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Rebuilding fish biomass for the world's marine ecoregions under climate change

William W. L. Cheung[1] | Juliano Palacios-Abrantes[1,2] | Thomas L. Frölicher[3,4] | Maria Lourdes Palomares[1] | Tayler Clarke[1] | Vicky W. Y. Lam[1] | Muhammed A. Oyinlola[1,5] | Daniel Pauly[1] | Gabriel Reygondeau[1] | U. Rashid Sumaila[1,6] | Lydia C. L. Teh[1] | Colette C. C. Wabnitz[1,7]

[1]Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, British Columbia, Canada

[2]Center for Limnology, University of Wisconsin, Madison, Wisconsin, USA

[3]Climate and Environmental Physics, Physics Institute, University of Bern, Bern, Switzerland

[4]Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland

[5]Institut National de la Recherche Scientifique – Centre Eau Terre Environnement, Quebec City, Quebec, Canada

[6]School of Public Policy and Global Affairs, The University of British Columbia, Vancouver, British Columbia, Canada

[7]Stanford Center for Ocean Solutions, Stanford University, Stanford, California, USA

Correspondence

William W. L. Cheung, Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, BC, Canada.
Email: w.cheung@oceans.ubc.ca

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Abstract

Rebuilding overexploited marine populations is an important step to achieve the United Nations' Sustainable Development Goal 14—Life Below Water. Mitigating major human pressures is required to achieve rebuilding goals. Climate change is one such key pressure, impacting fish and invertebrate populations by changing their biomass and biogeography. Here, combining projection from a dynamic bioclimate envelope model with published estimates of status of exploited populations from a catch-based analysis, we analyze the effects of different global warming and fishing levels on biomass rebuilding for the exploited species in 226 marine ecoregions of the world. Fifty three percent (121) of the marine ecoregions have significant (at 5% level) relationship between biomass and global warming level. Without climate change and under a target fishing mortality rate relative to the level required for maximum sustainable yield of 0.75, we project biomass rebuilding of 1.7–2.7 times (interquartile range) of current (average 2014–2018) levels across marine ecoregions. When global warming level is at 1.5 and 2.6°C, respectively, such biomass rebuilding drops to 1.4–2.0 and 1.1–1.5 times of current levels, with 10% and 25% of the ecoregions showing no biomass rebuilding, respectively. Marine ecoregions where biomass rebuilding is largely impacted by climate change are in West Africa, the Indo-Pacific, the central and south Pacific, and the Eastern Tropical Pacific. Coastal communities in these ecoregions are highly dependent on fisheries for livelihoods and nutrition security. Lowering the targeted fishing level and keeping global warming below 1.5°C are projected to enable more climate-sensitive ecoregions to rebuild biomass. However, our findings also underscore the need to resolve trade-offs between climate-resilient biomass rebuilding and the high near-term demand for seafood to support the well-being of coastal communities across the tropics.

1 | INTRODUCTION

Climate change is impacting marine biodiversity and ecosystem functions as well as human communities that depend on them (IPCC, 2019; Sumaila et al., 2019). The ocean has absorbed 90% of the additional heat energy (von Schuckmann et al., 2020) that is accumulating in the Earth system due to the increases in greenhouse gases and between 20% and 30% of the carbon dioxide (Friedlingstein et al., 2021) generated by burning fossil fuels and altering land use. Such assimilation is leading to increases in ocean heat content, loss of oxygen, acidification, and increases in the frequency and intensity of extreme events such as marine heatwaves (Frölicher et al., 2018; IPCC, 2021). These ocean changes are impacting marine ecosystems by shifting species distributions generally toward higher latitudes or deeper waters, changing phenology and body size, altering trophic interactions, and overall, affecting ecological structure and functions, such as biomass production (Bindoff et al., 2019; Poloczanska et al., 2016; Provost et al., 2017; Thackeray et al., 2010). Marine capture fisheries have been affected by these climate-induced ecological changes, with observed impacts including changes in catch composition (Cheung et al., 2013), decreases in potential catches of targeted species (Free et al., 2019), shifts in stock distributions, and losses in revenues and jobs (Lam et al., 2020; Palacios-Abrantes et al., 2022; Sumaila et al., 2020). These impacts on fisheries are projected to continue throughout the 21st century, and the intensity of these impacts is strongly related to the level of greenhouse gas emissions and global warming (Cheung, Frölicher, et al., 2016; Cheung, Jones, et al., 2016; Lotze et al., 2019; Tittensor et al., 2021).

Rebuilding marine populations that are overexploited or depleted is an important step toward a sustainable use of marine resources and central to achieving the United Nations' Sustainable Development Goals (SDG), such as Life Below Water (Danovaro et al., 2021; Duarte et al., 2020; Melnychuk et al., 2021; Sumaila, 2021; Sumaila et al., 2012; Teh & Sumaila, 2020). Rebuilding fisheries is also considered an adaptation measure to reduce climate impacts on biodiversity with substantial co-benefits in achieving conservation and food provision goals (Cheung et al., 2018; Free, Mangin, et al., 2020; Sumaila & Tai, 2020). Rebuilding target is usually expressed as fishing mortality relative to the level required to achieve maximum sustainable yield (MSY; F/F_{MSY}) and/or biomass relative to unexploited level of biomass (B/B_0) (Melnychuk et al., 2021). Some fisheries in the world already have rebuilding plans in place, although their progress of implementation and effectiveness in achieving rebuilding targets vary substantially (Hilborn et al., 2020). In addition, current fisheries' management approaches may not be sufficient to achieve rebuilding, with climate change being one of the major uncertainties in the effectiveness of rebuilding plans (Bell et al., 2018; Memarzadeh et al., 2019; Punt, 2011).

Climate change is expected to impact the rebuilding of fish stock biomass. Here, the term "fish stock" is used generically in the fisheries context and includes exploited fishes and invertebrates. Previous modeling studies have shown that, overall, projected changes in global biomass of marine animals is negatively related to warming levels, with important regional differences (Cheung et al., 2018; Cheung, Reygondeau, & Frölicher, 2016; Lotze et al., 2019; Tittensor et al., 2021). This scaling relationship is driven largely by temperature and net primary production (Heneghan et al., 2021), while ocean acidification is expected to steepen the negative scaling particularly for invertebrate fisheries (Tai et al., 2021). Climate impacts on marine species and fisheries also vary largely between regions, with tropical areas generally being among the most at risk to climate impacts while fisheries in some high latitude regions may gain from having more diverse and abundant fish stocks (Lam et al., 2020; Lam, Cheung, & Sumaila, 2016). Tropical regions are projected to have a steeper negative scaling while some high latitude regions have positive scaling because of the range expansion of exploited species and increases in primary production (Cheung, Frölicher, et al., 2016; Cheung, Jones, et al., 2016). Thus, climate change is expected to alter the potential gains from biomass rebuilding and the impacts will vary between regions.

Understanding the effects of climate change on the rebuilding of fish stock biomass is important in developing effective restoration plans. Here, we aim to project the effects of climate change under different global warming levels on achieving fish biomass rebuilding targets for the world's marine ecoregions. We combine published estimates of the status of exploited populations from a catch-based analysis with projected changes in exploited fish and invertebrate populations from a dynamic bioclimate envelope model (DBEM; Cheung, Jones, et al., 2016). Next, we analyze the effects of different global warming levels on achieving population biomass rebuilding targets. We then examine the impacts of achieving (or not) global climate mitigation commitments and targets for population rebuilding and its contribution to climate-resilient fisheries (Mason et al., 2021). We hypothesize that climate change will reduce the possibility of achieving rebuilding targets for most marine ecoregions (Hypothesis a) and have positive effects in some regions (Hypothesis b) (Figure 1a,b, respectively). Moreover, we hypothesize that for some regions, there is no or a weak relationship between biomass and global warming levels (Hypothesis c) (Figure 1c).

2 | MATERIALS AND METHODS

2.1 | Estimating status of fish stocks in marine ecoregions

We adopted a Bayesian modeling approach using catch at maximum sustainable yield (hereafter called CMSY method) to estimate the status of fish stocks (i.e., the amount of fish biomass in the water)

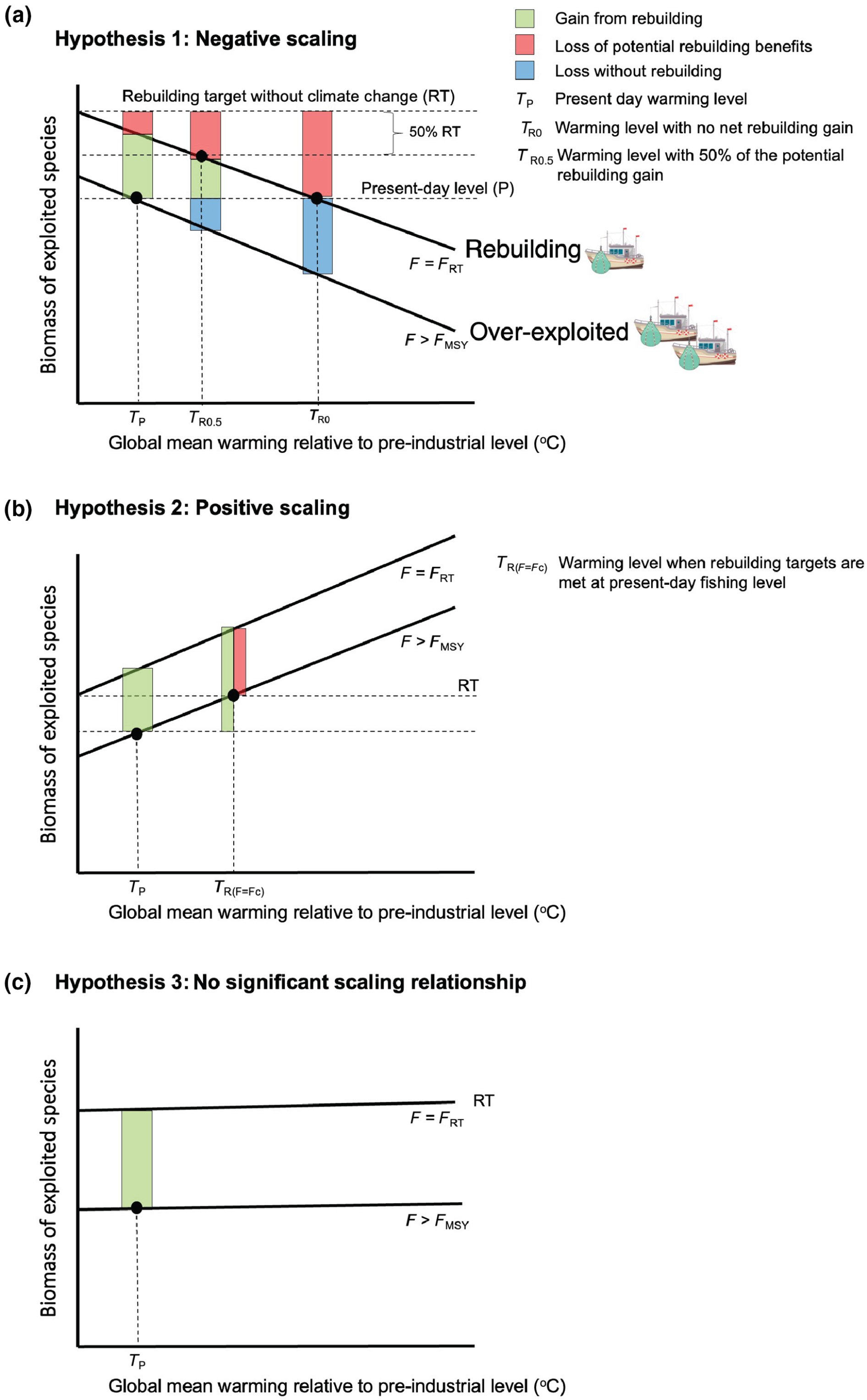

FIGURE 1 Expected impacts of climate change on fisheries rebuilding depend on the scaling between stock biomass and global warming levels. (a) Loss of potential rebuilding benefits and lowered possibility of achieving rebuilding targets. (b) Gain in potential rebuilding benefits and increased possibility of achieving rebuilding targets. (c) No change in rebuilding benefits and possibility of achieving rebuilding targets. Rebuilding targets are computed by simulating changes in biomass under a specified reference target (RT) and different fishing mortality rates for rebuilding. Impacts of climate change on biomass rebuilding are indicated by (1) present-day maximum potential biomass and scenarios of global warming levels under specified rebuilding reference targets, (2) loss of potential rebuilding benefits (in terms of biomass) relative to no climate change, (3) warming level at when all the benefits from rebuilding biomass are lost (T_{R0}) and (4) warming level at when 50% of the benefits from rebuilding biomass are lost ($T_{R0.5}$). [Colour figure can be viewed at wileyonlinelibrary.com]

across the marine ecoregions of the world (for details of the CMSY method, see Froese et al., 2018; Martell & Froese, 2013; Palomares et al., 2020). Spalding et al. (2007) define 232 marine ecoregions representing a global biogeographic system of coastal and shelf areas. This study included 226 of those marine ecoregions where analysis using the CMSY method has been previously applied (Palomares et al., 2020). While traditional stock assessment methods use biomass data to estimate catch rates, the CMSY method uses catch data to estimate biomass. The CMSY approach has been applied to undertake numerous assessments across the world's oceans (e.g., Andrašūnas et al., 2022; Barman et al., 2020; Ren & Liu, 2020; Schijns et al., 2021).

In brief, the CMSY method follows a dynamic Schaefer (surplus production) model, which assumes that population is determined by the current stock biomass, the carrying capacity of the environment for the stock (k) and its intrinsic rate of population increase (r) (Schaefer, 1954, 1957). Following Palomares et al. (2020), we defined a species in a marine ecoregion as a stock unit (see online supplementary data for the list of stocks included in this study). For each stock, we applied the CMSY method to compute the historical time series of biomass and catch using a dynamic surplus production model, given different values of r and k. The r and k values were sampled from a uniform probability distribution with the minimum and maximum parameter values determined based on the life-history characteristics of targeted species. Life-history values were obtained from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org) for fish and invertebrate species, respectively (Froese et al., 2017).

The CMSY method compares the predicted historical catches with observational-based catches (from the Sea Around Us catch reconstruction from 1950 to 2018, Zeller et al., 2016) and computes posterior probability distributions for r and k, and estimates fishing mortality rates (F) and biomass over time for each stock (Palomares et al., 2020). The CMSY method applied here incorporated publicly available results from about 200 assessments conducted by fisheries management bodies, including the United Nations' Food and Agriculture Organization (FAO), National Oceanic and Atmospheric Administration in the USA, Fisheries and Oceans Canada, International Council for the Exploration of the Seas in Europe, and other Regional Fisheries Management Organizations. The assessment results used to inform the CMSY analysis include independently derived time series of estimated biomass or its indicators, for example, catch per unit effort data (Palomares et al., 2020). About 40% of the CMSY analyses used catch-per-unit-effort and other relative abundance data from scientific studies, including biomass estimations from swept area methods with trawl survey (a method commonly employed by the FAO in their assessments). These assessment data are used as priors for the Bayesian algorithm in the CMSY methods applied here (see Palomares et al., 2020 for details). Using the published estimates of biomass and carrying capacity from the CMSY analyses (Palomares et al., 2020), we estimated the F required to attain MSY (F_{MSY}) for each stock. We also calculated mean current (2014–2018) F relative to F_{MSY} ($F_{current}/F_{MSY}$) and biomass relative to unexploited levels (carrying capacity) ($B_{current}/B_0$). We then calculated the median $F_{current}/F_{MSY}$ and $B_{current}/B_0$ across stocks in each marine ecoregion.

We acknowledge that there is a higher uncertainty associated with CMSY estimates from more data-limited regions. These data-limited regions, for which fisheries survey data and assessments are lacking, are concentrated in the tropics, where there is also higher risk and vulnerability to the effects of climate change on the oceans (Bindoff et al., 2019). While we acknowledge this uncertainty, only focusing efforts on regions where fisheries survey data are available and rigorous fisheries assessments have been undertaken would bias attention toward developed countries in mid- and high-latitude regions. Such biases would limit us from informing biomass rebuilding under climate change in tropical areas where such information is likely to be needed the most.

2.2 | Earth system models projection and climate scenarios

We used outputs from three Earth system models that participated in the Coupled Model Intercomparison Project Phase 6 (CMIP6) under two contrasting emission scenarios. The three Earth system models included are the Geophysical Fluid Dynamics Laboratory (GFDL)-ESM4 (Dunne et al., 2020), the Institut Pierre-Simon Laplace (IPSL)-CM6A-LR (Boucher et al., 2020), and the Max Planck Institute Earth System Model (MPI)-ESM1.2 (Gutjahr et al., 2019). The variables that we extracted from each Earth system model simulation include global mean surface atmospheric temperature, sea surface and bottom temperature, dissolved oxygen concentration and salinity, vertically integrated total net primary production, sea ice extent, and surface advection. Projections follow two contrasting scenarios—shared socio-economic pathway (SSP) 1—representative concentration pathway (RCP) 2.6 (SSP1-2.6) and SSP5-8.5 (Gütschow et al., 2021; Meinshausen et al., 2020). The SSP1-2.6 and SSP5-8.5 represent a "strong mitigation" low-emissions pathway and a "no mitigation" high-emissions pathway, respectively.

2.3 | Projecting potential biomass and fishing scenarios

We used the DBEM to simulate changes in the distribution and abundance of exploited marine fish and invertebrate species (Cheung, Jones, et al., 2016; Cheung, Reygondeau, & Frölicher, 2016). We summarize pertinent aspects of the model here. The current distributions of commercially exploited species, representing the average pattern of relative abundance in recent decades (i.e., 1970–2000), were reproduced using an algorithm developed by the Sea Around Us (Zeller et al., 2016). The algorithm predicts the relative abundance of a species on a 0.5° latitude × 0.5° longitude grid based on the species' depth range, latitudinal range, and known FAO statistical areas and polygons encompassing their known occurrence regions. The distributions were further refined by assigning habitat preferences to each species, such as affinity to the shelf (inner, outer), estuaries, and coral reef habitats. The required habitat information was obtained from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org), databases which contain key information on the distribution of the species in question, and on their known occurrence region.

We calculated an index of habitat suitability for each species in each spatial cell of the world ocean from temperature (bottom and surface temperature for demersal and pelagic species, respectively), bathymetry, specific habitats (coral reef, continental shelf, shelf slope, and seamounts), salinity (bottom and surface salinity for demersal and pelagic species, respectively), and sea ice extent with 30-year averages of outputs from 1971 to 2000 from the three Earth system models. Movement and dispersal of adults and larvae were modeled through advection–diffusion–reaction equations for larvae and adult stages. Carrying capacity in each cell is assumed to be a function of the unfished biomass of the population, the estimated habitat suitability, and net primary production in each cell. We assumed that the average of the top 10 annual historical catches since 1950 was roughly equal to the MSY of the species. Fernandes et al. (2013) showed that the top 10 annual catches are strongly and significantly correlated with MSY estimated from survey-based stock assessment. In some cases, the top 10 annual catches may be higher than MSY, with species, therefore, being overexploited, or the approach may underestimate MSY if the species are underexploited. However, this would not substantially alter the main results from DBEM, which focuses largely on the relative changes across time instead of absolute biomasses or catches. Changes in carrying capacity in each year are proportional to changes in predicted habitat suitability and net primary production. The model simulates changes in relative abundance by solving the advection–diffusion relationships and modeling population growth through a logistic growth function. In addition to the abundance, DBEM calculates a characteristic weight representing the average mass of an individual in the cell. The model simulates how changes in temperature and oxygen content would affect the growth of the individual using a submodel derived from a generalized von Bertalanffy growth function. The DBEM has a spin-up period of 100 years using the climatological average oceanographic conditions from 1971 to 2000 simulated from the Earth system models, thereby allowing the species to reach equilibrium before it is perturbed with oceanographic changes. Previous studies have found strong correlation between catch data and DBEM projections from marine regions (Cheung, Jones, et al., 2016).

Annual fishing mortality rate (F) was applied to an entire stock (species—marine ecoregion unit) for the simulation time period (1950–2100) to calculate changes in abundance. In DBEM, biomass was calculated from the simulated population mean body weight, abundance, and the specified fishing mortality rate (Cheung, Jones, et al., 2016). When the fishing mortality rate is set to be equal to the natural mortality rate from such fishing levels, it represents the maximum equilibrium surplus production or maximum catch potential.

We applied five scenarios of fishing mortality rate under each of the two climate scenarios. These fishing scenarios were expressed relative to fishing mortality at MSY for each exploited species: (1) "no fishing" ($F = 0$), (2) "conservation focus" ($F/F_{MSY} = 0.5$), (3) "sustainable target" ($F/F_{MSY} = 0.75$), (4) "catch maximization" ($F/F_{MSY} = 1$), (5) "overexploitation" ($F/F_{MSY} = 1.5$).

2.4 | Assessing stock rebuilding under climate change and fishing scenarios

For each marine ecoregion, we examined the linear scaling relationship between total biomass of the studied fish stocks and the global mean surface atmospheric warming. First, using DBEM and outputs from each of the three Earth system models, we simulated changes in potential biomass for each exploited species from 1950 to 2100 under each of the five fishing scenarios and the two climate change scenarios (SSP1-2.6 and SSP5-8.5). Second, for each marine ecoregion, we computed annual total potential biomass from all the exploited species under each scenario. Third, for each fishing scenario, we examined the relationship between annual total potential biomass with global average atmospheric surface warming (relative to pre-industrial levels, i.e., average between 1881 and 1900) projected by the respective Earth system model using a linear mixed model (*lmer* function in the package *lme4* in R). In this linear mixed model, the response variable was the biomass projected from DBEM. The fixed effect independent variable was the global warming level, while the random effect of the slope is represented by different Earth system models. We developed a mixed model for each marine ecoregion and fishing scenario, and tested the hypotheses that total biomass in a marine ecoregion scales positively, negatively, or has no relationship with global atmospheric warming level.

For the marine ecoregions with significant scaling between total biomass and global warming level, we used the established linear mixed models to project the expected total biomass at different warming levels. Specifically, we examined five reference global warming levels: (1) 0°C (representing pre-industrial global temperature); (2) 1.09°C representing the average temperature between 2011 and 2020 level (IPCC, 2021); (3) 1.5°C representing the Paris agreement target; (4) 2.6°C representing projected warming levels under the pledges and targets of nations in 2021 (Carbon Action Tracker, 2021); and (5) 3.5°C representing ineffective mitigation (Carbon Action Tracker, 2021). Total biomass across the exploited stocks considered were calculated for each fishing scenario. We predicted total biomass by using the specific warming and targeted fishing levels as inputs into the developed linear mixed effect model for each marine ecoregion.

We computed indicators to examine the potential limit to stock rebuilding under climate change (Table 1). Biomass relative to the unexploited level (B/B_0) has been commonly used as an indicator to assess the conservation status of fish stocks (Sibert et al., 2006). To assess the effects of climate change and fishing on stock status, we estimated the unexploited biomass level using the developed linear mixed model for each marine ecoregion with atmospheric temperature at pre-industrial level under the no fishing scenario ($B_{0,T=0}$) as well as different levels of fishing (F) and global warming (T) ($B_{F,T}/B_{0,T=0}$) (Table 1). Moreover, we assumed that $B/B_{0,T=0}$ under the "sustainable target" (F/F_{MSY} = 0.75) and the "catch maximization" (F/F_{MSY} = 1) scenarios as alternative biomass rebuilding targets. Using the established linear mixed models, we computed the global warming levels expected to reduce differences between these rebuilding targets and current biomass levels (average of 2014–2018) by 50% ($T_{R=50\%}$) and 100% ($T_{R=100\%}$), respectively.

3 | RESULTS

Our results indicate that over half of the ecoregions analyzed (121 of 226, 53%) have an estimated slope of the relationship between unexploited biomass and global warming level that is significantly different from 0 (i.e., estimated 95% confidence interval higher or lower than 0; Figure 2). Among these 121 marine ecoregions, 103 (85%) of them have predicted total unexploited biomass levels that scale negatively with projected global warming levels (Figure 2a). The median of the estimated slopes, expressed as percentage relative to predicted unexploited biomass without global warming, is −6.3 and −7.4%°C^{-1} for all 226 ecoregions and only those that have significant scaling (121), respectively. Tropical ecoregions are projected to have the steepest slopes between total unexploited biomass and global atmospheric warming, particularly those in the Indo-Pacific (e.g., Palawan/North Borneo, Sunda Shelf/Java Sea, Sulawesi Sea/Makassan Strait, Halmahera ecoregions), central and south Pacific (East Caroline Island, Gilbert/Eillis Islands ecoregions), Eastern Tropical Pacific (e.g., Mexican Tropical Pacific, Chiapas-Nicaragua, Central Peru, Humboldtian ecoregions), and West Africa (e.g., Gulf of Guinea, Angolan ecoregions; Figure 2b).

All but one (225 of 226) marine ecoregions have estimated current (average of 2014–2018) biomass relative to unexploited levels below the rebuilding targets under the "sustainable target" scenario without climate change. Comparing with a benchmark of projected biomass from our models at F_{MSY} and without climate change, average CMSY estimated $B_{current}/B_0$ of the studied marine ecoregions is 38 ± 18% below our benchmark biomass. The low biomass is associated with high fishing mortality rates for most marine ecoregions. Our estimated average fishing mortality rate relative to the fishing level required to achieve MSY (F/F_{MSY}) is 1.5 ± 0.6 across marine ecoregions.

Rebuilding of biomass is projected to be impacted by higher fishing intensity and reduced levels of climate mitigation (Figure 3). We estimated biomass levels from the regression models between biomass and global warming for each marine ecoregion and focused on those with significant (5% level) relationship (121 marine regions). Without global warming (i.e., warming = 0°C), median biomass relative to the current level across marine ecoregions is projected to be 1.9 (1.7–2.4 interquartile ranges) under the "conservation focus," 1.5 (1.4–2.0) under the "sustainability target," and 1.2 (1.1–1.5) under the "catch maximization" scenarios, respectively (Figure 3a–c). Increasing global warming levels from 1.5 to 3.5°C reduces the median biomass relative to current level from 1.3 to 1.2 under the "sustainable target" scenario, respectively. However, such increase in warming levels is projected to increase the number of ecoregions that show no increase or a decrease in biomass relative to the current level by 3.8 times from 10% to 38% of the ecoregions (Figure 3e–g). The "worst-case" scenario of a 3.5°C global warming and "overexploitation" scenario is projected to result in biomass being only 36% (26%–51%) relative to the current level across the marine ecoregions (Figure 3h).

Our projections indicate that without strong climate mitigation measures biomass rebuilding across many marine ecoregions will not be possible (Figure 4). Overall, the median global warming level at or above which no biomass rebuilding is projected across marine regions is 1.8, 4.5, and 6.2°C, under the "catch maximization," "sustainable target," and "conservation focus" scenarios, respectively. Under the "sustainable target" scenario (F/F_{MSY} = 0.75) and "catch maximization" scenario (F/F_{MSY} = 1), 6% and 24% of the marine ecoregions are projected to show no biomass rebuilding unless global warming

TABLE 1 Key indicators of biomass rebuilding under climate change

Indicators	Global warming levels (in °C relative to pre-industrial level)	Fishing scenario (F/F_{MSY})	Description
Biomass relative to unexploited levels at different warming levels ($B_T/B_{0,T=0}$)	1.09, 1.5, 2.6, 3.5	0.5, 0.75, 1, 1.5	Predicted biomass using the linear regression model of biomass versus global warming levels for the respective fishing scenarios; expressed as a ratio relative to $B_{0,T=0}$
Global warming levels projected to reduce the expected potential rebuilding biomass targets from current levels by 50% ($T_{R=50\%}$)	—	0.75, 1	Using the respective linear regression model, we predicted T at when: $(B_{F,T}-B_{current})/(B_{F,T=0}-B_{current}) = 0.5$
Global warming levels projected to reduce the expected potential rebuilding biomass targets from current levels by 100% ($T_{R=100\%}$)	—	0.75, 1	Using the respective linear regression model, we predicted T at when $(B_{F,T}-B_{current})/(B_{F,T=0}-B_{current}) = 0$

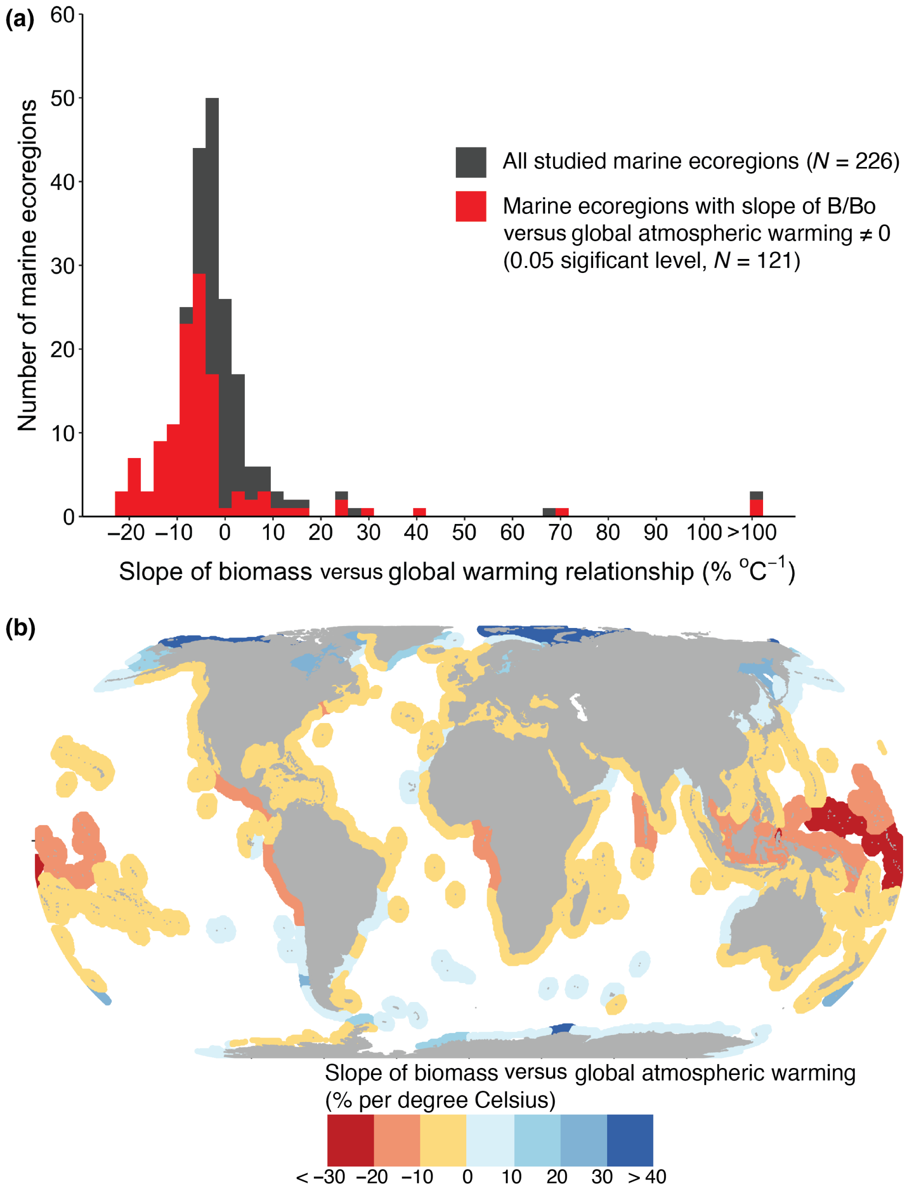

FIGURE 2 Estimated slope of the relationship between unexploited biomass (B_0) and global warming levels. (a) Frequency distribution of marine ecoregions with different projected slopes of $B_0/B_{0,T=0}$ against global warming level. Red bars represent those marine ecoregions (121 out of 226) with estimated slopes that are significantly (at the 0.05 level) different from 0. (b) Map of marine ecoregions with the estimated slopes of the relationship between projected unexploited biomass relative to preindustrial levels (B_0/B_0,$T = 0$) and global atmospheric warming levels. [Colour figure can be viewed at wileyonlinelibrary.com]

is at 1.5°C relative to pre-industrial levels, respectively. These marine ecoregions are located mostly in the tropics. Furthermore, if global warming level is at 2.6°C, our projections show that we would not be able to rebuild biomass from the current levels in 47% and 19% of the marine ecoregions under the "catch maximization" and "sustainable target" scenario, respectively.

For eight marine ecoregions, fishing mortality levels under the "catch maximization" scenario would be too high for any biomass rebuilding, even without climate change (i.e., global warming level = 0°C). These marine ecoregions are either in the Arctic where many exploited species are slow-growing and late-maturing (South and West Ireland, Gulf of Alaska, USA) or in regions currently with high fishing mortality rates (Bismarck Sea, Papua New Guinea; northern Indian Ocean, Northern Monsoon Current Coast). Only four marine ecoregions, mainly at high latitudes (e.g., Eastern Bering Sea, Sea of Okhotsk, East Greenland Shelf ecoregions), are projected to be able to rebuild more biomass under higher warming levels. We acknowledge that the circulation and biogeochemistry of some of the semi-enclosed seas such as the Sea of Okhotsk and the Red Sea are not well resolved by the Earth system models used in this study (Stock et al., 2011). Thus, detailed interpretation of the projections specifically for these regions should be done with caution.

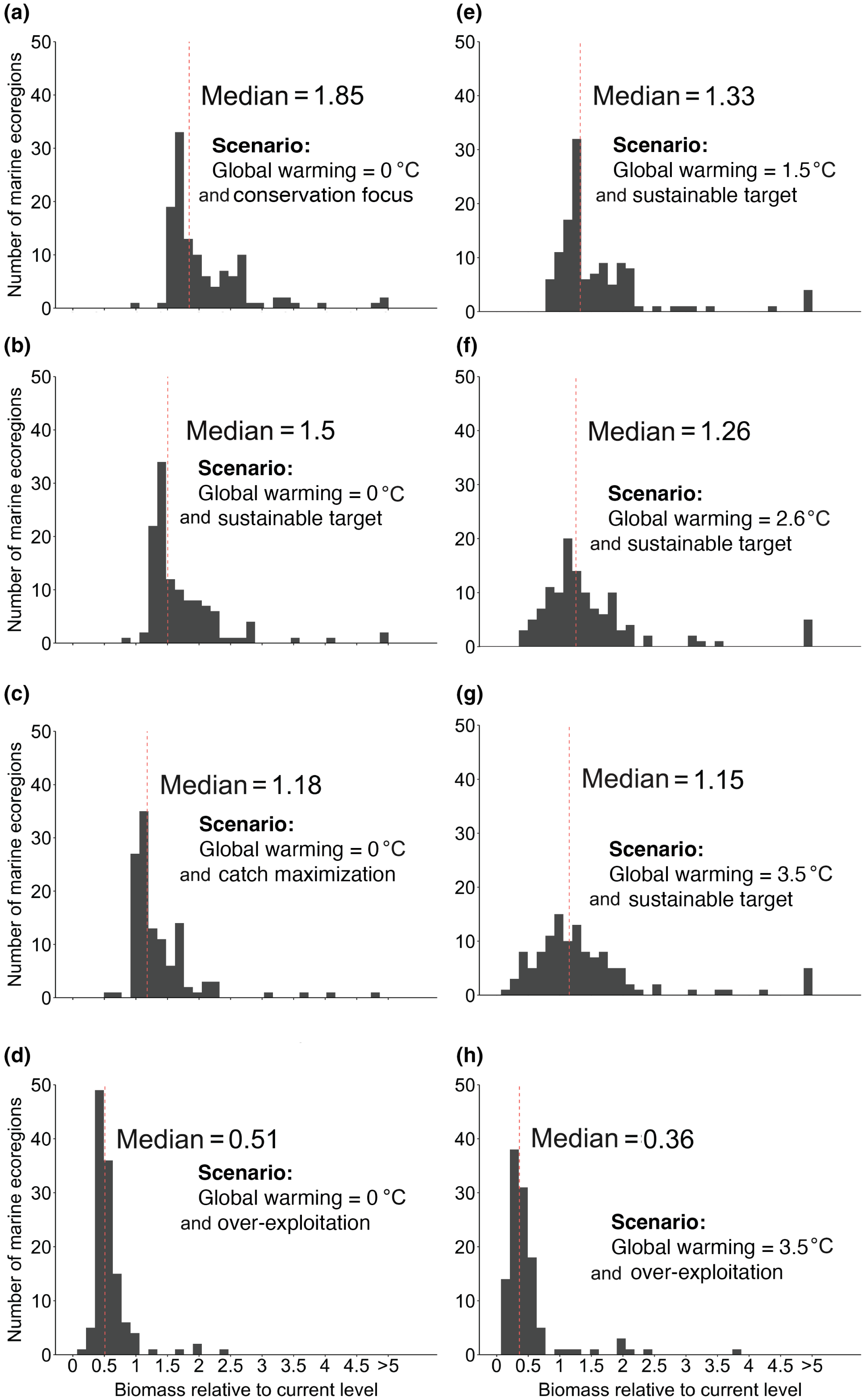

FIGURE 3 Projected biomass relative to the current (2014–2018) level ($B_{T,F}/B_{T=0,F=0}$) for the studied marine ecoregions under different scenarios of global warming (T) and fishing levels (F/F_{MSY}). Only marine ecoregions for which the slope of the relationship between biomass and global warming levels is significantly (at the 0.05 level) different from zero are included here ($N = 121$). Reference unexploited biomass does not include global warming ($T = 0°C$). Scenarios of global warming and fishing levels include (a) $T = 0°C$ and $F/F_{MSY} = 0.5$, (b) $T = 0°C$ and $F/F_{MSY} = 0.75$, (c) $T = 0°C$ and $F/F_{MSY} = 1$, (d) $T = 0°C$ and $F/F_{MSY} = 1.5$, (e) $T = 1.5°C$ and $F/F_{MSY} = 0.75$, (f) $T = 2.6°C$ and $F/F_{MSY} = 0.75$, (g) $T = 3.5°C$ and $F/F_{MSY} = 0.75$, (h) $T = 3.5°C$ and $F/F_{MSY} = 1.5$. Median values across marine ecoregions for each scenario are highlighted by red dashed lines and the annotated median values.

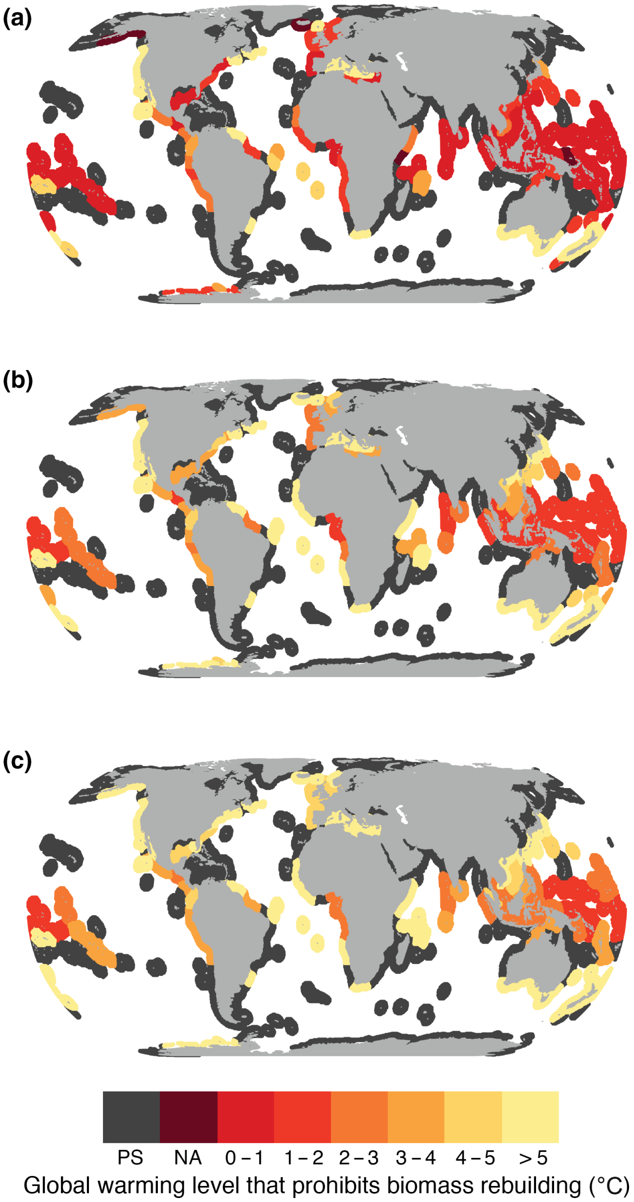

FIGURE 4 The maximum global warming levels at or above which we project we would not be able to rebuild biomass from current (average 2010–2014) levels for marine ecoregions of the world under the three rebuilding scenarios. (a) 'Catch maximization' scenario ($F/F_{MSY} = 1$), (b) 'sustainable target' scenario ($F/F_{MSY} = 0.75$), (c) 'conservation focus' scenario ($F/F_{MSY} = 0.5$). PS indicates that the marine ecoregion has a positive relationship between biomass rebuilding and global warming levels or the relationship is insignificant at 0.05 level. NA indicates that no biomass rebuilding can be attained even without climate change (global warming = 0°C). [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Climate change is projected to globally impact the biomass rebuilding needed for most marine ecoregions to help us achieve the United Nations' Sustainable Development Goal 14—Life Below Water. For most marine ecoregions with significant scaling between biomass and global warming levels (Hypothesis a or b, Figure 1), our results project that climate change will negatively impact biomass rebuilding capacity (Hypothesis a) with a clear spatial pattern in the magnitude of impacts. Particularly, in marine ecoregions with negative scaling between biomass rebuilding and global warming level, existing rebuilding efforts are likely to have already been impacted by the current level of climate change, although fishing has been a dominant factor driving changes in fish biomass across most ecoregions. Without recognizing the negative impacts of climate change, biomass rebuilding targets and anticipated ecological responses to rebuilding plans will become unrealistic.

Our study indicates that the effectiveness of fisheries reforms in climate adaptation is more constrained when rebuilding objectives, in addition to maximization of profits and yields (Gaines et al., 2018), are considered. In contrast, for marine ecoregions with positive scaling between biomass rebuilding and global warming level, the apparent achievement of targets with consideration of climate change may overestimate the effectiveness of rebuilding plans. Thus, our findings underline previous recommendations to urgently develop climate-adapted and resilient rebuilding plans (Bell et al., 2018; Punt, 2011). In addition, as the existence of biomass rebuilding plans and their effective implementation, if such plans are available, vary largely between countries and regions, it is important to ensure rebuilding plans are indeed effectively implemented and to monitor progress toward targets (Froese et al., 2018; Hilborn et al., 2020).

Our model projects that global warming below 1.5°C relative to pre-industrial level would be sufficient to prevent exploited stock biomass to rebuild in some marine ecoregions, particularly if fishing effort is not kept at a relatively lower level (i.e., more conservation focused). For example, Atlantic cod (*Gadus morhua*) in the Gulf of Maine (Pershing et al., 2015) and Pacific salmon (*Oncorhynchu* spp.) in British Columbia (Beamish, 2022) did not rebuild as expected, despite substantial investment and activities in support of conservation efforts. Climate change impacts on these species is likely one of the reasons for lack of success in rebuilding efforts (Meng et al., 2016; Pershing et al., 2015). It should be noted that the biological tolerance levels of some species may be more sensitive to the changes in ocean conditions associated species global warming above 1.5°C as their upper thermal tolerance set a biological limit to adaptation to ocean warming and deoxygenation (Clarke et al., 2022; Pörtner & Peck, 2010). However, these stocks have some additional scope to adjust through distribution shifts within given ecoregions, mainly to higher latitude or deeper waters or following local temperature gradients. Thus, the estimated global warming level at or above which no biomass rebuilding is projected in an ecoregion is generally higher than the biological upper thermal tolerance of the exploited species.

Climate change represents a big barrier for countries managing their marine resources to achieve SDG-14, particularly across the tropics—countries which bear the most significant cost of, and yet are the least responsible for, current global warming levels (Sumaila et al., 2019). Most of the 32 marine ecoregions that are unable to rebuild biomass if global warming exceeds 1.5°C relative to pre-industrial levels are in the tropics. These tropical marine ecoregions, such as those located around Indonesia and the Philippines, are among the most biodiverse systems on earth, yet also represent some of the systems that are the most over-fished and threatened by other human stressors (Lam et al., 2020; O'Hara et al., 2021). Moreover, tropical regions are facing high risk of climate impacts on food security as their agriculture and fisheries systems are projected simultaneously to be negatively impacted by climate change (Cinner et al., 2022; Thiault et al., 2019). In addition, plans to rebuild exploited marine populations are still largely limited to temperate regions, where funding and research capacity have been available to expend to relevant data collection and the development of targeted rebuilding plans. Yet, as highlighted in our study, marine ecoregions that are likely to be the most affected by loss of rebuilding potential under recent global warming levels are mostly situated in the tropics. Our findings highlight the need to expand and significantly support efforts to examine the past and current effects of climate change on ecosystem rebuilding in tropical regions (Lam et al., 2020), to strengthen means of data collection as well as relevant human and financial capacity.

Our projections suggest that a further increase in global warming levels would demand more stringent limitations of fishing effort to reach, or get closer to, biomass rebuilding targets—particularly across tropical marine ecoregions. However, such restrictions will need to consider social impacts resulting from their implementation given that fisheries across many of these tropical marine ecoregions contribute substantially to food and nutrition security, revenue and employment as well as cultural practices (Batista et al., 2014; Bell et al., 2021; Cheung et al., 2021; Gillett, 2016; Golden et al., 2016; Lam, Cheung, Reygondeau, et al., 2016; Teh & Sumaila, 2013; Wabnitz et al., 2018). Particularly in areas where communities are strongly dependent on fisheries and have limited alternative livelihood opportunities and/or capacity to cope, substantial efforts are needed to support communities' adaptation and resilience in the face of reductions in fishing activities. Biomass rebuilding in most extra-tropical marine ecoregions would also be increasingly impacted by climate change under fisheries management aimed at production maximization.

A portfolio of marine conservation measures, that are practical and explicitly consider justice principles, would be needed to support effective biomass rebuilding under climate change. When implemented “right,” such measures would therefore extend the global warming level at or below which biomass can be rebuilt. However, the effectiveness of these conservation measures would also be impacted by climate change. Planning and implementation of these measures with long-term resilience in mind can help increase their climate adaptability (Bates et al., 2019; Wilson et al., 2020). The effectiveness of these conservation measures requires substantial human and knowledge capital as well as financial investments, resources that are often limited in the most climate-sensitive marine ecoregions identified in this study, putting a disproportionately large burden on areas that have contributed least to emissions. Indeed, given an often poor track record in or lack of concern for social equity considerations in conservation efforts to date, future efforts will need to expressly commit to the pursuit of socially equitable conservation (Bennett et al., 2021; Gill et al., 2019; Kockel et al., 2020). Although addressing climate change in biomass rebuilding efforts would increase implementation costs, over the long term, these investments will have substantial pay-offs for the well-being of communities as they will help secure climate-resilient economic and social development and the biodiversity that is necessary to support this development (Mason et al., 2021; Pörtner et al., 2021).

Extending the global warming level at or below which biomass can be rebuilt in marine ecoregions would require a global coordinated effort and support of resources (Blasiak & Wabnitz, 2018; Hannah, 2010; Reed et al., 2020; Waldron et al., 2013). For example, in the western and central Pacific, fisheries play key roles not only in providing communities with key sources of food but also key sources of income (Bell et al., 2021; Gillett, 2016), yet their projected global warming level for biomass rebuilding to be able to occur is among the lowest and requires more stringent limits on fishing activities to achieve greater biomass rebuilding potential. Resolving tensions between biodiversity, social, and climate nexus challenges would require more in-depth understanding of the ways in which marine biodiversity contributes to livelihood and economies. Such information would help forge means to secure sustainable and equitable social and economic support through, for instance, adaptive governance mechanisms and fisheries management measures (Cisneros-Montemayor et al., 2021). Specific examples of financing approaches to support climate-adaptive biomass rebuilding include innovative revenue generation mechanisms from distant-water fishing operations in a country's adjacent high seas (Bell et al., 2021), or targeted, co-designed, and well-structured overseas development aid mechanisms (Blasiak & Wabnitz, 2018) that respond to nationally identified needs and priorities.

We highlight several sources of uncertainties that need to be considered when interpreting model projections. First, the CMSY method utilized to evaluate the past and current status of exploited fish and invertebrate species in marine ecoregions is associated with inherent uncertainties (Froese et al., 2018; Ovando et al., 2021). Second, the ESMs and DBEM projections of climate change effects on ocean conditions and changes in biomass have multiple sources of uncertainties that have been examined and explored in detail in previous studies (Cheung et al., 2021; Cheung, Jones, et al., 2016; Lotze et al., 2019; Séférian et al., 2020). The use of multimodel ensembles to estimate relative biomass and fishing mortalities can help explore such uncertainties in future analyses (Cheung, Frölicher, et al., 2016; Free, Jensen, et al., 2020; Tittensor et al., 2021). Moreover, the representation of the species included in this study is biased toward marine ecoregions in developed countries where scientific data are generally more available. However, we have selected modeling methods that are less data demanding, allowing them to be applicable to most marine ecoregions. In the future, expanding data collection efforts and developing better methods to account for Indigenous, traditional, and local knowledge will be important to help reduce the information gaps between regions. Despite current caveats in projections, the low global warming levels below which biomass rebuilding can occur in the tropics and the stronger limitation on fishing effort that is needed to rebuild stocks across tropical regions should be robust to these uncertainties, even if the numerical projections are likely to have larger variabilities. Future studies could apply alternative modeling approaches and analyses using multimodel ensembles to facilitate the exploration of uncertainties and improve the robustness of the findings.

5 | CONCLUSIONS

In summary, climate change is challenging biomass rebuilding in marine ecoregions globally. A prerequisite for effective biomass rebuilding efforts worldwide is to achieve the global warming target set under the Paris Agreement. Moreover, more conservation—instead of catch maximization—focused rebuilding plans would substantially increase the climate resilience of biomass rebuilding. However, even with strong conservation efforts, projections show that many tropical marine ecoregions will be unable to rebuild biomass if global warming goes beyond 1.5°C relative to pre-industrial level. Many fisheries in these tropical marine ecoregions also face trade-offs between the need to engage in more conservation intensive pathways for climate adaptation and the loss of important social, cultural, and economic benefits derived from and associated with fisheries. Climate change will thus increase the demand for additional resources and community support to help reduce trade-offs between biodiversity conservation, food, and livelihood provisioning and climate adaptation to facilitate effective biomass rebuilding. A portfolio of marine conservation measure, that are practical and explicitly consider justice principles will be needed to support effective biomass rebuilding under climate change (Cisneros-Montemayor et al., 2021; Khan & Neis, 2010). Development and implementation of these measures would require global coordinated efforts and support of human as well as financial resources (Sumaila et al., 2021). These investments will have substantial pay-off for the well-being of communities in the long term as it will help secure climate-resilient economic and social development and the biodiversity that is necessary to support the achievement of the sustainable development goals.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be available in Dryad: https://doi.org/10.5061/dryad.79cnp5hzf.

ORCID

William W. L. Cheung https://orcid.org/0000-0001-9998-0384
Juliano Palacios-Abrantes https://orcid.org/0000-0001-8969-5416
Tayler Clarke https://orcid.org/0000-0002-9438-5794
Muhammed A. Oyinlola https://orcid.org/0000-0001-5177-854X
Colette C. C. Wabnitz https://orcid.org/0000-0002-5076-9163

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