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Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change

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While the physical dimensions of climate change are now routinely assessed through multimodel intercomparisons, projected impacts on the global ocean ecosystem generally rely on individual models with a specific set of assumptions. To address these single-model limitations, we present standardized ensemble projections from six global marine ecosystem models forced with two Earth system models and four emission scenarios with and without fishing. We derive average biomass trends and associated uncertainties across the marine food web. Without fishing, mean global animal biomass decreased by 5% ($\pm 4\%$ SD) under low emissions and 17% ($\pm 11\%$ SD) under high emissions by 2100, with an average 5% decline for every 1 °C of warming. Projected biomass declines were primarily driven by increasing temperature and decreasing primary production, and were more pronounced at higher trophic levels, a process known as trophic amplification. Fishing did not substantially alter the effects of climate change. Considerable regional variation featured strong biomass increases at high latitudes and decreases at middle to low latitudes, with good model agreement on the direction of change but variable magnitude. Uncertainties due to variations in marine ecosystem and Earth system models were similar. Ensemble projections performed well compared with empirical data, emphasizing the benefits of multimodel inference to project future outcomes. Our results indicate that global ocean animal biomass consistently declines with climate change, and that these impacts are amplified at higher trophic levels. Next steps for model development include dynamic scenarios of fishing, cumulative human impacts, and the effects of management measures on future ocean biomass trends.

climate change impacts | marine food webs | global ecosystem modeling | model intercomparison | uncertainty

Climate change is altering the abundance and distribution of marine species (1–5), with consequences for ocean ecosystem structure and functioning, seafood supply, and marine management

Significance

Climate change can affect the distribution and abundance of marine life, with consequences for goods and services provided to people. Because different models can lead to divergent conclusions about marine futures, we present an integrated global ocean assessment of climate change impacts using an ensemble of multiple climate and ecosystem models. It reveals that global marine animal biomass will decline under all emission scenarios, driven by increasing temperature and decreasing primary production. Notably, climate change impacts are amplified at higher food web levels compared with phytoplankton. Our ensemble projections provide the most comprehensive outlook on potential climate-driven ecological changes in the global ocean to date and can inform adaptive management and conservation of marine resources under climate change.

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The authors declare no conflict of interest.

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and conservation (6–8). Quantifying future trends and uncertainties is critical to inform ongoing global assessments (1), including the Intergovernmental Panel for Climate Change (IPCC) and Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, and guide viable pathways toward achieving key policy objectives, such as the United Nations Sustainable Development Goals (SDGs). Various modeling approaches exist to assess current and future impacts on marine ecosystems (8–12), yet each individual model is necessarily an incomplete simplification of the natural world, with different assumptions, structures, and processes (13). One approach to overcoming any single-model limitations is to force a suite of models with standardized climate change scenarios and combine them into ensemble projections to estimate mean future trends and associated intermodel spread (13). Such model intercomparison projects (MIPs) have become a “gold standard” in climate science and have proven critical for enhancing credibility and understanding of the physical and biochemical climate change projections (14) and associated impacts on Earth’s terrestrial biosphere (15–17), yet can only now be attempted for the global ocean ecosystem (13).

Over the past decade, a number of global fisheries and marine ecosystem models (MEMs) have been developed (13). Some of these have been used individually to project future changes in species distribution, biomass, or potential fisheries catch (8–12), but it remains unclear how consistent and comparable these results are, and thus how applicable for providing robust insight and advice. The Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP; ref. 13) was created to bring these various models and modeling groups together to produce ensemble projections under standardized climate change scenarios.

Here we assess projected changes in global marine animal biomass over the 21st century through ensemble projections with six published global MEMs from Fish-MIP, forced with standardized outputs from two contrasting Earth system models (ESMs) and four emission scenarios [Representative Concentration Pathways (RCPs)]. The MEMs range from size-structured [Bioeconomic Marine Trophic Size-spectrum (BOATS), Macroecological] and trait-based [Dynamic Pelagic Benthic Model (DPBM), Apex Predators Ecosystem Model (APECOSM)] to species distribution [Dynamic Bioclimate Envelope Model (DBEM)] and trophodynamic models (EcoOcean) (*SI Appendix, Tables S1 and S2*). The ESMs span the range of available Coupled Model Intercomparison Project Phase 5 (CMIP5) projections, from low [Geophysical Fluid Dynamics Laboratory Climate Model (GFDL-ESM2M)] to high Institute Pierre Simon Laplace Climate Model (IPSL-CM5A-LR) increases in sea surface temperature (SST) and associated changes in net primary production (NPP), while other drivers were more similar (ref. 14 and *SI Appendix, Figs. S1 and S2*). The RCPs range from a low-emission strong mitigation scenario (RCP2.6) to a high-emission business-as-usual scenario (RCP8.5), with two intermediate scenarios (RCP4.5 and RCP6.0). All climate change scenarios were run for historical (1970–2005) and future (2006–2100) periods without fishing to isolate the climate signal, and with fishing to evaluate how climate responses differ in an ocean fished at current levels of intensity (13). The six MEMs generated standardized outputs of total animal biomass (except zooplankton) and biomass of animals of >10 cm and >30 cm. Since not all MEMs could run the full set of scenarios, due to MEM or ESM limitations, we analyzed all available runs for each scenario, and performed sensitivity analyses on subsets, which revealed similar results (*SI Appendix, Table S3*).

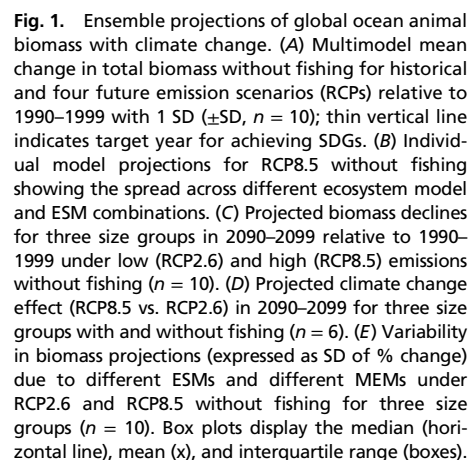
The goals of this study were to examine the consistency of projections across MEMs over a range of climate change scenarios globally and regionally from 1970 to 2100. We also evaluated how ocean animal biomass changes correspond with those in the physical environment and the extent to which projected climate impacts on primary producers and zooplankton (18) are transmitted to higher food web levels.

Results and Discussion

Ensemble Projections of Global Ocean Animal Biomass. Our ensemble projections revealed consistent declines in global marine animal biomass from 1970 to 2100 across all emission scenarios (RCPs, Fig. 1A). Almost all scenarios and MEM–ESM combinations predicted decreasing animal biomass (*SI Appendix, Table S3*), although the magnitude of decline varied among models. This general trend can be explained by warming causing increased ocean stratification, which reduces nutrient availability in the upper ocean, leading to decreased primary production and lower energy supply for higher trophic levels (14, 18), and changes in metabolic rates, among others (19). Without fishing, mean total biomass declines ranged from 4.8% ($\pm 3.5\%$ SD) under low emissions (RCP2.6) to 17.2% ($\pm 10.7\%$ SD) under high emissions (RCP8.5) by 2090–2099 relative to 1990–1999 (Fig. 1A). All four emission scenarios projected similar declines by 2030, the target year of many SDGs, and through to midcentury, after which they began to diverge. Projected mean biomass declines were similar for animals of >10 cm and >30 cm (Fig. 1C), albeit slightly lower and more variable for those of >30 cm (*SI Appendix, Fig. S5 and Table S3*). Thus, the consequences of different emission scenarios may not be distinguishable over the next two to three decades but differ markedly in the long term.

Climate Change Effects in a Fished and Unfished Ocean. Three MEMs were also able to run simulations with fishing, including time-varying historical and constant future fishing pressure (*SI Appendix, SI Methods*), which we used to compare projected climate change effects (RCP8.5 vs. RCP2.6) with and without fishing. The magnitude and variability of the climate change effect were similar (Fig. 1D), suggesting that fishing, at least under current levels of intensity, may not substantially alter the relative effect of climate change. The slightly weaker climate change effects with fishing (mean difference 2 to 3%; Fig. 1D and *SI Appendix, Fig. S6A*) may be due to an indirect effect: Warming enhances both growth and predation rates, yet predation rates are reduced due to selective fishing of larger animals and lower predator abundance (20, 21) which may indirectly enhance prey biomass and weaken the relative climate change effect (19). This is a relatively small effect, however, compared with the large direct effect of fishing itself, which resulted in 16 to 80% lower biomass for animals of >10 cm and 48 to 92% for animals of >30 cm compared with unfished conditions in 2100 under RCP2.6, and slightly lower values under RCP8.5. We note that the absolute magnitude of the fishing effect is not directly comparable across MEMs, due to inherent differences in how fishing pressure and commercial versus noncommercial taxa are incorporated (*SI Appendix, SI Methods*). We also caution that our future constant fishing scenario is simplistic and does not incorporate potential changes in effort, technology, management, and conservation (11, 21–23), which are likely to strongly affect future biomass trends. Nevertheless, a possible consistent climate change effect is an important consideration in the context of marine management and conservation.

Variability among Model Projections. Although ensemble means revealed global biomass declines across all emission scenarios (Fig. 1A), there was considerable variation among MEMs and ESMs (Fig. 1B). The latter largely reflects differences in SST increases and NPP reductions among ESMs (*SI Appendix, Fig. S1*), in addition to other physical and biochemical drivers (14), and reinforces previous work highlighting the importance of ESM and scenario uncertainty in future projections of fish biomass or fisheries production (24, 25). Interestingly, the variability in projected biomass changes among ESMs was of similar magnitude to that among MEMs (Fig. 1E), suggesting similar levels of uncertainty associated with physical and biological models. Since the field of global ecosystem modeling is relatively new compared with Earth system modeling (13, 14), one might have expected higher variability across MEMs. Other MIPs also found that uncertainties in both ESMs and climate impact models contribute to overall projection



Trends in Relation to Global Temperature Changes. Many policy processes use the change in global air temperature since pre-industrial times as a reference for the effects of climate change (34, 35). For our ensemble projections, this revealed a consistent linear relationship with an average 5% drop in total animal biomass with every 1 °C of Earth surface warming in the absence of fishing

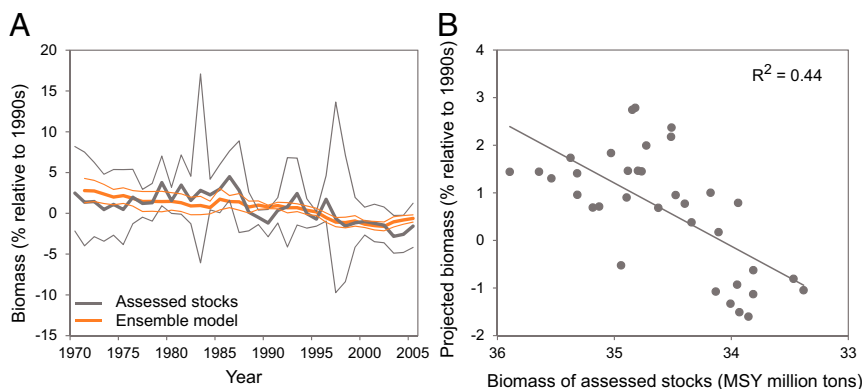


Fig. 2. Empirical validation of ensemble projections. Shown is the relative biomass change (animals of >10 cm) for our multimodel mean without fishing (orange line, $\pm 95\%$ CI, $n = 10$) compared with temperature-dependent hindcasts of MSY for 235 assessed fish stocks that are independent of fishing effects (gray lines, $\pm 95\%$ CI; ref. 30). Both projected and empirical biomass trends are displayed as (A) time series and (B) yearly scatter plot with a linear regression fit. A similar analysis of biomass trends with fishing is shown in *SI Appendix, Fig. S4*.

(Fig. 4). Similar declines were found for animals of >10 cm and >30 cm (*SI Appendix, Fig. S7*). These relationships may be slightly less negative in a fished ocean, given the dampening effect described above, yet overall biomass reductions remain substantial (i.e., 15% instead of 17% decline under highest warming; *SI Appendix, Fig. S6B*). Individual ecosystems may well show more-complex responses to warming (3, 36), but these simple relationships represent well-founded approximations for a global average response. Recent results hindcasting temperature effects on biomass of 235 assessed fish stocks found a 4.1% drop in MSY from 1930 to 2010, a period that saw an average 0.6 °C of warming (30). This reconstructed rate of change is consistent with our 5% drop in biomass per 1 °C of warming throughout the 21st century. According to these results, limiting future warming to 1.5 °C to 2.0 °C above preindustrial levels would limit biomass declines to 4 to 6% by 2100, underscoring the potential impact of climate change mitigation according with the Paris Agreement (34, 35).

Spatial Patterns of Biomass Change. Not all ocean regions respond similarly to climate warming (Fig. 5 and *SI Appendix, Fig. S8*). Our ensemble projections revealed strong increases in total animal biomass in polar regions and widespread declines in temperate to tropical regions under RCP8.5 (Fig. 5B), with qualitatively similar but less pronounced patterns under RCP2.6 (Fig. 5A). The climate change effects were spatially similar with and without fishing (*SI Appendix, Fig. S9*). However, our ensemble projections differed spatially from previous single-model results highlighted in the IPCC's Fifth Assessment Report (1): We found strong biomass declines (not increases) in many temperate to subtropical regions and increases (not declines) around Antarctica. The magnitude of regional changes also varied from other single-model results (8–11). Generally, warming waters and enhanced primary production are expected to facilitate species expansions and biomass increases in polar regions, while tropical areas may experience pronounced species losses as thermal thresholds are exceeded. In temperate regions, warming is expected to change species composition, and reduced primary production due to enhanced stratification will result in biomass declines (3, 4, 30). Our ensemble projections showed high model agreement on the direction of change in many ocean regions (75 to 100%; Fig. 5 E and F), providing confidence in our multimodel results that combine different ecosystem structures and processes. Many models also agreed relatively well on the magnitude of projected changes in temperate to tropical regions but showed considerable intermodel variability in many polar and coastal regions (Fig. 5 C and D), reflecting differences among ESMs and MEMs (*SI Appendix, Figs. S10 and S11*). These results again underscore the importance of model intercomparison in identifying uncertainties and constraining expected outcomes of ecosystem changes in the ocean.

Conclusions

Our ensemble projections demonstrate that global ocean animal biomass consistently declines with climate change, and that impacts are amplified at higher trophic levels. Our hindcasts support recent empirical work that shows ongoing climate impacts on fish biomass (30, 37), and project elevated climate-driven declines in ocean ecosystems, with magnitudes dependent on emission pathways. Amplification of biomass declines for higher trophic levels represents a particular challenge for human society, including meeting the SDGs for food security (SDG2), livelihoods (SDG1), and well-being (SDG3) for a growing human population while also sustaining life below water (SDG14). Our ensemble projections indicate the largest decreases in animal biomass at middle to low latitudes, where many nations depend on seafood and fisheries, and where marine biodiversity is already threatened by multiple human activities (6, 38). In turn, the largest increases are projected at high latitudes, highlighting new opportunities for—and potential conflict over—resource use, but also an urgent need for protecting sensitive species and rapidly changing ecosystems. Overall, our results clearly highlight the benefits to be gained from climate change mitigation, as all impacts were substantially reduced under

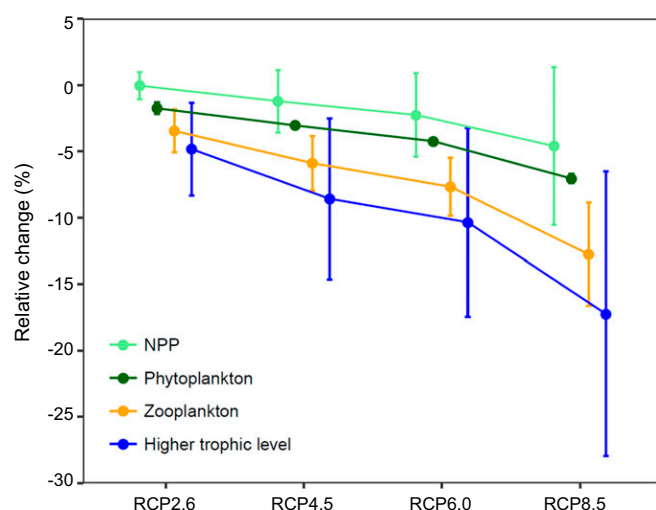


Fig. 3. Trophic amplification of marine biomass declines. Shown is the magnitude of projected mean changes in 2090–2099 relative to 1990–1999 (percent, \pm SD) for NPP, phytoplankton, and zooplankton biomass derived from ESMs ($n = 2$) and higher trophic levels from MEMs across four RCPs ($n = 10$ for RCP2.6 and RCP8.5; $n = 8$ for RCP4.5 and RCP6.0). All ecosystem models use either NPP or phytoplankton biomass as forcing variables, and some also use zooplankton biomass.

Climate Change Scenarios. The two ESMs from CMIP5 (<https://pcmdi.llnl.gov/cmip5/>) provided the necessary physical and biochemical outputs to force our MEMs, particularly monthly depth-resolved fields of phytoplankton and zooplankton size groups (*SI Appendix, SI Methods and Table S2*). Average trends of GFDL-ESM2M and IPSL-CM5A-LR reflect the multimodel mean and range of a broad set of CMIP5 models (14). The four RCPs represent standard IPCC informed emission scenarios (*SI Appendix, SI Methods*).

Simulations. All MEMs ran simulations without fishing, and three MEMs ran simulations with fishing for historical (1970–2005) and future (2006–2100) periods. Historical fishing reflected time-varying effort or mortality rates depending on MEM requirements, and future fishing was kept constant at 2005 levels (*SI Appendix, SI Methods*). Not all MEMs performed all simulations, and sensitivity analyses cross-checked subsets of results (*SI Appendix, Table S3*).

Analyses and Validation. Annual outputs of total animal biomass density (grams carbon per square meter) and animal biomass of >10 cm and >30 cm were derived on a 1×1 degree grid. We calculated time series of % biomass change from 1970 to 2100 relative to 1990–1999 (reference period), and % biomass change in 2090–2099 vs. 1990–1999 for each simulation, as absolute biomass densities were not strictly comparable across MEMs. Relative changes were combined into ensemble means and SD. The climate change effect [(RCP8.5 – RCP2.6)/RCP2.6] was calculated in a fished and unfished ocean within and across MEMs. Empirical validation was achieved by comparing historical projections with biomass trends of assessed fish stocks in a fished ocean (B/B_{MSY} ; ref. 29) and temperature-dependent biomass hindcasts (MSY) of assessed stocks without fishing (30), in addition to published individual MEM validations with empirical data (*SI Appendix, Fig. S3*). Trophic amplification was evaluated by comparing mean (\pm SD) changes (2090s vs. 1990s) in NPP and total phytoplankton and zooplankton biomass from ESMs

with higher trophic level biomass from MEMs across RCPs. Mean biomass changes were also compared with global air temperature changes since preindustrial times (1861–1870) from ESMs. Spatial patterns were mapped as mean % biomass changes in 2090–2099 vs. 1990–1999, the SD of the mean to assess intermodel variability in the magnitude of change, and the % model agreement on the direction of change (14). We also mapped the climate change effect with and without fishing and the variability of results across ESMs and MEMs. For further details, see *SI Appendix, SI Methods*.

Data Accessibility. All data reported in this paper are archived (45) and publicly available at <http://dataservices.gfz-potsdam.de/pik/showshort.php?id=escidoc:2956913>.

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