

# Ocean Biomass and Climate Change

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## Abstract

Climate change is having profound impacts on marine life and ocean ecosystems. Changes in physical and chemical parameters are influencing biological processes on all levels of organisation, altering food web structure and ecosystem dynamics. This chapter provides a brief overview on observed climate change impacts on marine populations and ecosystems, and then synthesizes state-of-the-art ensemble model projections on global and coastal ocean biomass at different trophic levels. We highlight relevant consequences of projected biomass changes for fisheries and human development and discuss necessary adaptations in marine management, conservation, and governance to mitigate some climate change effects.

## Glossary

APECOSM	Apex Predators Ecosystem Model
BOATS	BiOeconomic MArine Trophic Size-spectrum model
CMIP5	Coupled Model Intercomparison Project Round 5
CMIP6	Coupled Model Intercomparison Project Round 6
DBEM	Dynamic Bioclimate Envelope Model
DBPM	Dynamic Benthic-Pelagic Model
EEZ	Exclusive Economic Zone
ESM	Earth System Model
FAO	Food and Agriculture Organization
FEISTY	FishErLes Size and functional TYpe model
Fish-MIP	Fisheries and marine ecosystem Model Intercomparison Project
GCM	General Circulation Model
GDP	Gross Domestic Product
GFDL	Geophysical Fluid Dynamics Laboratory
GHG	Greenhouse Gas
HDI	Human Development Index
HTL	Higher Trophic Level
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

IPCC	Intergovernmental Panel for Climate Change
IPSL	Institute Pierre Simon Laplace
IUCN	International Union for Conservation of Nature
MEM	Marine Ecosystem Model
MIP	Model Intercomparison Project
MPA	Marine Protected Area
NPP	Net Primary Production
RCP	Representative Concentration Pathway
SDG	Sustainable Development Goal
SSP	Shared Socio-economic Pathway
SST	Sea Surface Temperature
ZOOMS	ZOOplankton Model of Size spectra

### Key Points

- Overview on physical, chemical, and biological changes in the ocean with climate change.
- Description of ensemble model projections in marine ecosystems.
- Synthesis of climate-induced future changes in global and coastal ocean biomass.
- Consequences of climate change impacts for fisheries dependent societies and human development.
- Implications for climate change adaptation in marine conservation and ocean governance.

## 1 Introduction

Climate change is altering a range of physical and chemical properties in the ocean that are influencing biological processes on all levels of organisation (IPBES, 2019a,b; IPCC, 2019a,b, 2022; Letcher, 2021). This includes the growth, reproduction and survival of individual organisms, the abundance and distribution of populations and species, the composition and dynamics of marine food webs, and the diversity and productivity of entire ocean ecosystems (Lotze *et al.*, 2021; Worm and Lotze, 2021). Together, these changes affect the amount of ocean biomass at various spatial and temporal scales and at different taxonomic and trophic levels (Bryndum-Buchholz *et al.* 2019; Kwiatkowski *et al.*, 2020; Lotze *et al.*, 2019). Although some impacts of climate change are already observed and measured in the ocean today, a better understanding of projected future impacts of continued climate change will help to anticipate the consequences of marine ecosystem and ocean biomass changes for seafood supply, fisheries, tourism, and other human uses of the ocean (Blanchard *et al.*, 2017; Boyce *et al.*, 2020; Eddy *et al.*, 2021). This will provide insight into the adaptations needed in fisheries management, ocean governance, and marine conservation to mitigate some climate change impacts (Bryndum-Buchholz *et al.*, 2021, 2022; Tittensor *et al.*, 2019).

Over the past two decades, great progress has been made in the modelling of marine ecosystem dynamics and the projection of climate change impacts on marine species, food webs and ocean biomass (Lotze *et al.*, 2019; Tittensor *et al.*, 2018, 2021). This has been fuelled by the increased scientific understanding of the blue realm, the rapidly growing availability of data and information, and the enhanced computational power and modelling capacity. Climate-impact modelling now includes a range of possible approaches, from species distribution models to trophic, size structure and composite ecosystem models, which can be designed for regional or global scales (Tittensor *et al.*, 2018). There is also a range of climate models and climate change scenarios available to force the ecological models and project future trajectories.

Overall, the impacts of climate change are projected to increase into the future, but the magnitude of projected changes depends on the model used and climate change scenario applied (IPCC, 2019a, 2022; Lotze *et al.*, 2019; Tittensor *et al.*, 2021). The impacts also depend on other human activities, for example, extensive fishing that may intensify or mitigate climate change effects (Blanchard *et al.*, 2017; Galbraith *et al.*, 2017). Climate change projections from ecosystem models are typically highly variable and largely incomparable; however, the recent use of ensemble modelling and model intercomparisons have helped overcome some limitations and have provided more refined climate-impact projections, including mean trends and estimates of uncertainty (Tittensor *et al.*, 2018, 2021; Lotze *et al.*, 2019).

In this chapter, we first provide a brief overview on the major climate change drivers in the ocean followed by their general consequences on marine species and ecosystems. We then describe different modelling approaches to derive climate change projections of ocean biomass, and how to combine them into an ensemble modelling approach. Results from such a model ensemble are then used to outline projected 21<sup>st</sup> century changes in biomass in the global ocean, and in the national waters of countries around the world, as this is where people most strongly depend on direct access to marine resources. In the final section, we highlight the implications of projected ocean biomass changes for fisheries and human societies, and how marine management, conservation and governance can adapt to climate change to mitigate some of the consequences for ocean ecosystems and human societies.

## 2 Climate Change Drivers in the Ocean

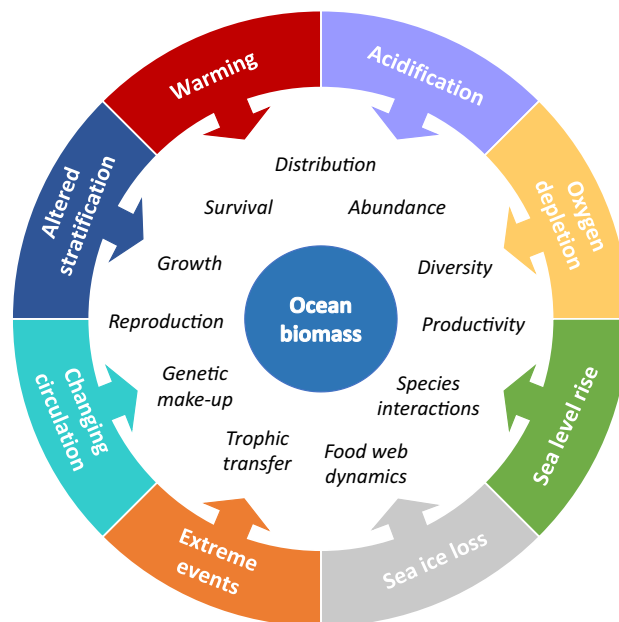
One major consequence of anthropogenic greenhouse gas (GHG) emissions into the atmosphere is the warming of the ocean — from its surface layers into the deep sea, from the poles to the equator, and from shallow coasts to the open ocean (Bindoff *et al.*, 2019; IPCC, 2019a, 2022; Kwiatkowski *et al.*, 2020; Williamson and Guinder, 2021). Despite a general trend of warming, the magnitude and rate of warming are not the same everywhere, with high spatial variability both vertically and horizontally. Surface waters and shallow seas are warming relatively fast compared to more slow changes in the interior ocean, although the latter may have more long-term momentum (IPCC, 2019a, 2022; Williamson and Guinder, 2021). There are also differences in the rate of warming among ocean basins (Bryndum-Buchholz *et al.* 2019; Schlunegger *et al.*, 2020), and notable hotspots of warming in the Northwest Atlantic Ocean and large regions in southeastern Australia (Hobday and Pecl, 2014).

Unequal warming of waterbodies results in altered patterns of ocean circulations, shifts in the strength of ocean currents and upwelling, and enhanced stratification of the water column, which in turn affect the availability, vertical and horizontal transport of nutrients, oxygen, and other ocean properties (Worm and Lotze, 2021). For example, warming waters in combination with altered ocean circulation reduce the concentration of subsurface oxygen (O<sub>2</sub>), which most marine life depends upon (Shepherd *et al.*, 2017). Stronger water column stratification reduces the influx of nutrients from deeper ocean layers to surface waters, a resource primary production heavily relies on (Bopp *et al.*, 2001; Li *et al.*, 2020; Lotze *et al.*, 2022). Warming waters also lower the extent of sea ice, and enhanced input of meltwater and freshwater result in rising sea levels (IPCC, 2019a, 2022). The enhanced uptake of carbon dioxide (CO<sub>2</sub>) in ocean water causes acidification by lowering the pH (Bopp *et al.*, 2013), an important chemical property for many forms of marine life, particularly those with calcified shells or structures (Hofmann *et al.*, 2010; Cornwall *et al.*, 2021).

These physical and chemical changes affect biological organisms and processes in the ocean (Fig. 1). It is important to note, that many climate change effects are not linear and underlie increasing variability, which can lead to more frequent extreme events, including storms and marine heatwaves (Oliver *et al.*, 2018). Furthermore, climate change drivers, such as warming and acidification, do not act in isolation. Cumulative impacts as well as potentially complex interactions between climate change and other anthropogenic drivers, such as fishing, challenge the understanding and management of human impacts on socio-ecological systems (Williamson and Guinder, 2021; Worm and Lotze, 2021).

## 3 Biological Consequences in the Ocean

Changes in physical and chemical ocean properties influence all levels of biology and ecology in the ocean and, ultimately, ocean biomass on various temporal and spatial scales (Fig. 1) (IPCC, 2022; Williamson and Guinder, 2021; Worm and Lotze, 2021). This includes the basic survival, growth and reproduction of individual organisms, the distribution and abundance of populations, the interaction of species within communities, the dynamics and trophic transfer in food webs, and the biodiversity and productivity of ecosystems (Fig. 1) (IPBES, 2019a; IPCC, 2019a, 2022; Williamson and Guinder, 2021; Worm and Lotze, 2021). Consequently, climate change drivers can have



**Fig. 1** Conceptual graph of the physical and chemical climate change drivers (outer circle) and their influences on marine organisms, populations, communities, and ecosystems, all of which affect ocean biomass (inner circle).

differing impacts depending on the species, life-history stage, or age class. Currently, about 16% of the species listed as vulnerable, endangered, or critically endangered by the International Union for Conservation of Nature (IUCN) around the world are directly or indirectly threatened by climate change (Lotze, 2021). Many of these species are also threatened by other human activities, and the ecological response to these combined impacts is challenging to disentangle or understand in its entirety (Heneghan *et al.*, 2021). In the following, we therefore provide a broad overview of observed changes in marine ecosystems at different levels of organization that inform marine ecosystem modelling and climate change projections (see below).

All marine organisms depend on a range of physical and chemical conditions to perform their physiological processes, including growth and reproduction (Fig. 1). If conditions are in their preferred range or around their optimum, physiological performance is highest, while suboptimal conditions result in reduced performance, and conditions outside their tolerance level can be lethal. Younger age groups or life-history stages can be more sensitive to change than adults, with consequences for reproduction and recruitment (Britten *et al.*, 2016; Dahlke *et al.*, 2020). The effects of changing environmental characteristics also depend on background conditions. For example, ocean warming seems to reduce growth and body size of many fishes in warmer regions, where species are already at their upper temperature limit, compared to increased growth and size in cold regions, where temperature was limiting previously (Cheung *et al.*, 2013a; Shackell *et al.*, 2010; Sheridan and Bickford, 2011). If warming exceeds the tolerance or preferred range for a species, individuals may die or move in search for colder conditions to deeper, polar, or offshore waters. Together, this can affect the distribution and abundance of a population or species as well as its size structure or genetic make-up (Pinsky *et al.*, 2013, 2019; Scheffers *et al.*, 2016; Trisos *et al.*, 2020). If conditions reach extreme levels, populations may collapse or become regionally or globally extinct (Caputi *et al.*, 2016; Cavole *et al.*, 2016; Pershing *et al.*, 2015; Oliver *et al.*, 2017). Alternatively, some species may be able to adapt or show evolutionary responses to climate change that may alter their tolerance for warming waters or other climate-driven impacts (Scheffers *et al.*, 2016; Worm and Lotze, 2021).

With climate-induced changes in the ocean environment and marine organisms, many populations and species will increase or decrease in abundance in certain areas and shift their distribution on local to global scales (Fig. 1). Resulting range shifts have already been observed for many fish and invertebrate species (Nye *et al.*, 2009; Simpson *et al.*, 2011) and are projected to continue in the future (Jones and Cheung, 2015; Shackell *et al.*, 2014). For example, warming waters in many temperate regions are leading to an influx of warm-adapted species from the south, such as in the North Sea (Hiddink and Hofstede, 2008) and the Gulf of Maine (Friedland *et al.*, 2020), a process known as tropicalization. At the same time, cold-adapted species are declining or disappearing as they move further north, deeper, or offshore in search for colder waters (Cheung *et al.*, 2013a; Pinsky *et al.*, 2013). On a global scale, both observed and predicted range shifts are leading to an overall poleward shift of many marine species, whereas polar and sea-ice dependent species decline or disappear (Cheung *et al.*, 2009; Jones and Cheung, 2015; Michel *et al.*, 2012). Declines and extinctions also occur in tropical waters where temperatures exceed maximum tolerances (Cheung *et al.*, 2009; Jones and Cheung, 2015; Trisos *et al.*, 2020).

Not all species move or change at the same pace or in the same direction, resulting in a restructuring of marine communities and ecosystems (Fig. 1). Prey species, predators and competitors may shift on different temporal and spatial scales leading to mismatches in trophic relationships and altered food web dynamics (Asch, 2015; Beaugrand *et al.*, 2003; Frank *et al.*, 2006, 2007; Petrie *et al.*, 2009). Thereby, changes at the bottom of marine food webs, such as in plankton and microbial communities have repercussions at higher trophic levels (Boyce *et al.*, 2015; Boyce and Worm, 2015; Cavicchioli *et al.*, 2019; Kwiatkowski *et al.*, 2018, 2019; Lefort *et al.*, 2015). Similarly, shifts in the distribution and abundance of habitat-building species, such as coral reefs, seagrass beds, or kelp forests alter the availability of nursery, breeding and foraging grounds and opportunities for shelter and settlement (Hughes *et al.*, 2017; Wernberg *et al.*, 2016; Wilson and Lotze, 2019; Wilson *et al.*, 2019) with consequences on habitat-dependent or -associated species. Climate change can also enhance the prevalence of marine infectious diseases, alter parasite-host relationships, and intensify harmful algal blooms with consequences for affected populations and communities (Burge *et al.*, 2014; Harvell *et al.*, 2002).

Together, these variable and complex changes in species distribution, abundance and interactions alter biodiversity patterns and the fundamental structure and functioning of marine food webs and ecosystems with consequences for ocean biomass (Fig. 1). Resolving all climate change effects in marine ecosystems is difficult and represents a key challenge in our understanding of climate-induced changes in the ocean (Coll *et al.*, 2020; Lotze *et al.*, 2019; Tittensor *et al.*, 2018). At an ecosystem level, however, climate change will affect the basic amount of primary production available to secondary producers and higher trophic levels (Chassot *et al.* 2010; Eddy *et al.*, 2021). For example, warming decreases the cell size and biomass of many phytoplankton species and alters species composition (Boyce and Worm, 2015; Lewandowska *et al.*, 2014; Morán *et al.*, 2010). This will alter the abundance and quality of food and the flux of organic matter and energy to consumers at higher trophic levels, with consequences for secondary production and biomass levels (Eddy *et al.*, 2021). Thus, both observational and modelling studies suggest that basic environmental changes are amplified at higher food web levels (Lefort *et al.*, 2015; Lotze *et al.*, 2019). Ultimately, this will affect human societies through changes in the supply of seafood, fisheries production, livelihoods, tourism, and other ocean benefits (Blanchard *et al.*, 2017; Boyce *et al.*, 2020).

#### 4 Modelling Climate Change Impacts on Marine Ecosystems

Over the past decades, a range of modelling approaches has been developed aimed at predicting the present and future distribution, abundance and interactions of marine species, size classes, functional or trophic groups with climate change on global and regional scales. This generally requires a global or regional climate model (see below), the output of which (Table 1) then forces an ecological model representing parts of or whole marine ecosystems. For example, Cheung *et al.* (2011) developed a

global species distribution model based on bioclimatic envelopes or niches (DBEM) for 892 fish and invertebrate species (Table 2). Galbraith *et al.* (2017) developed a global size-structure model (BOATS) that calculates the production of commercially harvested fish across multiple size spectra, and Jennings and Collingridge (2015) developed a size-structure model (Macroecological) to calculate mean size composition and abundance of 180 body mass classes (Table 2). Blanchard *et al.* (2012) developed a dynamic size- and trait-based model (DBPM) that incorporates a pelagic predator and a benthic detritivore size spectrum (Table 2). Christensen *et al.* (2015) developed a global trophodynamic model (EcoOcean) based on species interactions and energy transfer across trophic levels among 51 species and functional groups, and Maury (2010) developed a composite (hybrid) 3D dynamic energy budget model of three size-based communities, including epipelagic, mesopelagic, and migratory components (APE-COSM). Heneghan *et al.* (2020) developed a global size-spectrum model (ZoomSS) that resolves zooplankton composition specifically (Table 2). Each of these models has its advantages and limitations, as each model is a necessary simplification of the overall ocean ecosystem, with its own set of structures, processes, and resolutions.

In the first attempts of climate change projections, most studies usually combined one climate model with one ecosystem model, which represents only one possible combination of ideas of how marine ecosystems may respond to climate change. Moreover, different studies used a variety of temporal time frames and spatial regions or resolutions, so that the projected outcomes are difficult to compare (Lotze *et al.*, 2019; Tittensor *et al.*, 2018). Another issue concerns the advantages and disadvantages of regional versus global models. Whereas regional models or regionally downscaled global models can provide higher temporal and spatial resolution and include more ecological details and complexity, they also have higher parameter needs, which makes the projection of continuous climate change impacts challenging (Laurent *et al.*, 2021; Tittensor *et al.*, 2018). In comparison, global models have larger spatial and temporal coverage but coarser resolution and less details, which often compromises projections particularly for more complex coastal or polar regions but can reduce parameter needs (Laurent *et al.*, 2021; Lotze *et al.*, 2019; Tittensor *et al.*, 2021). Computational run-time is another important aspect to consider when comparing regional versus global models, run-time typically increases with model complexity, spatial resolution and coverage of the model, and with the time frame examined.

To overcome the limitations of individual climate or ecosystem models, model intercomparison projects (MIP) have been established that use standardized climate change forcings to produce projections that are comparable in magnitude and direction of change (Bryndum-Buchholz *et al.*, 2019; Kwiatkowski *et al.*, 2020; Lotze *et al.*, 2019; Tittensor *et al.*, 2018). Furthermore, these standardized projections can be combined into an ensemble mean change, and the inter-model standard deviation (SD) can be calculated as a measure of variability or uncertainty around this mean (Tittensor *et al.*, 2018). One can also calculate a model agreement, indicating how many models agree in the direction of change, either positive (increase) or negative (decline) (Bryndum-Buchholz *et al.*, 2019; Lotze *et al.*, 2019). What is more, by combining a standardized set of ecosystem models, differences in model outputs can be assessed systematically which is important for continuous model improvement (Heneghan *et al.*, 2021). By including a variety of model structures and processes, the combined model ensemble represents more possible climate and ecosystem outcomes, with higher reliability of projected trends compared to any individual model result (Bopp *et al.*, 2013; Tittensor *et al.*, 2018). Such MIPs can be done on a global scale with global models or for specific regions involving both regional and global models (Laurent *et al.*, 2021; Tittensor *et al.*, 2018).

Using an ensemble model approach has been well established in the climate sciences by the Coupled Model Intercomparison Project (CMIP; WCRP World Climate Research Programme), which is currently in its 6<sup>th</sup> iteration (CMIP6). CMIP results have been used to inform policy and governance, for example, through results published by the IPCC (2019a,b, 2022). To project future climate-driven changes in the ocean, general circulation models (GCMs) are used to project changes in physical and chemical parameters, such as temperature, salinity, oxygen, pH, currents, and sea ice (Bopp *et al.*, 2013). These can be coupled with a biochemical model to form an Earth system model (ESM) that also projects net primary production and the biomass of phytoplankton and zooplankton as important foundations for marine food webs (Bopp *et al.*, 2013; Kwiatkowski *et al.*, 2020). ESMs are then forced with standardized emissions scenarios following representative concentration pathways (RCPs) linked to the shared socio-economic pathway (SSP) framework (Kwiatkowski *et al.*, 2020; O'Neill *et al.*, 2014). These range from a strong mitigation and low emissions scenario (RCP2.6; Van Vuuren *et al.*, 2011) to a low mitigation and high emissions scenario (RCP8.5; Riahi *et al.*, 2011), with two intermediate scenarios (RCP4.5, RCP6.0; Masui *et al.*, 2011; Thomson *et al.*, 2011).

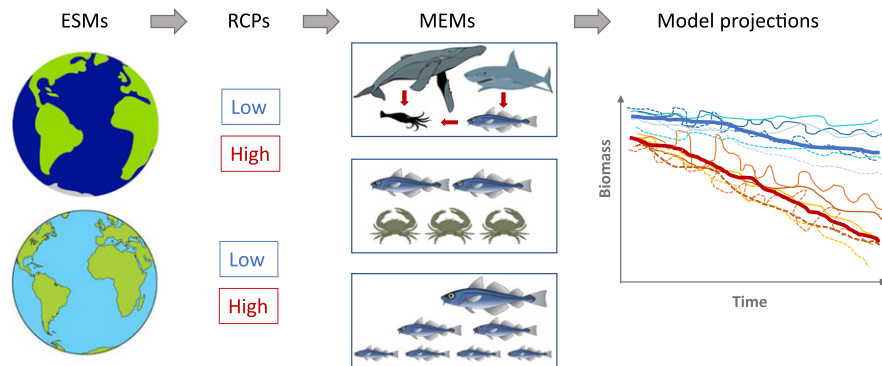
Of the CMIP5 round, which has been used for many of the marine ecosystem projections over the past decade, an ensemble of  $n = 10$  models has been used for marine ESM analyses (Bopp *et al.*, 2013; Kwiatkowski *et al.*, 2019, 2020). Results suggest a general increase in sea surface temperature (SST) by the end of the 21<sup>st</sup> century, from an average of  $+1.15^{\circ}\text{C}$  under RCP2.6 to  $+3.04^{\circ}\text{C}$  under RCP8.5 since the late 19<sup>th</sup> century (Table 1). These rates of warming are accompanied by decreases in pH (stronger acidification), dissolved  $\text{O}_2$  (deoxygenation), upper ocean nutrient availability ( $\text{NO}_3^-$  nitrate concentration) and net primary production (NPP), and these decreases become stronger with higher RCPs (Table 1). The next generation CMIP6 round, which incorporated several improvements over CMIP5 (Kwiatkowski *et al.*, 2020; Ruane *et al.*, 2016; Tittensor *et al.*, 2021) has only become available recently, and an ensemble of  $n = 13$  models has been used for marine ESM analyses (Kwiatkowski *et al.*, 2020). In terms of future climate conditions, CMIP6 generally projects more severe increases in SST and more severe decreases in pH,  $\text{O}_2$  and  $\text{NO}_3^-$  under every combined emissions scenario (SSP-RCP), except for less severe yet more variable changes in NPP (Table 1).

The standardized climate change projections produced by different ESMs and RCPs (CMIP5) or SSP-RCPs (CMIP6) can be used as standardized forcings for a range of marine ecosystem models to evaluate the impacts of climate change in the ocean (Fig. 2). Such an ensemble modelling approach has been established in the Fisheries and Marine Ecosystem Modelling Intercomparison Project (Fish-MIP, Tittensor *et al.*, 2018). In its first round of simulations, Fish-MIP included 6 global marine ecosystem models that were forced with CMIP5 outcomes (Lotze *et al.*, 2019; Table 2). In its second round of simulations, Fish-MIP included 9 global marine ecosystem models forced with CMIP6 outcomes (Tittensor *et al.*, 2021; Table 2). Fish-MIP also contains a variety of

**Table 1** Comparison of global changes in sea surface temperature (SST), surface ocean pH, subsurface dissolved oxygen concentration ( $O_2$  at 100–600 m) and upper-ocean nitrate concentration ( $NO_3^-$  at 0–100 m) across CMIP5 ( $n = 10$ ) and CMIP6 ( $n = 13$ ) ensembles. Results represent mean ( $\pm$  SD) anomalies in 2080–2099 relative to 1870–1899 and are listed for different emissions scenarios as RCPs for CMIP5 and SSPs-RCPs in CMIP6. Data from Kwiatkowski *et al.* (2020).

	CMIP5				CMIP6			
	RCP2.6	RCP4.5	RCP6.0	RCP8.5	SSP1–2.6	SSP2–4.5	SSP3–6.0	SSP5–8.5
$\Delta$ SST [ $^{\circ}$ C]	+1.15 (0.33)	+1.74 (0.44)	+1.82 (0.54)	+3.04 (0.62)	+1.42 (0.32)	+2.10 (0.43)	+2.89 (0.61)	+3.48 (0.78)
$\Delta$ pH	–0.14 (0.001)	–0.21 (0.002)	–0.27 (0.004)	–0.38 (0.005)	–0.16 (0.002)	–0.26 (0.003)	–0.35 (0.003)	–0.44 (0.005)
$\Delta O_2$ [ $mmol\ m^{-3}$ ]	–3.71 (2.47)	–6.16 (2.86)	–6.56 (3.27)	–9.51 (2.13)	–6.36 (2.92)	–8.14 (4.08)	–12.44 (4.40)	–13.27 (5.28)
$\Delta NO_3^-$ [ $mmol\ m^{-3}$ ]	–0.38 (0.15)	–0.51 (0.14)	–0.60 (0.18)	–0.66 (0.49)	–0.53 (0.23)	–0.66 (0.32)	–0.87 (0.43)	–1.07 (0.45)
$\Delta$ NPP [%]	–3.42 (2.47)	–5.06 (3.56)	–4.82 (3.60)	–8.54 (5.88)	–0.56 (4.12)	–1.13 (5.81)	–1.40 (7.25)	–2.99 (9.11)

Note: Reproduced from Kwiatkowski, L., Torres, O., Bopp, L., *et al.*, 2020. Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. *Biogeosciences* 17, 3439–3470.



**Fig. 2** Conceptual graph showing the process of ensemble modelling where standardized outputs of selected Earth System Models (ESMs) and emissions scenarios (RCPs) are combined with different marine ecosystem models (MEMs) to project a range of individual ecosystem trajectories (thin lines) which can then be combined into an ensemble mean (thick lines).

regional marine ecosystem models, but the results of global and regional projections have not yet been compared systematically, so we focus on results from global model projections here. We note that not all ESMs provide all the necessary physical and biochemical parameters needed to force the range of marine ecosystems, which all have different parameter requirements (Tittensor *et al.*, 2018). Thus, only outcomes of Geophysical Fluid Dynamics Laboratory (GFDL) climate model GFDL-ESM2M (CMIP5) or GFDL-ESM4.1 (CMIP6) and the Institute Pierre Simon Laplace (IPSL) climate model IPSL-CM5A-LR (CMIP5) or IPSL-CM6A-LR (CMIP6) were used, but these span the possible range of low (GFDL) to high (IPSL) results, and their ensemble mean is a good representation of average CMIP5 or CMIP6 outcomes (Lotze *et al.*, 2019; Tittensor *et al.*, 2018, 2021).

In addition to the effects of climate change, other forcings can also be used in some marine ecosystems, for example, fishing pressure as an important impact on many marine species, food webs and ecosystems (Galbraith *et al.*, 2017; Lotze *et al.*, 2019). In the first round of Fish-MIP, a ‘no-fishing’ scenario, and a ‘fishing’ scenario with constant 2005 fishing effort levels were used (Lotze *et al.*, 2019), as temporally and spatially resolved future fishing scenarios were not yet available. However, more refined future fishing scenarios have been conceptualized (Maury *et al.*, 2017) and are currently being developed for numerical integration into marine ecosystem models. Moreover, future scenarios of other human impacts, such as developments in aquaculture, diet and consumer changes, and marine management and conservation efforts, are also being developed to be included in future projections of marine ecosystems and ocean biomass (Maury *et al.*, 2017).

## 5 Ocean Biomass Changes

In the following sections, we first share the projected climate change impacts on global ocean biomass from Fish-MIP with CMIP5, as described in the previous section, and compare these to the magnitude of projections from CMIP6 where possible. To evaluate

**Table 2** Overview of different marine ecosystem models used in the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP) with CMIP5 and CMIP6. Note that EcoTroph, FEISTY, and ZooMSS were not included in the analyses by (Lotze *et al.*, 2019) but was used for comparison of both CMIPs in (Tittensor *et al.*, 2021)

<i>Model abbreviation</i>	<i>Full name</i>	<i>Type</i>	<i>CMIP5</i>	<i>CMIP6</i>	<i>Key reference</i>
APECOSM	Apex Predators ECOSystem Model	Composite model (size- and trait-based; functional group structure)	x	x	Maury (2010); Maury and Poggiale (2013)
BOATS	BiOeconomic mARine Trophic Size-spectrum model	Size-based model	x	x	Carozza <i>et al.</i> (2016, 2017)
DBEM	Dynamic Bioclimate Envelope Model	Species distribution model	x	x	Cheung <i>et al.</i> (2011, 2016)
DBPM	Dynamic Benthic-Pelagic Model	Size-based model	x	x	Blanchard <i>et al.</i> (2012)
EcoOcean	–	Composite model (trophodynamic and species distribution model)	x	x	Christensen <i>et al.</i> (2015); Coll <i>et al.</i> (2020)
EcoTroph	–	Trophic-based model		x	Gascuel <i>et al.</i> (2011); Du Pontavice <i>et al.</i> (2021)
FEISTY	Fisheries Size and Functional Type Model	Composite model		x	Petrik <i>et al.</i> (2019)
Macroecological	–	Size-based model	x	x	Jennings and Collingridge (2015)
ZooMSS	Zooplankton Model of Size Spectra	Composite (size- and trait-based; functional group structure)	x	x	Heneghan <i>et al.</i> (2020)

Note: Reproduced from Lotze, H.K., Tittensor, D.P., Bryndum-Buchholz, A., *et al.*, 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences of the United States of America* 116, 12907–12912. Tittensor, D.P., Novaglio, C., Harrison, C.S., *et al.*, 2021. Next-generation ensemble projections reveal higher climate risks for marine ecosystems. *Nature Climate Change* 11, 973–981.

changes in coastal waters, we extracted the projected biomass changes from the global Fish-MIP with CMIP5 outcomes for Exclusive Economic Zones (EEZs) of nations around the world. These are described in detail for different countries, regions, and trophic levels, and compared to projected changes at the global scale.

### 5.1 Global Ocean Changes

The ensemble of 6 marine ecosystem models (MEMs) combined with 2 ESMs and 4 RCPs from Fish-MIP with CMIP5 (Table 2) revealed general declines in global marine biomass that intensified with stronger emissions scenarios (Fig. 3, left panel). Considering just the climate change effect and no fishing, mean global animal biomass decreased by 4.8% ( $\pm 3.5\%$  SD) under the low emissions or strong mitigation scenario (RCP2.6) and 17.2% ( $\pm 10.7\%$  SD) under the high emissions scenario (RCP8.5) in 2090–2099 relative to 1990–1999 (Lotze *et al.*, 2019). However, projected biomass declines were similar for all RCPs until approximately 2030, after which they begin to diverge. Across all RCPs, biomass declined by an average of 5% for every 1°C of Earth surface warming (IPCC, 2019a,b; Lotze *et al.*, 2019).

All individual model projections also showed general declines in global marine animal biomass, although with strong variation in the magnitude – but not direction – of declines (Fig. 3, right panel). This highlights the uncertainties in different model structures and processes in both the ESMs and MEMs (Heneghan *et al.*, 2021; Lotze *et al.*, 2019), whereas the ensemble mean provides an average across different model outcomes. Incorporating a constant fishing scenario at 2005 levels in a subset of MEMs revealed that fishing did not alter the general climate change effect (Lotze *et al.*, 2019). However, the direct effect of fishing on marine biomass declines can be substantial, but more refined and standardized fishing scenarios are needed to make effective comparisons among ecosystem models (see above).

Recently, the same Fish-MIP ensemble model simulations were performed with the next generation of ESMs from CMIP6 (Tittensor *et al.*, 2021) and the inclusion of more MEMs (Table 2). Compared to CMIP5-forced results, mean projected global marine animal biomass from CMIP6-forced MEMs showed significantly stronger declines by 2100, particularly from 2030 forward (Fig. 4). Resulting biomass declines were –19% ( $\pm 6.57\%$  SD) by 2099 under the high emissions scenario relative to 1990–1999, and –6.75% ( $\pm 2.88\%$  SD) under the strong mitigation scenario, about 2% stronger than in CMIP5-forced MEMs (Tittensor *et al.*, 2021). Moreover, the variability, expressed as standard deviation (SD) around the ensemble mean, was lower in CMIP6- compared to CMIP5-forced MEMs, suggesting a reduction in projection uncertainty, possibly due to improvements made in next generation CMIP6 climate models as well as the inclusion of a wider range of marine ecosystem models (Tittensor *et al.*, 2021).

Despite overall global declines, the direction and magnitude of projected biomass changes varies across ocean regions (Fig. 4). Spatially heterogeneous patterns are found in both CMIP5 and CMIP6 (Lotze *et al.*, 2019; Tittensor *et al.*, 2021), with 71% of global grid cells showing the same direction of change for the ensemble mean biomass (Tittensor *et al.*, 2021). Generally, there are consistent projections of biomass declines in tropical and many temperate regions, whereas biomass increases are projected in many polar regions in both CMIP5 (Fig. 4) and CMIP6 (Lotze *et al.*, 2019; Tittensor *et al.*, 2021). The general patterns of increased biomass production in polar regions and decreased production in temperate to tropical regions have also been shown for phytoplankton and zooplankton communities (Fig. 5) and are related to the trends in SST and NPP, with stronger warming and decreasing primary production in temperate to tropical regions (Kwiatkowski *et al.*, 2018; Tittensor *et al.*, 2021), although other climate change drivers, such as pH, O<sub>2</sub>, and sea ice loss, also play a role (see above; Fig. 5).

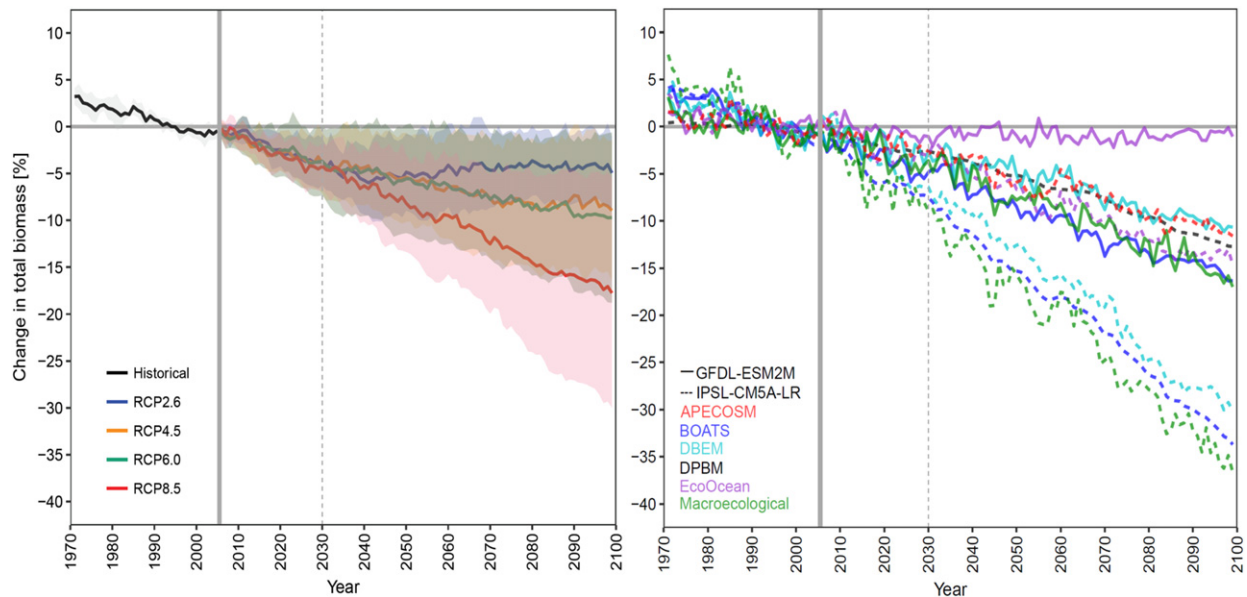
When comparing changes in marine animal biomass across ocean basins, the North Atlantic Ocean showed the strongest declines ( $-31.7\% \pm 14.1\%$  SD) in 2090–2099 relative to 1990–1999 under RCP8.5, followed by the North Pacific Ocean ( $-25.4\% \pm 16.9\%$  SD), and the South Atlantic, South Pacific and Indian Oceans showed declines between  $-14.3\%$  and  $-20.4\%$  (Bryndum-Buchholz *et al.*, 2019). In the Southern and Arctic Oceans, however, marine animal biomass was projected to increase by  $19.2\% (\pm 35.6\%$  SD) and  $82.0\% (\pm 201.1\%$  SD), respectively; these increases were associated with large variability indicating high uncertainty in polar ocean projections (Bryndum-Buchholz *et al.*, 2019). Overall, these changes in marine animal biomass will have consequences for both global and regional fisheries, seafood production, and other ocean ecosystem services (see below).

Taken together, global projections across multiple food web levels suggest that the effects of climate change amplify at higher trophic levels, meaning that higher trophic levels show stronger declines in response to warming than lower trophic levels, a process called trophic amplification (Fig. 6). This amplification has been shown within plankton communities (Kwiatkowski *et al.*, 2018, 2019), fish communities (Lefort *et al.*, 2015) and overall marine food webs (Coll *et al.*, 2020; Lotze *et al.*, 2019). For CMIP5-forced Fish-MIP projections (Fig. 6), mean declines in phytoplankton, zooplankton, and higher trophic level biomass amount to  $-1.8\%$ ,  $-3.5\%$ , and  $-4.8\%$ , respectively, under RCP2.6; and  $-7.1\%$ ,  $-12.8\%$ , and  $-17.2\%$ , respectively, under RCP8.5 by the end of the 21<sup>st</sup> century relative to the 1990s (Lotze *et al.*, 2019). These results clearly show the process of trophic amplification which becomes more severe with stronger emissions scenarios (Fig. 6).

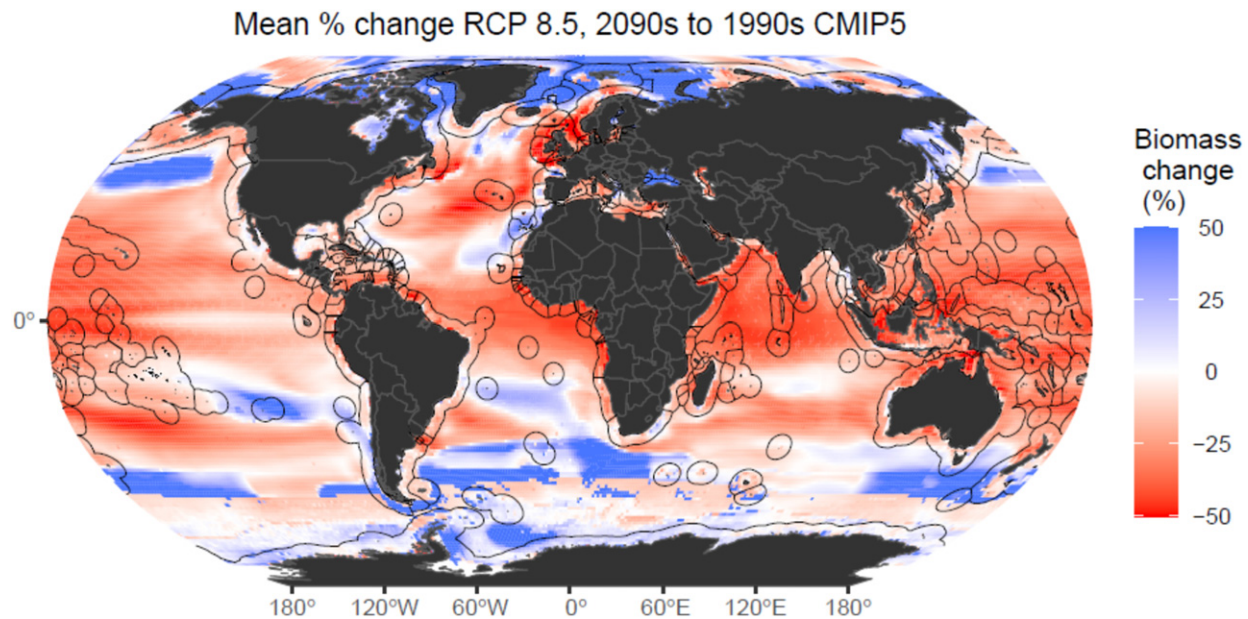
### 5.2 Coastal Ocean Changes

To more closely evaluate changes in total marine animal biomass and key environmental variables in coastal waters, we extracted results from the global CMIP5-forced Fish-MIP datasets (Table 2, Lotze *et al.*, 2019; Tittensor *et al.*, 2021; ISIMIP Repository, 2022), which were available on a 1 x 1 degree grid, for each Exclusive Economic Zone (EEZ, see outlines in Fig. 4) around the world





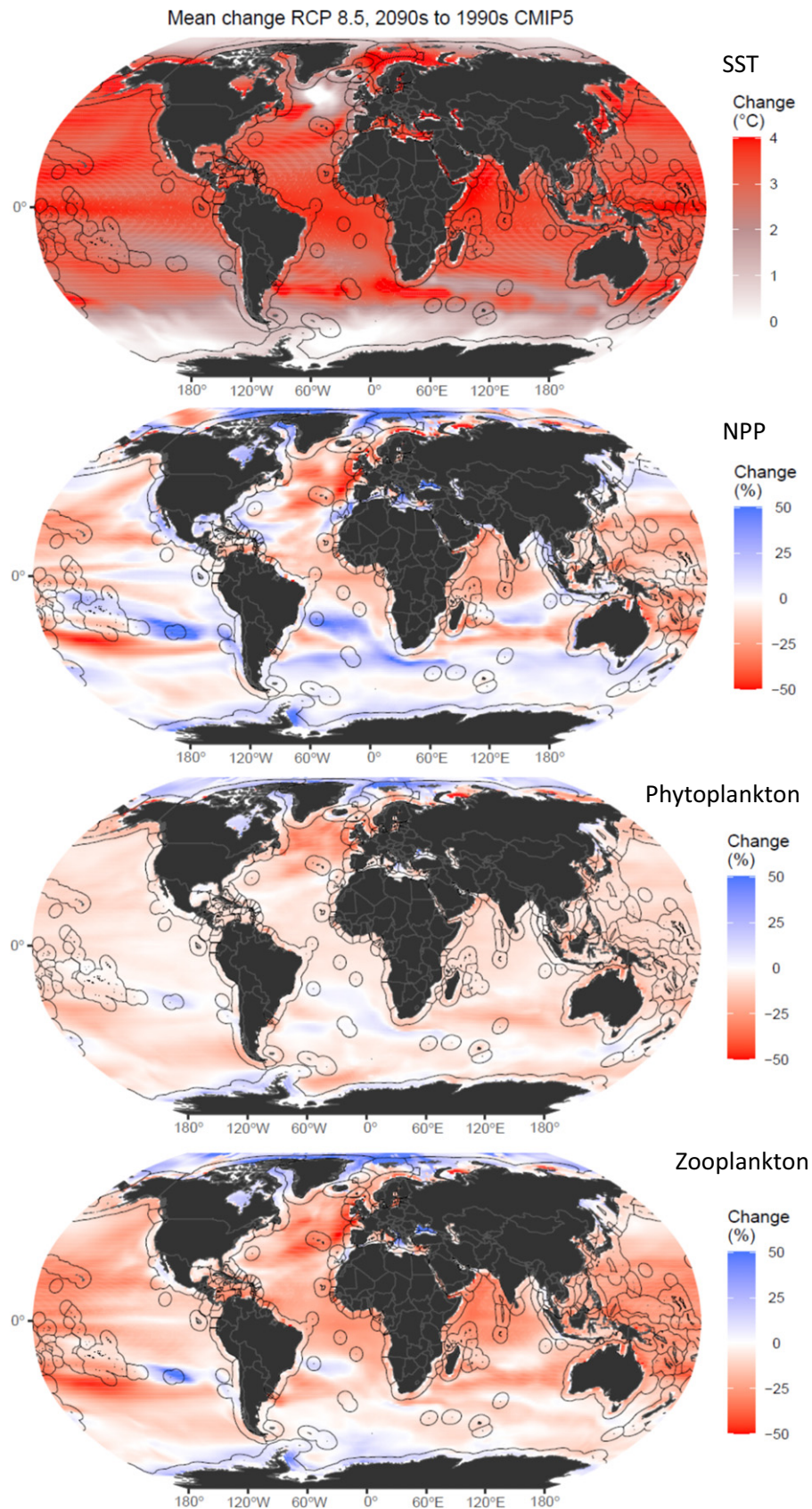
**Fig. 3** Projections of global changes in marine animal biomass based on the ensemble of marine ecosystem models under four different emissions scenarios (RCPs) (left panel) and individual ecosystem model projections with either GFDL-ESM2M or IPSL-CM5A-LR under RCP8.5 (right panel). All values represent % biomass change relative to 1990–1999. The vertical grey line indicates the separation of the historical and future projection period, and the dotted line marks the year 2030. All model projections are based on Fish-MIP with CMIP5 (Table 2). Redrawn with permission from Lotze *et al.* (2019).



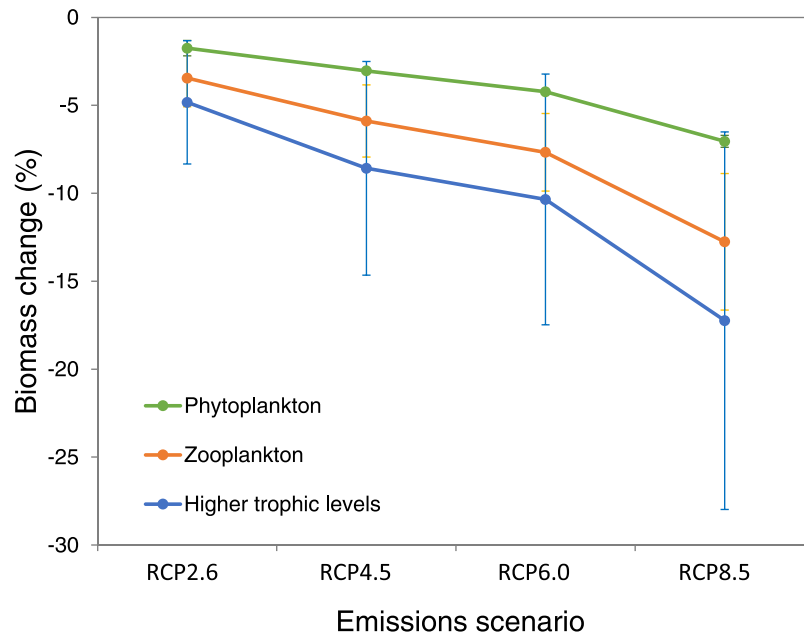
**Fig. 4** Global distribution of ensemble mean changes in marine animal biomass in the 2090s relative to the 1990s under RCP8.5 in CMIP5-forced marine ecosystem models. Blue colours indicate biomass increases and red colours biomass decreases. The thin black lines depict the Exclusive Economic Zones (EEZs) of nations around the world. EEZ data from “Relevant Websites” section. Data from Fish-MIP redrawn from Tittensor *et al.* (2021).

provided by the Flanders Marine Institute (2019). Of all  $n = 231$  nations with an EEZ, we only evaluated those with a coastline of more than 100 km and at least two  $1 \times 1$  degree grid cells ( $n = 143$ ) within its EEZ boundary to calculate a mean and SD. Other EEZs ( $n = 88$ ) were deemed too small with less reliable results.

Across all 143 EEZs, 22 (15.4%) showed increases in biomass under the high emissions scenario compared to 121 (84.6%) which showed decreases (Fig. 7). Nations with the strongest increases were those with EEZs including polar oceans either in the Arctic, such as Canada, Russia, United States of America (USA) and Iceland, or in the Southern Ocean, such as Argentina, Chile and



**Fig. 5** Global distribution of mean changes in sea surface temperature (SST), net primary production (NPP), phytoplankton biomass and zooplankton biomass in the 2090s relative to the 1990s under RCP8.5 across two CMIP5 ESMs (GFDL-ESM2M and IPSL-CM5A-LR). SST increases are depicted in red as are warming-related decreases in NPP and plankton biomass. The thin black lines depict the Exclusive Economic Zones (EEZs) of nations around the world that are discussed below. EEZ data from “Relevant Websites” section. Data from Fish-MIP redrawn from [Tittensor et al. \(2021\)](#).



**Fig. 6** Trophic amplification shown in global projections of climate-induced changes at different trophic levels, including phytoplankton biomass (green), zooplankton biomass (orange), and higher trophic level biomass (blue) based on CMIP5 projections. Shown are ensemble mean changes ( $\% \pm \text{SD}$ ) in the 2090s relative to 1990s under four emissions scenarios (RCPs). Adapted from Lotze *et al.* (2019)

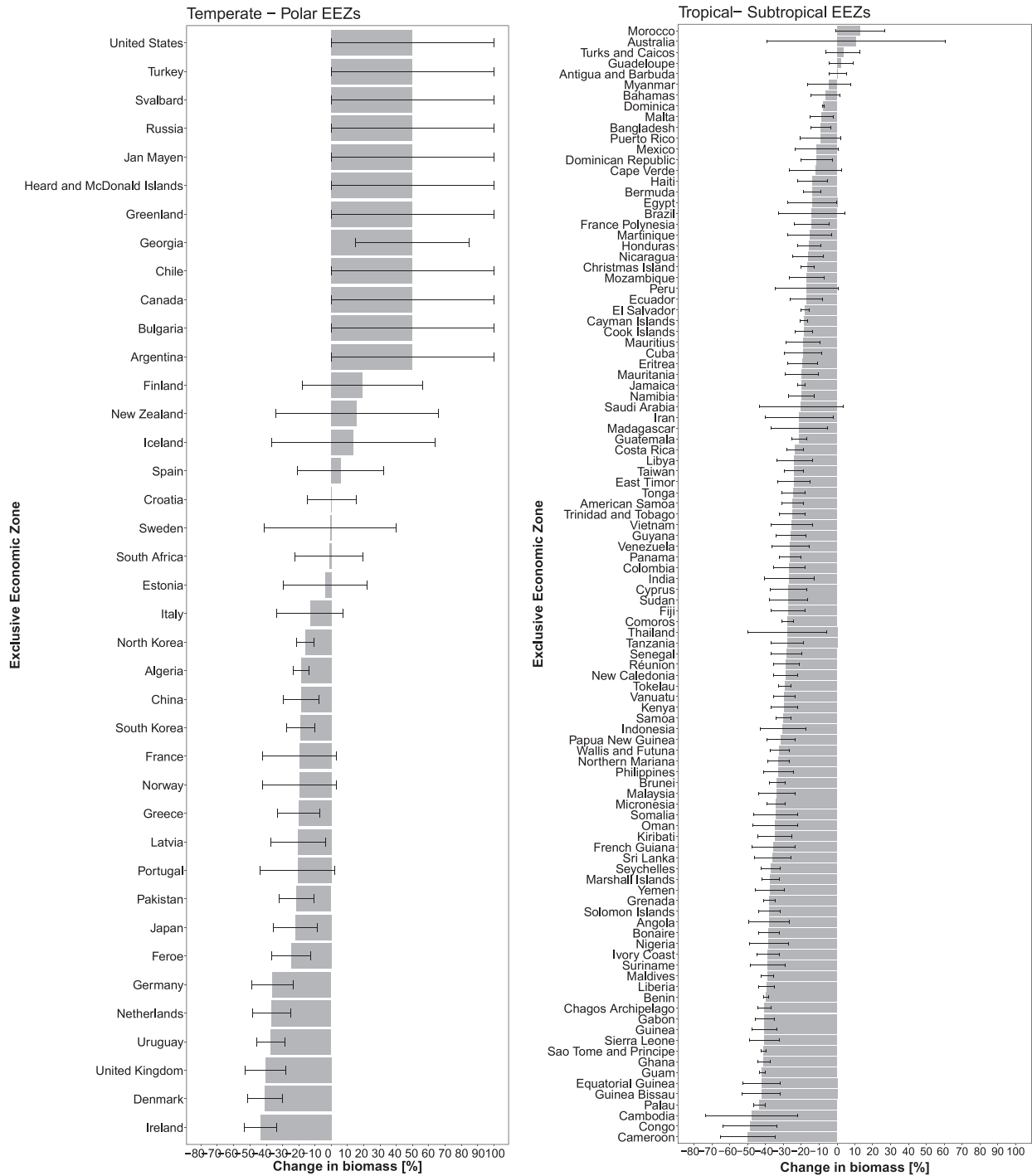
New Zealand (Fig. 7). It is important to note, however, that these countries will also experience biomass declines in their respective temperate waters (Fig. 4), for example Canada in its Atlantic and Pacific temperate regions (Bryndum-Buchholz *et al.*, 2020a,b). In comparison, nations with the strongest decreases in biomass included many nations in Western Africa (e.g., Congo, Ghana, Guinea Bissau, Sierra Leone), Southeast Asia (e.g., Cambodia) and Europe (e.g., Ireland, United Kingdom, Denmark). Across all EEZs, marine animal biomass decreased by  $-17.6\% (\pm 24.7\% \text{SD})$  on average. However, the high variability around ensemble means, particularly in countries with increasing biomass around polar and coastal regions as well as in marginal seas (e.g., Turkey's EEZ in the Black Sea), highlights considerable projection uncertainty.

As on the global scale, the changes in marine animal biomass in coastal waters are influenced by several climate change drivers and biomass changes at lower trophic levels. Generally, most tropical-subtropical countries show stronger warming of SST ( $>3^\circ\text{C}$ ) and associated NPP declines in their coastal waters, whereas temperate-polar countries show more variable SST and NPP changes (Figs. 8 and 9). Across all nations, SST warming generally coincides with decreases in NPP (Fig. 8), although at lower rates of warming, NPP can be both increasing or decreasing.

Patterns of trophic amplification, where biomass changes are stronger with each higher trophic level, are also clearly visible across most tropical and temperate EEZs in which marine animal biomass (HTL) decreases (Fig. 9). Averaged across the 143 EEZs, mean phytoplankton biomass decreased by  $-7.7\% (\pm 5.9\% \text{SD})$ , mean zooplankton biomass by  $-15.6\% (\pm 14.1\% \text{SD})$  and mean higher trophic level biomass by  $-17.6\% (\pm 24.7\% \text{SD})$  by the end of the 21<sup>st</sup> century under RCP8.5. This trophic amplification in coastal waters is slightly stronger than globally, with  $-7.1\% (\pm 0.3\% \text{SD})$ ,  $-12.8\% (\pm 3.9\% \text{SD})$ , and  $-17.2\% (\pm 10.7\% \text{SD})$  for phytoplankton, zooplankton, and higher trophic levels, respectively. However, for nations with increasing marine animal biomass (HTL), which are generally EEZs that include polar regions (see above), these patterns of trophic amplification disappear. Such a latitudinal gradient of trophic amplification has also been shown within plankton communities (Kwiatkowski *et al.*, 2019) and may be related to the rapidly changing ocean conditions that enhance primary production in polar waters with positive effects on higher trophic levels. Unfortunately, these processes are poorly understood and not well represented in global climate or ecosystem models, which may explain the high variability and uncertainty around projected changes in polar regions.

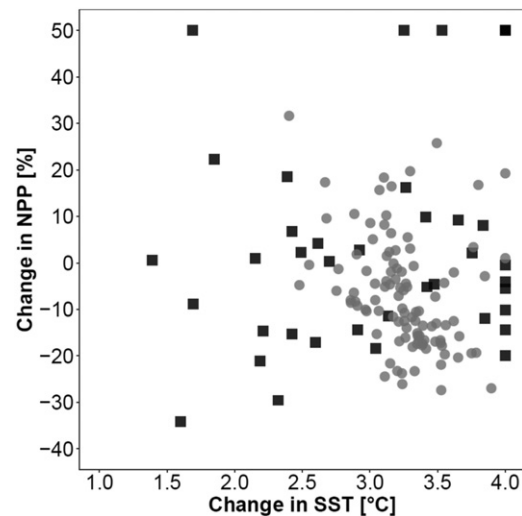
## 6 Implications

Climate-driven changes in the abundance and distribution of marine species and marine animal biomass will have implications for human well-being globally and nationally (Blanchard *et al.*, 2017; Boyce *et al.*, 2020; Sala *et al.*, 2021). Based on projected biomass changes with climate change, it appears that both the global ocean and many temperate and tropical nations will experience lower primary production with warming waters and related decreases in marine animal biomass. This has important implications for fisheries, management, and conservation as those biomass decreases will likely lead to seafood shortages, reduced



**Fig. 7** Relative change in marine animal biomass (%) in 2090–2099 relative to 1990–1999 in each Exclusive Economic Zone (EEZ) of nations around the world. Data represent the CMIP5-forced Fish-MIP projections under RCP8.5 and are shown as the ensemble mean change ( $\pm$  SD) per EEZ ordered by magnitude from biomass increases (top) to biomass decreases (bottom). We note that maximum increases or decreases were cut-off at  $\pm 50\%$  due to high uncertainties in polar oceans and to facilitate visualization. Fish-MIP data derived from [Tittensor et al. \(2021\)](#).

livelihoods, biodiversity loss and other consequences for human well-being. In contrast, polar regions, and nations with polar waters in their EEZs will likely benefit from warming waters due to enhanced primary production and marine animal biomass. This also has important implications for fisheries, management and conservation as projected biomass increases will provide new opportunities for resource exploitation and livelihoods, yet also provide challenges for biodiversity conservation and the equality among nations.



**Fig. 8** Relationship between changes in sea surface temperature (SST) and net primary production (NPP) in 2090–2099 relative to 1990–1999 under RCP8.5 across temperate-polar (squares) and tropical (circles) nations' Exclusive Economic Zones (EEZs). Data are ensemble means of two CMIP5 ESMs (GFDL-ESM2M and IPSL-CM5A-LR) that were used in Fish-MIP. Fish-MIP data derived from [Tittensor et al. \(2021\)](#).

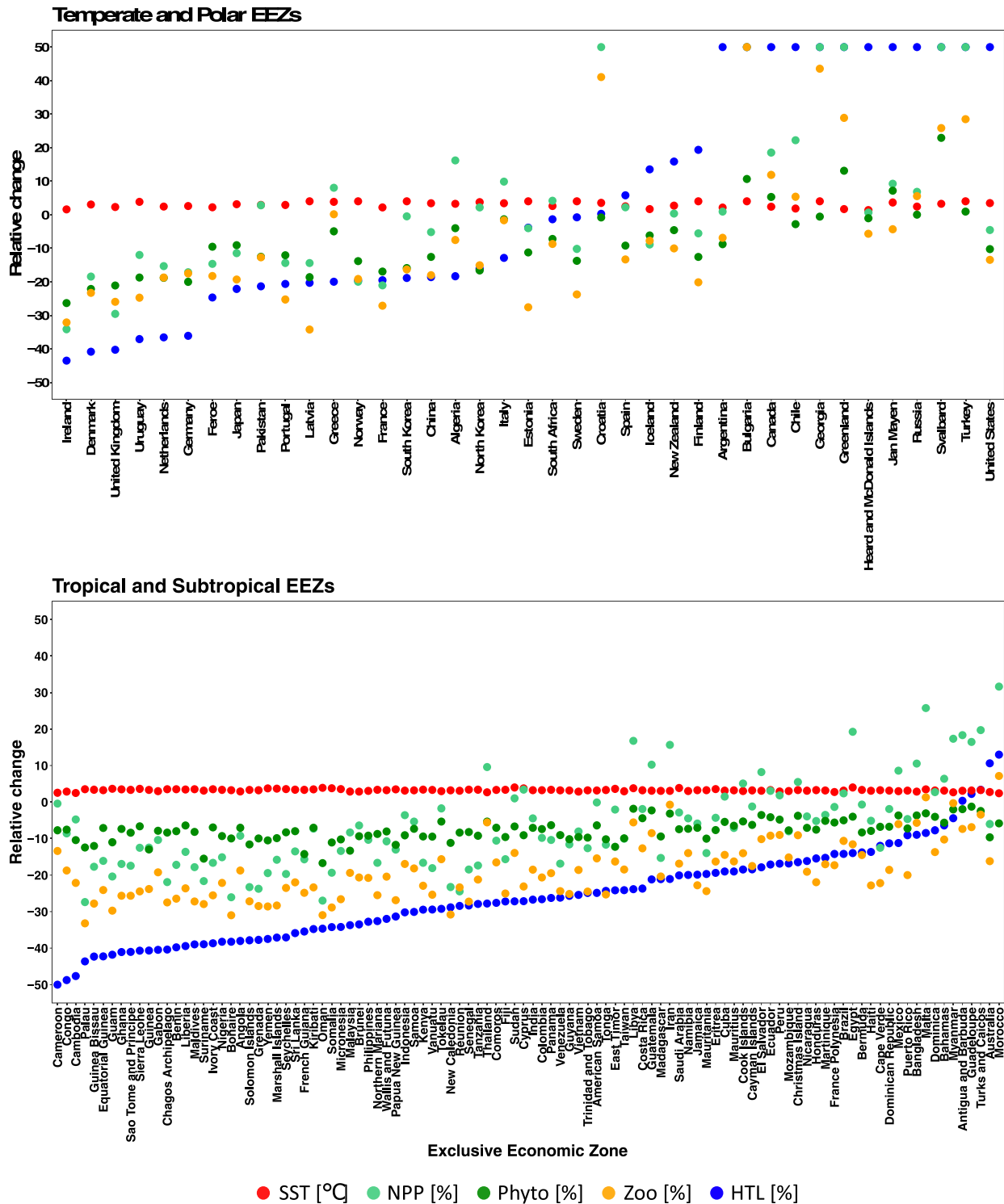
## 6.1 Fisheries

Shifting ranges of target species and changing biomass levels will affect the location and potential fisheries catch within and across nations ([Boyce et al., 2020](#); [Bryndum-Buchholz et al., 2020a](#)). Over the past decade, several changes have been observed in fish stocks around the world and have been related to the effects of climate change. These changes include decreased growth and body size ([Cheung et al., 2013a](#); [Shackell et al., 2010](#); [Sheridan and Bickford, 2011](#)), reduced recruitment ([Britten et al., 2016](#)), changes in abundance, biomass, and productivity ([Britten et al., 2017](#); [Cheung et al., 2010, 2013b](#); [Free et al., 2019](#); [Tai et al., 2019](#)), shifts in phenology ([Asch, 2015](#); [Platt et al., 2003](#); [Poloczanska et al., 2013, 2016](#)), and altered spatial distribution ([Cheung et al., 2010](#); [MacKenzie et al., 2014](#); [Nye et al., 2009, 2011](#); [Pershing et al., 2015](#); [Pinsky et al., 2013](#)) including local disappearances or extirpations as well as new appearances or invasions. Fishers, fisheries operations, and fisheries management need to adapt to these changes as they affect the availability of target species, catch rates, and fishing locations with consequences for livelihoods, seafood supply and sustainability ([Cheung et al., 2010, 2013b](#); [Lotze et al., 2018](#)).

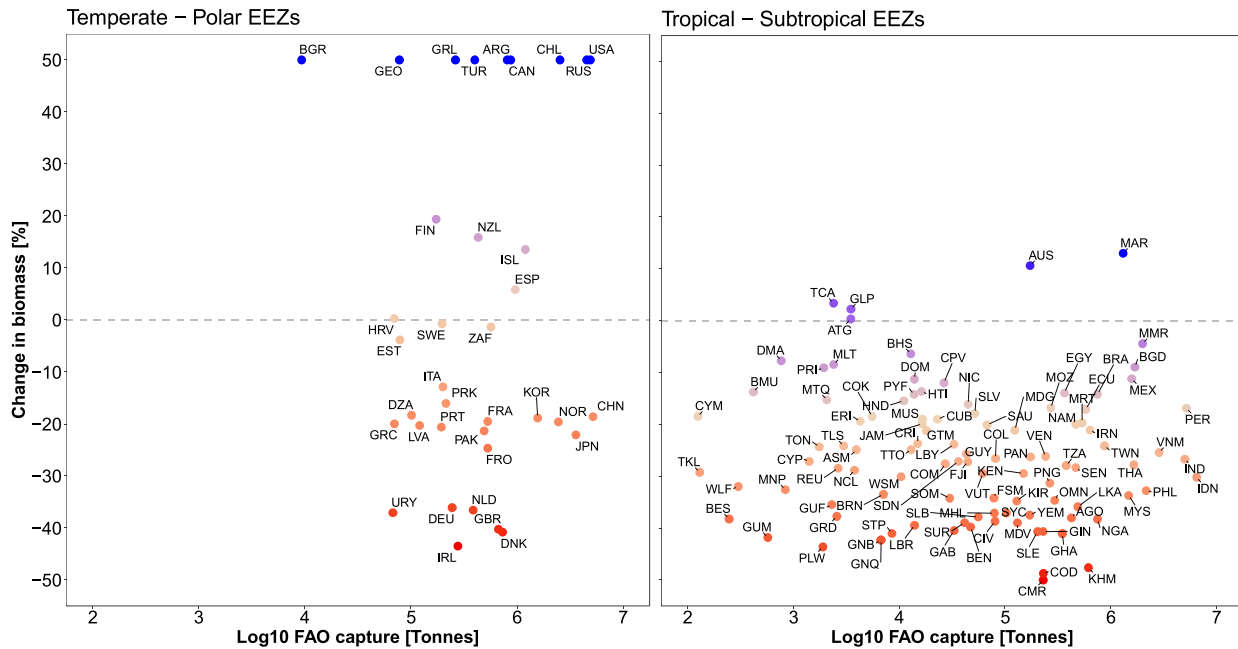
As seen in the projections of marine animal biomass over the 21<sup>st</sup> century, not all climate change effects are negative in terms of biomass loss, and particularly polar regions, and nations with polar areas in their EEZs, are likely to experience biomass increases with potential benefits for their fisheries ([Fig. 7](#)). For example, Canada and the USA are projected to have overall biomass increases, although they will experience biomass decreases in their temperate waters ([Fig. 4](#); [Bryndum-Buchholz et al., 2020a,b](#)). When we relate projected climate-induced biomass changes per EEZ to the current magnitude of each nation's capture fisheries, most temperate and tropical countries will experience future biomass declines independent of their current fisheries catch ([Fig. 10](#)). This indicates that future fisheries losses are a universal and global problem. In contrast, among the winners are mostly temperate-polar countries that already are among the bigger fishing nations in terms of catch, such as Russia, the USA, and Canada in the Northern Hemisphere, and Chile and Argentina in the Southern Hemisphere ([Fig. 10](#)). However, even these nations will experience a redistribution of catches and fishing opportunities within their EEZs. In Atlantic Canada, for example, northern polar and subpolar fisheries management regions near Baffin Island and Labrador that historically had low catches will experience strong biomass increases, whereas more southern temperate fisheries regions, such as the Scotian Shelf and Gulf of Maine, which historically had high fisheries catches, will experience strong biomass declines ([Bryndum-Buchholz et al., 2020a](#)).

The above data ([Fig. 10](#)) suggest that all nations need to adapt their fisheries management in response to climate change. A recent review on climate change adaptations in fisheries management, policy and legislation, however, suggests that – although the need for climate change adaptation is widely recognized – progress on the implementation of climate-adapted fisheries management is limited ([Bryndum-Buchholz et al., 2021](#)). This is often due to a lack of political and institutional incentives and inertia to adapt policies and established management approaches to change ([Skern-Mauritzen et al., 2016](#); [Termeer et al., 2016](#); [Dubik et al., 2019](#)). Ideally, fisheries management should be rooted in policies and legislation that explicitly acknowledge climate change and allow for flexible and timely management responses in the face of climate-induced ecosystem changes that can have wide-reaching consequences for fisheries ([Bryndum-Buchholz et al., 2021](#); [Karp et al., 2019](#)).

A promising fisheries management approach for effective adaptation to climate change is climate-enhanced Ecosystem-based Fisheries Management (EBFM) ([Bryndum-Buchholz et al., 2021](#); [Fig. 11](#)). EBFM integrates the notion that climate change affects no single species in isolation, but rather marine ecosystems as a whole ([Skern-Mauritzen et al., 2018](#)). Managing fisheries with



**Fig. 9** Relative changes in sea surface temperature (SST), net primary production (NPP) and the biomass of phytoplankton (Phyto), zooplankton (Zoo), and higher trophic level marine animal biomass (HTL) in 2090–2099 relative to 1990–1999 under RCP8.5 across 143 nations' Exclusive Economic Zones (EEZs). Data are sorted by marine animal biomass changes as in Fig. 8, and represent ensemble means of CMIP5-forced Fish-MIP models. Fish-MIP data derived from [Tittensor et al. \(2021\)](#).



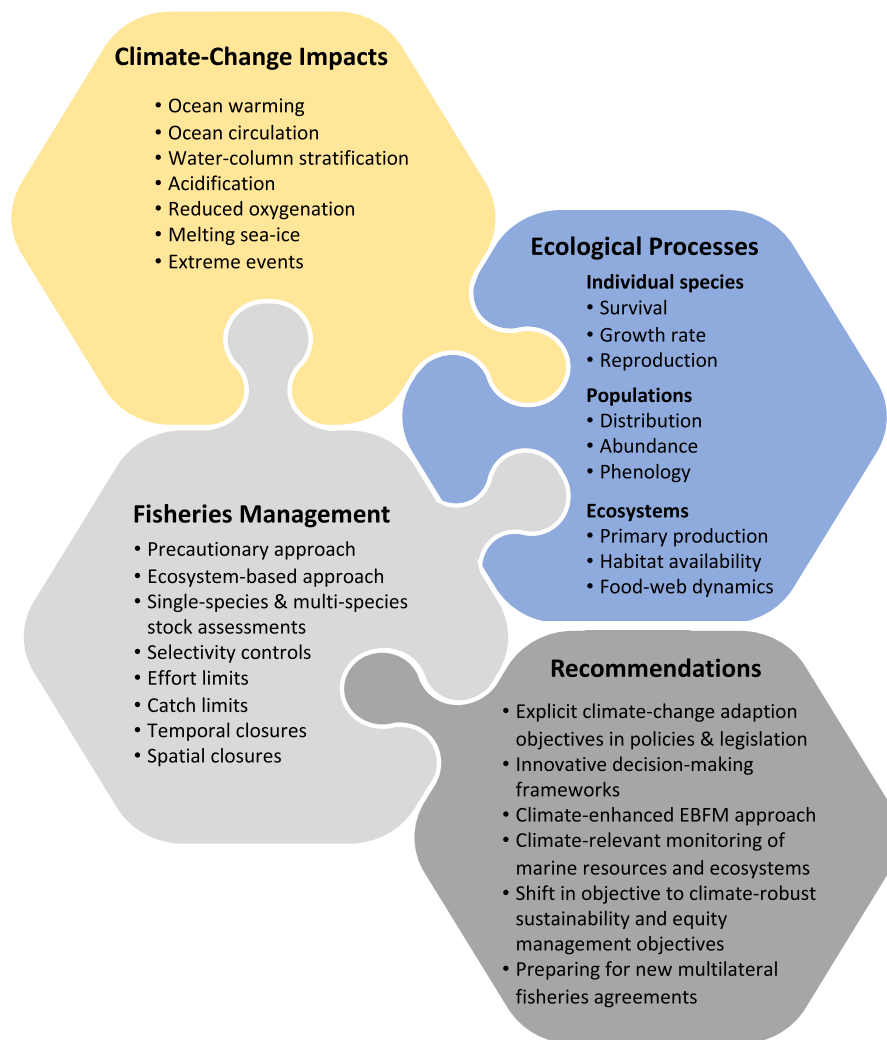
**Fig. 10** Relationship between projected biomass changes and current levels of fishing across nations. Shown are the changes in marine animal biomass (%) in 2090–2099 relative to 1990–1999 in each Exclusive Economic Zone (EEZ) of 138 (out of 143) nations in temperate-polar (left) and tropical (right) areas worldwide; 5 EEZs had to be excluded due either no data or no fisheries catches: Chagos Archipelago, Christmas Island, Heard and McDonald, Svalbard, and Jan Mayen. Biomass data represent the ensemble mean of CMIP5-forced Fish-MIP projections under RCP8.5 (note that maximum increases were cut-off at  $\pm 50\%$  due to high uncertainties in polar oceans). Colors indicate magnitude of projected biomass increase (blue) and decrease (red). Fisheries data represent average landings for each nation from 2010–2019 (Log10 metric tonnes) based on the Food and Agriculture Organization capture production statistics (FAO, 2021).

EBFM can address climate-driven shifts in ecosystems that affect fisheries, including species distribution and ecosystem productivity, and can allow for necessary adjustments in the management system, facilitating long-term sustainable fisheries under climate change (Bryndum-Buchholz *et al.*, 2021). This system level management ideally includes multiple climate-enhanced management tools and approaches (Fig. 11), for example, climate vulnerability assessments (e.g., Hare *et al.*, 2016; Hobday *et al.*, 2011), ecosystem-level indicators that can inform existing harvest rules (e.g., Link, 2010; Link and Watson, 2019; Tam *et al.*, 2017), as well as climate-relevant ecosystem monitoring and regular ecosystem status reports (e.g., Busch *et al.*, 2016; Logan *et al.*, 2020).

### 6.2 Human Development

Current and projected changes in marine animal biomass will also have consequences for overall human well-being and development within and across nations (Blanchard *et al.*, 2017; Boyce *et al.*, 2020; Maire *et al.*, 2021; Sala *et al.*, 2021). In addition to the effects on seafood supply and fisheries-dependent livelihoods, as discussed above, this includes key implications on a long and healthy life, a decent standard of living, and on education and knowledge. These key dimensions of human development are summarized in the Human Development Index (HDI), which was created by the United Nations Development Program (UNDP, 2021) to emphasize that people and their capabilities should be the criteria for assessing a country’s development instead of economic growth as commonly measured by the gross domestic product (GDP). Within the HDI, human health is measured by the life expectancy at birth, the standard of living is measured by the gross national income per capita, and education is measured by years of schooling (UNDP, 2021). There are several other dimensions of human development, for example, inequality, security, and empowerment which are not captured by the HDI; however, it is a useful index to evaluate the impacts of climate change on some aspects of human societies (UNDP, 2021).

Relating projected 21<sup>st</sup> century marine animal biomass changes under RCP8.5 to the HDI across nations reveals that almost all tropical and many temperate countries lose biomass in the future, largely independent of their HDI. However, most of the countries that will benefit from biomass increases are countries with already high or very high human development (HDI > 0.8 or 0.9) (Fig. 12). This suggests that climate-induced changes in the marine environment will likely enhance inequality among nations with respect to access to living marine resources, which may promote conflict unless governments and the international community alleviate these uneven consequences. Here, coastal developing nations (HDI 0.5–0.8) have the highest climate vulnerability along with low adaptive capacity to respond to projected marine animal biomass changes, because climate change is an



**Fig. 11** Overview of climate change impacts on marine ecosystem processes and fisheries management, and recommendations to achieve climate-adaptive fisheries management on the level of policy, legislative and implementation. Redrawn with permission from Bryndum-Buchholz *et al.* (2021).

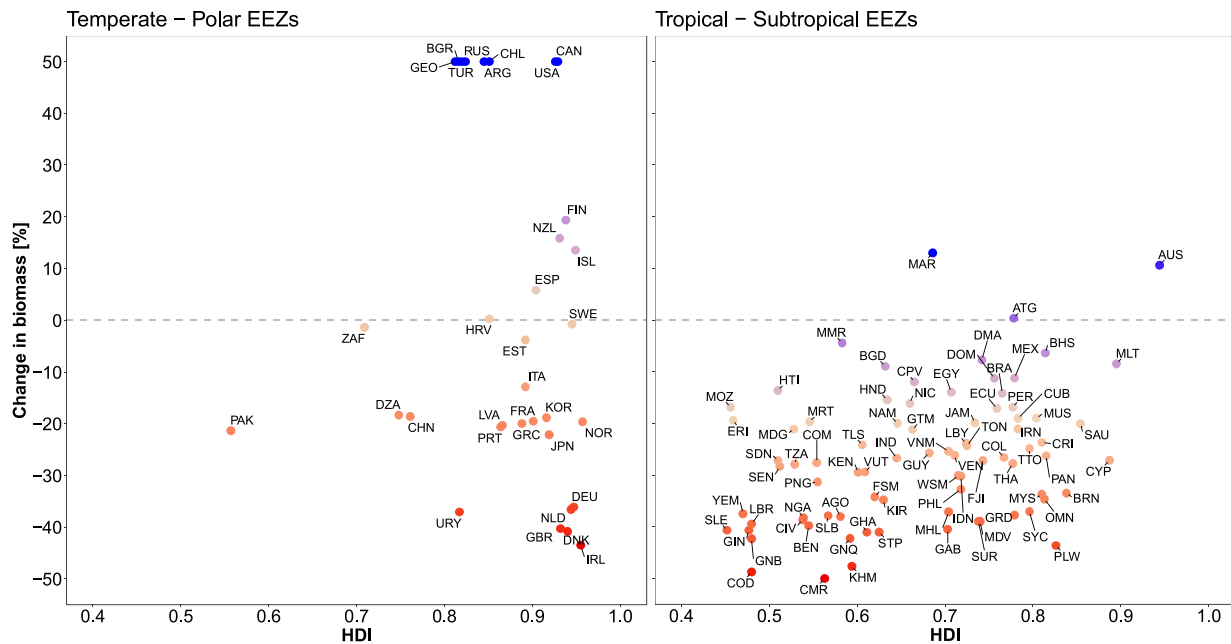
additional pressure to already existing challenges, such as higher levels of poverty, undernourishment, food insecurity and fisheries dependence (Blanchard *et al.*, 2017; Boyce *et al.*, 2020). Effective, internationally binding GHG emissions mitigation policies are likely to prevent such adverse climate-related consequences (Boyce *et al.*, 2020).

Human development and well-being have always been linked to the ability to adapt to changes in the environment (Pecl *et al.*, 2017). Today, developing nations with high fisheries dependence that are threatened by climate-driven changes in their traditional fishing grounds can respond by investing in livelihood and dietary diversification, which can also facilitate fisheries sustainability and poverty alleviation (Blanchard *et al.*, 2017; Quaas *et al.*, 2016; Roscher *et al.*, 2022). This response is ideally embedded in regional, climate-resilient fisheries management and marine conservation measures to ensure long-lasting adaptation and human well-being in a changing climate. Ultimately, a targeted and effective reduction of GHG emissions on a global level in combination with efforts to increase adaptive capacity across nations is the most direct response to the global climate emergency that can provide a pathway to avoid the disproportionate socio-economic burden on nations (Blanchard *et al.*, 2017; Boyce *et al.*, 2020).

### 6.3 Conservation

Marine biodiversity is the key foundation for the structure and functioning of ocean ecosystems and for providing essential service and benefits for human societies, on local, regional, and global scales (Lotze, 2021). Unsustainable and destructive human activities, such as pollution, habitat destruction, and overexploitation are threatening global marine biodiversity (Lotze, 2021).





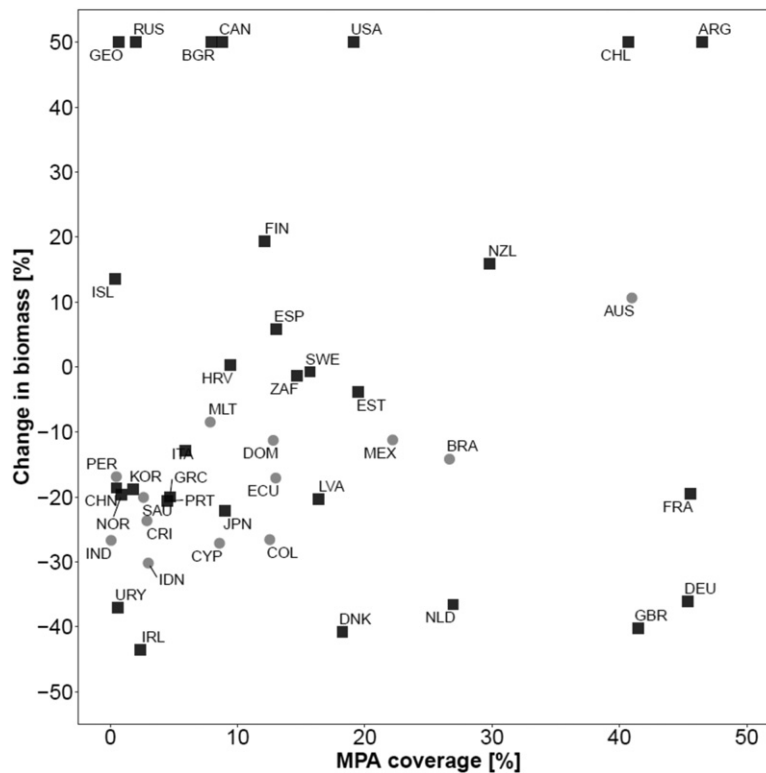
**Fig. 12** Relationship between projected biomass changes and current levels of the human development index (HDI) across nations. Shown are the relative changes in marine animal biomass (%) in 2090–2099 relative to 1990–1999 in each Exclusive Economic Zone (EEZ) of 114 (out 143) nations (HDI values were not available for all nations) in temperate-polar (left) and tropical-subtropical (right) areas worldwide. Biomass data represent the ensemble mean of CMIP5-forced Fish-MIP projections under RCP8.5 (note that maximum increases were cut-off at  $\pm 50\%$  due to high uncertainties in polar oceans). Colors indicate magnitude of projected biomass increase (blue) and decrease (red). HDI data represent 2019 values from the United Nations Development Program (see “Relevant Websites”).

Unabated climate change is an additional threat and, today, considered a major driver of marine biodiversity loss (IPBES, 2019a, IPCC, 2019a, 2022). For example, wide reaching ecosystem and species responses due to climate change include range expansions or contractions (Morley *et al.*, 2018), changes in species composition (e.g., García Molinos *et al.*, 2016) and species interactions (e.g., Asch, 2015; Grady *et al.*, 2019), and shifting phenology (e.g., Wilson *et al.*, 2016), all of which impact ecosystem function and biodiversity (Eddy *et al.*, 2021; Lotze *et al.*, 2019; Du Pontavice *et al.*, 2020).

Conservation efforts such as marine protected areas (MPAs), MPA networks and marine reserves aim to counteract this biodiversity loss. With the United Nation Initiative “High Ambition Coalition for People and Nature” (HAC), nations across the world have committed to protect 30% of their waters and land by 2030 with the auxiliary aim to address the global climate crisis (HAC, n.d.). These targets are non-binding, but the hope is that they will spur new conservation actions around the world. Currently, only 7.7% of the world’s ocean is under some form of protection, which is considered inadequate to achieve sufficient biodiversity conservation that is needed to bring its continuous loss to a halt (Marine Conservation Institute, 2022). HAC member nations, such as Canada (CAN), Ecuador (ECU), Japan (JPN) or Norway (NOR) have a long way ahead to meet their “30 by 30” commitment (Fig. 13). For example, if Canada is to reach this ambitious target, it requires to more than double the marine area protected currently under some form of biodiversity conservation measure within the next ten years (Bryndum-Buchholz *et al.*, 2022). Many other countries face similar challenges (Fig. 13). In comparison, among those nations that already have relatively high MPA coverage, some will experience strong biomass increases, such as Chile (CHL) and Argentina (ARG) within their polar waters in the Southern Ocean, whereas European nations such as Great Britain (GBR), France (FRA) and Germany (DEU) will experience strong biomass declines that may weaken their MPA effectiveness (Fig. 13).

As species move to more suitable regions with ongoing climate-driven ecosystem changes, some species might leave established protected areas which will render them ineffective or even obsolete. Despite an increasing international and national recognition of the global climate emergency, effects of climate change on marine ecosystems and/or individual populations are not often considered in marine conservation planning and management (O’Regan *et al.*, 2021; Rilov *et al.*, 2020; Tittensor *et al.*, 2019; Wilson *et al.*, 2020). To account for the climate-driven changes in biodiversity patterns and ecosystem dynamics, existing marine conservation efforts need to become innovative, climate-smart and adapt their underlying planning and management to a more dynamic and less certain future (Future Earth, 2021; Lotze, 2021; Stephenson *et al.*, 2021). Doing this, ocean protection can sustain long-term benefits ranging from unique biodiversity protection, seafood provision, and carbon storage (Martin *et al.*, 2021).

To move toward climate-smart marine biodiversity conservation that ensures long-term effectiveness in protecting marine biodiversity and ecosystem services, adaptive and operational conservation measures need to be implemented across nations (Tittensor *et al.*, 2019), ideally targeting policies, protected area design and placement as well as planning and management



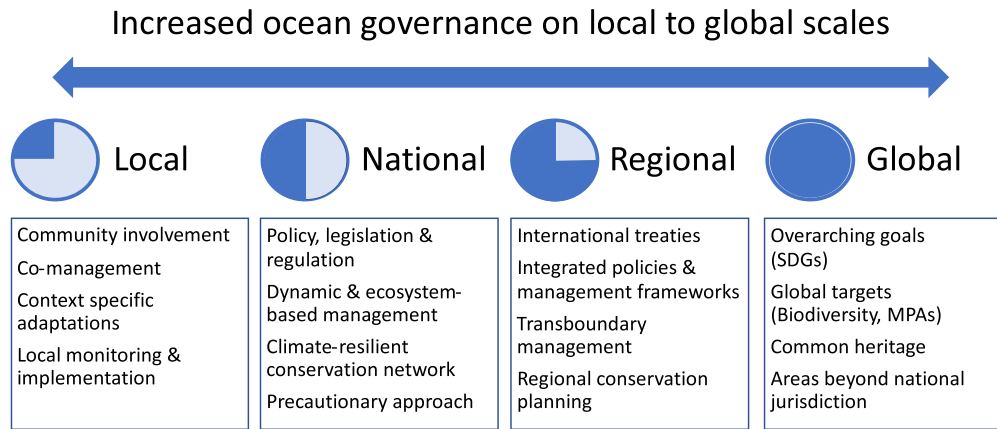
**Fig. 13** Relationship between changes in marine animal biomass [%] in 2090–2099 relative to 1990–1999 under RCP8.5 and coverage of Marine Protected Areas (MPAs) [%] across 43 (out of 143) EEZs (Not all EEZs are represented due to data availability). Temperate-polar nations are indicated by black squares and tropical by grey circles. Projected biomass changes are ensemble means of two CMIP5 ESMs, GFDL and IPSL, that were used in Fish-MIP. The MPA coverage data was derived from OECD (2022) and is based on the World Database on Protected Areas.

(Wilson *et al.*, 2020). National marine conservation policies need to explicitly integrate climate change objectives that ensure effective protection under ongoing climate change (Bryndum-Buchholz *et al.*, 2022). The design and placement of new conservation measures should be approached in the context of a dynamic network of protected areas, including areas of identified hot spots of threatened biodiversity, areas that represent a range of habitats and biomes, and areas with little projected change that can act as climate refugia, to holistically sustain marine biodiversity into the future (Lotze, 2021; Martin *et al.*, 2021). Climate-smart networks of protected areas should further aim to facilitate connectivity and species migration via protected corridors or stepping-stones, and dynamic management around MPAs to adequately respond to observed or projected changes (Lotze, 2021; Tittensor *et al.*, 2019; Wilson *et al.*, 2020). Protected area planning and management targets need to consider climate change impacts across planning and management components, such as protected area objectives (e.g., protection of key habitat, species, population), the strategies to fulfill said objectives, as well as protected area monitoring and ecosystem indicators (O'Regan *et al.*, 2021; Tittensor *et al.*, 2019). Ultimately, implementing effective, climate-smart protected area networks in waters of coastal nations as well as across the high seas can not only contribute to fulfilling the United Nation's Sustainable Development Goal (SDG) 14 *Life Below Water* but also significantly contribute towards SDG 13 *Climate Action* (Gissi *et al.*, 2022).

#### 6.4 Governance

Ocean governance includes various actors, formal and informal institutions, and nations (Haas *et al.*, 2022). Climate change is and will continue to impact all aspects of marine life; however, ocean governance is still largely ill-prepared for ongoing and projected climate-driven consequences in waters across coastal nations (Ison and Straw, 2020). The climate-driven changes in ocean dynamics places ocean management in a novel space with respect to decision-making and governance, challenging current governance systems and their path towards sustainability (Stephenson *et al.*, 2021). Meeting these challenges requires governance that can anticipate and adapt to rapidly changing conditions, while also minimize negative consequences and avoid inter- and intranational inequalities and injustices related to climate change (Pecl *et al.*, 2017; Martin *et al.*, 2021).

Historically, ocean governance primarily focused on individual, activity-based marine management (i.e., fisheries, shipping). In the past two decades, governance and management of marine activities have evolved in terms of recognizing that improved coastal and ocean management for long-lasting sustainability can only be achieved through more comprehensive approaches that



**Fig. 14** Conceptual graph of implications for local to global ocean governance and stewardship. Adapted from Future Earth (2021).

consider the dynamic nature and activities within marine systems (Stephenson *et al.*, 2021). Indeed, past governance and management successes exist, such as exploitation bans and restrictions, endangered species legislation, habitat protection and restoration, and invasive species and pollution controls (Martin *et al.*, 2021). Nevertheless, pervasive challenges remain as cumulative impacts of human activities interact with each other, including habitat destruction and modification, pollution, invasive species, direct exploitation, all exacerbated by the global climate emergency (Tittensor *et al.*, 2019). Globally, to tackle these challenges, the United Nations Sustainable Development Goals (SDGs) were launched to achieve a comprehensive governance transformation that aims at marine conservation and management that protects marine biodiversity in the long-term on all scales (UN United Nations, 2015).

Effective marine biodiversity conservation in a changing climate should be guided by reformed, multi-level ocean governance that recognizes the interconnectedness of the ocean, is adaptive and iterative, coordinated across different levels (i.e., local, regional, national, global) and responsive to shifting ecological and climate dynamics (Fig. 14; Haas *et al.*, 2022; Martin *et al.*, 2021; Ward *et al.*, 2022). A transformed ocean governance system will address pervasive issues regarding the necessity to improve ecosystem resilience and ocean health, by removing unjust and uneven marine resource access, as well as elitist and exclusive decision-making (Blythe *et al.* 2021; Haas *et al.*, 2022). On a local scale, this could entail community involvement, co-management, and context specific adaptation efforts (Fig. 14). On a national scale, future governance should establish or continue decision-making based on the precautionary approach, but also implement context-specific, adaptive, dynamic, and ecosystem-based policies and management regimes that are inclusive of local knowledge holders (Fig. 14). On a regional level, reformed ocean governance will need to incorporate shifting marine populations, requiring innovative transboundary management systems as well as reformed or novel international treaties (Fig. 14). Finally, on a global level, the UN SDGs and the international call for protecting areas beyond national jurisdiction (ABNJ), provide a chance for nations across the globe to move towards comprehensive ocean governance that protects marine biodiversity on all levels in the face of climate change, facilitating long-term ocean and human health.

## 7 Conclusions & Outlook

Climate change impacts ocean and coastal life with profound effects on marine ecosystems and associated human societies. Changes in physical and chemical parameters are influencing biological processes on all levels of organization, altering food web structure and ecosystem dynamics, which in turn has far-reaching consequences for marine fisheries, human well-being and development, as well as ocean governance. Marine biomass is largely projected to decline in temperate and tropical regions globally and nationally; however, increases are projected in polar regions and nations, albeit with high projection uncertainty. Overall, ensemble modelling is a useful approach to improve our understanding of future trajectories of climate-driven changes in the ocean and to inform policy, conservation and management.

To date, ensembles of marine ecosystem models do not integrate dynamic fishing scenarios (so far only constant fishing effort has been implemented), which is the next important step to reflect possible future changes in fishing activities over time and space. This would improve model output and the understanding of potential future ecosystem changes with climate change and fisheries. Further, scenarios of ocean responses to interacting, cumulative human impacts that go beyond fishing (for example, pollution, invasive species and habitat destruction), as well as scenarios of different management and governance regimes need to be developed to better inform policy and governance. Developing projections under those scenarios requires also regional down-scaling of global climate and ecosystem models to provide projections on scales relevant for coastal management and governance. Global initiatives such as CMIP, Fish-MIP and ISI-MIP are well suited to tackle these modelling issues and promote and improve model development to provide more refined and adjusted projections to inform the IPCC, IPBES and UN SDGs as well as other organizations and national governments around the world.

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