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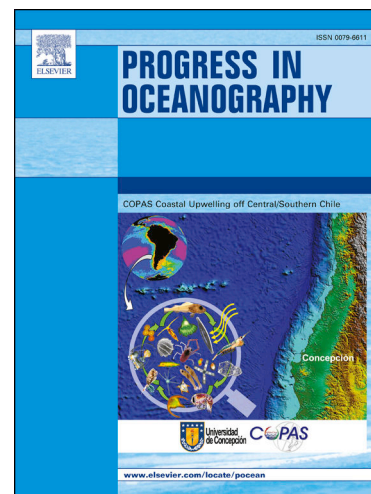
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1 **Title**

2 Disentangling diverse responses to climate change among global marine ecosystem models

3

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54

55 **Abstract**

56 Climate change is warming the ocean and impacting lower trophic level (LTL) organisms.

57 Marine ecosystem models can provide estimates of how these changes will propagate to

58 larger animals and impact societal services such as fisheries, but at present these estimates

59 vary widely. A better understanding of what drives this inter-model variation will improve our

60 ability to project fisheries and other ecosystem services into the future, while also helping to

61 identify uncertainties in process understanding. Here, we explore the mechanisms that

62 underlie the diversity of responses to changes in temperature and LTLs in eight global marine

63 ecosystem models from the Fisheries and Marine Ecosystem Model Intercomparison Project

64 (FishMIP). Temperature and LTL impacts on total consumer biomass and ecosystem structure

65 (defined as the relative change of small and large organism biomass) were isolated using a

66 comparative experimental protocol. Total model biomass varied between -35% to +3% in

67 response to warming, and -17% to +15% in response to LTL changes. There was little

68 consensus about the spatial redistribution of biomass or changes in the balance between

69 small and large organisms (ecosystem structure) in response to warming, and LTL impacts on

70 total consumer biomass varied depending on the choice of LTL forcing terms. Overall, climate

71 change impacts on consumer biomass and ecosystem structure are well approximated by the

72 sum of temperature and LTL impacts, indicating an absence of nonlinear interaction between

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

79

80 **Keywords**

81 *Climatic change, modelling, fishery oceanography, marine ecology, FishMIP, structural*
82 *uncertainty*

83

84

85 1. Introduction

86 Water temperature and primary production play critical roles in marine processes. Higher
87 temperatures accelerate reaction rates, with consequences ranging from the molecular to
88 ecosystem scale, while primary production provides the fundamental source of energy for
89 almost all marine life (Brown et al. 2004; Chavez et al. 2011). Climate change impacts on both
90 water temperature and primary production will thus alter marine ecosystems in fundamental
91 ways (Pörtner et al. 2014). For example, a first-order expectation of these impacts is that
92 accelerated metabolic rates will consume energy more quickly in a warmer ocean, all else
93 being equal, so that less biomass could be supported by a given level of primary production
94 (Heneghan et al, 2019). Yet, ecosystem-level effects emerge from individual-level processes
95 and interactions, which could lead to nonlinear effects and changes in ecosystem structure,
96 while shifting thermal habitats may influence the distribution of species, transforming food-
97 webs to previously unknown states (Coll et al. 2020; Pinsky et al. 2020; Poloczanska et al.
98 2016).

99
100 There is a growing need to quantify and project climate change impacts on marine ecosystems
101 to motivate mitigation (Bryndum-Buchholz et al. 2020), provide insight into potential future
102 threats to food security (Barange et al. 2014; Blanchard et al. 2017a; Boyce et al. 2020), and
103 identify needs for biodiversity conservation (Brito-Morales et al. 2020; Waldron et al. 2020).
104 Thus, there has been a recent proliferation of spatially-explicit marine ecosystem models that
105 simulate higher trophic level biomass and ecosystem structure at regional and global scales,
106 driven by output from climate-ocean-biogeochemical models (Tittensor et al. 2018). These
107 ecosystem models differ significantly in their design, level of complexity and implementation,
108 reflecting different choices for how to represent fundamental marine ecosystem processes,

109 as well as a diversity of model purpose and scope. As a result, there is considerable
110 uncertainty in model projections of climate change impacts on higher trophic levels (e.g. Lotze
111 et al., 2019), with projections from each model dependent upon decisions around the
112 inclusion or simplification of many candidate processes. Structural diversity in model
113 projections is a strength for gaining a rich view of possible outcomes, given that each model
114 reflects a different subset of established physiological and process knowledge, implemented
115 using different mathematical representations (Knutti, 2010; Brander et al. 2013; Lefevre et al.
116 2017; Payne et al. 2016). At the same time, this diversity reflects fundamental uncertainty in
117 our understanding of processes. Thus, identifying sources of structural uncertainty in
118 ensemble projections can point to critical weaknesses and thereby accelerate model
119 improvement.

120

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

133 uncertainty, which is problematic for the goal of using these models to provide assessments
134 of climate impacts on marine ecosystems and the societal services they provide.

135

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

152

153 Here, we identify sources of structural uncertainty in marine ecosystem models, by
154 disentangling the effects of temperature and LTL changes on model projections using eight
155 global models from the FishMIP ensemble. We first summarise how temperature and LTL
156 processes are incorporated in these models, highlighting common representations and

157 differences across the ensemble. We then isolate the impact of changes in temperature and
158 LTL processes on consumer biomass and ecosystem structure (which we define as the relative
159 change in small <30 cm and large ≥ 30 cm consumer biomass) in a simulation protocol
160 involving a combination of pre-industrial, historical and RCP 8.5 forcings. By illuminating key
161 sources of structural uncertainty in marine model projections, we identify critical areas of
162 future research necessary to improve not only climate impact projections but also our
163 understanding of the marine ecosystem.

164

165 **2. Methods**

166 We used projections from eight marine ecosystem models from the Fisheries and marine
167 ecosystem Model Intercomparison Project (FishMIP, www.fishmip.org; Tittensor et al. 2018).

168 There are several model types (see Tables 1 and 2 for a summary of each model and key
169 references). First, models that draw on the strongly size-structured nature of marine
170 ecosystem processes to represent the ecosystem purely by body size (BOATS,
171 Macroecological) or trophic level (EcoTroph). Second, trait-based size-structured models
172 (APECOSM, DBPM, FEISTY, ZooMSS), which move beyond a purely size-based representation
173 to include different communities and groups using functional traits other than body size. Last,
174 DBEM is a habitat suitability-based species-distribution model that resolves the biomass and
175 spatial distribution of >1200 fish and invertebrate species using observational data, and
176 includes other mechanisms such as species ecophysiology and dispersal. There is large
177 variation in the structural complexity of the models, and a detailed description of how each
178 model incorporates temperature and lower trophic level (LTL) impacts, including relevant
179 equations and temperature parameters, can be found in the Supplementary Information S2.

180 Here we summarise the key similarities and differences of each model as they pertain to

181 temperature, LTLs and other drivers in Sections 2.1, 2.2, 2.3 and Table 1 and 2. We then
182 explain the experimental protocol and model outputs in Section 2.4.

183

184 **2.1. How do models incorporate temperature impacts?**

185 Across all models, individuals gain mass through anabolic processes such as food uptake and
186 assimilation, while they lose mass through catabolic processes such as respiration.

187 Populations can also gain individuals through reproduction, and lose individuals through
188 mortality (Table 2). These processes are all influenced by temperature. As a result, changes

189 in ecosystem structure depend on how models resolve: (i) temperature effects on individual
190 anabolic and catabolic processes across different functional groups, body sizes or trophic

191 levels; and (ii) how these variations drive changes in ecological interactions (Table 2).

192 Temperature effects on these processes are represented in all models as an exponential
193 scaling, with parameters varying widely between models (Supplementary Information S2).

194 However, within models the same temperature scaling parameters are used across all
195 functional groups and ecosystem components, excluding EcoTroph, which uses different
196 scalings depending on the ecosystem's biome.

197

198 The representation of anabolic and catabolic processes varies across models (Table 2).

199 Macroecological and EcoTroph have the simplest representations, with individual mass
200 changes resolved implicitly in each model by a single individual metabolic rate that scales with

201 temperature and body size (for Macroecological) or trophic level (for EcoTroph). For these

202 models, total biomass at a given body size/trophic level is determined by the metabolic

203 carrying capacity of that size/trophic level, divided by the metabolic rate of individuals. In

204 these two models, individual metabolic rates increase with temperature while total metabolic

205 carrying capacity at a given body size/trophic level is determined by net primary production.
206 Thus, as warming drives an increase in individual metabolism, total biomass decreases even
207 if primary production remains constant. The BOATS model uses a similar framework to
208 Macroecological and EcoTroph to determine maximum supported biomass at each body size
209 class. However, in BOATS individual mortality is resolved separately and the growth of
210 individuals from one size class to the next is explicitly resolved. As temperatures rise,
211 individual growth rates in BOATS increase, increasing the speed of biomass flow from small
212 to large size classes, but also increasing mortality and reducing the maximum biomass that
213 can be supported at each body size. Taken together, these processes mean that warming
214 causes total biomass to decrease in BOATS.

215

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

229

230 For trait-based models (APECOSM, DBPM, FEISTY and ZooMSS), individual growth is fuelled
231 by ingesting smaller organisms, with individual ingestion rates scaling with temperature and
232 body size. For APECOSM, DBPM and FEISTY this scaling is also modulated with the density of
233 prey. Thus, food uptake for individuals at one size is fuelled by predation of smaller size
234 individuals, and in some cases predators can compete with each other for the same prey.
235 These models also include other sources of mortality (destruction of population biomass).
236 APECOSM, DBPM and ZooMSS incorporate at least one size-dependent mortality term, and
237 FEISTY includes a single natural mortality term that is independent of body size. These
238 additional mortality sources increase with temperature (except for senescence mortality,
239 which increases with body size, in DBPM and natural mortality, which is independent of body
240 size, in FEISTY), causing population biomass to decrease with increasing temperature. In
241 FEISTY, maintenance costs increase faster with both body size and temperature than do
242 ingestion rates. APECOSM and FEISTY also explicitly resolve size and temperature-dependent
243 costs of maintaining existing biomass (metabolism). In these models, as temperature
244 increases, maintenance costs also increase, reducing the available energy for growth and
245 reproduction. If maintenance costs of existing biomass exceed energy intake from ingestion,
246 biomass decreases. As food becomes limited in APECOSM, ingestion rates scale more slowly
247 with temperature than maintenance costs, limiting the scope for new growth and potentially
248 inducing biomass to decrease as maintenance costs outpace ingestion.

249

250 In APECOSM, DBPM, FEISTY and ZooMSS, temperature affects anabolic and catabolic
251 processes differently across ecosystems, which has cascading effects on how the different
252 components of ecosystems (e.g. predators and prey) interact. In APECOSM, FEISTY and

253 ZoomSS for example, the scaling of maintenance costs (in APECOSM and FEISTY) and
254 senescence mortality (in APECOSM and ZoomSS) with body size and temperature mean that
255 large organisms are more vulnerable to warming compared to small organisms. Everything
256 else being equal, a warming-induced decrease in large organism biomass would reduce
257 predation mortality on smaller organisms, thus favouring small organisms in these models.

258

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

268

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

275

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

284

285 **2.2. How do models incorporate lower trophic level processes?**

286 Net primary production sustains essentially all non-photosynthetic life in the oceans, and
287 limits the biomass of higher trophic levels (Ryther, 1969; Friedland et al. 2012). Solar energy
288 captured and organic matter synthesized by primary producers flow through food webs,
289 primarily by larger organisms preying on smaller organisms. FishMIP models focus on higher
290 trophic levels, so lower trophic level processes are driven by a range of Earth system model
291 forcings (Table 1). The role of lower trophic levels in setting the limits to growth for higher
292 trophic levels is represented across the eight FishMIP models in two ways. First, for BOATS,
293 DBEM, Macroecological and EcoTroph, net primary production is used to determine limits of
294 consumer growth rates and total biomass according to trophic transfer functions. Second, in
295 the trait-based models (APECOSM, DBPM, FEISTY and ZooMSS), plankton biomass and export
296 production are consumed by the size classes or functional groups that feed on them. This
297 energy is then transferred to higher trophic levels through size-based predation. However, all
298 eight models considered here are one-way forced (run offline), so there is no feedback from
299 higher trophic levels to lower trophic level biomass or production. This means that for the

300 trait-based models, ingestion-fuelled growth of higher trophic level predators is not explicitly
301 matched by predation mortality in the plankton.

302

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

324

325

326 2.3. How do models incorporate other impacts?

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

341

342

343

344

345

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347

348

349 **Table 1** Summary of temperature, lower trophic level (LTL) and other drivers sourced from
 350 earth system models, used by each model in the FishMIP ensemble, as well as the ecosystem
 351 representation of each model. All drivers used by the models in this experiment had a monthly
 352 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 15µg– 120kg.
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 10g–100kg.
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 1mg 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 1mg and 125kg.
Macroecological Jennings and Collingridge (2015)	2D sea surface temperature	2D depth-integrated net primary production	NA	All marine animals between 1mg 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 1mg and 10 tonnes.

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

357

358

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.

361 2.4. Experimental protocol

362 To isolate the impact of temperature and LTL processes on the FishMIP ensemble, we
363 conducted four simulations (Table 3) following the general approach of Carozza et al. (2018).
364 In each simulation, all models were forced with different combinations of temperature, LTL
365 and other (for APECOSM and DBEM) drivers from pre-industrial, historical and high emissions
366 scenarios (RCP 8.5; IPCC, 2014) from the CESM1-BGC earth system model (Moore et al. 2013).
367 simulation submitted for the Coupled Model Intercomparison Project 5 (CMIP5; IPCC, 2014).
368 For RCP 8.5 in the CMIP5 multi-model ensemble, CESM-BGC is average in temperature
369 sensitivity and less than average in global mean NPP and export production decline (Bopp et
370 al. 2013). All forcings were provided to modellers with a monthly temporal resolution. We do
371 not use a range (from low to high) of emission scenarios for the future, or source forcings
372 from multiple Earth system models, as our purpose here is to isolate sources of structural
373 uncertainty within the FishMIP model ensemble itself (Payne et al. 2016). Under the RCP 8.5
374 scenario, the CESM1-BGC model projects a global sea surface temperature increase, which is
375 particularly marked at high latitudes (Figure 1b); net primary production declines across most
376 of the tropics and mid-latitudes, but increases at high latitudes and in the eastern South
377 Pacific (Figure 1d); phytoplankton and zooplankton biomass declines across most of the
378 world's oceans, except in polar regions (Figure 1f, h). The mean change in sea surface
379 temperature across the global ocean from 1950 to 2100 under historical (averaged over 1950-
380 1960) and RCP 8.5 (averaged over 2090-2100) scenarios is +3.2°C, and for net primary
381 production, phytoplankton and zooplankton carbon the mean change was -14%, -8% and -
382 21%, respectively.

383

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

397

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

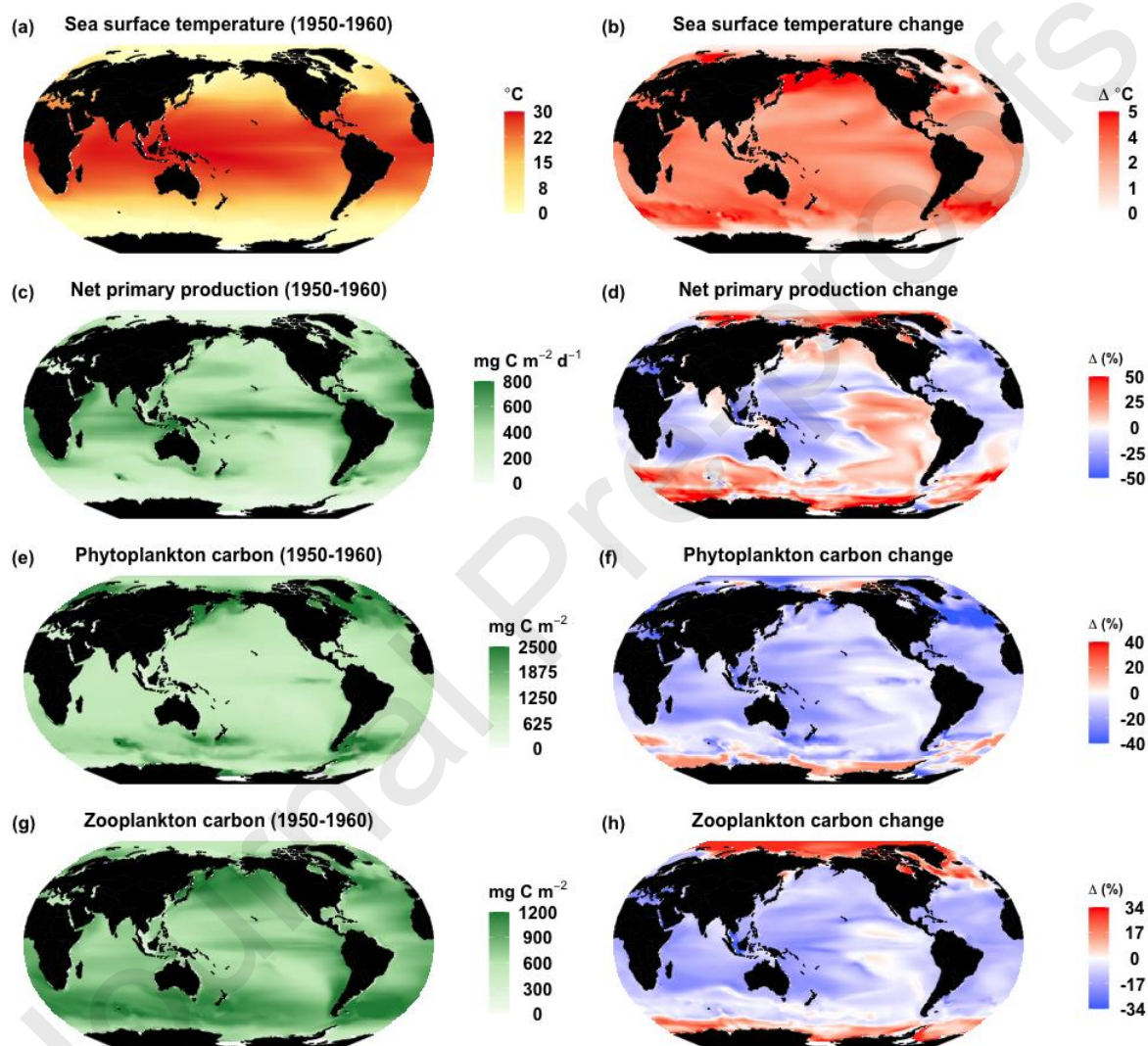
	Simulation							
	Control		Temperature Change		LTL Change		All (Climate) Change	
Drivers	<u>1950-2005</u>	<u>2006-2100</u>	<u>1950-2005</u>	<u>2006-2100</u>	<u>1950-2005</u>	<u>2006-2100</u>	<u>1950-2005</u>	<u>2006-2100</u>
Temperature	PI	PI	H	RCP 8.5	PI	PI	H	RCP 8.5

LTL	PI	PI	PI	PI	H	RCP 8.5	H	RCP 8.5
Other	PI	PI	PI	PI	PI	PI	H	RCP 8.5

403

404

405



406

407 **Figure 1** Control (historical averaged over 1950-1960) forcing variables and the change in

408 those variables from climate change (RCP 8.5) from the CESM1-BGC earth system model; a,b)

409 Sea surface temperature, c,d) Net primary production, e,f) Phytoplankton carbon, g,h)

410 Zooplankton carbon. The change in each variable is measured as the mean over 2090-2100

411 under the RCP 8.5 scenario minus the mean over 1950-1960 (for sea surface temperature), or

412 the percentage change between the mean in 1950-1960 and 2090-2100 (for net primary
413 production, phytoplankton carbon and zooplankton carbon).

414

415

416 **3. Results**

417 **3.1. Global changes in total consumer biomass**

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

426

427 The LTL Change simulation also showed globally averaged biomass decreases for most
428 models, except BOATS and Macroecological, which projected global biomass increases (Figure
429 2b). For these two models, the trajectory of global biomass change was switched in the LTL
430 Change simulation from negative change to positive in comparison with the warming only
431 simulation. In contrast, APECOSM projected global consumer biomass to increase slightly with
432 warming, but decrease with LTL changes. APECOSM projected a 7% decrease in total
433 consumer biomass globally, while BOATS and Macroecological projected increases of 10-15%
434 in response to LTL changes in isolation. Maximum decreases of biomass in LTL simulations are
435 half the magnitude (up to 15%) of the decreases in warming simulations. The smallest

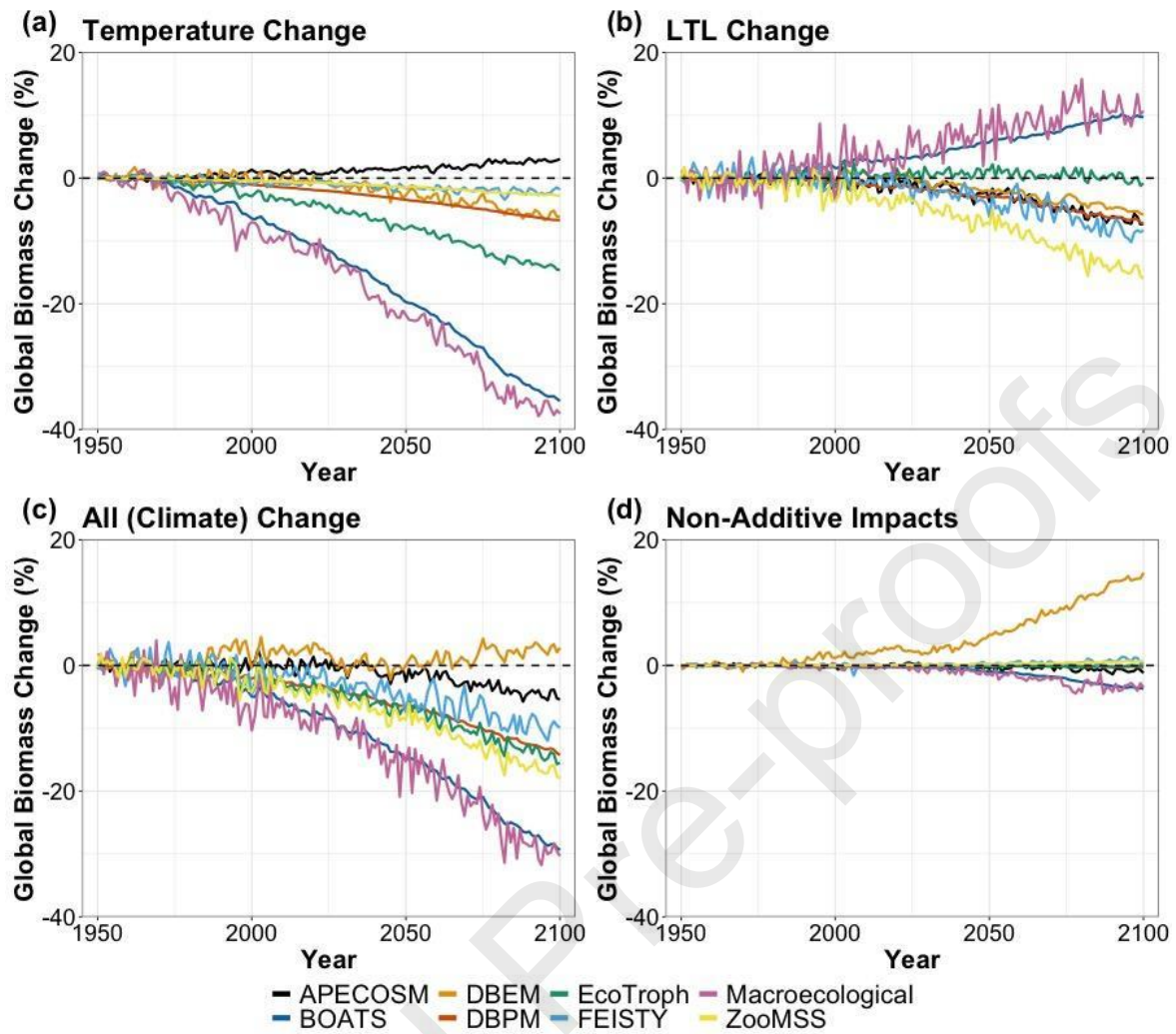
436 response to LTL changes was from EcoTroph, which projected a total consumer biomass
437 change of <-1%. Trends in total consumer biomass from the other five models (DBEM, DBPM,
438 FEISTY and ZooMSS) were grouped within a range between -5% (DBEM) and -15% (ZooMSS).

439

440 The combined temperature and LTL changes led to a decline in globally averaged consumer
441 biomass across all models except DBEM (Figure 2c). By the end of the 21st century, changes
442 in global consumer biomass in the All (Climate) Change simulation ranged from around -30%
443 for BOATS and Macroecological, to +3% for DBEM. The other five models (APECOSM, DBPM,
444 EcoTroph, FEISTY and ZooMSS) had changes in total global consumer biomass of between -
445 5% (for APECOSM) and -17% (for ZooMSS). For all models except BOATS, DBEM and
446 Macroecological, climate change impacts at the global scale were largely the sum of the
447 separate global impacts of warming and LTL change, with almost no non-additive impact
448 (Figure 2d). For BOATS and Macroecological, climate change impacts caused total consumer
449 biomass to decline by about 4% more than the sum of separate warming and LTL impacts. In
450 DBEM, total consumer biomass under climate change was ~15% higher than under the
451 combined, separate impacts of warming and LTL impacts, indicating some non-additive
452 impact of cumulative temperature and LTL changes. Non-additive impacts in DBEM may also
453 be caused by additional impacts from changes in pH and oxygen levels. APECOSM, the only
454 other model to incorporate non-temperature or LTL drivers, had negligible non-additive
455 impacts, indicating these other drivers had little effect compared to warming and LTL shifts.

456

457



458

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

464

465 3.2. Spatial changes in total consumer biomass

466 Globally averaged time-series of total consumer biomass change conceal considerable spatial
 467 variation across regions within each model, and between models in each experiment.
 468 Temperature-induced shifts in the spatial distribution of total consumer biomass (Figure 3,

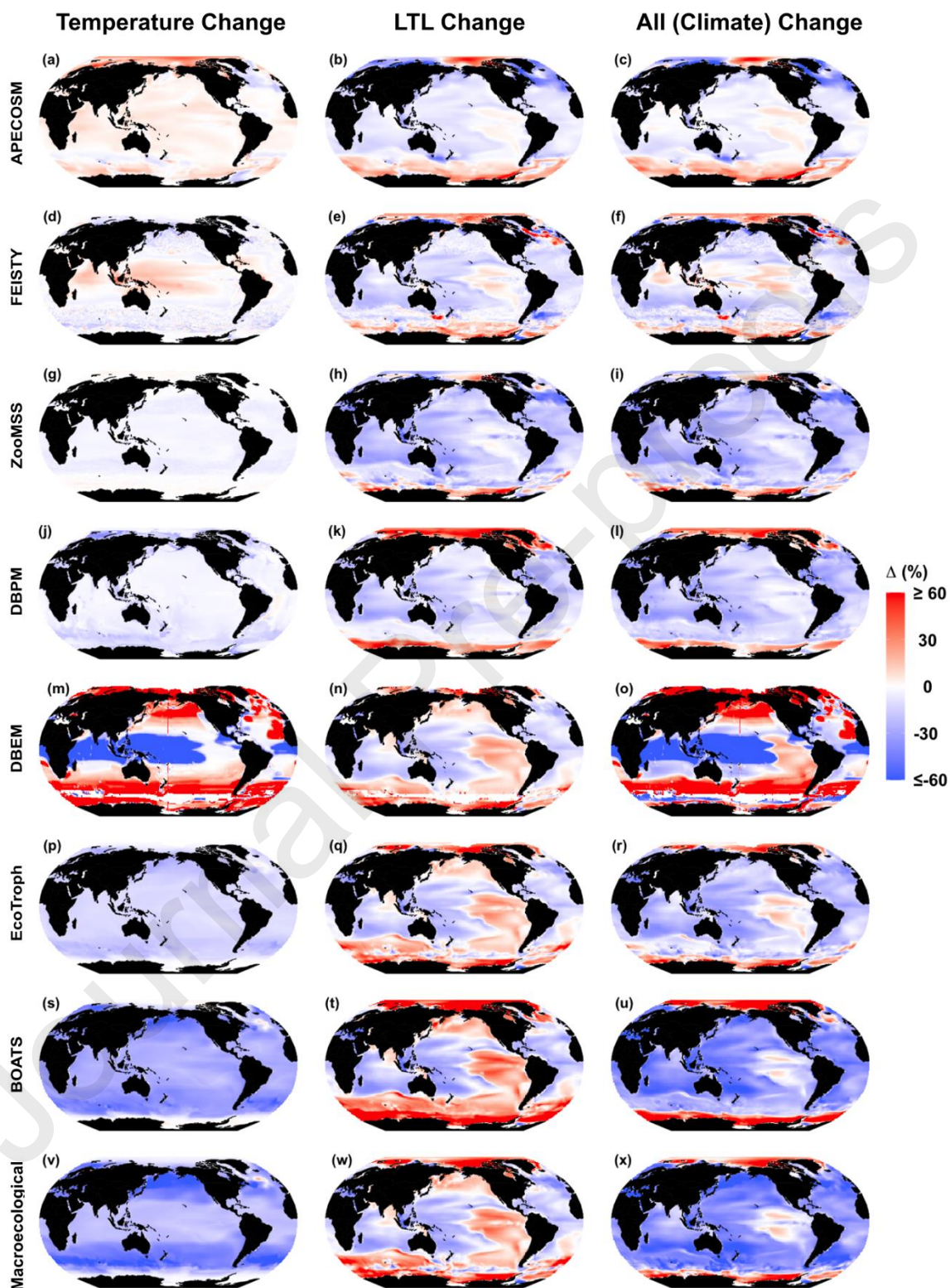
469 left column) varied from increases in many regions for APECOSM, to decreases across the
470 global ocean in DBPM, ZooMSS, EcoTroph, BOATS and Macroecological. The magnitude of the
471 total consumer biomass changes generally followed the magnitude of change in temperature
472 (Figure 1b); temperate regions that experienced the strongest warming (Figure 1b) exhibited
473 the largest decreases in biomass for these five models. FEISTY and ZooMSS consumer biomass
474 also decreased with increased temperature in many of the regions with the greatest warming.
475 However, in warm regions (Figure 1a) with relatively small temperature increases such as the
476 eastern Pacific or northern Indian Ocean, FEISTY consumer biomass increased, and small
477 increases in ZooMSS consumer biomass occurred almost entirely in very high latitude polar
478 regions where temperature change was relatively small (Figure 1b). In contrast, APECOSM
479 consumer biomass increased across most of the global ocean in response to warming. The
480 exception to this pattern was in patches where phytoplankton biomass was highest (Figure
481 1c) such as the North Atlantic, the Bering Strait or the South Pacific around New Zealand. In
482 DBEM, temperature-induced changes in consumer biomass were greatest in the warmest
483 waters around the equator, where DBEM consumer biomass decreased by 60-100%. In cold
484 high latitude waters, DBEM consumer biomass increased by $\geq 60\%$ in response to warming.
485
486 For all models, lower trophic level (LTL) induced shifts in the distribution of consumer biomass
487 (Figure 3, centre column) show more agreement in their patterns of change; most models
488 show biomass decreases in equatorial regions, and increases towards the poles. The
489 exceptions here are APECOSM, FEISTY and ZooMSS which show a mix of positive and negative
490 consumer biomass toward the north pole. Consumer biomass shifts generally followed
491 changes in the distribution of the main LTL forcings used by each model (Figure 1d, f, h).
492 APECOSM, DBPM, FEISTY and ZooMSS use plankton biomass inputs (Table 2), and for these

493 models, consumer biomass generally decreased with decreasing phytoplankton carbon
494 (Figure 1f) and increases were isolated to polar regions. DBEM, EcoTroph, BOATS and
495 Macroecological use net primary production as their LTL forcing and the spatial distribution
496 of changes in consumer biomass followed spatial shifts in net primary production (Figure 1d),
497 with increases in biomass not only in polar regions, but also in the North Pacific and in the
498 South East Pacific.

499

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

515



516

517 **Figure 3** Maps of relative total consumer biomass averaged over 2090-2100, compared to the
 518 Control (over 2090-2100), for the Temperature (left column), Lower Trophic Level (LTL) and

519 All Change simulations for a-c) APECOSM, d-f) FEISTY, g-i) ZooMSS, j-l) DBPM, m-o) DBEM, p-
520 r) EcoTroph, s-u) BOATS, v-x) Macroecological. Maps are ordered by the magnitude (from
521 smallest to greatest) of the negative warming impact on consumer biomass.

522

523 **3.3. Disentangling temperature and lower trophic level impacts on total consumer** 524 **biomass**

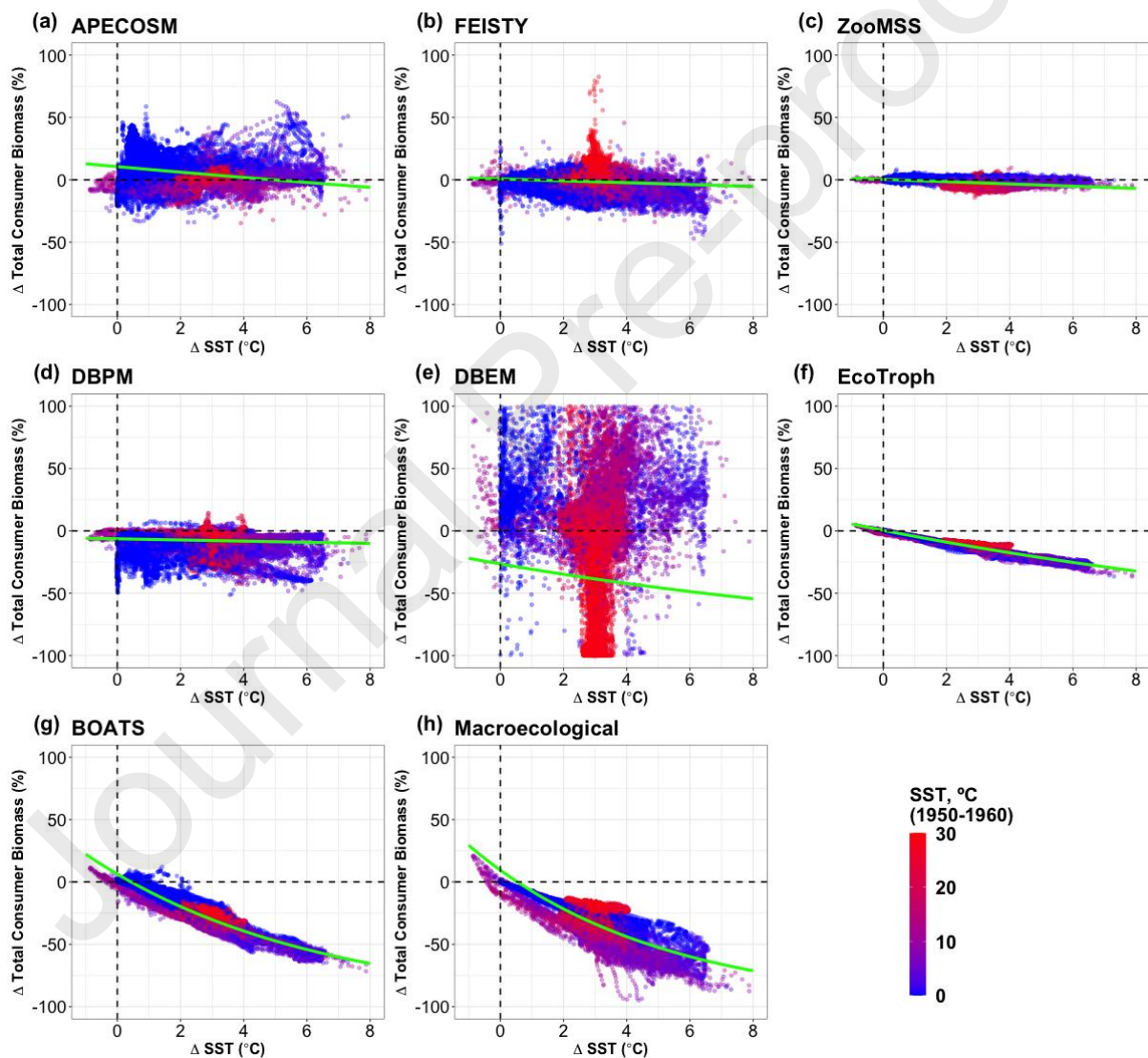
525 Figure 4 compares the forced changes in sea surface temperature (SST) with the co-located
526 simulated changes in biomass for all grid cells in the global ocean. Regressions give negative
527 exponential slopes for all models, but with substantial variation (Supplementary Table S1).
528 Globally,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

536

537 Figure 5 shows the corresponding plots for LTL forcing. For all models, changes in total
538 consumer biomass were positively correlated with changes in their respective aggregated
539 lower trophic level (LTL) forcing (Figure 5). A 1% change in LTL forcings caused a change in
540 total consumer biomass of between 0.6% in DBPM to 1.7% in BOATS (Supplementary Table
541 S4). Positive correlations between consumer biomass and LTL changes ranged from $r = 0.39$
542 for DBPM, to $r = 0.98$ for EcoTroph. For all models except DBPM, the greatest correlation

543 was between change in total consumer biomass and change in total LTL production, or
 544 biomass, of the model's chosen LTL forcing (Supplementary Table S3). In models that used
 545 size-fractionated LTL inputs, or additional secondary LTL inputs, changes in consumer biomass
 546 were less correlated with changes in their main aggregated LTL forcing (APECOSM, DBPM,
 547 FEISTY) compared to models that did not use size-fractionated or multiple LTL forcings
 548 (BOATS, DBEM, EcoTroph, Macroecological, ZooMSS).

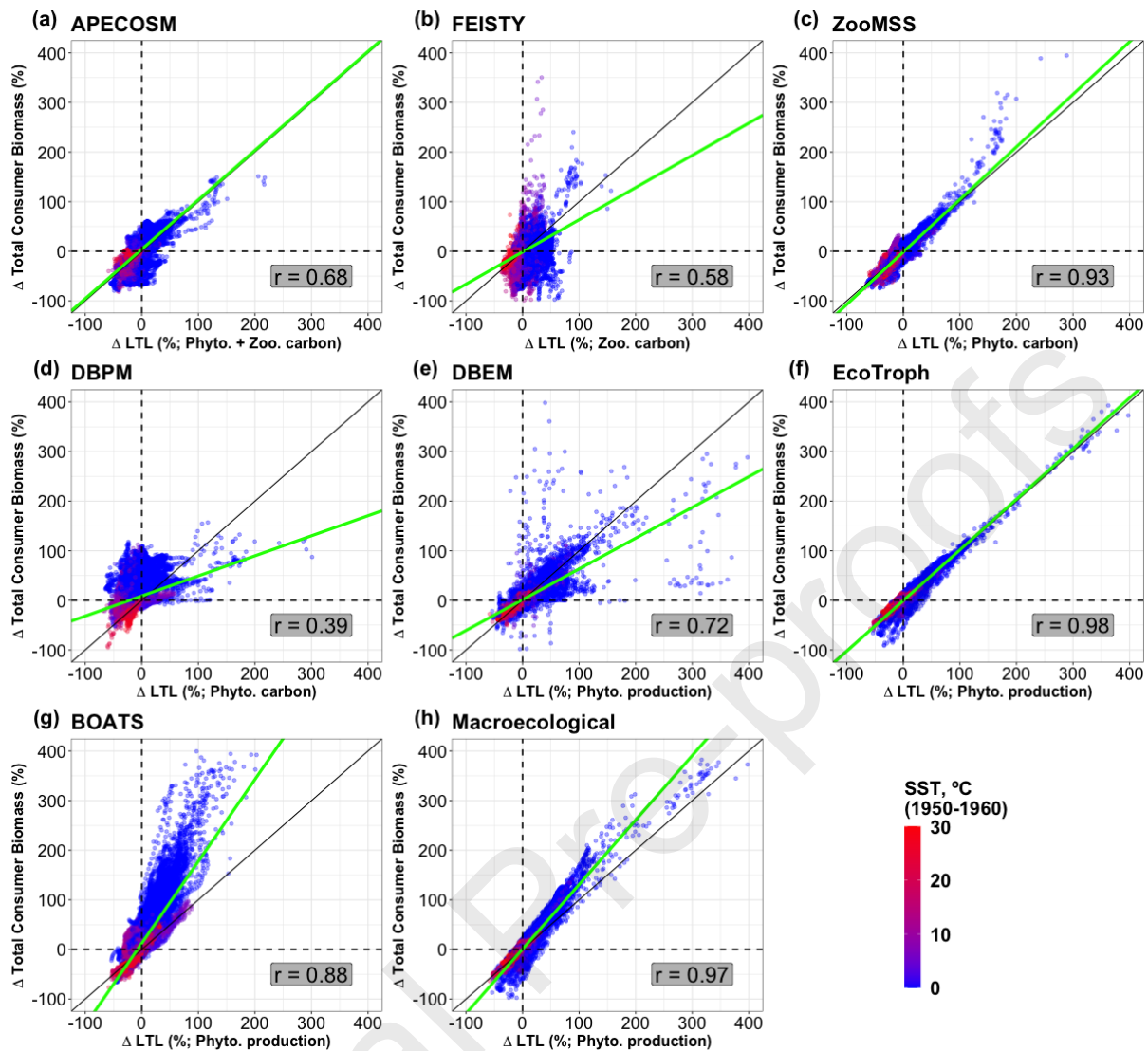
549



550

551 **Figure 4** Change in total consumer biomass (%) against the mean change in sea surface
 552 temperature (SST) over 2090-2100, for individual 1° grid squares, under the Temperature

553 Change simulation, compared to the Control simulation, for a) APECOSM, b) FEISTY, c)
554 ZooMSS, d) DBPM, e) DBEM, f) EcoTroph, g) BOATS, h) Macroecological. Each point is coloured
555 according to the mean 1950-1960 historical SST in its grid cell. Dotted horizontal and vertical
556 black lines indicate where % change in total consumer biomass and change in temperature
557 are zero, respectively. The green line is the fitted regression (Δ Total Consumer Biomass =
558 $\exp(\beta_0 + \beta_1 \Delta \text{SST}) + \varepsilon$) for the change in consumer biomass with warming. We use
559 exponential regression to calculate the line of best fit here since all models incorporate
560 temperature effects using an exponential function (see Supplementary Information).
561 Information about the fitted regression is in Supplementary Table S1 and S4.
562



563

564 **Figure 5** Change in total consumer biomass (%) against change in aggregated lower trophic

565 level forcings (LTL), from 2090-2100 under the LTL Change simulation, against the Control, for

566 individual 1° grid squares, compared to the Control simulation for a) APECOSM, b) FEISTY, c)

567 ZooMSS, d) DBPM, e) DBEM, f) EcoTroph, g) BOATS, h) Macroecological, with Pearson's

568 correlation coefficient (r) reported for each. Each point is coloured according to the average

569 1950-1960 historical sea surface temperature (SST) in its corresponding grid cell. The black

570 solid line is the 1:1 line, and the dotted horizontal and vertical black lines indicate where %

571 change in total consumer biomass and % change in LTL are zero, respectively. The green line

572 is the fitted regression ($\Delta\text{Total Consumer Biomass} = \beta_0 + \beta_1\Delta\text{LTL} + \epsilon$) for the change in

573 consumer biomass with warming. For models that use more than one LTL variable
574 (APECOSM), or size-fractionated LTL (FEISTY and DBPM), Δ LTL is calculated from the sum of
575 all LTL forcings. Information about the fitted regression is in Supplementary Table S2 and S4.

576

577 **3.4. Impacts of warming and lower trophic level change on ecosystem structure**

578 In response to warming, there was little consensus in the relative change of small (<30 cm)
579 and large (\geq 30 cm) mean global consumer biomass (Figure 6a), with four models (BOATS,
580 EcoTroph, Macroecological, ZooMSS) showing a decrease of both and the other three models
581 (APECOSM, DBPM, FEISTY) showing a mixture of responses. Small consumer biomass
582 increased by ~2% in both APECOSM and FEISTY in response to warming, but large consumer
583 biomass increased in APECOSM by 5% while decreasing in FEISTY by >10%. Similarly, although
584 small consumer biomass in DBPM and ZooMSS decreased by 3% and 6% respectively, these
585 models disagreed on the direction of change for large consumer biomass. In response to
586 warming total large consumer biomass in DBPM increased by 15%, and over 60% in some
587 regions (Supplementary Figure S2n), but in ZooMSS total large consumer biomass declined by
588 ~2% overall. Finally, small and large consumer biomass declined in EcoTroph, BOATS and
589 Macroecological, and the spatial pattern of decline across was similar both across models and
590 across small and large consumer biomass (Supplementary Figure S2). There was no difference
591 in the magnitude of the decline of small and large consumer biomass in Macroecological,
592 however in EcoTroph and BOATS the magnitude of the decline in large consumer biomass was
593 greater than the decline in small consumer biomass.

594

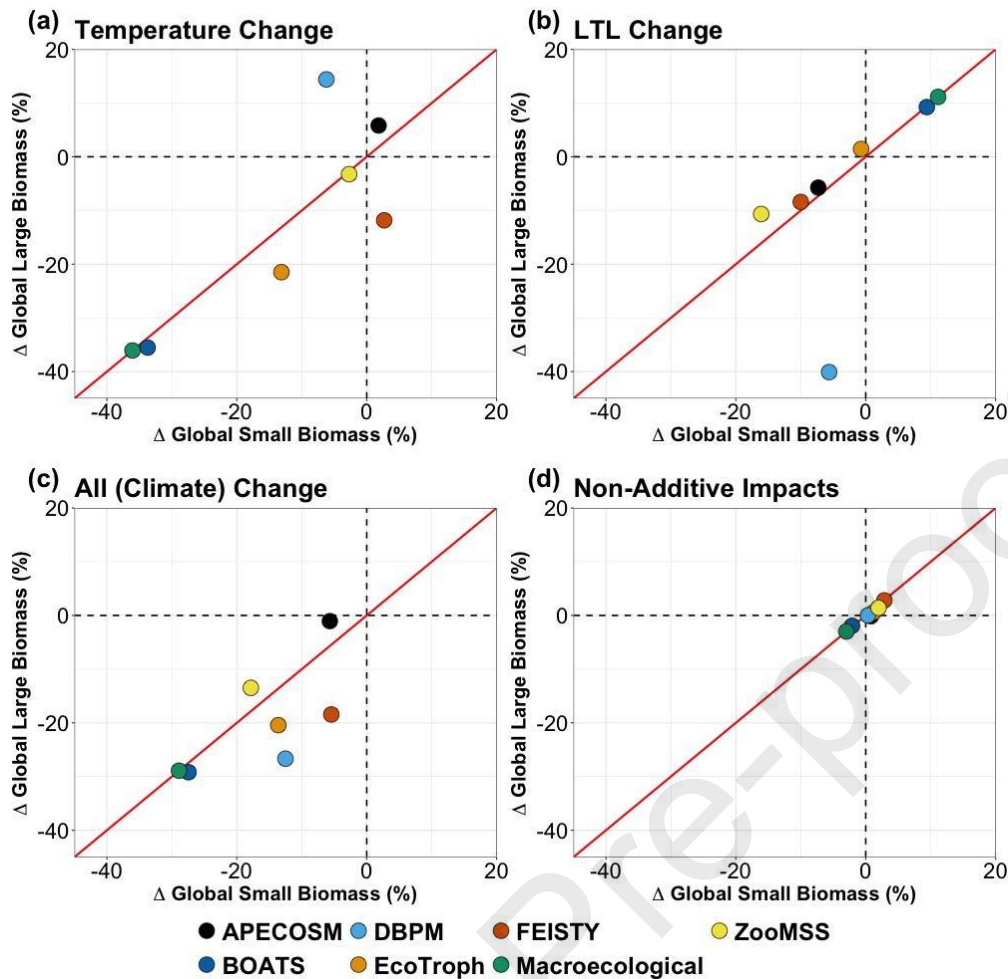
595 Changes in total small and large consumer biomass in response to lower trophic level (LTL)
596 changes show more agreement (Figure 6b). The change in total small and large consumer

597 biomass was similar in APECOSM, FEISTY, ZooMSS, EcoTroph, BOATS and Macroecological,
598 and again the spatial pattern of change in small and large consumer biomass generally
599 followed each model's respective LTL forcings (Supplementary Figure S2; Figure 1f-h).
600 However, in DBPM, total large consumer biomass declined by 40%, while small consumer
601 biomass declined by only 10%. This was reflected in the spatial patterns of biomass change
602 for DBPM, with large consumer biomass varying by over $\pm 60\%$ and small consumer biomass
603 varying by less than $\pm 30\%$ across non-polar regions of the global ocean (Supplementary
604 Figure S2 o,p).

605

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

615



616

617 **Figure 6** Change in total small (<30 cm) consumer biomass versus change in global large
 618 (>30cm) consumer biomass averaged between 2090-2100 relative to Control simulation for
 619 each model (excluding DBEM, which did not provide small and large consumer biomass) in
 620 the a) Temperature Change simulation b) Lower Trophic Level (LTL) Change simulation, c) All
 621 Change simulation and d) the non-additive impacts of temperature and LTL changes,
 622 calculated by taking the difference between the All Change and the sum of the Temperature
 623 and LTL Change simulations. The red solid line is the 1:1 line, and the dotted horizontal and
 624 vertical black lines indicate where the percentage change in global large and small consumer
 625 biomass are zero, respectively.

626

627

628 4. Discussion

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

644

645 4.1. Warming impacts are complex

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

652 scalings are irrelevant, but rather that the emergent results depend on the interactions of
653 multiple temperature-dependent processes, operating within the structural context of each
654 model.

655

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

670

671 DBEM aside, four of the models included here (APECOSM, DBPM, FEISTY and ZooMSS) project
672 much smaller warming impacts on consumer biomass than the remaining three
673 models (BOATS, EcoTroph and Macroecological). Although there are many differences
674 between these models, one particularly salient feature is that the low-sensitivity models all
675 use LTL biomass as Earth-system model (ESM) drivers for the projections, together with

676 temperature-dependent feeding rates. In contrast, the high-sensitivity models use ESM net
677 primary production to directly limit the growth rates of upper trophic levels. We suggest that
678 the discrepancy in temperature sensitivity between the model groups can be attributed, at
679 least in part, to an inconsistency that arises from the 1-way forcing of marine models with LTL
680 biomass. The relationship between LTL biomass (B_{LTL}), LTL production (P_{LTL}) and higher
681 trophic level predation ($Pred_{HTL}$) through time t can be represented as:

$$682 \quad \frac{dB_{LTL}}{dt} = P_{LTL}(t) - Pred_{HTL}(t).$$

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

696

697 Our results also explored the warming impacts on ecosystem structure, defined as the relative
698 biomass of small versus large organisms. Here, there was little consensus between models.

699 DBPM and FEISTY provide a striking example of divergent projections of ecosystem structure
700 with warming. In DBPM, ingestion-fuelled anabolism outpaces senescence-induced mortality
701 in large organisms as waters warm (Blanchard et al. 2012), causing their biomass to increase.
702 This raises predation pressure on smaller organisms, which when coupled with warming-
703 induced increases in natural mortality, causes their biomass to decline. By contrast, in FEISTY,
704 biomass respiration increases faster with both body size and temperature compared to
705 ingestion-fuelled anabolism (Petrik et al. 2019) reducing the scope for growth and causing
706 large organism biomass to decline with warming. Declines in large consumer biomass in
707 FEISTY with increasing temperature relieve predation pressure on small consumers, resulting
708 in an increase in their biomass, especially in tropical waters. The divergent impacts of warming
709 on individual processes and ecosystem structure reflects the lack of consensus among
710 modellers of how temperature impacts on individuals translate into ecosystem impacts.

711

712 **4.2. Lower trophic level impacts are influenced by choice of forcing**

713 The choice of LTL forcings differed between models, with each model using either biomass or
714 production variables at the phytoplankton or zooplankton level, with significant impacts on
715 the results. Generally, spatial changes in consumer biomass were most correlated with
716 changes in the distribution of the LTL forcing used. The sensitivity of models to the choice of
717 LTL forcing again indicates a lack of common understanding of how to link lower trophic levels
718 production with higher trophic levels, with no consensus on whether production rates or
719 standing-stock biomass should be used. We believe this problem fundamentally arises out of
720 practical necessity because of each model's one-way, offline coupling with the Earth system
721 model—were higher trophic levels and LTLs to be fully coupled, and predation feedbacks on
722 LTLs resolved, there should theoretically be no disagreement between models that use

723 production or biomass variables, everything else being equal. However, in the absence of two-
724 way coupled models in the FishMIP ensemble, the development of which is a tremendous
725 technical challenge (see Aumont et al., 2018), this problem remains to be addressed. As
726 mentioned above, this problem also leads to inconsistency in the temperature response when
727 plankton biomass versus net primary production rates are used.

728

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

743

744 **4.3. Cumulative warming and lower trophic level impacts are largely additive**

745 Across the model ensemble, climate change impacts on total consumer biomass and
746 ecosystem structure were generally well-approximated by the sum of separate warming and

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

763

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

771 the lack of nonlinear interactions in marine climate change projections to our present lack of
772 ability to resolve them in the models.

773

774 **4.4. Improving marine ecosystem models with observational constraints**

775 In this study, we have identified key sources of structural uncertainty that drive disparate
776 projections of climate change impacts on the global marine ecosystem. As a first step, the
777 marine modelling community can work to reduce this structural uncertainty and increase the
778 credibility of ecosystem projections by constraining models with independent observations.

779 An increasingly popular approach to confront model projections with observations is to use
780 emergent constraints, which relate the long-term climate sensitivity of an observable
781 ecosystem feature - such as total biomass change (Free et al. 2019) or size-spectrum slope
782 (Blanchard et al. 2017; Heneghan et al. 2019) - to its short-term, observed variability (Allen &
783 Ingram, 2002; Eyring et al. 2019). Models that give a closer fit to short-term observed
784 variability of an ecosystem feature are hypothesised to provide more reliable projections of
785 its long-term variability from climate change (Kwiatkowski et al. 2017; Veytia et al. 2020).

786 Moreover, within a model ensemble, each model's weighting can be linked to its ability to
787 capture the emergent constraint (Eyring et al. 2019). This provides a more sophisticated and
788 credible way to weight model projections within an ensemble, over the standard approach
789 where all models are given equal weighting (known as model democracy), irrespective of
790 performance (Knutti, 2010). Emergent constraints do not require or necessarily reward any
791 particular ecosystem representation. This is important as differing representations of the
792 marine ecosystem across the FishMIP ensemble not only represent our present uncertainty
793 of the most important drivers structuring marine ecosystems, but also the diversity of
794 purpose and scope for which models have been built.

795

796 Finally, it is possible for models to perform well against whole-ecosystem emergent
797 constraints, while neglecting fundamental physiological or ecosystem processes (Knutti,
798 2010). Therefore, if we are to improve marine models, it is also necessary to consider
799 observational constraints on physiological processes such as the balance between growth and
800 respiration with temperature, or ecosystem processes such as the coupling of lower and
801 higher trophic levels. Improving our understanding of how physiological processes such as
802 ingestion and metabolism respond to warming, and how changes in LTL processes propagate
803 through marine ecosystems, are critical steps towards model improvement and more robust
804 climate impact projections.

805

806 **5. Concluding remarks**

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

812

813 Our harmonized experimental protocol clearly showed that the responses to the two most
814 important drivers of change – warming and LTL shifts – differ widely among models.
815 Uncertainty in the temperature sensitivities of competing processes, including both
816 physiology and ecological interactions, undermine confidence in the emergent sensitivities,
817 and can only be improved with better observational constraints. Meanwhile, the outcome of
818 changes in both water temperature and LTL production depends strongly on the feedback of

819 consumers on the LTL biomass itself, a process which is not captured by any of the one-way
820 forcings available at present, and can only be rectified with fully two-way coupling, which is
821 itself sure to raise many new questions.

822

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

832

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

839

840 **Code and data availability**

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

844

845 **Author contributions**

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

852

853 **Competing interests**

854 The authors declare that they have no conflict of interest.

855

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868

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Journal Pre-proofs

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1090 **Title**

1091 Disentangling diverse responses to climate change among global marine ecosystem models

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1093 **Highlights**

- 1094 • Experimental study identifying uncertainty sources in FishMIP global model
1095 ensemble
- 1096 • Warming and lower trophic level (LTL) impacts on model predictions isolated
- 1097 • Coupling of lower and higher trophic levels a key driver of model warming response
- 1098 • LTL impacts driven primarily by each model's choice of LTL driver

- 1099 • Overall climate projections mostly a linear combination of warming and LTL impacts

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1101 **Declaration of interests**

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1103 The authors declare that they have no known competing financial interests or personal
1104 relationships that could have appeared to influence the work reported in this paper.

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1106 The authors declare the following financial interests/personal relationships which may be
1107 considered as potential competing interests:

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