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Disentangling diverse responses to climate change among global marine ecosystem models

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ABSTRACT

Climate change is warming the ocean and impacting lower trophic level (LTL) organisms. Marine ecosystem models can provide estimates of how these changes will propagate to larger animals and impact societal services such as fisheries, but at present these estimates vary widely. A better understanding of what drives this inter-model variation will improve our ability to project fisheries and other ecosystem services into the future, while also helping to identify uncertainties in process understanding. Here, we explore the mechanisms that underlie the diversity of responses to changes in temperature and LTLs in eight global marine ecosystem models from the Fisheries and Marine Ecosystem Model Intercomparison Project (FishMIP). Temperature and LTL impacts on total consumer biomass and ecosystem structure (defined as the relative change of small and large organism biomass) were isolated using a comparative experimental protocol. Total model biomass varied between −35% to +3% in response to warming, and -17% to +15% in response to LTL changes. There was little consensus about the spatial redistribution of biomass or changes in the balance between small and large organisms (ecosystem structure) in response to warming, an LTL impacts on total consumer biomass varied depending on the choice of LTL forcing terms. Overall, climate change impacts on consumer biomass and ecosystem structure are well approximated by the sum of temperature and LTL impacts, indicating an absence of

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nonlinear interaction between the models' drivers. Our results highlight a lack of theoretical clarity about how to represent fundamental ecological mechanisms, most importantly how temperature impacts scale from individual to ecosystem level, and the need to better understand the two-way coupling between LTL organisms and consumers. We finish by identifying future research needs to strengthen global marine ecosystem modelling and improve projections of climate change impacts.

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1. Introduction

Water temperature and primary production play critical roles in marine processes. Higher temperatures accelerate reaction rates, with consequences ranging from the molecular to ecosystem scale, while primary production provides the fundamental source of energy for almost all marine life (Brown et al., 2004; Chavez et al., 2011). Climate change impacts on both water temperature and primary production will thus alter marine ecosystems in fundamental ways (Pörtner et al., 2014). For example, a first-order expectation of these impacts is that accelerated metabolic rates will consume energy more quickly in a warmer ocean, all else being equal, so that less biomass could be supported by a given level of primary production (Heneghan et al., 2019). Yet, ecosystem-level effects emerge from individual-level processes and interactions, which could lead to nonlinear effects and changes in ecosystem structure, while shifting thermal habitats may influence the distribution of species, transforming food-webs to previously unknown states (Coll et al., 2020; Pinsky et al., 2020; Poloczanska et al., 2016).

There is a growing need to quantify and project climate change impacts on marine ecosystems to motivate mitigation (Bryndum-Buchholz et al., 2020), provide insight into potential future threats to food security (Barange et al., 2014; Blanchard et al., 2017a; Boyce et al., 2020), and identify needs for biodiversity conservation (Brito-Morales et al., 2020; Waldron et al., 2020). Thus, there has been a recent proliferation of spatially-explicit marine ecosystem models that simulate higher trophic level biomass and ecosystem structure at regional and global scales, driven by output from climate-ocean-biogeochemical models (Tittensor et al., 2018). These ecosystem models differ significantly in their design, level of complexity and implementation, reflecting different choices for how to represent fundamental marine ecosystem processes, as well as a diversity of model purpose and scope. As a result, there is considerable uncertainty in model projections of climate change impacts on higher trophic levels (e.g. Lotze et al., 2019), with projections from each model dependent upon decisions around the inclusion or simplification of many candidate processes. Structural diversity in model projections is a strength for gaining a rich view of possible outcomes, given that each model reflects a different subset of established physiological and process knowledge, implemented using different mathematical representations (Knutti, 2010; Brander et al., 2013; Lefevre et al., 2017; Payne et al., 2016). At the same time, this diversity reflects fundamental uncertainty in our understanding of ecosystem processes. Thus, identifying sources of structural uncertainty in ensemble projections can point to critical weaknesses and thereby accelerate model improvement.

The Fisheries and Marine Ecosystem Model Intercomparison Project (FishMIP) was created to explore this uncertainty and provide more robust assessments of climate impacts on marine ecosystems through the analysis of multi-model ensembles (Tittensor et al., 2018). A recent FishMIP study (Lotze et al., 2019) found that projections of mean changes in animal biomass from a model ensemble typically compared better with empirical data than individual models, emphasising the benefits of ensemble climate impact projections. However, uncertainty in ensemble projections of higher trophic level biomass is significant: Lotze et al. (2019) found that the spread of changes across the FishMIP ensemble in 21st century marine consumer biomass under the high emissions, representative concentration pathway 8.5 (RCP 8.5) climate change scenario (0 to −35%) was larger than the multi-model mean consumer biomass change between the RCP 2.6 (low emissions) and RCP 8.5 scenarios (-5% to −20%). This means that structural uncertainty across global marine models is greater than climate scenario uncertainty, which is problematic for the goal of using these models to provide assessments of climate impacts on marine ecosystems and the societal services they provide.

For all global models in the FishMIP ensemble, temperature and lower trophic level (LTL) forcings such as net primary production, phytoplankton and zooplankton biomass, and export carbon are the two main drivers of projected climate change impacts (Tittensor et al., 2018), yet their implementations vary. Although there is some agreement on how temperature impacts physiological processes in general (e.g. Kooijman, 2010), there is less agreement on how these impacts vary across functional groups, body sizes, and different processes such as growth and metabolism (van Denderen et al., 2020). Similarly, although it is universally understood that LTL biomass and production provide the source of energy that supports higher trophic levels, there is less understanding about how the physiology and structure of LTLs affects transfer efficiency and ecosystem structure, and how to couple lower and higher trophic levels (Eddy et al., 2020; Heneghan et al., 2016; Stock et al., 2017). Previous multi-model ensemble studies have explored structural model uncertainty in projections of consumer biomass and species distribution shifts under climate change (e.g. Jones et al., 2012; Woodworth-Jefcoats et al., 2015), but these studies did not disentangle the effects of temperature and lower trophic level (LTL) changes, a strategy that can provide mechanistic insight on underlying processes (Carozza et al., 2018).

Here, we identify sources of structural uncertainty in marine ecosystem models, by disentangling the effects of temperature and LTL changes on model projections using eight global models from the FishMIP ensemble. We first summarise how temperature and LTL processes are incorporated in these models, highlighting common representations and differences across the ensemble. We then isolate the impact of changes in temperature and LTL processes on consumer biomass and ecosystem structure (which we define as the relative change in small <30 cm and large ≥30 cm consumer biomass) in a simulation protocol involving a combination of pre-industrial, historical and RCP 8.5 forcings. By illuminating key sources of structural uncertainty in marine model projections, we identify critical areas of future research necessary to improve not only climate impact projections but also our understanding of the marine ecosystem.

2. Methods

We used projections from eight marine ecosystem models from the Fisheries and marine ecosystem Model Intercomparison Project (FishMIP, www.fishmip.org; Tittensor et al., 2018). There are several model types (see Tables 1 and 2 for a summary of each model and key references). First, models that draw on the strongly size-structured nature of marine ecosystem processes to represent the ecosystem purely by body size (BOATS, Macroecological) or trophic level (EcoTroph). Second, trait-based size-structured models (APECOSM, DBPM, FEISTY, ZooMSS), which move beyond a purely size-based representation to include different communities and groups using functional traits other than body size. Last, DBEM is a habitat suitability-based species-distribution model that resolves the biomass and spatial distribution of >1200 fish and invertebrate species using observational data, and includes other mechanisms such as species ecophysiology and dispersal. There is large variation in the structural complexity of the models, and a detailed description of how each model incorporates temperature and lower trophic level (LTL) impacts, including relevant equations and temperature parameters, can be found in the Supplementary Information S2. Here we summarise the key similarities and differences of each model as they pertain to temperature, LTLs and other drivers in Sections 2.1–2.3 and Tables 1 and 2. We then explain the experimental protocol and model outputs in Section 2.4.

2.1. How do models incorporate temperature impacts?

Across all models, individuals gain mass through anabolic processes such as food uptake and assimilation, while they lose mass through catabolic processes such as respiration. Populations can also gain individuals through reproduction, and lose individuals through mortality (Table 2). These processes are all influenced by temperature. As a result, changes in ecosystem structure depend on how models resolve: (i) temperature effects on individual anabolic and catabolic processes across different functional groups, body sizes or trophic levels; and (ii) how these variations drive changes in ecological interactions (Table 2). Temperature effects on these processes are represented in all models as an exponential scaling, with parameters varying widely between models (Supplementary Information S2). However, within models the same temperature scaling parameters are used across all functional groups and ecosystem components, excluding EcoTroph, which uses different scalings depending on the ecosystem's biome.

The representation of anabolic and catabolic processes varies across models (Table 2). Macroecological and EcoTroph have the simplest representations, with individual mass changes resolved implicitly in each model by a single individual metabolic rate that scales with temperature and body size (for Macroecological) or trophic level (for EcoTroph). For these models, total biomass at a given body size/trophic level is determined by the metabolic carrying capacity of that size/trophic level, divided by the metabolic rate of individuals. In these two models, individual metabolic rates increase with temperature while total metabolic carrying capacity at a given body size/trophic level is determined by net primary production. Thus, as warming drives an increase in individual metabolism, total biomass decreases even if primary production remains constant. The BOATS model uses a similar framework to Macroecological and EcoTroph to determine maximum supported biomass at each body size class. However, in BOATS individual mortality is resolved separately and the growth of individuals from one size class to the next is explicitly resolved. As temperatures rise, individual growth rates in BOATS increase, increasing the speed of biomass flow from small to large size classes, but also increasing mortality and reducing the maximum biomass that can be supported at each body size. Taken together, these processes mean that warming causes total biomass to decrease in BOATS.

Within BOATS, Macroecological and EcoTroph, ecological interactions such as predator-prey encounters or predator-predator competition are not explicitly resolved. Thus, temperature and LTL drivers do not explicitly change interactions among individuals. However, in BOATS and Macroecological, all primary producers are represented by a single body size, which is inversely related to temperature; as temperature increases, the single representative body size of primary producers decreases according to an empirical equation. This in turn decreases the production of higher trophic level organisms, as the number of trophic steps that net primary production must be transferred through to reach any given body size increases. However, since trophic transfer efficiency in these models is not temperature-dependent, an increase in the number of trophic levels is not expected to change the ratio of small and large organism biomass. In contrast, transfer efficiency decreases with warming in Ecotroph. This means that warmer waters in Ecotroph will support relatively less biomass at high trophic levels (large body sizes) than what they will at low trophic levels (small body sizes).

For trait-based models (APECOSM, DBPM, FEISTY and ZooMSS), individual growth is fuelled by ingesting smaller organisms, with individual ingestion rates scaling with temperature and body size. For APECOSM, DBPM and FEISTY this scaling is also modulated with the density of prey. Thus, food uptake for individuals at one size is fuelled by predation of smaller size individuals, and in some cases predators can compete with each other for the same prey. These models also include other sources of mortality (destruction of population biomass). APECOSM, DBPM and ZooMSS incorporate at least one size-dependent

Table 1
Summary of temperature, lower trophic level (LTL) and other drivers sourced from Earth system models, used by each model in the FishMIP ensemble, as well as the ecosystem representation of each model. All drivers used by the models in this experiment had a monthly temporal resolution.

Model and key references	Temperature drivers	LTL drivers	Other drivers	Taxonomic scope
APECOSM Maury et al. (2007a, 2007b), Maury (2010), Maury and Poggiale (2013)	3D water temperature	3D small and large phytoplankton, 3D small and large zooplankton biomass*, 3D export carbon flux	3D oxygen concentration, 3D photosynthetically active radiation, 3D current velocities	All epipelagic, mesopelagic and migratory heterotrophic marine animals in the pelagic ecosystem between 15 μg and 120 kg.
BOATS Carozza et al. (2016, 2017)	2D water temperature (averaged over top 75 m)	2D depth-integrated net primary production	NA	All commercial animal biomass from 10 g to 100 kg.
DBEM Cheung et al. (2008, 2010, 2011, 2016)	2D sea surface temperature	2D depth-integrated net primary production	2D surface and bottom oxygen concentration, salinity and pH, sea ice, mixed layer depth, 3D current velocities	>1200 fish and invertebrate species.
DBPM Blanchard et al. (2009, 2012)	2D sea surface and bottom water temperature	2D depth-integrated small and large phytoplankton biomass	NA	All benthic and pelagic marine animals, weighing between 1 mg and 1 tonne.
EcoTroph Gascuel and Pauly (2009), du Pontavice et al. (2020)	2D sea surface temperature	2D depth-integrated net primary production	NA	All marine animals with trophic level ≥ 2.
FEISTY Petrik et al. (2019)	2D upper pelagic (averaged over 100 m) and bottom water temperature	2D depth-integrated (top 100 m) small and large zooplankton biomass*, 2D export carbon flux to the sea floor	NA	Forage, large pelagic and demersal fish, as well as benthic invertebrates, between 1 mg and 125 kg.
Macroecological Jennings and Collingridge (2015)	2D sea surface temperature	2D depth-integrated net primary production	NA	All marine animals between 1 mg and 1 tonne.
ZooMSS Heneghan et al. (2020)	2D sea surface temperature	2D sea surface phytoplankton biomass	NA	Nine zooplankton groups, from flagellates to jellyfish and all marine animals between 1 mg and 10 tonnes.

[*] Where small and large zooplankton biomass are not provided by an Earth system model (as is the case with CESM1-BGC, the Earth system model used in this study) FishMIP splits total zooplankton biomass using the fraction of total phytoplankton biomass from small and large phytoplankton.

mortality term, and FEISTY includes a single natural mortality term that is independent of body size. These additional mortality sources increase with temperature (except for senescence mortality, which increases with body size, in DBPM and natural mortality, which is independent of body size, in FEISTY), causing population biomass to decrease with increasing temperature. In FEISTY, maintenance costs increase faster with both body size and temperature than do ingestion rates. APECOSM and FEISTY also explicitly resolve size and temperature-dependent costs of maintaining existing biomass (metabolism). In these models, as temperature increases, maintenance costs also increase, reducing the available energy for growth and reproduction. If maintenance costs of existing biomass exceed energy intake from ingestion, biomass decreases. As food becomes limited in APECOSM, ingestion rates scale more slowly with temperature than maintenance costs, limiting the

Table 2
Summary of temperature and lower trophic level impacts in the FishMIP model ensemble.

Model	Temperature effect on:		Lower trophic level effect on:	
	Individual anabolic and catabolic processes	Ecosystem structure	Individual anabolic and catabolic processes	Ecosystem structure
APECOSM	Ingestion and thus predatory mortality scale with temperature and vary with predator size as well as the density and size of prey. Assimilation, maintenance, and non-predation mortality rates also scale with temperature. Temperature effects are stronger where prey density is high. In food-limited areas, catabolic processes increase faster than anabolic processes, causing individual mass to decrease. In food-rich areas, catabolic and anabolic processes increase in the same proportion, accelerating life-cycles.	Growth and mortality rates increase with temperature. In food limited situations, this leads to less biomass, especially for large organisms. In prey-rich regions, temperature does not drive biomass down but drives a faster transfer toward large sizes causing an increase in large organisms and a decrease of small organisms due to top-down control.	Small and large plankton biomass is the primary food source of small consumer organisms. More plankton biomass increases satiation and maximizes individual growth and reproduction, thus driving increases in biomass.	More plankton biomass supports more ecosystem biomass and reduces the trophic amplification of food limitation with size. This leads to biomass increase of large organisms and the presence of larger species in the communities.
BOATS	Warming drives higher individual growth and mortality rates, which reduces the maximum biomass that can be supported by a given level of primary production.	Phytoplankton size decreases with warming. Smaller phytoplankton means longer food chains causing biomass declines for all sizes.	Net primary production sets the limits to growth across all body size classes. Higher production means more biomass.	Phytoplankton size decreases with decreasing production. Smaller phytoplankton mean longer food chains causing biomass declines for all sizes.
DBEM	Biomass creation occurs after catabolism is deducted from anabolism. Catabolism increases faster with warming than anabolism. Thus, biomass decreases with warming.	Catabolism increases with size faster than anabolism, so warming affects large species more and drives shifts in spatial distribution of species.	In all regions, net primary production is a key part of what sets the limits to maximum biomass across all higher trophic levels.	Lower net primary production means less consumer biomass can be supported.
DBPM	Ingestion-driven growth, and mortality rates from predation and natural sources scale with temperature at the same rate. Thus, temperature effects largely balance, except in low food regions where natural mortality is relatively large and causes biomass to decrease.	Natural mortality costs scale with temperature but decrease with body size. Thus, warming increases mortality relatively more for small organisms compared to large, potentially causing their biomass to decrease faster.	Small and large phytoplankton biomass set the slope and intercept of the phytoplankton size-spectrum, which is the primary food source of small pelagic organisms. More phytoplankton means more biomass.	Relatively more small phytoplankton with less phytoplankton biomass, which reduces food for small organisms and increases food chain length. This should decrease overall biomass, especially for larger sizes, as senescence increases with size.
EcoTroph	Warming drives higher individual turnover rates, and lower trophic transfer efficiency, which means fewer individuals can be supported, causing biomass to decrease.	Trophic transfer efficiency decreases with warming, causing higher trophic level biomass to decrease more than lower trophic level biomass.	Net primary production is a driver of total biomass across all trophic levels. Higher production means more biomass.	Lower net primary production means less biomass can be supported across all trophic levels.
FEISTY	Maintenance costs, ingestion-driven growth, and mortality rates from predation scale with temperature. Maintenance costs increase faster with warming compared to ingestion, so warming reduces the scope for growth, causing biomass to decrease.	Maintenance costs increase faster than ingestion-driven growth with body size and temperature. Thus, warming will reduce the scope for large organism growth more than small organisms.	Zooplankton is food for all small consumers and medium pelagic consumers. Export production fuels benthic growth. More zooplankton biomass and export production mean more ecosystem biomass overall.	Less zooplankton biomass supports lower pelagic biomass, and more small zooplankton biomass may reduce large fish biomass due to an increase in the number of trophic steps between zooplankton and a narrower scope for growth than smaller sizes.
Macroecological	Warming drives higher individual metabolic rates, which means fewer individuals can be supported by a given level of primary production, causing total biomass to decrease.	Phytoplankton size decreases with warming, lengthening food chains and reducing how much energy is transferred to higher trophic levels.	Net primary production is a key determinant of total biomass. Higher net primary production means more biomass.	Phytoplankton size decreases with decreasing production. Smaller phytoplankton support longer food chains, thus less biomass across all sizes.
ZooMSS	Ingestion-driven growth and mortality rates from predation and senescence scale with temperature at the same rate. Thus, temperature effects largely balance, except where senescence mortality is large, causing biomass to decrease.	Warming negatively impacts large organisms more than small by increasing senescence. If large organism biomass declines more than small, small biomass will increase from reduced predation.	The phytoplankton spectrum—set by total phytoplankton biomass—is the main food of microzooplankton. More phytoplankton means more consumer biomass.	Less phytoplankton biomass means less food for small organisms, and relatively more small phytoplankton. Drives shifts in zooplankton composition, which stabilise food chain length.

scope for new growth and potentially inducing biomass to decrease as maintenance costs outpace ingestion.

In APECOSM, DBPM, FEISTY and ZooMSS, temperature affects anabolic and catabolic processes differently across ecosystems, which has cascading effects on how the different components of ecosystems (e.g. predators and prey) interact. In APECOSM, FEISTY and ZooMSS for example, the scaling of maintenance costs (in APECOSM and FEISTY) and senescence mortality (in APECOSM and ZooMSS) with body size and temperature mean that large organisms are more vulnerable to warming compared to small organisms. Everything else being equal, a warming-induced decrease in large organism biomass would reduce predation mortality on smaller organisms, thus favouring small organisms in these models.

Unlike what happens in the size and trait-based models, anabolic and catabolic processes in DBEM are not driven explicitly by net primary production or by the ingestion of smaller organisms. Instead, individual mass increases in DBEM when anabolism exceeds catabolism, both of which are affected by temperature and other drivers (see Section 2.3). Similar to APECOSM, FEISTY and BOATS, the explicit balance between anabolic and catabolic processes drives an organism's scope for growth–if catabolism outpaces anabolism, an individual's mass will decline. In DBEM, anabolism accelerates more slowly with warming compared to catabolism. Thus, as waters warm, an organism's potential for growth becomes increasingly limited, and their maximum size decreases.

Organisms do not interact in DBEM. Rather, temperature and other forcings drive the spatial distribution of species across the ocean, with species' relative abundance in a region changing with respect to temperature depending on their thermal preference, and the prevailing water temperature. Thus, as waters warm, ecosystem structure changes by individual organisms becoming smaller on average, and by different species shifting their spatial boundaries to follow their thermal preferences.

Finally, energy transfer from small to large organisms through size-based predation is not the only way that different parts of the ecosystem interact; in APECOSM, BOATS, DBPM, DBEM and FEISTY, energy moves from large to the smallest size classes through reproduction. In these models, the flux of small organism biomass entering the population through reproduction can increase or decrease, depending on the relative impacts of warming on large organisms. In FEISTY for example, if large organisms are more adversely affected by warming than small organisms, the reproduction rate in larger size classes would also decline, leading to less biomass overall.

2.2. How do models incorporate lower trophic level processes?

Net primary production sustains essentially all non-photosynthetic life in the oceans, and limits the biomass of higher trophic levels (Ryther, 1969; Friedland et al., 2012). Solar energy captured and organic matter synthesized by primary producers flow through food webs, primarily by larger organisms preying on smaller organisms. FishMIP models focus on higher trophic levels, so lower trophic level processes are driven by a range of Earth system model forcings (Table 1). The role of lower trophic levels in setting the limits to growth for higher trophic levels is represented across the eight FishMIP models in two ways. First, for BOATS, DBEM, Macroecological and EcoTroph, net primary production is used to determine limits of consumer growth rates and total biomass according to trophic transfer functions. Second, in the trait-based models (APECOSM, DBPM, FEISTY and ZooMSS), plankton biomass and export production are consumed by the size classes or functional groups that feed on them. This energy is then transferred to higher trophic levels through size-based predation. However, all eight models considered here are one-way forced (run offline), so there is no feedback from higher trophic levels to lower trophic level biomass or production. This means that for the trait-based models, ingestion-fuelled growth of higher trophic level predators is not explicitly matched by predation mortality in the plankton.

The correlation of mean phytoplankton size with total primary production is an important driver of ecosystem structure (Boyce et al., 2015). Phytoplankton are generally larger in more productive waters (Barnes et al., 2011; Finkel et al., 2010). Given the size-structured nature of the marine ecosystem (Trebilco et al., 2013), smaller phytoplankton support longer food chains, which are thought to support relatively less consumer biomass (Eddy et al., 2020; Ryther, 1969). All models explicitly represent this phenomenon with the exception of EcoTroph and DBEM. EcoTroph uses trophic level instead of body size to represent the marine ecosystem. In DBEM, changes in net primary production affect the carrying capacity of modelled species disregarding the size of primary producers. In BOATS and Macroecological, changes in food chain length are represented by a varying representative size of phytoplankton, the size increasing with net primary production according to empirical equations. In DBPM and ZooMSS, the phytoplankton size-spectrum, which is the relationship between primary producer abundance N and body size $w, N = aw^b$, is continuous, with the intercept a and slope b set by phytoplankton biomass. In these two models, the plankton size-spectrum intercept is lower and the slope is steeper in less productive waters, meaning relatively more small producers but less biomass overall. APECOSM and FEISTY use size-fractionated phytoplankton and zooplankton biomass inputs from earth system models to directly set the biomass of small and large phytoplankton and zooplankton groups, with a fixed size-spectrum slope assigned to each LTL group in APECOSM. APECOSM and FEISTY also use export carbon to represent detrital flux across the entire water column (in APECOSM) or to the seafloor to fuel the growth of benthic invertebrates (in FEISTY).

2.3. How do models incorporate other impacts?

All models in the FishMIP ensemble are driven solely by temperature and LTL drivers, with the exception of APECOSM and DBEM (Table 1). In these two models, movement of organisms between adjacent grid cells is resolved, so both models incorporate current speeds. Since APECOSM resolves the 3D density of animal biomass, the model also uses 3D photosynthetically active radiation to resolve water clarity and light penetration across the water column. Thus, in APECOSM areas with the highest consumer biomass are not necessarily regions with the highest LTL biomass, due to active and passive horizontal movements in response to temperature, light, food availability and the strength of currents. Both APECOSM and DBEM also incorporate oxygen concentration, which impacts anabolic processes; lower oxygen concentration reduces the scope for organism growth in both models, and thus reduces total biomass. DBEM also resolves the negative impacts of acidification on catabolic processes, by incorporating pH forcings. DBEM also uses salinity, sea ice and mixed layer depth forcings, alongside temperature, to establish the spatial extent of each of the $>$1200 fish and invertebrate species the model resolves.

2.4. Experimental protocol

To isolate the impact of temperature and LTL processes on the FishMIP ensemble, we conducted four simulations (Table 3) following the general approach of Carozza et al. (2018). In each simulation, all models were forced with different combinations of temperature, LTL and other (for APECOSM and DBEM) drivers from pre-industrial, historical and high emissions scenarios (RCP 8.5; IPCC, 2014) from the CESM1-BGC earth system model (Moore et al., 2013). simulation submitted for the Coupled Model Intercomparison Project 5 (CMIP5; IPCC, 2014). For RCP 8.5 in the CMIP5 multi-model ensemble, CESM-BGC is average in temperature sensitivity and less than average in global mean NPP and export production decline (Bopp et al., 2013). All forcings were provided to modellers with a monthly temporal resolution. We do not use a range (from low to high) of emission scenarios for the future, or source forcings from multiple Earth system models, as our purpose here is to isolate

Table 3
Summary of the experimental simulations and corresponding environmental driver combinations. Temperature: all temperature-related drivers (e.g., sea surface temperature); LTL: all lower trophic level drivers (e.g., phytoplankton biomass); Other: any drivers that are not related to temperature or lower trophic levels (e.g., pH). The abbreviations for forcings are: PI = pre-industrial control, H = historical, RCP 8.5 = RCP 8.5.

	Simulation							
	Control		Temperature Change		LTL Change		All (Climate) Change	
Drivers	1950-2005	2006-2100	1950-2005	2006-2100	1950-2005	2006-2100	1950-2005	2006-2100
Temperature	PI	PI	H	RCP 8.5	PI	PI	H	RCP 8.5
LTL	PI	PI	PI	PI	H	RCP 8.5	H	RCP 8.5
Other	PI	PI	PI	PI	PI	PI	H	RCP 8.5

sources of structural uncertainty within the FishMIP model ensemble itself (Payne et al., 2016). Under the RCP 8.5 scenario, the CESM1-BGC model projects a global sea surface temperature increase, which is particularly marked at high latitudes (Fig. 1b); net primary production declines across most of the tropics and mid-latitudes, but increases at high latitudes and in the eastern South Pacific (Fig. 1d); phytoplankton and zooplankton biomass declines across most of the world's oceans, except in polar regions (Fig. 1f, h). The mean change in sea surface temperature across the global ocean from 1950 to 2100 under historical (averaged over 1950–1960) and RCP 8.5 (averaged over 2090–2100) scenarios is +3.2 °C, and for net primary production, phytoplankton and zooplankton carbon the mean change was −14%, −8% and −21%, respectively.

To enable the model comparison, two standardized outputs - total

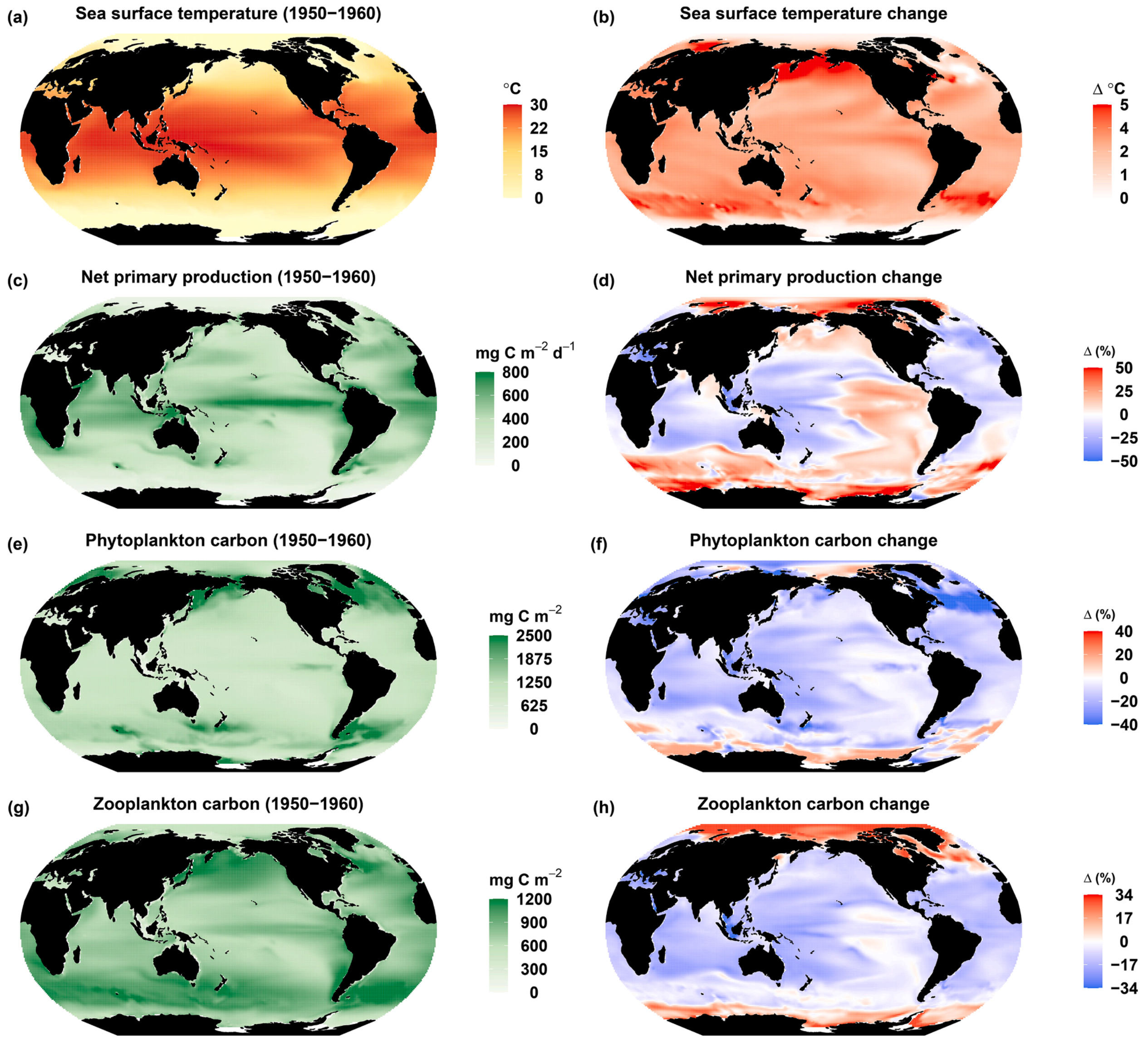

Fig. 1. Control (historical averaged over 1950–1960) forcing variables and the change in those variables from climate change (RCP 8.5) from the CESM1-BGC earth system model; a, b) Sea surface temperature, c, d) Net primary production, e, f) Phytoplankton carbon, g, h) Zooplankton carbon. The change in each variable is measured as the mean over 2090–2100 under the RCP 8.5 scenario minus the mean over 1950–1960 (for sea surface temperature), or the percentage change between the mean in 1950–1960 and 2090–2100 (for net primary production, phytoplankton carbon and zooplankton carbon).

consumer biomass (which broadly includes all consumer with trophic level >1, see Table 1) and the biomass of large consumers (≥30 cm; see Tittensor et al., 2018 for details) - were calculated from each ecosystem model. All models supplied both outputs, except DBEM which did not provide the biomass of large consumers. Outputs were reported as depth integrated carbon biomass (g m^{-2}) and aggregated to a spatial grid with a resolution of 1° on a monthly or annual time step, depending on model capability. Owing to differences in model formulation total consumer biomass varies widely amongst models, all else being equal (Tittensor et al., 2018). Since our focus was not on explaining these differences in total biomass, but rather the differences in the responses of the models to temperature and LTL changes, we compared model outputs using biomass change relative to biomass levels under the preindustrial control. Further, as our focus was isolating impacts of temperature and LTL processes, simulations were run in the absence of fishing.

3. Results

3.1. Global changes in total consumer biomass

All models projected a decline of globally averaged consumer biomass in the Temperature Change simulation, with the exception of APECOSM (Fig. 2a). The spread of total global consumer biomass change in response to warming ranged from around −35% for Macroecological and BOATS, to +3% for APECOSM by the end of the 21st century. EcoTroph produced the third largest change after BOATS and Macroecological of around −13%. The remaining four models (DBEM, DBPM, FEISTY, ZooMSS) simulated modest changes in global consumer biomass of between −2% (FEISTY) to −7% (DBPM) in response to changes in temperature alone.

The LTL Change simulation also showed globally averaged biomass decreases for most models, except BOATS and Macroecological, which projected global biomass increases (Fig. 2b). For these two models, the trajectory of global biomass change was switched in the LTL Change simulation from negative change to positive in comparison with the warming only simulation. In contrast, APECOSM projected global consumer biomass to increase slightly with warming, but decrease with LTL changes. APECOSM projected a 7% decrease in total consumer biomass globally, while BOATS and Macroecological projected increases of 10–15% in response to LTL changes in isolation. Maximum decreases of biomass in LTL simulations are half the magnitude (up to 15%) of the decreases in warming simulations. The smallest response to LTL changes was from EcoTroph, which projected a total consumer biomass change of <−1%. Trends in total consumer biomass from the other five models (DBEM, DBPM, FEISTY and ZooMSS) were grouped within a range between −5% (DBEM) and −15% (ZooMSS).

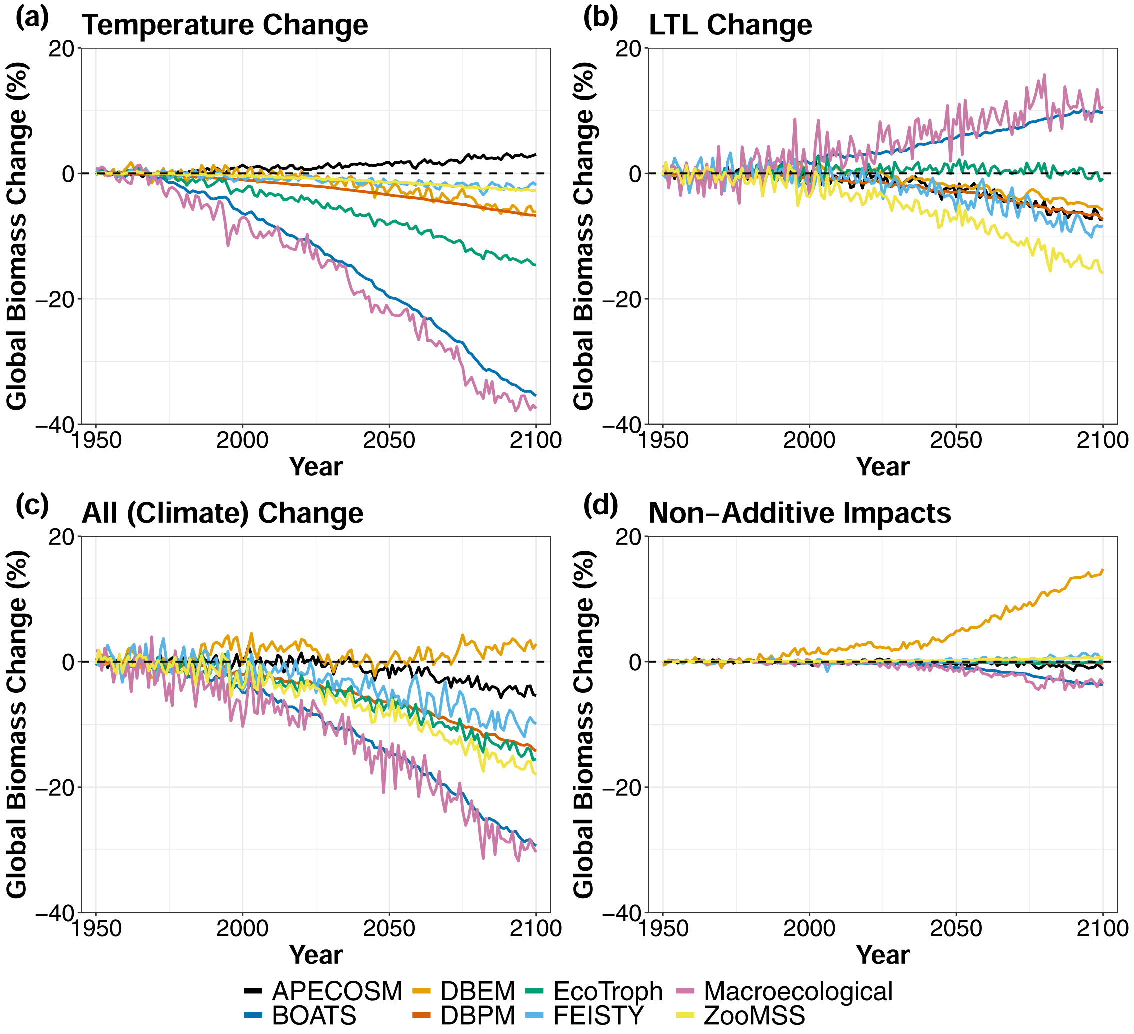

Fig. 2. Model projections of percentage change in global consumer biomass, relative to the Control, from 1950 to 2100 for the: a) Temperature Change simulation, b) Lower Trophic Level (LTL) Change simulation, c) All (Climate) Change simulation and d) the non-additive impacts of temperature and LTL changes. Non-additive impacts are calculated by taking the difference between the All Change and the sum of the Temperature and LTL Change simulations.

The combined temperature and LTL changes led to a decline in globally averaged consumer biomass across all models except DBEM (Fig. 2c). By the end of the 21st century, changes in global consumer biomass in the All (Climate) Change simulation ranged from around −30% for BOATS and Macroecological, to +3% for DBEM. The other five models (APECOSM, DBPM, EcoTroph, FEISTY and ZooMSS) had changes in total global consumer biomass of between −5% (for APECOSM) and −17% (for ZooMSS). For all models except BOATS, DBEM and Macroecological, climate change impacts at the global scale were largely the sum of the separate global impacts of warming and LTL change, with almost no non-additive impact (Fig. 2d). For BOATS and Macroecological, climate change impacts caused total consumer biomass to decline by about 4% more than the sum of separate warming and LTL impacts. In DBEM, total consumer biomass under climate change was ~15% higher than under the combined, separate impacts of warming and LTL impacts, indicating some non-additive impact of cumulative temperature and LTL changes. Non-additive impacts in DBEM may also be caused by additional impacts from changes in pH and oxygen levels. APECOSM, the only other model to incorporate non-temperature or LTL drivers, had negligible non-additive impacts, indicating these other drivers had little effect compared to warming and LTL shifts.

3.2. Spatial changes in total consumer biomass

Globally averaged time-series of total consumer biomass change conceal considerable spatial variation across regions within each model, and between models in each experiment. Temperature-induced shifts in the spatial distribution of total consumer biomass (Fig. 3, left column) varied from increases in many regions for APECOSM, to decreases across the global ocean in DBPM, ZooMSS, EcoTroph, BOATS and Macroecological. The magnitude of the total consumer biomass changes generally followed the magnitude of change in temperature (Fig. 1b); temperate regions that experienced the strongest warming (Fig. 1b) exhibited the largest decreases in biomass for these five models. FEISTY and ZooMSS consumer biomass also decreased with increased temperature in many of the regions with the greatest warming. However, in warm regions (Fig. 1a) with relatively small temperature increases such as the eastern Pacific or northern Indian Ocean, FEISTY consumer biomass increased, and small increases in ZooMSS consumer biomass occurred almost entirely in very high latitude polar regions where temperature change was relatively small (Fig. 1b). In contrast, APECOSM consumer biomass increased across most of the global ocean in response to warming. The exception to this pattern was in patches where phytoplankton biomass was highest (Fig. 1c) such as the North Atlantic, the Bering Strait or the South Pacific around New Zealand. In DBEM, temperature-induced changes in consumer biomass were greatest in the warmest waters around the equator, where DBEM consumer biomass decreased by 60–100%. In cold high latitude waters, DBEM consumer biomass increased by ≥60% in response to warming.

For all models, lower trophic level (LTL) induced shifts in the distribution of consumer biomass (Fig. 3, centre column) show more agreement in their patterns of change; most models show biomass decreases in equatorial regions, and increases towards the poles. The exceptions here are APECOSM, FEISTY and ZooMSS which show a mix of positive and negative consumer biomass toward the north pole. Consumer biomass shifts generally followed changes in the distribution of the main LTL forcings used by each model (Fig. 1d, f, h). APECOSM, DBPM, FEISTY and ZooMSS use plankton biomass inputs (Table 2), and for these models, consumer biomass generally decreased with decreasing phytoplankton carbon (Fig. 1f) and increases were isolated to polar regions. DBEM, EcoTroph, BOATS and Macroecological use net primary production as their LTL forcing and the spatial distribution of changes in consumer biomass followed spatial shifts in net primary production (Fig. 1d), with increases in biomass not only in polar regions, but also in the North Pacific and in the South East Pacific.

When both temperature and LTL drivers changed simultaneously in the All (Climate) Change simulation, shifts in the distribution of consumer biomass for each model were a combination of the shifts driven by separate temperature and LTL effects (Fig. 3, right column; Supplementary Fig. S1). Across all models, temperature-induced declines in consumer biomass were generally exacerbated in regions where LTL changes negatively impacted consumer biomass. Overall, consumer biomass generally increased in polar waters, where all LTL variables increased but temperature changed relatively little. Increases in consumer biomass in DBEM were greater in polar regions under climate change, compared to the sum of the separate impacts of warming and LTL shifts (Supplementary Fig. S1e). Outside of polar regions, the magnitude and direction of change in consumer biomass varied among models, depending on their individual responses to temperature and LTL changes. For BOATS and Macroecological, the magnitude of positive and negative changes in consumer biomass from LTL shifts in isolation were attenuated when combined with the impacts of warming in the Climate Change simulation (Supplementary Fig. S1g, h), however these non-additive effects largely cancelled at the global scale (Fig. 2d).

3.3. Disentangling temperature and lower trophic level impacts on total consumer biomass

Fig. 4 compares the forced changes in sea surface temperature (SST) with the co-located simulated changes in biomass for all grid cells in the global ocean. Regressions give negative exponential slopes for all models, but with substantial variation (Supplementary Table S1). Globally, consumer biomass changed between −0.5% and −2.0% for every 1 °C of sea surface warming for APECOSM, FEISTY, DBPM and ZooMSS, and between −4.8% and −15.4% per 1 °C across EcoTroph, BOATS and Macroecological (Supplementary Table S4). The models vary in their degree of linearity, with DBEM projecting the greatest nonlinearity in the impacts of warming between cold and warm waters (Fig. 4e; Supplementary Table S4). DBEM consumer biomass increased by ~50% in cold waters (<15 °C SST) in response to warming (Fig. 4e), and decreased on average by >27% for each 1 °C warming in warm (≥15 °C SST) waters.

Fig. 5 shows the corresponding plots for LTL forcing. For all models, changes in total consumer biomass were positively correlated with changes in their respective aggregated lower trophic level (LTL) forcing (Fig. 5). A 1% change in LTL forcings caused a change in total consumer biomass of between 0.6% in DBPM to 1.7% in BOATS (Supplementary Table S4). Positive correlations between consumer biomass and LTL changes ranged from $r = 0.39$ for DBPM, to $r = 0.98$ for EcoTroph. For all models except DBPM, the greatest correlation was between change in total consumer biomass and change in total LTL production, or biomass, of the model's chosen LTL forcing (Supplementary Table S3). In models that used size-fractionated LTL inputs, or additional secondary LTL inputs, changes in consumer biomass were less correlated with changes in their main aggregated LTL forcing (APECOSM, DBPM, FEISTY) compared to models that did not use size-fractionated or multiple LTL forcings (BOATS, DBEM, EcoTroph, Macroecological, ZooMSS).

3.4. Impacts of warming and lower trophic level change on ecosystem structure

In response to warming, there was little consensus in the relative change of small (<30 cm) and large (≥30 cm) mean global consumer biomass (Fig. 6a), with four models (BOATS, EcoTroph, Macroecological, ZooMSS) showing a decrease of both and the other three models (APECOSM, DBPM, FEISTY) showing a mixture of responses. Small consumer biomass increased by ~2% in both APECOSM and FEISTY in response to warming, but large consumer biomass increased in APECOSM by 5% while decreasing in FEISTY by >10%. Similarly, although small consumer biomass in DBPM and ZooMSS decreased by 3% and 6% respectively, these models disagreed on the direction of

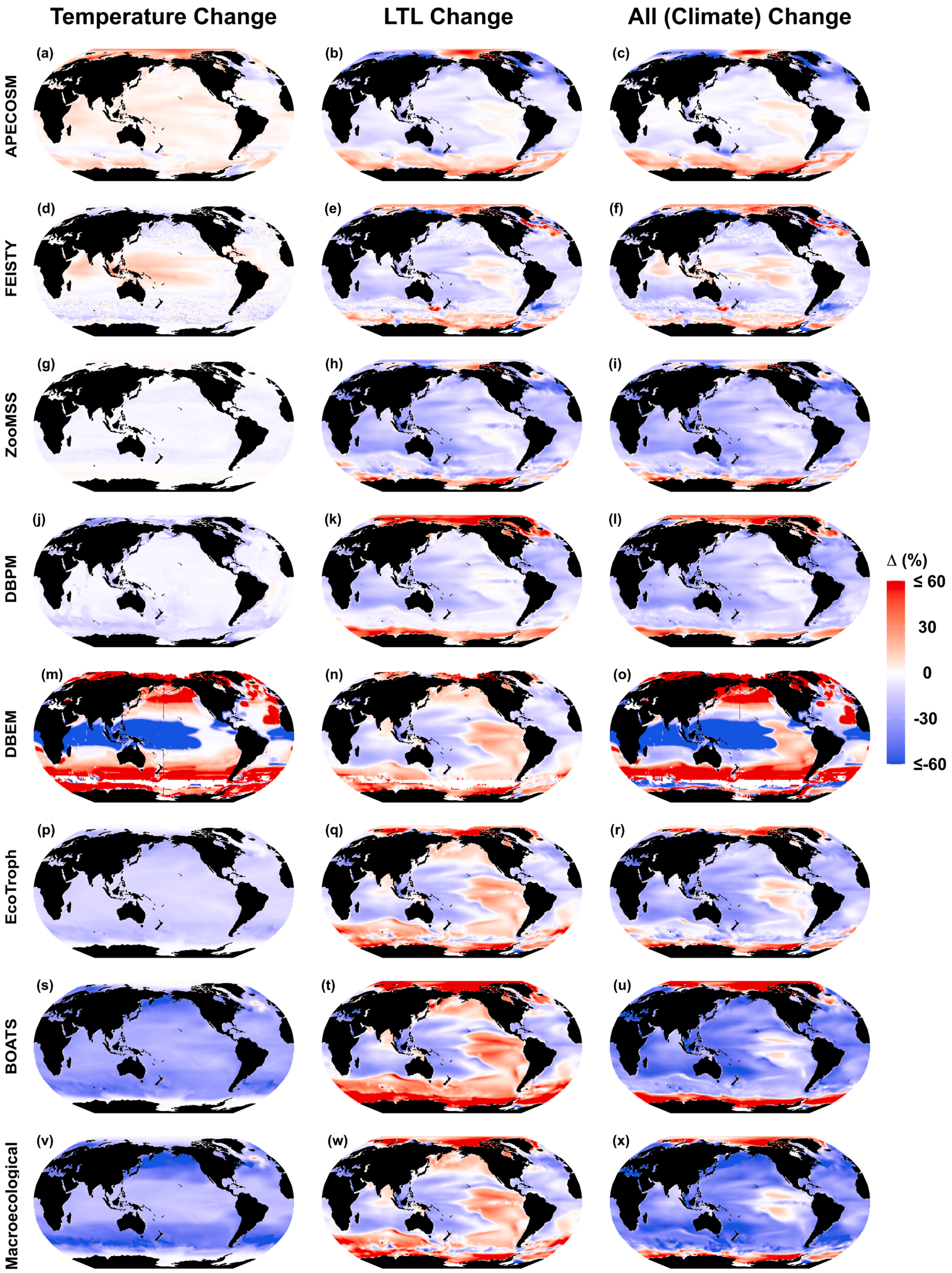

Fig. 3. Maps of relative total consumer biomass averaged over 2090–2100, compared to the Control (over 2090–2100), for the Temperature (left column), Lower Trophic Level (LTL) and All Change simulations for a-c) APECOSM, d-f) FEISTY, g-i) ZooMSS, j-l) DBPM, m-o) DBEM, p-r) EcoTroph, s-u) BOATS, v-x) Macroecological. Maps are ordered by the magnitude (from smallest to greatest) of the negative warming impact on consumer biomass.

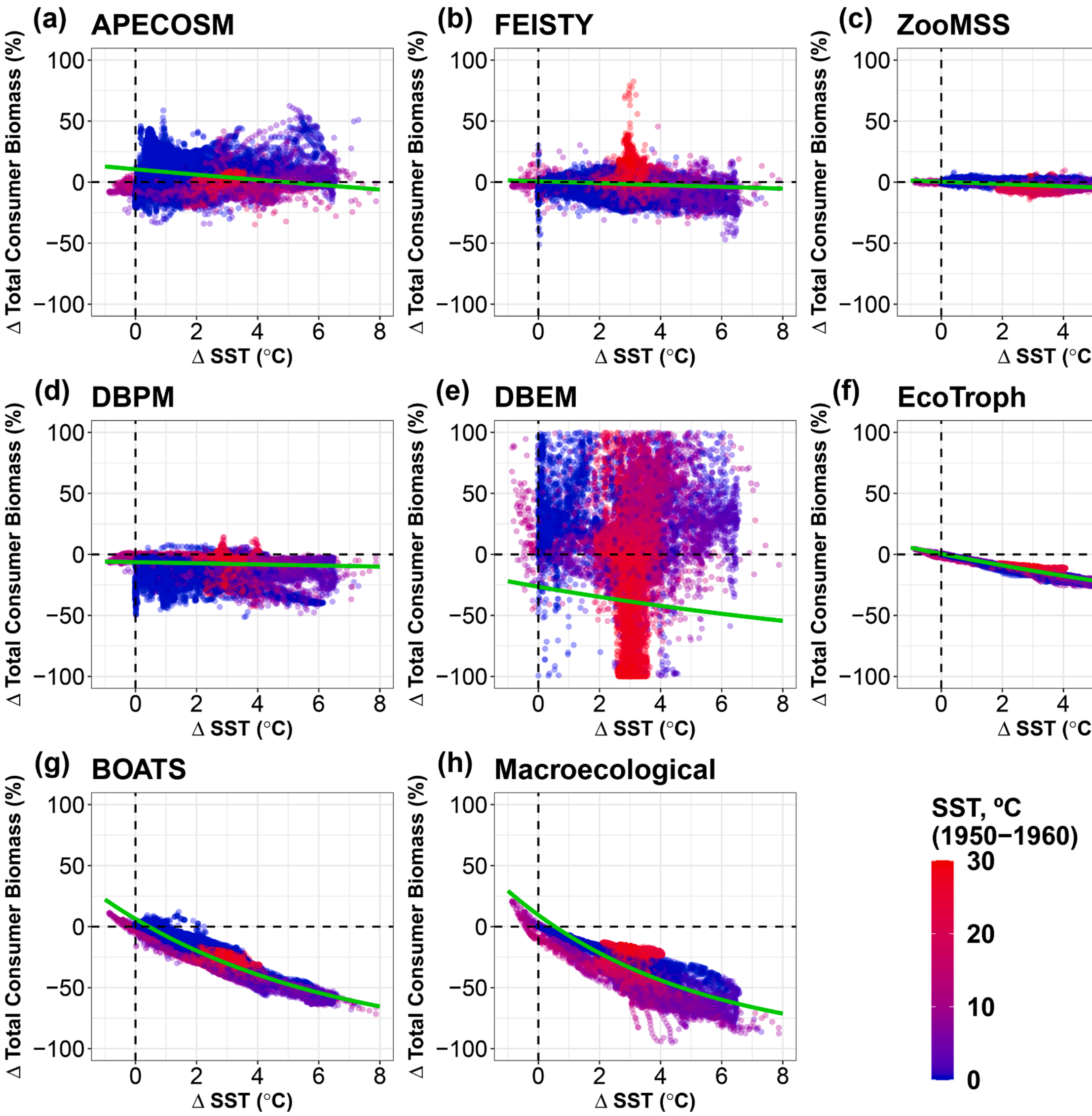

Fig. 4. Change in total consumer biomass (%) against the mean change in sea surface temperature (SST) over 2090–2100, for individual 1° grid squares, under the Temperature Change simulation, compared to the Control simulation, for a) APECOSM, b) FEISTY, c) ZooMSS, d) DBPM, e) DBEM, f) EcoTroph, g) BOATS, h) Macroecological. Each point is coloured according to the mean 1950–1960 historical SST in its grid cell. Dotted horizontal and vertical black lines indicate where % change in total consumer biomass and change in temperature are zero, respectively. The green line is the fitted regression ($\Delta \text{Total Consumer Biomass} = \exp(\beta_0 + \beta_1 \Delta \text{SST}) + \varepsilon$) for the change in consumer biomass with warming. We use exponential regression to calculate the line of best fit here since all models incorporate temperature effects using an exponential function (see Supplementary Information). Information about the fitted regression is in Supplementary Table S1 and S4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

change for large consumer biomass. In response to warming total large consumer biomass in DBPM increased by 15%, and over 60% in some regions (Supplementary Fig. S2n), but in ZooMSS total large consumer biomass declined by ~2% overall. Finally, small and large consumer biomass declined in EcoTroph, BOATS and Macroecological, and the spatial pattern of decline across was similar both across models and across small and large consumer biomass (Supplementary Fig. S2). There was no difference in the magnitude of the decline of small and large consumer biomass in Macroecological, however in EcoTroph and BOATS the magnitude of the decline in large consumer biomass was greater than the decline in small consumer biomass.

Changes in total small and large consumer biomass in response to lower trophic level (LTL) changes show more agreement (Fig. 6b). The change in total small and large consumer biomass was similar in APECOSM, FEISTY, ZooMSS, EcoTroph, BOATS and Macroecological, and again the spatial pattern of change in small and large consumer biomass generally followed each model's respective LTL forcings (Supplementary Fig. S2; Fig. 1f-h). However, in DBPM, total large consumer biomass declined by 40%, while small consumer biomass declined by only 10%. This was reflected in the spatial patterns of biomass change for DBPM, with large consumer biomass varying by over ±60% and small consumer biomass varying by less than ±30% across non-polar regions of the global ocean (Supplementary Fig. S2 o,p).

Small and large consumer biomass declined for all models (except DBEM, which was excluded from this part of the analysis since it did not provide size-fractionated biomass) in response to climate change (simultaneous temperature and LTL changes) impacts (Fig. 6c). Large consumer biomass declined more than small consumer biomass in BOATS, DBPM, EcoTroph and FEISTY. In contrast, small consumer biomass declined more than large consumer biomass in APECOSM and ZooMSS, and there was no difference between small and large consumer biomass change in Macroecological. For all models, the impacts of climate change on small and large consumers were largely the sum of temperature and LTL impacts, with relatively small non-additive impacts (Fig. 6d).

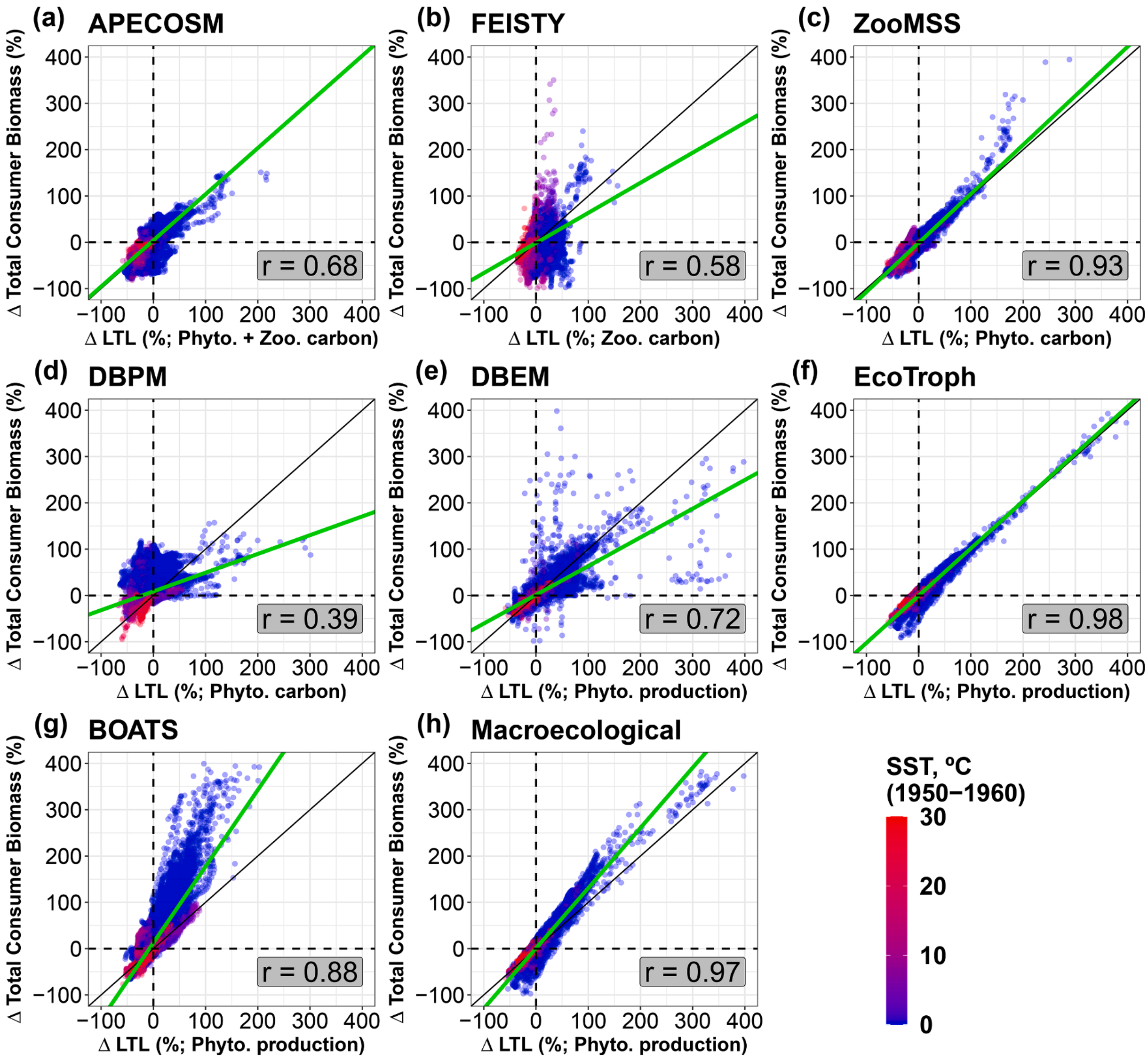

Fig. 5. Change in total consumer biomass (%) against change in aggregated lower trophic level forcings (LTL), from 2090 to 2100 under the LTL Change simulation, against the Control, for individual 1° grid squares, compared to the Control simulation for a) APECOSM, b) FEISTY, c) ZooMSS, d) DBPM, e) DBEM, f) EcoTroph, g) BOATS, h) Macroecological, with Pearson's correlation coefficient (*r*) reported for each. Each point is coloured according to the average 1950–1960 historical sea surface temperature (SST) in its corresponding grid cell. The black solid line is the 1:1 line, and the dotted horizontal and vertical black lines indicate where % change in total consumer biomass and % change in LTL are zero, respectively. The green line is the fitted regression ($\Delta\mathrm{TotalConsumerBiomass} = \beta_0 + \beta_1\Delta\mathrm{LTL} + \varepsilon$) for the change in consumer biomass with warming. For models that use more than one LTL variable (APECOSM), or size-fractionated LTL (FEISTY and DBPM), ΔLTL is calculated from the sum of all LTL forcings. Information about the fitted regression is in Supplementary Table S2 and S4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The results of our experimental protocol reveal commonalities, as well as contrasts among the FishMIP models. All models agreed that the combination of warming and lower trophic level (LTL) shifts will cause substantial regional changes in consumer biomass. Furthermore, no model projected a significant increase in global biomass in response to climate change. However, the impacts of warming varied markedly between models, leading to large inter-model disagreements. Changes in LTL drivers were more directly correlated with the outcomes on consumer biomass, but with substantial variation among models, and strong dependence on each model's choice of LTL driver. For almost all models, the combined impacts of warming and LTL changes were largely additive at the global scale, showing little nonlinear interaction, and additional climate change drivers (e.g., oxygen, acidification, current speeds) were not significant global drivers in the models that included them (APECOSM and DBEM). By separating the marine ecosystem model responses to climate-driven warming versus LTL shifts, our results point toward the processes that need to be clarified to reduce the uncertainty of how these two dominant drivers impact marine ecosystems.

4.1. Warming impacts are complex

One straightforward expectation might be that the different responses to warming reflect differences in the temperature scalings used in each model. However, the differences in temperature scalings do not readily explain the variation in the results. For instance, DBPM and Macroecological use identical temperature scalings (see Supplementary Information S2.4 and S2.7), yet DBPM's projections of warming-induced biomass decline are almost an order of magnitude smaller than those of Macroecological. This does not mean the temperature scalings are irrelevant, but rather that the emergent results depend on the

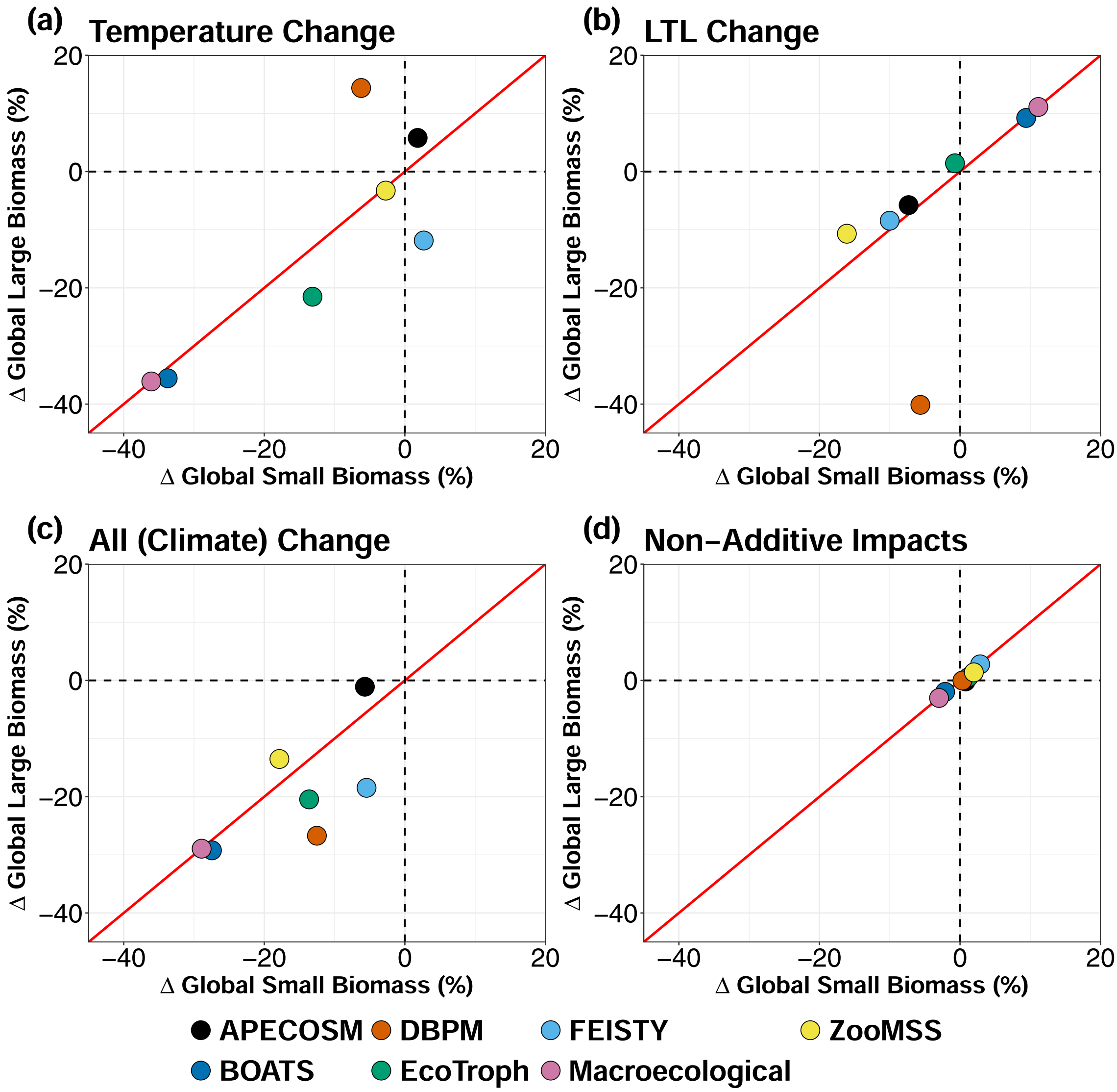

Fig. 6. Change in total small (<30 cm) consumer biomass versus change in global large (>30 cm) consumer biomass averaged between 2090 and 2100 relative to Control simulation for each model (excluding DBEM, which did not provide small and large consumer biomass) in the a) Temperature Change simulation b) Lower Trophic Level (LTL) Change simulation, c) All Change simulation and d) the non-additive impacts of temperature and LTL changes, calculated by taking the difference between the All Change and the sum of the Temperature and LTL Change simulations. The red solid line is the 1:1 line, and the dotted horizontal and vertical black lines indicate where the percentage change in global large and small consumer biomass are zero, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interactions of multiple temperature-dependent processes, operating within the structural context of each model.

For example, DBEM attempts to resolve preferred temperature ranges for different species, while the other models consider the effect of temperature on generalized physiological processes, implicitly assuming that species moving out of a region are replaced by species moving in with no change in ecosystem function. Although food web processes such as predator-prey interactions are not explicitly included in the DBEM species-distribution model, it projects an emptying of tropical waters and a corresponding build-up of biomass in polar waters, as species move poleward to follow their thermal preferences. This redistribution of the biomass of >1200 recorded commercial species included in the model reflects the absence of very warm water fish that can repopulate the tropics, and the small number of cold water fish in the initial state (Cheung et al., 2010). It also largely explains the model's combined impacts of warming, LTL shifts and other drivers being nonlinear: relative to extant species in polar waters, a larger number of species follow their thermal niche poleward and are able to take advantage of increased primary production in high latitude regions, compared to the regions they left behind.

DBEM aside, four of the models included here (APECOSM, DBPM, FEISTY and ZooMSS) project much smaller warming impacts on consumer biomass than the remaining three models (BOATS, EcoTroph and Macroecological). Although there are many differences between these models, one particularly salient feature is that the low-sensitivity models all use LTL biomass as Earth-system model (ESM) drivers for the projections, together with temperature-dependent feeding rates. In contrast, the high-sensitivity models use ESM net primary production to directly limit the growth rates of upper trophic levels. We suggest that the discrepancy in temperature sensitivity between the model groups can be attributed, at least in part, to an inconsistency that arises from the 1-way forcing of marine models with LTL biomass. The relationship between LTL biomass (B_{LTL}), LTL production (P_{LTL}) and higher trophic level predation ($Pred_{HTL}$) through time t can be represented as:

$$\frac{dB_{LTL}}{dt} = P_{LTL}(t) - Pred_{HTL}(t)$$

In reality, if warming accelerates predation rates, but lower trophic level production remains constant or does not increase as much, such that $P_{LTL}(t) < Pred_{HTL}(t)$, LTL biomass would decrease. However in the 1-way forcing used here, LTL biomass is determined externally by the Earth system model and is not affected by predation from higher trophic levels. Thus, increased predation rates from warming on fixed LTL biomass causes an increase in the flux of biomass energy into higher trophic levels that is decoupled from lower trophic level production. This increased energy input counters the increased metabolic rates and associated respiratory losses, dampening biomass declines from warming. This inconsistency in coupling between LTLs and higher trophic level consumers would tend towards an underestimate of warming impacts on consumer biomass. In contrast, in the production-driven models there is no spurious energy input under warming, so that warming-driven increases in consumer respiration costs and decreases in representative phytoplankton size act to drive biomass down strongly.

Our results also explored the warming impacts on ecosystem structure, defined as the relative biomass of small versus large organisms. Here, there was little consensus between models. DBPM and FEISTY provide a striking example of divergent projections of ecosystem structure with warming. In DBPM, ingestion-fuelled anabolism outpaces senescence-induced mortality in large organisms as waters warm (Blanchard et al., 2012), causing their biomass to increase. This raises predation pressure on smaller organisms, which when coupled with warming-induced increases in natural mortality, causes their biomass to decline. By contrast, in FEISTY, biomass respiration increases faster with both body size and temperature compared to ingestion-fuelled anabolism (Petrik et al., 2019) reducing the scope for growth and causing large organism biomass to decline with warming. Declines in large consumer biomass in FEISTY with increasing temperature relieve predation pressure on small consumers, resulting in an increase in their biomass, especially in tropical waters. The divergent impacts of warming on individual processes and ecosystem structure reflects the lack of consensus among modellers of how temperature impacts on individuals translate into ecosystem impacts.

4.2. Lower trophic level impacts are influenced by choice of forcing

The choice of LTL forcings differed between models, with each model using either biomass or production variables at the phytoplankton or zooplankton level, with significant impacts on the results. Generally, spatial changes in consumer biomass were most correlated with changes in the distribution of the LTL forcing used. The sensitivity of models to the choice of LTL forcing again indicates a lack of common understanding of how to link lower trophic levels production with higher trophic levels, with no consensus on whether production rates or standing-stock biomass should be used. We believe this problem fundamentally arises out of practical necessity because of each model's one-way, offline coupling with the Earth system model—were higher trophic levels and LTLs to be fully coupled, and predation feedbacks on LTLs resolved, there should theoretically be no disagreement between models that use production or biomass variables, everything else being equal. However, in the absence of two-way coupled models in the FishMIP ensemble, the development of which is a tremendous technical challenge (see Aumont et al., 2018), this problem remains to be addressed. As mentioned above, this problem also leads to inconsistency in the temperature response when plankton biomass versus net primary production rates are used.

Ecosystem structure did not change substantially in response to LTL changes, except in DBPM. Large organism biomass in DBPM declined by 40% and small organisms declined by <10% in response to decreases in phytoplankton biomass and resultant shifts in the size structure of the phytoplankton abundance spectrum. DBPM's relatively large decrease in large consumer biomass in response to phytoplankton biomass declines is a result of biomass destruction through senescence mortality, which increases with body size but does not depend on food density, outpacing ingestion-fuelled biomass creation. The other predation-explicit models—including ZooMSS and FEISTY, which also include biomass destruction processes independent of food density that increase with body size—did not exhibit similar declines in large organism biomass. This is because in these models, ingestion-fuelled growth outpaces biomass destruction from these processes, highlighting the sensitivity of model outputs to the parameterisation of these rates. In fact, across all models except DBPM, the change in large organism biomass with LTL change was equal to or slightly less than the change in small organism biomass.

4.3. Cumulative warming and lower trophic level impacts are largely additive

Across the model ensemble, climate change impacts on total consumer biomass and ecosystem structure were generally well-approximated by the sum of separate warming and LTL impacts. This lack of non-linearity is perhaps less surprising for the majority of models that only use temperature and LTL drivers to force their models (Tittensor et al., 2018), but remarkably it also holds for APECOSM, which incorporates other drivers such as oxygen, pH and current velocity. The fact that the overall climate change impact on consumer biomass in APECOSM was close to the sum of temperature and LTL impacts indicates that the additional forcings have a comparatively small effect. DBEM, which also includes additional environmental drivers, did show a much stronger non-additive impact of climate change on overall consumer biomass, but this appeared to be driven primarily by the relocation of species niches in DBEM in response to warming, rather than the other drivers. DBEM aside, only BOATS and Macroecological show significant non-linear interactions between temperature and LTL drivers. This can be attributed to the fact that, in BOATS and Macroecological, the representative size of phytoplankton used to force the models scales with both net primary production and temperature, increasing in cooler waters or regions with high net primary production (Dunne et al., 2005). For these two models, the spatial pattern of attenuation follows shifts in net primary production, indicating that warming attenuates the increases and decreases in biomass from shifts in net primary production.

It may be tempting to assume that the lack of nonlinear interactions in the models means that such nonlinearities are unlikely to exist in the ocean. However, an increasing number of experimental and observational studies indicate that cumulative impacts from climate change stressors such as warming, deoxygenation and acidification are likely to be nonlinear and amplifying (Sampaio and Rosa, 2020). Rather, given the rudimentary representation of many ecosystem processes in the models (e.g., no phenological or diversity-related mechanisms, simplistic or absent predation relationships), we suggest that it is more appropriate to ascribe the lack of nonlinear interactions in marine climate change projections to our present lack of ability to resolve them in the models.

4.4. Improving marine ecosystem models with observational constraints

In this study, we have identified key sources of structural uncertainty that drive disparate projections of climate change impacts on the global marine ecosystem. As a first step, the marine modelling community can work to reduce this structural uncertainty and increase the credibility of ecosystem projections by constraining models with independent observations. An increasingly popular approach to confront model projections with observations is to use emergent constraints, which relate the long-term climate sensitivity of an observable ecosystem feature - such as total biomass change (Free et al., 2019) or size-spectrum slope (Blanchard et al., 2017b; Heneghan et al., 2019) - to its short-term, observed variability (Allen & Ingram, 2002; Eyring et al., 2019). Models that give a closer fit to short-term observed variability of an ecosystem feature are hypothesised to provide more reliable projections of its long-term variability from climate change (Kwiatkowski et al., 2017; Veytia et al., 2020). Moreover, within a model ensemble, each model's weighting can be linked to its ability to capture the emergent constraint (Eyring et al., 2019). This provides a more sophisticated and credible way to weight model projections within an ensemble, over the standard approach where all models are given equal weighting (known as model democracy), irrespective of performance (Knutti, 2010). Emergent constraints do not require or necessarily reward any particular ecosystem representation. This is important as differing representations of the marine ecosystem across the FishMIP ensemble not only represent our present uncertainty of the most important drivers structuring marine ecosystems, but also the diversity of purpose and scope for which models have been built.

Finally, it is possible for models to perform well against whole-ecosystem emergent constraints, while neglecting fundamental physiological or ecosystem processes (Knutti, 2010). Therefore, if we are to improve marine models, it is also necessary to consider observational constraints on physiological processes such as the balance between growth and respiration with temperature, or ecosystem processes such as the coupling of lower and higher trophic levels. Improving our understanding of how physiological processes such as ingestion and metabolism respond to warming, and how changes in LTL processes propagate through marine ecosystems, are critical steps towards model improvement and more robust climate impact projections.

5. Concluding remarks

Projecting the global impact of climate change on marine ecosystems and fisheries is an important and challenging task. Marine ecosystem models represent the current understanding of how climate change could impact the food web and fisheries globally in the future. Yet, although these models have made great strides in recent years, our results show that the current understanding falls short in many respects.

Our harmonized experimental protocol clearly showed that the responses to the two most important drivers of change – warming and LTL shifts – differ widely among models. Uncertainty in the temperature sensitivities of competing processes, including both physiology and ecological interactions, undermine confidence in the emergent sensitivities, and can only be improved with better observational constraints. Meanwhile, the outcome of changes in both water temperature and LTL production depends strongly on the feedback of consumers on the LTL biomass itself, a process which is not captured by any of the one-way forcings available at present, and can only be rectified with fully two-way coupling, which is itself sure to raise many new questions.

What are the implications of our results for single ecosystem model studies? The eight models used here differ significantly in their design and ecosystem representation, having been built for different purposes (Tittensor et al., 2018). Although using common outputs across models has been useful here to identify shared weaknesses, this approach conceals the strengths of individual models to resolve certain processes and ecosystem components that other models do not. Thus, studies that explore the unique strengths and weaknesses of individual models remain important, in order to explore questions that each model has been designed to address. However, results of these single model studies should be interpreted within the greater context of sources of structural uncertainty shared across models identified here.

Attempting to summarise the vast complexity of the global marine ecosystem in a handful of equations is enormously difficult. The fact that independently constructed models with contrasting architectures have arrived at many similar conclusions is encouraging, while their diversity is useful to identify common weaknesses. These initial results from the FishMIP ensemble provide a glimpse into the great promise of multi-model comparisons to improve our understanding of the global marine ecosystem and its future under change.

6. Code and data availability

The experimental protocol in this paper has no code associated with it. Forcing data from CMIP5 used for the protocol, and the FishMIP model outputs presented in this paper are available on the ISIMIP servers (https://www.isimip.org/).

Author contributions

JLB, TDE, EDG and DPT led the conceptualisation and development of the protocol for this study, with contributions from the other authors. CH and RFH obtained and processed forcings for the modellers to complete the protocol, with assistance from JV. Model simulations were conducted by RFH, NB, CB, WC, MC, JDE, TDE, ME, JAG, DF, JG, OM, JP, CMP, HdP, JS, TCT, PAW. RFH conducted the analysis, with assistance from EDG and JLB. RFH led the writing of the text, with feedback and contributions from all authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102659.

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