sea species across the global ocean. Climatic hazards are projected to emerge from historical variabilities in all the recorded habitats of the studied species by the mid-twenty-first century. Species that are both at very high risk of climate impacts and highly vulnerable to fishing include Antarctic toothfish (*Dissostichus mawsoni*), rose fish (*Sebastes norvegicus*), roughhead grenadier (*Macrourus berglax*), Baird's slickhead (*Alepocephalus bairdii*), cusk (*Brosme brosme*), and Portuguese dogfish (*Centroscymnus coelepis*). Most exploited deep-sea fishes are likely to be at higher risk of local, or even global, extinction than previously assessed because of their high vulnerability to both climate change and fishing. Spatially, a high concentration of deep-sea species that are climate vulnerable is predicted in the northern Atlantic Ocean and the Indo-Pacific region. Aligning carbon mitigation with improved fisheries management offers opportunities for overall risk reduction in the coming decades. Regional fisheries management organizations (RFMOs) have an obligation to incorporate climate change in their deliberations. In addition, deep-sea areas that are not currently managed by RFMOs should be included in existing or new international governance institutions or arrangements.

Keywords Deep sea · Vulnerability · Climate change · Fisheries · Multi-stressors · Adaptation

Introduction

The ocean covers 70% or 360 million km^2 of the earth, and over 90% of this has deep seafloor at

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Data depository Data and source code are available: https://doi.org/10.5061/dryad.m37pvmd4n and documented in Appendix Tables 1 and 2.

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depths > 200 m. Once considered homogeneous and inhospitable, we now recognize the deep ocean hosts a diverse array of habitats and ecosystems, including sedimented slopes, abyssal plains, canyons, seamounts, biogenic (coral and sponge) reefs, mid ocean ridges, hydrothermal vents, and methane seeps and more (Ramirez-Llodra et al. 2010; Levin and Sibuet 2012). These ecosystems provide critical habitat and food to diverse fish, and some, such as continental slopes, seamounts, and canyons, host active deep-water, demersal fisheries to depths of 2500 m or more (Norse et al. 2012).

Conditions at the sea floor were once thought to be constant, with prevalence of low temperatures, darkness, and limited food; however, increased human access and the advent of deep-ocean observing instruments and programs has revealed that there are strong, often rapid connections between surface features and processes such as water mass properties, stratification, mesoscale eddies, and primary production that affect the seafloor (Danovaro et al. 2017; Louzao et al. 2017). Similarly, CO_2-induced warming, ocean deoxygenation, and ocean acidification are now experienced at the seafloor, or are projected to occur within this century (Levin and Le Bris 2015; Sweetman et al. 2017; Kwiatkowski et al. 2020).

The deep ocean is increasingly vulnerable to a range of human resource extraction activities, as well as contamination and debris (Ramirez-Llodra et al. 2011). In addition to increasingly deeper fishing (Watson and Morato 2013), energy (oil and gas) and minerals are being targeted at great depths (Mengerink et al. 2014). The confluence of climate change with physical or demographic disturbance caused by humans creates a need for ecosystem-based management in the deep ocean that includes humans, their direct impacts, and climate change (Levin et al. 2019).

Among deep-sea organisms, fishes may be the group best known taxonomically, though for many species, key life-history traits are undocumented. Deep-sea fishes are recognized as being mostly long-lived and slow to mature, with very low reproductive rates (Norse et al. 2012). This makes them vulnerable to the population effects of extraction, as well to disruption of habitat and changes in their physico-chemical environment (Cheung et al. 2005, 2007). Fish populations may be affected by fisheries even below fishing depths via carry over demographic effects (Bailey et al. 2009).

Here, we project the hazards of climate change that are threatening exploited deep-sea fishes and use this in combination with their life-history traits to assess their vulnerability to these climatic hazards and fishing. We predicted that climate change exposures combined with slow growth and maturation would lead to significant risk for some demersal species. Specifically, we first combine global biogeographical and fisheries datasets and Earth system model projections to determine the level of exposure of deep-sea fishes and invertebrates to climate hazards, in particular, ocean warming, deoxygenation, acidification, and decrease in export production. Based on life-history theory (Petrik 2019), we use a fuzzy logic algorithm to predict species' sensitivity and adaptive capacity to both climatic and fishing hazards. We then assess the conservation risk of these deep-sea species in the next few decades. Here, conservation risk is defined as the risk of extinction expressed in terms of the likelihood of being listed under the International Union for the Conservation of Nature (IUCN) Red List of Endangered Species (Cheung et al. 2018). We then discuss the scope for risk reduction through improved fisheries management and climate mitigation.

Materials and methods

Exploited demersal deep-sea species and their biological characteristics

We identified a subset of 32 deep-sea fishes and invertebrates living at or near the seafloor that were targeted by commercial fisheries in the 2000s (Table 1). These species, which occur both within and beyond national jurisdiction, were included because their catches were reported in the fisheries statistics of the United Nations' Food and Agriculture Organization. Thus, our list does not include species that were caught as by-catch but were not reported in the fisheries statistics. Each species considered has their reported main distribution extend beyond 200-m water depth. We collated biogeographic descriptions and estimates of their life-history characteristics from FishBase (for fishes, www.fishbase.org) and Sealifebase (for invertebrates, www.sealifebase.org). Temperature tolerance ranges were based on estimates given in Cheung et al. (2013).

Geo-referenced occurrence records were obtained from the Global Biodiversity Information

Table 1 Trait values of deep-sea commercial species used for climate vulnerability modeling. Habitat specificity scales between 0 and 1 indicating the diversity of the species' associated habitats based on information from FishBase and SeaLifeBase (see http://www.seaaroundus.org/catch-reconstruction-and-allocation-methods/#_Toc421534362 for details)

Common name	Scientific name	Maximum length (cm)	Temperature tolerance range (°C)	Latitudinal range (degree)	Depth range (m)	Fecundity (average number of eggs in a female)	Habitat specificity (0 to 1)
Fishes							
Alfonsino	*Beryx decadactylus*	100	22	136	890	NA	0.75
Antarctic toothfish	*Dissostichus mawsoni*	175	2	20	1599	796,204	0.10
Argentine	*Argentina sphyraena*	43	15	45	650	NA	0.25
Atlantic halibut	*Hippoglossus hippoglossus*	267	16	37	1950	2,133,073	0.10
Baird's slickhead	*Alepocephalus bairdii*	122	23	36	1335	1797	0.25
Beaked redfish	*Sebastes mentella*	55	11	31	1141	11,632	0.10
Black cardinalfish	*Epigonus telescopus*	75	10	108	1125	NA	0.25
Black scabbard-fish	*Aphanopus carbo*	134	18	36	1500	165	0.10
Blackbelly rosefish	*Helicolenus dactylopterus*	47	22	116	1050	116,649	0.10
Blue ling	*Molva dypterygia*	155	23	50	850	NA	0.25
European conger	*Conger conger*	300	26	54	1 170	4,898,979	0.25
Golden redfish	*Sebastes norvegicus*	100	8	34	900	81,653	0.10
Greater argentine	*Argentina silus*	85	15	30	1300	NA	0.10
Greenland halibut	*Reinhardtius hippoglossoides*	80	12	46	1999	45,166	0.10
Ling	*Molva molva*	200	15	45	900	34,641,016	0.25
Longtail southern cod	*Patagonotothen ramsayi*	44	8	19	450	NA	0.10
Orange roughy	*Hoplostethus atlanticus*	75	15	121	1629	59,161	0.80
Patagonian toothfish	*Dissostichus eleginoides*	215	14	51	3800	360,610	0.50
Portuguese dogfish	*Centroscymnus coelolepis*	120	17	112	3550	15	0.10
Rabbit fish	*Chimaera monstrosa*	150	22	38	960	NA	0.10
Roughhead grenadier	*Macrourus berglax*	110	13	45	900	25,510	0.10
Roundnose grenadier	*Coryphaenoides rupestris*	110	17	46	2420	23,467	0.10
Sablefish	*Anoplopoma fimbria*	120	16	32	2739	316,228	0.25
Silver scabbardfish	*Lepidopus caudatus*	210	16	113	578	NA	0.10

Table 1 (continued)

Common name	Scientific name	Maximum length (cm)	Temperature tolerance range (°C)	Latitudinal range (degree)	Depth range (m)	Fecundity (average number of eggs in a female)	Habitat specificity (0 to 1)
Slender armourhead	*Pseudopentaceros wheeleri*	53	8	30	654	NA	0.75
Splendid alfonsino	*Beryx splendens*	70	11	88	1275	426,907	0.75
Tusk	*Brosme brosme*	120	11	40	982	2,449,490	0.75
White hake	*Urophycis tenuis*	133	11	37	820	3,872,983	0.25
Invertebrates							
Deep-water rose shrimp	*Parapenaeus longirostris*	4	12	75	680	63,250	0.25
Giant red shrimp	*Aristaeomorpha foliacea*	6	2	110	1239	NA	0.10
Northern shrimp	*Pandalus borealis*	14	12	50	1441	1550	0.10
Snow crab	*Chionoecetes opilio*	20	10	55	1180	NA	0.10

Facility (GBIF, www.gbif.org) and the Ocean Biodiversity Information System (OBIS, www.obis.org). A total of 495,322 geospatial occurrence records of the 32 deep-sea species was obtained. The records were then gridded on a 0.5 degree latitude × 0.5 degree longitude resolution grid (Fig. 1). Since the focus is on deep-sea habitats, we only included pixels with a bathymetric depth of more than 200 m.

Exposure to climate hazards

We overlaid the gridded occurrences of these deep-sea species (Fig. 1) on projections of key ocean variables in the deep sea (> 200-m depth) that are important for exploited deep-sea species (export particulate organic matter or POC, oxygen concentration, pH, and temperature) from three global Earth system models that participated in the Coupled Models Intercomparison Project Phase 5 (CMIP5) (see online data). We used

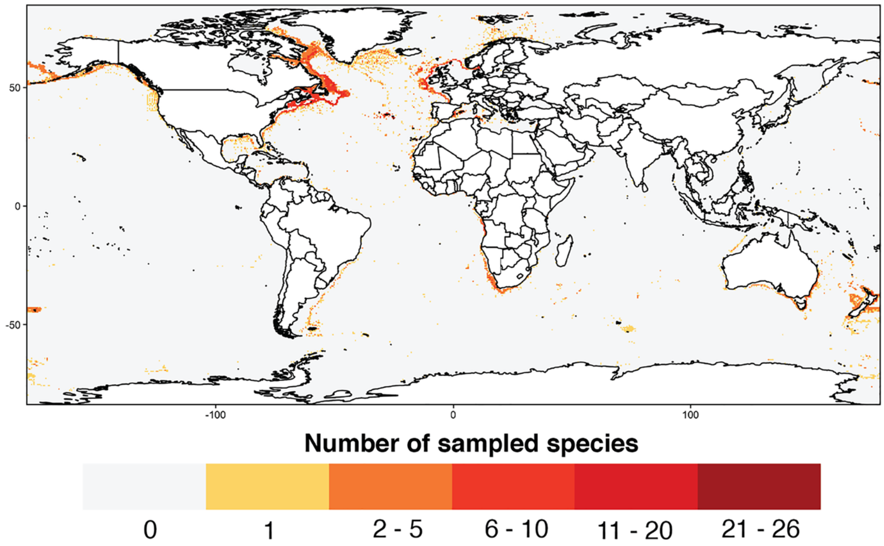

Fig. 1 Number of sampled deep-sea species included in this study in each 0.5 degree latitude × 0.5 degree longitude pixel. Only pixels that have bathymetry > 200 m were included in the sample tally

three-dimensional, fully coupled earth system models including the Geophysical Fluid Dynamics Laboratory's ESM 2G (Dunne et al. 2012), the Institut Pierre Simon Laplace's CM6-MR (Dufresne et al. 2013), and the Max Planck Institute's ESM-MR (Giorgetta et al. 2013). All models are part of CMIP5 and were downloaded from Earth System Grid Federation Peer-to-Peer enterprise system. These models were selected because they were used in the protocol for Fisheries and Marine Ecosystems Impact Model Intercomparison Project (FISHMIP) (Tittensor et al. 2018) and previous studies assessing climate change impacts on fish stocks and fisheries (Cheung et al. 2016b). The same models were also used in studies that investigated other dimensions of climate risks on deep sea biodiversity (Levin et al. 2020; Morato et al. 2020). Thus, the utilization of these Earth system model outputs in this study would facilitate comparison and harmonization of other climate risk and impact assessments for marine species and fisheries.

Within each model output, we extracted the downward flux of particle organic carbon at 100-m depth (*epc100*), seawater potential temperature (*thetao*), dissolved oxygen concentration (*o2*), and pH value (*ph*) for the historical time period from 1951 to 2000 and for representative concentration pathways (RCP8.5 and RCP2.6) until 2100. The monthly data (*epc100* and *thetao*) were averaged by year before any further calculation. We retained the bottom-most grid from each layer of *thetao*, *o2*, and *ph* to construct seafloor environmental conditions. The *epc100* was converted to export POC flux at the seafloor (*epc*) using the Martin curve (Martin et al. 1987) following the equation:

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

The export depth was set to 100 m and water depth was generated using the ETOPO1 Global Relief Model (Amante and Eakins 2009). We then re-projected these bottom grids to 0.5 by 0.5-degree grids based on bilinear interpolation and calculated the multi-model average of each interpolated grid. We calculated the average and standard deviation of *epc*, *o2*, *thetao*, and *ph* by year for 1951 to 2000, 2041 to 2060, and 2081 to 2100.

We quantified climate hazards by subtracting the historical average (1951–2000) from the future average (2041–2060 or 2081–2100). Exposure to climate change hazard (*ExV*) 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. Specifically, *ExV* for each variable (*V*) was calculated from:

$$ExV_i = \frac{\left|\overline{V}_{future,i} - \overline{V}_{historical,i}\right|}{\partial V_{historical,i}} \quad (2)$$

We expressed the exposure of all the 32 exploited species to each climatic hazard as the sum of the number of 0.5 degree × 0.5 degree spatial pixels in which the occurrences of the species overlap with particular levels of climatic hazards.

We compared the frequency distribution of species richness-pixel by hazard levels between sea bottom temperature, oxygen concentration, pH, and export POC flux. Richness-pixel refers to the sum of the number of spatial pixels across all species at specific hazard levels. Thus, a higher value of richness-pixel means that there are more species occupying larger areas of water at specific hazard levels.

Vulnerability and risk to climate hazards

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 based on pre-defined heuristic rules, implemented using a fuzzy logic expert system approach (the algorithm is described briefly here; see Jones and Cheung 2018 for details).

For each species, we categorized the level of exposure to each climate hazard (ExV, see Eq. 2) into four fuzzy sets representing low, medium, high, and very high categories. Fuzzy sets are frequently defined by subjective criteria, and although intrinsic vulnerability values for each species would vary depending on the definition of fuzzy sets, the overall vulnerability value or linguistic category of risk is relative to that calculated for other species and scenarios of climate change, irrespective of changes in the threshold values for the delineation of fuzzy sets (Jones and Cheung 2018). Specifically, exposure to climate hazards is low when changes in the ocean drivers are within historical variability, i.e., ExV < 1. Intermediate exposure values of 0.5 < ExV < 2 and 1 < ExV < 3 are considered moderate and high, respectively, while ExV > 2 is also considered very high. Thus, a spatial grid within a species' range can be categorized as two different levels of exposure to climate hazards at the same time, with different levels of membership in each category. The membership is defined by the fuzzy membership functions. We assumed trapezoid functions for the lower and upper categories (low and very high) and triangular functions for the intermediate categories (moderate and high). The fuzziness of the categories (as indicated by the degree of overlap between the fuzzy sets) represents our uncertainty in deciding the exposure level. Using projected ocean variables from the average of the Earth system models, the exposure categories and their membership were calculated for each spatial grid within each species' distribution range.

For temperature-related effects, sensitivity was based on species' temperature tolerance ranges and maximum body size. Temperature tolerance data were obtained from published calculations of each species' temperature preference profile (the relative suitability of particular temperatures). Fuzzy sets for temperature tolerance range (small, medium, large, very large) were defined based on the minimum, 10th percentile, 25th percentile, median, 75th percentile, 90th percentile, and maximum values across the set of species studied, respectively. These temperature tolerance range categories then correspond to very high, high, moderate, and low sensitivity. As species with large body sizes are suggested to be metabolically more sensitive to warming and ocean deoxygenation, species were also categorized into small, medium, large, and very large body size (thus low, medium, high, and very high sensitivity, respectively).

We ranked the order of sensitivity of the main groups of exploited marine species (negative impacts on growth, calcification, survivorship, or reproduction for similar level increase in acidity). For crustaceans, we assumed a moderate sensitivity (membership = 0.25, 0.50, and 0.75 from low, moderate, and very high sensitivity, respectively), and for fishes, we assumed a low to moderate sensitivity (membership = 0.75 and 0.25, respectively).

A species' adaptive capacity to climate change is low when habitat specificity is high because of the possible restriction of a species to respond to climate change–induced increase in sea temperature by range shift. All in all, small latitudinal or depth range, low fecundity, or very high habitat specificity corresponds to low adaptive capacity, and vice versa.

We concluded the level of vulnerability based on the sensitivity and adaptive capacity categories determined from the input variables and fuzzy membership functions. The conclusion was determined based on a set of IF–THEN rules (Table 2). These rules described 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. We used published heuristic rules described in Cheung et al. (2018). The level of vulnerability was expressed as four linguistic categories: (i) low; (ii) moderate; (iii) high; (iv) very high. As the conditional categories are joined by *AND*, the conclusion degree of membership is the minimum of the degrees of membership of the conditional categories.

The algorithm calculated the final degree of membership associated with each level of conclusions based on all the available input variables. Actions defined by each rule are operated when a threshold value of membership is exceeded (threshold is set at 0.2, with minimum and maximum membership values being 0 and 1, respectively), thereby defining the minimum required membership under the premise that an expert would expect for a particular rule to be activated.

The algorithm accumulated the degree of membership associated with each level of conclusions from the rules using an algorithm called MYCIN (Cheung et al. 2005), where:

$$\mathrm{AccMem}_{(i+1)} = \mathrm{AccMem}_{(i)} + \mathrm{Membership}_{(i+1)} \times (1 - \mathrm{AccMem}_{(i)}) \tag{3}$$

Table 2 Matrix of rules that determine the level of vulnerability based on species' sensitivity and adaptive capacity to climate change

	Sensitivity			
Adaptive capacity	Low	Moderate	High	Very high
High	Low	Low	Moderate	High
Moderate	Low	Moderate	High	High
Low	Moderate	High	High	Very high
Very low	High	High	Very high	Very high

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. The algorithm explicitly carried all the uncertainties from the inputs to the final 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. These values represent the centroids of the fuzzy membership functions applied to categorize the vulnerability levels. The final index of risk of impacts or vulnerability was calculated from the average index values weighted by their accumulated membership (Cheung et al. 2016b).

The risk of impact index (for both the 2050 and 2090 periods) was calculated for each spatial grid cell. The risk of impact of each species was then calculated as the average risk index across grid cell weighted by the cell's water area. The source code for the implementation of this algorithm in *R* is available from the online repository.

Comparison between vulnerability to climatic hazards and overfishing

We computed vulnerability to fishing for the 32 exploited species based on the algorithm and information available from Cheung et al. (2005). We compared our estimated climatic risk with their vulnerabilities to fishing. The study examined the relationship between climate risk and fishing vulnerability in the methods. Therefore, we plotted the climate risk index projected by 2041–2060 under RCP8.5 and fishing vulnerability index. We identified species at high risk to either or both climate and fishing hazards (indices > 75). These species are expected to have the highest conservation risk. Identifying these species can help inform the design of management and conservation measures.

Results

Globally, ocean conditions in the bathyal depths (> 200 m) will likely expose exploited species to climatic hazards that are significantly (> 2 times the standard deviation) above the historical (1951–2000) variabilities (detrended) by the end of the twenty-first century under RCP2.6 and RCP8.5 (Fig. 2). Particularly, under both the RCP8.5 and RCP2.6 scenarios, large areas of the world's seafloor will simultaneously be exposed to acidification and warming hazards, which are up to 20 times historical values (or variation) by 2081–2100 (Fig. 2). Regionally, the tropical deep-sea floor across the Pacific, Atlantic, and Indian oceans is projected to be exposed to large changes in the four climatic hazard variables (temperature, pH, O_2, and export POC flux). In the North Atlantic, although regional deep-sea cooling is projected, POC flux on average is projected to decline by 1.3 times (by 2041–2060) and 2.3 times (by 2081–2100) of its historical variability under RCP8.5. The average decline will be less in the Indian and the Pacific Oceans; however, the decline still amounts to 1.02 and 0.49 times (by 2041–2060) and 1.91 and 1.04 times (by 2081–2100) its historical variability, respectively. The extent of declining POC flux decreases substantially under RCP2.6. Large areas of the world's seafloor will likely experience deoxygenation hazard up to five times (by 2041–2060) and ten times (by 2081–2100) their historical variability under RCP8.5 (Fig. 2). The deoxygenation of regional hotspots in the Canadian high arctic, equatorial Atlantic and Pacific and Southern Ocean may exceed 10 times (by 2041–2060) and 20 times (by 2081–2100) of historical variability under RCP8.5. On average, the Atlantic bathyal habitats (200–2500 m) will likely 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. Regional hotspots of acidification and warming hazard may also occur in the Arctic Oceans, especially at bathyal depths.

Except for those in the Arctic and Southern Oceans, most of the exploited deep-sea species will likely be exposed to a decline in export POC flux up to two (by 2041–2060) and three times (by 2081–2100) historical (1951–2000) variability (Fig. 3). Specifically, under RCP8.5, 87% of species richness-pixel were projected to be exposed to seafloor warming by more than two times its historical (1951–2000) variability by 2041–2060, and this becomes 96% of pixels by 2081–2100 (Fig. 3(A, B)). In contrast, under RCP2.6, only 65% and 67% of pixels were exposed to that level of warming by the mid and end of the twenty-first century, respectively. Also, mean decrease in seafloor

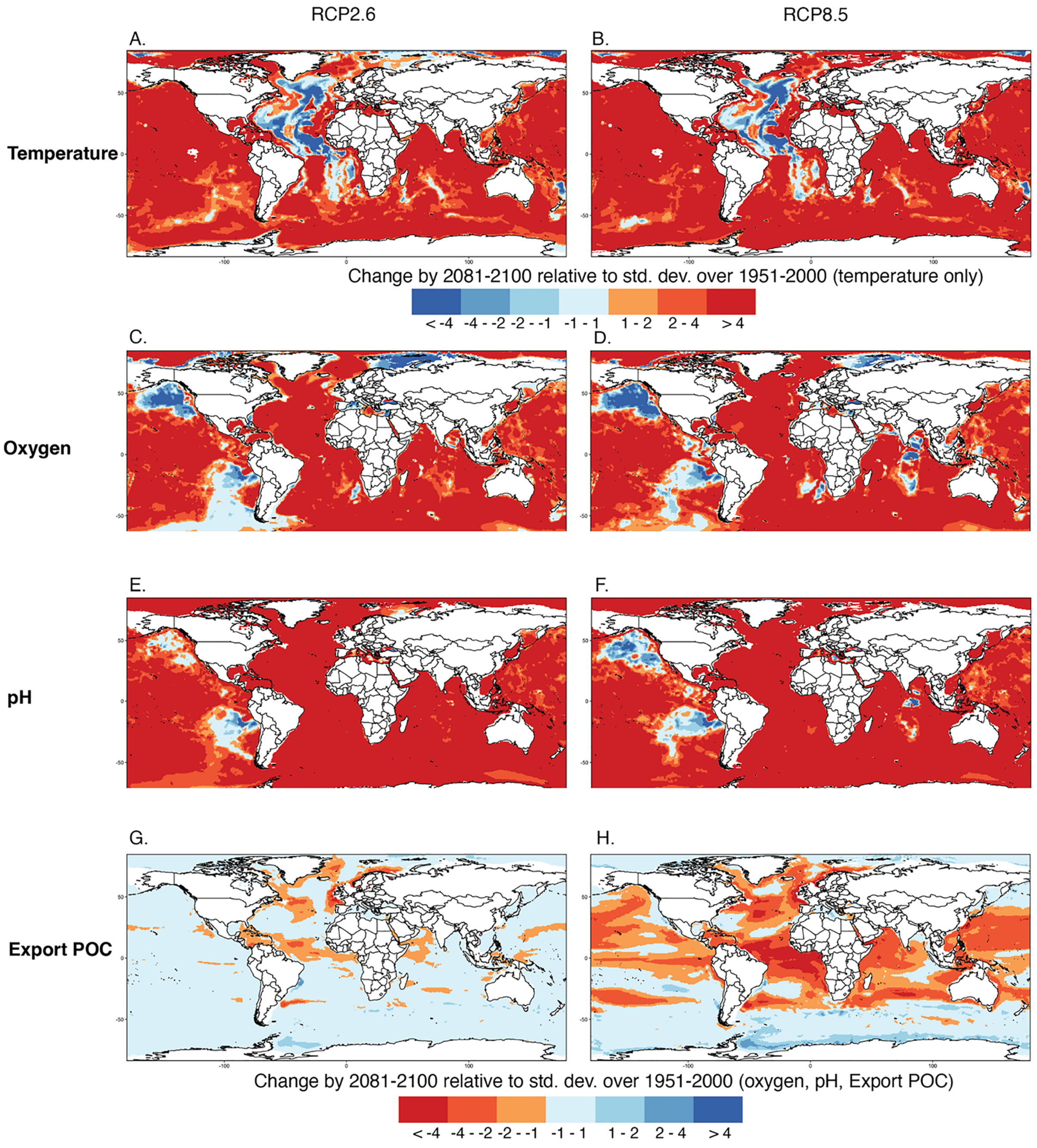

Fig. 2 Projected changes in ocean variables between the averages of 1951–2000 and 2081–2100, expressed relative to the standard deviation of the 1951–2000 period under RCP2.6 (A, C, E, G) and RCP8.5 (B, D, F, H). (**A**, **B**) Seafloor temperature, (**C**, **D**) seafloor oxygen, (**E**, **F**) seafloor pH, and (**G**, **H**) seafloor export particulate organic matter (POC). The color scale for C–H is opposite to A and B so that the red color scale indicates increasing climatic hazard to deep-sea species

oxygen concentration was twice the historical variability in 41% and 66% of the species-pixels by the mid and end of the twenty-first century, respectively, under RCP8.5 (Fig. 3(C, D)). Moreover, almost 100% of the species-pixels were projected to experience decline in seafloor pH that is two times above historical

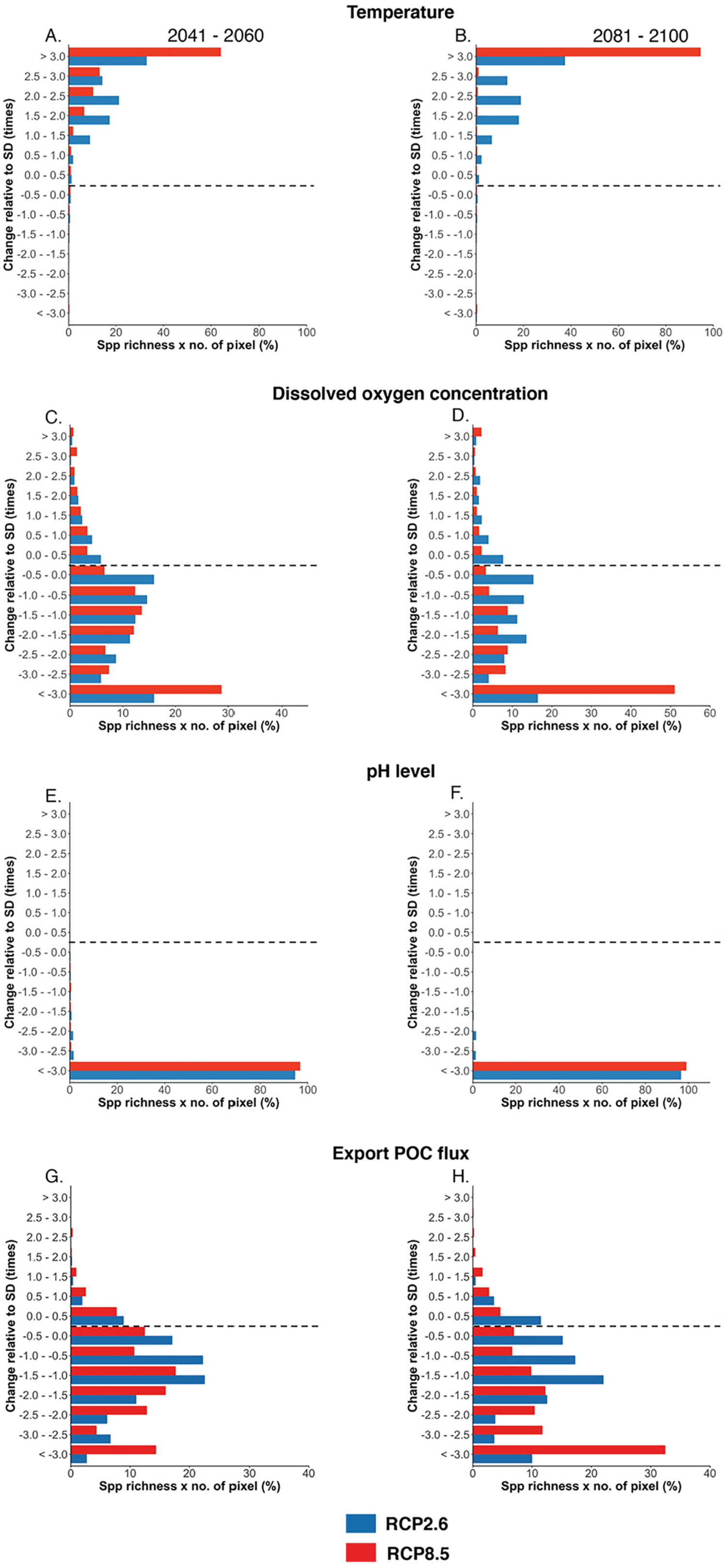

Fig. 3 Level of exposure to main climatic hazards that the 32 studied deep-sea species are projected to face. Exposure of climatic hazards was expressed through the changes in mean conditions by 2041–2060 (A, C, E, G) and 2081–2100 (B, D, F, H) relative to 1951–2000 (reference period) and divided by the standard deviation (detrended) of annual variabilities during the reference period. The climatic hazards including (**A**, **B**) ocean warming, (**C**, **D**) ocean deoxygenation, (**E**, **F**) ocean acidification, and (**G**, **H**) decrease in nutrient supplies from export POC. The dotted lines represent no change in the hazard variables. The blue and red bars represent RCP2.6 and RCP8.5 scenarios, respectively

variability by the mid-twenty-first century (Fig. 3(E, F)) while 36% and 59% of species-pixels were projected to experience decline in export POC flux to seafloor of twice the historical variability by the 2050s and 2090s, respectively (Fig. 3(G, H)).

The exploited deep-sea species are projected to face substantially larger climate hazards and risk of impacts under RCP8.5 than RCP2.6 (Fig. 4, Appendix Table 1). The median values of the exposure index of climate hazard are 69 (minimum and maximum = 54–81) and 76 (61–92), respectively, projected for 2050 (2041–2060) and 2100 (2091–2100) periods under the RCP8.5 scenario (100 being the highest level of exposure to climate hazard) (Fig. 4A). In contrast, the median exposure index declines by 42% and 50% under RCP 2.6 by 2050 and 2100, respectively. Species that are among the most exposed to climate hazards under RCP8.5 are Baird's slickhead (*Alepocephalus bairdii* index = 81 and 92 by 2050 and 2100, respectively), roughhead grenadier (*Macrourus berglax*, index = 80 and 89), and roundnose grenadier (*Coryphaenoides rupestris*, 78 and 87). Although the exposure to hazard of Patagonian toothfish (*Dissostichus eleginoides*, 59 and 63), Antarctic toothfish (*Dissostichus mawsoni*, 55 and 63), and sablefish (*Anoplopoma fimbria*, 55 and 63) are relatively lower than the other studied deep-sea species, they have high climate risk because of their high vulnerabilities to climate change.

A majority (24 out of 32) of the studied exploited deep-sea species simultaneously have climate risk and fishing vulnerability at high to very high levels (index value > 50) by the mid twenty-first century under RCP8.5 (Fig. 5, Appendix Table 2). The majority of our studied exploited deep-sea species are estimated to be experiencing high to very high risk of climate impacts (index value > 50) by 2051–2060 and 2081–2100 under RCP8.5. Species that are both at very high risk of climate impacts and highly vulnerable to fishing include Antarctic toothfish (*Dissostichus mawsoni*), rose fish (*Sebastes norvegicus*), roughhead grenadier (*Macrourus berglax*), Baird's slickhead (*Alepocephalus bairdii*), cusk (*Brosme brosme*), and Portuguese dogfish (*Centroscymnus coelepis*). Overall, we found a significantly positive correlation between risk of climate impacts and vulnerability to fishing among the 32 exploited deep-sea species ($p < 0.05$, $R = 0.7$, Pearson's product-moment correlation, R function "cor.test") (Fig. 5).

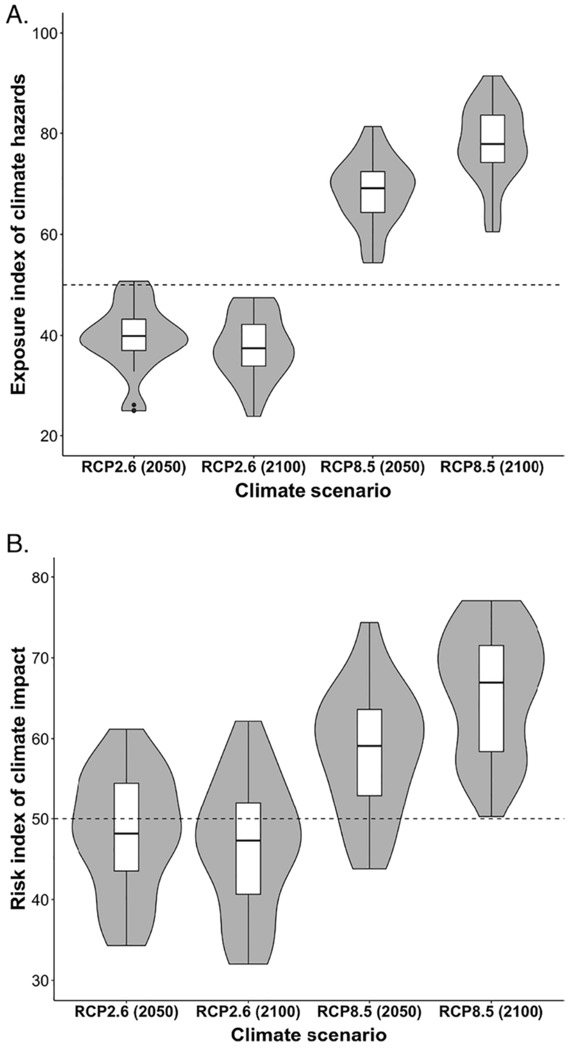

Fig. 4 Calculated exposure index of climate hazards and risk index of climate impacts of the 32 exploited deep-sea in the twenty-first century. Panels **A** and **B** are exposure index of climate hazards and **B** risk index of climate impacts, respectively, under the RCP2.6 and RCP8.5 scenarios by 2050 (2041–2060) and 2100 (2081–2100). The index value ranges from 1 to 100, with 100 indicating maximum risk of climate impact. Dash lines represent an index of 50 above which exposure to climate hazards and risk of climate impacts are associated with the high to very high categories

Discussion

This study shows that almost all deep-sea floor ecosystems and the 32 exploited species living therein are projected to face high level of hazards towards the end of the twenty-first century, challenging their long-term survival from multiple climatic stressors

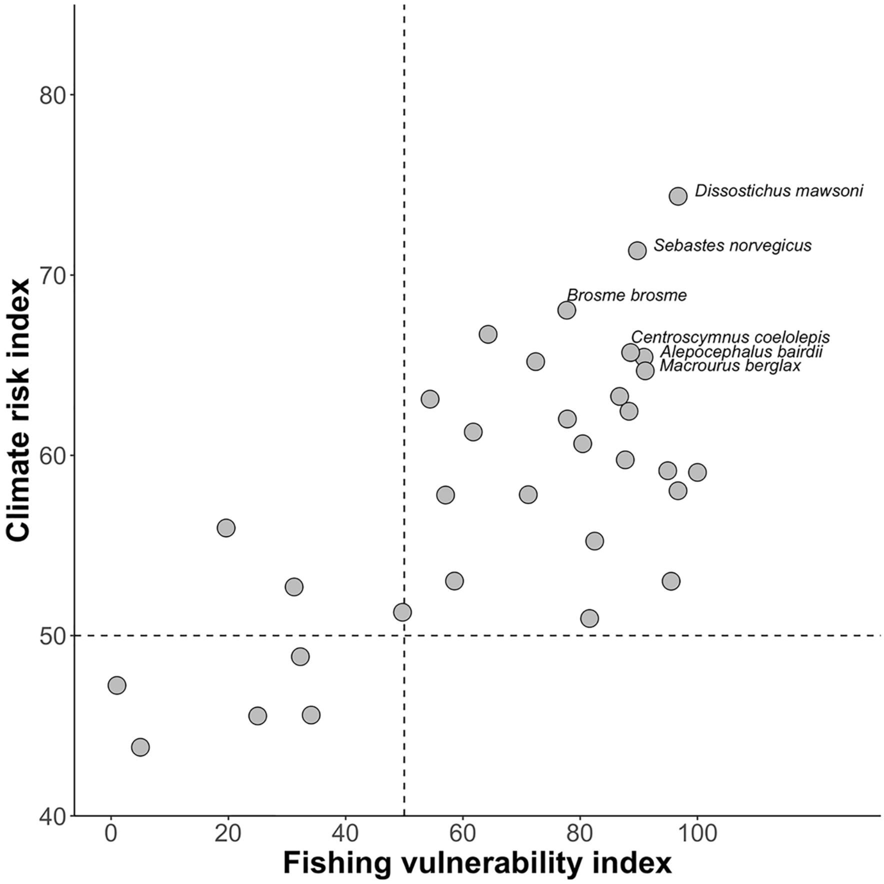

Fig. 5 Comparison of risk of climate risk index by 2041–2060 under RCP8.5 and fishing vulnerability index. The dashed lines indicate index values = 50 above which risk or vulnerability are considered as high to very high

that include ocean warming, deoxygenation, acidification, and decreasing food supplies. The life-history characteristics of some of our studied deep-sea exploited species such as large body size and narrow temperature tolerances (high sensitivity) and late maturation (low adaptive capacity) render them particularly vulnerable to these climatic hazards (Jones and Cheung 2018). Some of these life-history characteristics (large-bodied, long-lived) also indicate that these species have high fishing vulnerability (Cheung et al. 2005). As such, these species are at "double risk" from both climate change and overfishing, including those that are highly valued commercially, such as Antarctic toothfish. Our results highlight the need to tackle climate change, fisheries resources management, and conservation in an integrative manner, as highlighted by the recently published joint report by the International Panel on Climate Change and Intergovernmental Science-Policy platform on Biodiversity and Ecosystem Services (Pörtner et al. 2021).

Fast emergences of climate hazards but low species' adaptive capacity

The deep-sea floor environment was once considered to be isolated from the variabilities of the surface layer of the ocean, but strong rapid connections are now recognized through thermohaline circulation, gravitational sinking, animal migrations, and other processes (O'Leary and Roberts 2018). The effects of more than a century of greenhouse gas emissions from human activities since the industrial revolution have already affected many parts of the deep ocean despite a time-lag from changes in surface waters (Bindoff et al. 2019; Levin et al. 2020). Deep-sea environments are characterized as stable on ecological timescales (Costello and Chaudhary 2017), and therefore the projected ocean warming and acidification have high "signal-to-noise" ratios. Thus, secular changes in these climatic hazards are projected to emerge from historical variabilities in all the recorded habitats of the studied species in the first half of the twenty-first century (Figs. 2 and 3). A previous study also highlights more rapid projected temperature velocity in the deep sea than surface ocean in the twenty-first century (Brito-Morales et al. 2020). The rapid emergence of climatic hazards challenges both the capacity of organisms and management policies to respond in a timely way to the resulting impacts.

The studied deep-sea species are evolved to adapt to these relatively stable but extreme environmental conditions, resulting in life-history characteristics that span the gradient between "equilibrium" and "periodic." Equilibrium strategists are species that put substantial investment into caring for a small number of offspring to ensure their survival (King 2005; Winemiller 2005). For example, Portuguese dogfish (*Centroscymnus coelolepis*) included in our analysis is large-bodied, late-maturing, and ovoviviparous, which is an example of a species with an equilibrium strategy. These deep-sea species have low population turnover rates and long generation times that do not favour rapid evolutionary adaptive responses to the changing environment. In contrast, periodic strategists are characterized as having large body size, long lifespan, and high fecundity to hedge the uncertainties of successful recruitment (King 2005; Winemiller 2005). Many of our studied species such as Atlantic halibut (*Hippoglossus hippoglossus*) belong to the "periodic" strategist categories. Their large body sizes render them physiologically sensitive to climate change (Danovaro et al. 2017; Priede 2017). Such climate sensitivities are exacerbated by narrow thermal tolerance preferences for some species (e.g., Antarctic toothfish and golden redfish). While some species do not belong clearly to "equilibrium" or "periodic" strategies, their exposure to very high level of climatic hazards has rendered them at high risk to climatic impacts. The combination of rapid emergence of climatic hazards, high sensitivity, and low adaptive capacity explains the high risk of negative climate impacts on these exploited deep-sea species.

Multiple climatic and non-climatic stressors

Our study highlights that the compounded effects of multiple climatic stressors from warming, ocean acidification, deoxygenation, and declines in food supply exacerbate the risks to deep-sea species under climate change. Most of the studied species and their habitats are projected to be exposed to these four climatic stressors simultaneously by the mid-twenty-first century and increasingly towards the end of the twenty-first century. Particularly, our findings add to earlier studies on climate change impacts on deep-sea species that focus on the effects of temperature (Brito-Morales et al. 2020) or multiple climatic stressors (Gallo et al. 2020), suggesting that most of the exploited deep-sea fishes are likely to be at higher risk of local, or even global, extinction than previously assessed.

The risk of local or global extinction of deep-sea exploited species is further exacerbated when considering the addition of non-climatic stressors. Particularly, the vulnerability of the studied exploited deep-sea species to climate change and fishing are positively related as some of the life-history characteristics of deep-sea species that confer high vulnerability to climate change and fishing are similar. The climatic and fishing indices used in this study have been shown to be significantly related to the extinct risk categories of the IUCN Red List (Cheung et al. 2005, 2018). Many deep-sea fishes are already vulnerable or endangered because of overfishing (Norse et al. 2012; Watling et al. 2020). Moreover, deep-sea floor habitats that these exploited species are dependent on are vulnerable to physical damage from fishing activities such as bottom trawling (Pusceddu et al. 2014). Continential margin is particularly at risk because of its higher fishing activities relative to other deep-sea habitats, higher biodiversity, and exposure to climatic hazards (Levin and Sibuet 2012; Mora et al. 2013). Furthermore, recovery time for over-exploited populations or disturbed habitats in the deep sea can be decades to a century (Baker et al. 2009). The long recovery timeframe is at a similar scale as the emergence of climatic stressors in the deep sea. Thus, even if interventions addressing over-exploitation are implemented, climate change will adversely affect the effectiveness of such interventions (Johnson et al. 2018). In addition, the deep sea is also exposed to other non-climatic human stressors such as mining activities and plastic pollution (Chiba et al. 2018; Simon-Lledó et al. 2019; Levin et al. 2020). Understanding the combined risks and vulnerability of all the main climatic and non-climatic stressors would help more comprehensively elucidate the conservation challenges that deep-sea exploited species are facing.

Uncertainties and future research

There are a number of key uncertainties associated with the analysis in this study that could inform areas for future studies. Most climate models only focus on the surface ocean with progressively lower vertical resolution into deeper water. For example, the vertical resolution of the three models used in this study is 10 m for the top 70- to 200-m water depths; however, the resolution beyond 2000-m water depth is ~ 300 to 500 m. Therefore, the projected climate hazards may not represent the potential hazard faced by these exploited demersal fishes. As a result, the errors in model accuracy (i.e., comparison between historical projections and observations) and precision (i.e., standard deviation among models) are much higher on the seafloor than the surface ocean (Mora et al. 2013), highlighting the need for Earth system model to pay more attention on the deep ocean. Moreover, there is a general lack of observational data to understand the deep-sea species and ecosystems and their vulnerability to climate change (Levin et al. 2019). These observational data gaps include insufficient spatial and temporal coverage of biological and oceanographic sampling, particularly for the tropical Pacific and Indian Ocean (Levin et al. 2019). This underscores the importance of expanding and enhancing the capacity to monitor the deep ocean. In addition, future studies can use the latest generation of Earth system model outputs, e.g., from CMIP Phase 6 (Kwiatkowski et al. 2020), climatic, e.g., different shared socio-economic pathway-RCP and fishing scenarios, e.g., from FISH-MIP (Cheung et al. 2016a; Rounsevell et al. 2021). Future studies can also use a wider range of these models and scenarios to explore model and additional scenario uncertainties in the assessment of climatic and fishing risks for deep-sea species.

Implications for international policies

In 2016 the United Nations General Assembly passed resolution 71/123 which in Paragraph 185 calls upon States, individually and through regional fisheries management organizations and arrangements, "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." The FAO Common Oceans *ABNJ Deep Seas Project* has partnered with *The Deep-Ocean Stewardship Initiative* and its working group of climate change experts to better understand the consequences of climate change for deep-sea ecosystems and deep-sea fisheries (FAO 2019). This study represents one approach, with a focus on evaluating the impacts of climate change on commercially important deep-sea fish and shellfish.

The findings of this study speak to a need for both mitigation of greenhouse gas emissions to slow the effects of climate change, ocean acidification and ocean deoxygenation on the ocean environment, conservation of oceanic carbon stores (Hilmi et al. 2021), and adaptation of fisheries activities and practices to recognize and manage the consequences of climate change. The RFMOs can and should incorporate vulnerability to climate change in their management and planning, including using climate as a criterion for the designation of vulnerable marine ecosystems used by some of the species studied here, and fishing grounds where the species are harvested. Notably, not all international deep-sea waters are currently managed by RFMOs; those that are not should be included in existing or new international governance institutions or arrangements and these also should address climate change. Within exclusive economic zones, the 18 Region Seas Programs, engaging 146 countries, offer another opportunity for multilateral consideration of climate vulnerability in demersal fisheries management.

Fish and fisheries are not isolated from other changes in the ocean. Managing for the integrity of fish habitat, fish, and fisheries will require cooperation with other UN Agencies such as the IMO which manages shipping and dumping, and the ISA which currently issues mineral exploration contracts and is developing exploitation regulations for deep seabed mining. The UNFCCC under the Paris Agreement technically addresses emissions on land and ocean within national jurisdiction; the climate in areas beyond national jurisdiction (ABNJ) remains a key gap. The recent UNFCCC COP26 decision for the Subsidiary Body for Scientific and Technological Advice to hold an annual Ocean Dialogue offers new opportunities to address high seas and deep-sea climate issues relevant to fisheries. Some aspects of this gap also could be considered by a new treaty on biodiversity in ABNJ being negotiated by the UN General Assembly (Gjerde and Yadav 2021), particularly in the arenas of area-based management, marine spatial planning, and impact assessment, with potential benefits for the fish and fisheries of the high seas and deep seas. As many fish may be highly migratory, and straddle both EEZs and ABNJ in one or more life stages, they will be subject to other policy instruments (e.g., straddling stocks agreement), and national jurisdictions that should be consulted to maximize effective management.

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Declarations

Animal care or ethics committee Not applicable.

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