

1 Metabolic impacts of climate change on marine ecosys-  
2 tems: implications for fish communities and fisheries

3

4 Short running title: Climate and marine ecosystem metabolism

5

6 David A. Carozza<sup>1,2</sup>, Daniele Bianchi<sup>3</sup>, Eric D. Galbraith<sup>1,4,5</sup>

7 Corresponding Author: David A. Carozza

8

9 <sup>1</sup> Department of Earth and Planetary Sciences, McGill University, Montreal, Canada  
10 (david.carozza@gmail.com)

11 <sup>2</sup> Now at Département de mathématiques, Université du Québec à Montréal, Mon-  
12 treal, Canada

13 <sup>3</sup> Department of Atmospheric and Oceanic Sciences, University of California, Los An-  
14 geles, 520 Portola Plaza, Los Angeles, California, 90095, USA (dbianchi@atmos.ucla.edu)

15 <sup>4</sup> Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de  
16 Barcelona, 08193 Barcelona, Spain

17 <sup>5</sup> Institució Catalana de Recerca i Estudis Avançats (ICREA), 08010 Barcelona,  
18 Spain (eric.d.galbraith@gmail.com)

19 Acknowledgements: D.A.C was supported by the Social Sciences and Humanities  
20 Research Council of Canada through a Joseph-Armand Bombardier Canada Gradu-  
21 ate Scholarship, by the Marine Environmental Observation Prediction and Response  
22 (MEOPAR) Network through a doctoral fellowship and operational support, and the  
23 Birks Family Foundation through a doctoral bursary. Computational infrastructure  
24 was provided by the Canadian Foundation for Innovation (grant no. 25402). This  
25 project has received funding from the European Research Council (ERC) under the  
26 European Unions Horizon 2020 research and innovation programme (grant agree-  
27 ment No 682602). D.B. acknowledges support from NASA grant TunaScape award  
28 number 80NSSC17K0290, California Department of Resources - Ocean Protection  
29 Council grant C0100400, and a Faculty Research Grant from University of Califor-  
30 nia, Los Angeles. We thank Elizabeth A. Fulton for comments on an earlier version  
31 of this manuscript, and thank Ian A. Hatton for comments and discussions.

32

33 Author contributions: E.D.G. supervised the project and all authors contributed  
34 equally to the model development and experimental design. D.B. and D.A.C con-  
35 ducted simulations and analyses. D.A.C. and E.D.G. wrote the manuscript and  
36 prepared the figures, with input from D.B.

## 37 **Abstract**

38 **Aim:** Climate change will reshape marine ecosystems over the 21st century through  
39 diverse and complex mechanisms that are difficult to quantitatively assess. Here we  
40 characterize expectations for how marine community biomass will respond to the en-  
41 ergetic consequences of changes in primary production and temperature-dependent  
42 metabolic rates, under a range of fishing/conservation scenarios.

43 **Location:** Global ocean.

44 **Time period:** 1950-2100.

45 **Major taxa studied:** Commercially-harvested marine ectotherms ('fish').

46 **Methods:** We use a size-structured macroecological model of the marine ecosystem,  
47 coupled with a catch model that allows for calibration with global historical data  
48 and simulation of fishing. We examine the four energetic mechanisms that, within  
49 the model framework, determine the community response to climate change: net  
50 primary production, phytoplankton cell size, and the temperature dependencies of  
51 growth and natural mortality.

52 **Results:** Climate change decreases the modeled global fish community biomass by  
53 as much as 30% by 2100. This results from a diminished energy supply to upper  
54 trophic levels as photosynthesis becomes more nutrient-limited and phytoplankton  
55 cells shrink, and from a temperature-driven increase of natural mortality that, to-  
56 gether, overwhelm the effect of accelerated somatic growth rates. Ocean circulation  
57 changes drive regional variations of primary production, producing patterns of win-  
58 ners and losers that largely compensate each other when averaged globally, whereas  
59 decreasing phytoplankton size drives weaker but more uniformly-negative changes.

60 The climate impacts are similar across the range of conservation scenarios, but are  
61 slightly amplified in the strong conservation scenarios due to the greater role of nat-  
62 ural mortality.

63 Main conclusions: The spatial pattern of climate impacts is mostly determined by  
64 changes in primary production. The overall decline of community biomass is at-  
65 tributed to a temperature-driven increase of natural mortality, alongside an overall  
66 decrease in phytoplankton size, despite faster somatic growth. Our results highlight  
67 the importance of the competition between accelerated growth and mortality in a  
68 warming ocean.

## 69 **Keywords**

70 conservation, fisheries, global climate change, marine communities, marine ecosystem  
71 model, metabolic impacts, net primary production, temperature change

## 72 **Introduction**

73 Energy is supplied at the base of the marine ecosystem by Net Primary Produc-  
74 tion (NPP), generally thought to be dependent on water temperature, sunlight, and  
75 the availability of nutrient elements at the ocean surface (Moore et al., 2013). This  
76 energy, embodied as organic matter, is then transferred to marine heterotrophic or-  
77 ganisms, which span many orders of magnitude in size, through feeding relationships.  
78 At each trophic step in the ecosystem, some portion of the biomass-energy is used  
79 to construct the tissues of the consumer, while the remainder is either egested or  
80 respired. Thus, the fate of the available NPP, as it is distributed through trophic  
81 links in the ecosystem and is ultimately respired, determines the abundance and  
82 size-distributions of animals in the marine ecosystem.

83 Climate change is now altering both the total NPP and the trophic links in the  
84 ecosystem. These alterations are brought about by multiple drivers, including warm-  
85 ing the water, changing the distribution and composition of phytoplankton, altering  
86 habitat, modifying ecosystem structure, reducing dissolved oxygen concentrations,  
87 increasing acidification and shifting seasonality (Prtner et al., 2014). Although most  
88 of these changes are difficult to predict, water temperature and net primary produc-  
89 tion (NPP) are routinely projected by the current generation of Earth System Models  
90 (Bopp et al., 2013), as emergent properties of physics and biogeochemistry in response  
91 to atmospheric forcing. The temperature and NPP changes should have direct im-  
92 pacts on ecosystem metabolism, since NPP plays a role in limiting whole ecosystem  
93 biomass (Ware and Thomson, 2005; Chassot et al., 2010), and the metabolic rates  
94 of growth and respiration depend strongly on temperature, as evident both at the

95 physiological level of individual animals (Kooijmann, 2000; Pörtner, 2002; Schulte,  
96 2015) and at the level of whole ecosystems (Brown et al., 2004). Here, we quanti-  
97 tatively estimate these metabolic consequences, as driven by the temperature and  
98 NPP changes predicted by an Earth System Model for the 21st century, through the  
99 lens of a model of global fish communities.

100 Earth System Models generally predict that as surface waters are warmed as a  
101 result of rising atmospheric carbon dioxide, the nutrient supply to the sunlit surface  
102 is reduced, and the rate of net primary production declines (Bopp et al., 2013). In  
103 addition, observations have shown that warmer, less nutrient-rich waters tend to host  
104 smaller phytoplankton cells (Daufresne et al., 2009; Dutkiewicz et al., 2004), which  
105 are preferentially eaten by small zooplankton, leading to longer trophic chains (Ry-  
106 ther, 1969). Because most of the energy consumed at a given trophic level is lost to  
107 respiration, lengthening the trophic chain reduces the fraction of energy from primary  
108 production that can be transferred to larger organisms (Ryther, 1969; Woodworth-  
109 Jefcoats et al., 2012; Stock et al., 2017). Warming of waters also affects ectothermic  
110 organisms by increasing their metabolic rates (Gillooly et al., 2001; Clarke and Fraser,  
111 2004) and is commonly expected to produce more rapid growth alongside more rapid  
112 respiration, activity, and predation (Pepin, 1991). Different species react differently  
113 to changes in temperature, a process that can further depend on other physiological,  
114 chemical, and ecological variables (Rall et al., 2012; Seebacher et al., 2014; Deutsch  
115 et al., 2015). The net impact of temperature on variables such as production and  
116 biomass at the species or ecosystem level is therefore difficult to ascertain.

117 The wild-capture fishery offers a perspective on the global marine ecosystem that  
118 can help resolve these questions, while simultaneously playing a major role as the

119 dominant top predator in the oceans (Darimont et al., 2015). Although the high  
120 cost of accessing and sampling most of the ocean, compounded by the mobility of  
121 many marine organisms, has impeded the development of comprehensive scientific  
122 assessments of global marine biomass, marine organisms are intensively sampled by  
123 fishers in search of commercially marketable organisms. Fishing vessels are active  
124 throughout most of the world ocean (Kroodsma et al., 2018), and the global catch has  
125 recently approached, or slightly exceeded, the total production capacity for exploited  
126 species (Pauly and Zeller, 2016; Galbraith et al., 2017). Historical fish catch records  
127 therefore represent a valuable source of scientific information on the marine ecosystem  
128 - but one which is filtered through the economic drivers of fisheries, and which has  
129 also altered the marine ecosystem through time. Interpreting the output of this  
130 filter requires a framework that can simultaneously take into account both the natural  
131 ecosystem dynamics and the behaviour of fishers. At the same time, fisheries reshape  
132 the ecosystem directly in a way that will interact with future climate change.

133 Here we apply a number of macroecological principles with broad empirical sup-  
134 port to better understand some of the interactive impacts that climate change and  
135 fishing activities could have on marine ecosystems. Specifically, we present a first-  
136 order assessment of how changes in water temperature and NPP could affect the  
137 global marine fish community through ecosystem metabolism, considering multiple  
138 future fisheries regulation scenarios. We use BOATS, a bioenergetically-constrained  
139 size-based global model that represents the harvested fraction of the marine ecosys-  
140 tem with a generalized, low level of ecological detail (Carozza et al., 2016), integrated  
141 with a simple prognostic representation of fisheries economics (Carozza et al., 2017).  
142 The model does not explicitly resolve individual species, which are certain to migrate

143 and evolve as conditions change (Sunday et al., 2012). Instead, the model implicitly  
144 assumes that, on a multi-decadal timescale, migration and evolution will adjust local  
145 ecosystems to result in a stationary relationship with a given set of environmental  
146 conditions. In other words, the model assumes that as environmental conditions  
147 shift, the ecosystem shifts along with them, which is likely to be an optimistic as-  
148 sumption. Nor do we resolve changes in species assemblage, which are likely to be  
149 important additional consequences of both fisheries regulations and climate change  
150 (Pecl et al., 2017), but focus instead on the total abundance of fish.

151 We use a model ensemble in which parameters are optimized against historical  
152 fish catch and stock assessment data from ecosystems throughout the ocean, ensur-  
153 ing a realistic rate of fish production as a function of NPP and water temperature  
154 (Carozza et al., 2017). We subdivide the simulated effects of climate change into four  
155 mechanistic elements, as represented within the model: 1) the total energy available  
156 to the community from net primary production, 2) the impact of phytoplankton  
157 size on trophic transfer, 3) the temperature dependence of somatic growth, and 4)  
158 the temperature dependence of natural fish mortality. Although we use only one  
159 model architecture in our ensemble, which contributes to unavoidable uncertainty in  
160 the quantitative accuracy of our results, we focus the analysis on general patterns  
161 and principles that are likely to apply to the real ocean, while identifying important  
162 outstanding uncertainties in need of further investigation.



## 163 **Methods**

### 164 **Macroecological model**

165 The BiOeconomic mArine Trophic Size-spectrum model (BOATS) model is described  
166 in detail by Carozza et al. (2016) and Carozza et al. (2017), which focus on the  
167 ecosystem and the parameter optimization procedure, respectively. The model is  
168 publicly available for download at <https://github.com/davidcarozza/boats0d-review>,  
169 (see the Data Availability Statement below). Here we provide a general overview of  
170 the model, focusing on the most relevant aspects for the current work. Supporting  
171 Information Appendix S1 provides a descriptive example for the use of the BOATS.

172 BOATS is designed to run on a 2-dimensional horizontal grid of the ocean, and  
173 evolves over time in response to environmental and human factors. It uses the shal-  
174 low subsurface water temperature (top 75 meters) and vertically-integrated NPP in  
175 each grid cell as inputs, which determine the flow of energy through the commu-  
176 nity and its accumulation as biomass (Figure 1). The simulations here represent  
177 all harvested marine ectotherms, which we refer to as fish, within three spectra of  
178 size classes, i.e. continuous ranges of logarithmically-spaced size classes from 10  
179 g (juveniles) to a spectrum-dependent maximum size. The model employs empiri-  
180 cal parameterizations to describe phytoplankton community structure, the trophic  
181 transfer of primary production from phytoplankton to fish, natural mortality, and  
182 recruitment. Avoiding the need to compute feeding relationships simplifies model  
183 dynamics and reduces computational expense, allowing extensive global-scale cali-  
184 bration and ensemble simulations

185 In BOATS, the total energy input to growth (somatic and reproductive) of an

186 individual fish is determined by the local primary production and ecosystem trophic  
187 transfer efficiency, to an upper limit that is the maximum rate at which a well-fed  
188 fish can grow (von Bertalanffy, 1949; Andersen and Beyer, 2015). Water tempera-  
189 ture modifies the upper limit growth rate through a van't Hoff–Arrhenius tempera-  
190 ture dependence, which is parameterised with a representative activation energy of  
191 metabolism (Gillooly et al., 2001). The fraction of the resulting input energy that is  
192 allocated to reproduction, as opposed to somatic growth, increases as fish approach  
193 their maximum size (Andersen and Beyer, 2015). The somatic growth rate of a fish  
194 within a given size spectrum therefore depends on the local energy source from NPP  
195 (i.e. within the local grid cell), the local trophic transfer efficiency, and the local  
196 temperature which determines the upper limit.

197 The trophic transfer of NPP to fish depends on the size structure of phytoplank-  
198 ton, which we estimate using the empirical algorithm of Dunne et al. (2005). This  
199 algorithm predicts the fraction of primary production that is generated by large phy-  
200 toplankton in each grid cell from the in situ NPP and water temperature. We employ  
201 this large fraction to estimate the average phytoplankton size. The trophic level of a  
202 fish of a given size is then calculated from the mass ratio of that fish to the average  
203 phytoplankton, and using an average predator-to-prey mass ratio for the community.  
204 The fraction of NPP that can be taken up by fish of a given size is then given by its  
205 trophic level and the average trophic efficiency. This simple approach captures the  
206 basic size-dependence of energy distribution within the community, while avoiding  
207 the complexity of explicit feeding relationships. Implicitly, it assumes that most fish  
208 are opportunistic feeders, and that variations in predator-to-prey mass ratios tend  
209 to be approximately compensated by opposing changes in trophic efficiency, leading

210 to constant efficiencies of total energy transfer to fish of a given size.

211 To represent natural mortality, defined here as all non-harvesting sources of fish  
212 mortality and including losses to predation, parasitism, disease, old age, and star-  
213 vation (Brown et al., 2004), we apply the empirical mortality rate of Gislason et al.  
214 (2010). This formulation varies mortality as a function of individual fish mass and  
215 asymptotic mass, and depends on temperature through a van't Hoff–Arrhenius re-  
216 lationship. To capture physiological differences between growth and predation rates  
217 (Rall et al., 2012), we employ a different activation energy of metabolism parameter  
218 in each of the van't Hoff–Arrhenius temperature dependence relationships for growth  
219 and mortality.

220 BOATS simulates fishing activity from simple economic principles, as described  
221 in detail by Carozza et al. (2017). In brief, the fish caught in a grid cell is calculated  
222 as the product of catchable biomass, effort (the fishing energy exerted per unit area),  
223 and a catchability constant that represents the fraction of biomass that is caught for  
224 a unit amount of effort. The effort is either imposed at the level that achieves the  
225 Maximum Sustainable Yield, or allowed to vary independently in each cell according  
226 to an Open Access dynamic. Using one of these two general frameworks for the  
227 fishing rate, we consider four fishing scenarios that are described further below and  
228 summarized in Table 1.

229 Model parameters were optimized using a Monte Carlo Approximate Bayesian  
230 Computation approach (Csillry et al., 2010), using the global catch data of the Sea  
231 Around Us Project and the RAM Legacy Stock Assessment database as observational  
232 constraints (Ricard et al., 2011). Supporting Information Appendix S1 details the  
233 parameter optimization approach (Carozza et al., 2017). Importantly, this procedure

234 includes comparing the modeled fish catches among all Large Marine Ecosystems  
235 to those observed, to ensure a realistic production rate of fish biomass under the  
236 global range of present-day NPP and water temperatures. From a subset of 100  
237 acceptable parameter combinations, we chose a subsample of six different parameter  
238 combinations. We refer to the collection of six parameter combinations as the model  
239 ensemble, and to each of the individual parameter combinations as an ensemble  
240 member. Supporting Information Appendix S2 details the parameter values and  
241 global characteristics of the six ensemble members used in this study.

242 Like any model, BOATS provides a simplified representation of reality. The  
243 model ignores a multitude of potential stressors, such as the impact of phenology  
244 on recruitment (Asch, 2015), explicit inter-species interactions, decreased oxygen  
245 concentrations (Cheung et al., 2013; Prtner and Peck, 2010) and ocean acidification  
246 (Fabry et al., 2008; Briffa et al., 2012). BOATS also does not resolve movement  
247 between oceanic grid cells (Watson et al., 2015), which could be important for the  
248 adaptation of large predatory fish to changing food patterns, or changes to ecosystems  
249 due to bottom-trawling (Puig et al., 2012). Nonetheless, the structural simplicity of  
250 the model is necessary in order to allow the parameter optimization with historical  
251 fishing observations, which ensures a well-calibrated response to water temperature  
252 and NPP. In addition, the inclusion of prognostic fishing effort allow it to estimate  
253 how basic macroecological impacts of long-term climate change could interact with  
254 conservation efforts.

## 255 **Simulation strategy**

256 To estimate the relative roles of the energetic mechanisms that affect fish communities  
257 under changing NPP and water temperature, we conducted six sets of simulations,  
258 summarized in Table 1. Each of the first four sets isolates a specific aspect of the  
259 macroecological response to climate change, by allowing anthropogenic changes in  
260 NPP and/or water temperature to apply only to that aspect. The fifth set allows  
261 all elements to change together, and the last represents a constant climate over the  
262 period of analysis. In detail, the sets of simulations are:

- 263 1. **NPP**. Isolates the effects of changes in the input of energy to the base of the  
264 food web by photosynthesis. In the model, an individual fish of size  $m$  is limited  
265 by the proportion of NPP that is transferred to all fish of size  $m$  through the  
266 local food web, divided by the number of fish in that size class. Because this  
267 energy is partitioned uniformly among all fish of size  $m$ , the individual growth  
268 rate will increase (up to a maximum physiological rate) when NPP increases  
269 and/or the number of fish decreases. The fraction of NPP that can reach size  
270  $m$  depends on the trophic efficiency and the predator to prey mass ratio, both  
271 of which are global constants that differ for each ensemble member. Greater  
272 NPP also improves larval survival by increasing the flux of biomass from mature  
273 individuals that enters the smallest size classes (recruitment).
- 274 2. **PhytoSize**. Isolates the effects of changes in phytoplankton size structure on  
275 fish growth rates. The transfer of energy from NPP to fish of size  $m$  depends  
276 on phytoplankton cell size, since this contributes to determining the trophic  
277 distance (Ryther, 1969; Woodworth-Jefcoats et al., 2012; Stock et al., 2017).

278 In BOATS, the empirical model of Dunne et al. (2005) is used to estimate the  
279 fraction of primary production that is attributed to large phytoplankton as a  
280 function of temperature and NPP. Higher productivities and lower tempera-  
281 tures favor larger phytoplankton sizes.

282 3. **TempGrowth.** Isolates the impact of temperature on the maximum physio-  
283 logical growth rate of fish. In the model, individual fish cannot grow faster than  
284 a maximum rate that follows the widely-used von Bertalanffy growth formu-  
285 lation (von Bertalanffy, 1949; Hartvig et al., 2011; Andersen and Beyer, 2015)  
286 and depends on the individual fish size (relative to its maximum size) as well  
287 as temperature, following the van’t Hoff–Arrhenius equation. As temperature  
288 increases, so does the maximum physiological growth rate.

289 4. **TempMortality.** Isolates the impact of temperature on natural fish mortal-  
290 ity. BOATS represents the natural (i.e. non-fishing) mortality rate using the  
291 empirical formulation of Gislason et al. (2010), as the product of a natural  
292 mortality constant, a temperature-dependent term that is based on the van’t  
293 Hoff–Arrhenius equation, individual mass, and the asymptotic mass (Carozza  
294 et al., 2016). Note that temperature in the model affects fish growth and mor-  
295 tality rates differently, consistent with the distinct physiological and ecological  
296 processes controlling somatic growth vs. respiration and predation rates (Gis-  
297 lason et al., 2010; Rall et al., 2012). The magnitudes of the two activation  
298 energies are allowed to vary independently of each other in the Monte Carlo  
299 procedure, so that the six-member ensemble includes six different combinations  
300 of the activation energies.

301 5. **Total.** Simulates the overall climate impact by including all four of the above  
302 mechanisms simultaneously.

303 6. **Constant Climate.** Simulates no climate change. Forces the model with  
304 a constant climate of the monthly averages calculated from the preindustrial  
305 period of 1851-1900.

## 306 **Simulation design**

307 We force the six optimal model ensemble members described above with net pri-  
308 mary production and temperature output from the Institut Pierre Simon Laplace  
309 IPSL-CM5A-LR global climate model (Dufresne, et al., 2013), which employs the  
310 PISCES biogeochemical model (Aumont and Bopp, 2006), under the business as  
311 usual RCP8.5 scenario (Moss, et al., 2010). Figure 2a,b show the preindustrial water  
312 temperature and NPP (average of years 1851-1900) used for our constant climate  
313 scenario, respectively, of the IPSL-CM5A-LR model output, while Figure 2c,d show  
314 the change in water temperature and NPP between 1851-1900 and 2081-2100. Simi-  
315 larly, Supporting Information Appendix S3 presents the preindustrial phytoplankton  
316 size and its change compared to 2081-2100, respectively, estimated with the method  
317 of Dunne et al. (2005).

318 For each of the six ensemble members, we conduct simulations under four idealized  
319 regulation scenarios that span a broad range of possible futures (Table 1) following  
320 Galbraith et al. (2017). These scenarios are intended to illustrate the bounds of  
321 possibility, rather than being detailed attempts at future predictions. The base  
322 scenario has no fishing effort, which we call the 'Perfect Conservation' case, while

323 a second scenario allows fishing effort at the level 'Optimized for Human Food'  
324 production, commonly known as the Maximum Sustainable Yield (MSY) fishing  
325 rate. The remaining two scenarios do not include regulations, but simulate profit-  
326 driven fishing effort following the open-access principle (Carozza et al., 2017) under  
327 the assumption of either a near-future stabilization (No Conservation scenario), or  
328 a continuing intensification of fishing (Intense Overfishing scenario). Supporting  
329 Information Appendix S1 further details the simulation protocol.

## 330 **Results**

### 331 **Global changes of total biomass**

332 Under Perfect Conservation, climate change reduces the globally-integrated marine  
333 biomass by 32 % (lower estimate -33, upper estimate -29 %) by 2100 (Figure 3a;  
334 Figure 4). The increase in the natural mortality rate (simulation TempMortality)  
335 brought on by a warming ocean has the single greatest negative impact on biomass,  
336 resulting in a decrease of 43 % (-46, -33 %) by 2100. Net primary production (simula-  
337 tion NPP) has a minor negative or negligible impact on globally-integrated biomass,  
338 reducing it by only 3 % (-5, 1 %), whereas the shift to smaller phytoplankton cells  
339 (simulation PhytoSize) accounts for a more significant biomass reduction of 13 % (-  
340 15, -9 %). Warming waters have a positive impact on biomass through their impact  
341 on the growth rate upper limit (simulation TempGrowth), raising biomass by 18 %  
342 (16, 28 %).

343 The impact of climate change on fish biomass in the Optimized for Human Food  
344 scenario is similar to the Perfect Conservation scenario (Figure 3b; Figure 4), with



345 an overall decline of 32 % (-35, -29 %). As in the case with Perfect Conservation,  
346 this decline is mostly driven by increasing mortality under warming, reinforced by  
347 declines in productivity and phytoplankton size, which are only partially offset by  
348 faster growth rates. Interestingly, the range of variability among ensemble members  
349 is much larger for the TempMortality and TempGrowth simulations (Figure 4), re-  
350 vealing a large sensitivity to the uncertain parameters. However, this sensitivity is  
351 greatly reduced in the Total simulations, indicating that the temperature sensitivity  
352 of growth is correlated with the temperature sensitivity of mortality in any given  
353 ensemble member. This correlation is consistent with the constraint identified in  
354 Carozza et al. (2017) that, for realistic global harvests to arise from the mdel param-  
355 eters, temperature-driven increases in growth must be balanced by parallel increases  
356 in mortality.

357 Under the No Conservation scenario (Figure 3c; Figure 4), the negative impacts  
358 of climate change are significantly damped relative to the Perfect Conservation and  
359 Optimized for Human Food cases. Here, climate change only results in a loss of 15  
360 % (-20, -12 %) of biomass by 2100. The reduced climate impact is mainly driven  
361 by a weakened negative impact of the mortality rate; because fishing and natural  
362 mortality both act to reduce fish abundance, Intense Overfishing reduces the rela-  
363 tive importance of natural mortality. Biomass changes due to primary production  
364 (simulation NPP) and temperature-dependent growth (simulation TempGrowth) are  
365 similar to those without fishing, but the impact of phytoplankton size (simulation  
366 PhytoSize) is significantly damped, since when the number of fish is reduced, growth  
367 rates are determined by the size-dependent physiological upper limit rather than by  
368 primary production (Carozza et al., 2016).

369 In the extreme Intense Overfishing scenario, the impacts of the NPP and Phyto-  
370 Size mechanisms disappear almost entirely, and the overall impact of climate change  
371 to year 2100 is equivocal (Figure 4). The extremely intense fishing rate further damps  
372 the negative impact of TempMortality, which causes a biomass fall of only 7 % (-37,  
373 1 %), which is then entirely compensated by the more rapid growth rates. However,  
374 we caution that this effect only occurs in the model under extreme, and likely un-  
375 realistic values of harvesting technologies, at which point ecosystems are decimated  
376 and the average global fish catch is very small (Supporting Information Appendix  
377 S4g).

### 378 **Spatial patterns of change**

379 As shown in Figure 5a, the net reduction of global biomass under climate change  
380 does not reflect a uniform global decrease, but a patchwork of increases and decreases  
381 that largely compensate each other in the global sum. Reductions over the tropics  
382 and mid- to high-latitudes are partially counteracted by increases in subtropical (e.g.  
383 South Pacific and South Atlantic gyres) and polar regions (in particular the Southern  
384 Ocean), and over eastern boundary upwelling systems (California, Chile, and Canary  
385 Islands).

386 The pattern of net change closely resembles the responses driven by primary  
387 production (simulation NPP, Figure 5b), and to a lesser extent by phytoplankton  
388 size structure (PhytoSize, Figure 5c). However, the latter are generally shifted to-  
389 ward more negative values due to the effect of warming, which tends to decrease  
390 phytoplankton size everywhere. Thus, whereas NPP changes result in regional pat-  
391 terns that largely cancel each other out, phytoplankton size changes produce weaker

392 regional contrasts but a more significant negative global impact.

393 The uniquely temperature-dependent impacts on growth and mortality (simula-  
394 tions TempGrowth and TempMortality, Figure 5d,e) are more spatially homogeneous  
395 than those driven by net primary production, due to the homogeneous distribution of  
396 warming (Figure 2) and have opposite and nearly compensating effects on biomass.  
397 The activation energy of mortality is more sensitive to temperature than that of  
398 growth in all but one of our ensemble members (Supporting Information Appendix  
399 S2). Increases of biomass relative to the constant climate scenario only occur in re-  
400 gions where NPP increases enough to overcome the combined effect of enhanced mor-  
401 tality and shrinking phytoplankton cells. The simulated changes in fisheries catches  
402 (harvest) are qualitatively similar to the simulated biomass changes, as shown in  
403 Supporting Information Appendix S7.

## 404 Discussion

405 Our results show a large negative impact of climate change on marine fish commu-  
406 nities from metabolic effects, when summed at the global scale. The main ecological  
407 mechanisms driving this decrease are the temperature-sensitivity of natural mortal-  
408 ity, which reflects enhanced dissipation of biomass by respiration in warmer water,  
409 and a decrease in phytoplankton size, which reduces the energy available to fish by  
410 trophic transfer for a given rate of NPP. These deleterious effects are opposed by the  
411 increase of growth rates at higher temperatures, but this is insufficient to compensate  
412 for the negative effects in any of our six ensemble members. Under intense levels of  
413 overfishing, the negative impacts of climate are lessened because of a reduced impor-

414 tance of natural mortality, a diminished competition for resources, and an increased  
415 importance of growth when fish populations are greatly impoverished.

416 We find significant regional variability in the impacts of climate change, mostly  
417 driven by the spatial patterns of NPP changes simulated by the Earth System Model.  
418 While most of the tropics and mid-latitudes show a decline in fish biomass, some re-  
419 gions actually show an increase of these quantities, particularly in the Southern  
420 Ocean, South Pacific and South Atlantic gyres, and some Eastern Boundary Up-  
421 welling Systems. The current generation of Earth System models indicates a sub-  
422 stantial degree of uncertainty in projections for NPP (Bopp et al., 2013) and the  
423 details of this mosaic of winners and losers should therefore be viewed with caution.  
424 Nonetheless, the spatial heterogeneity of NPP changes typically simulated by mod-  
425 els, compared to the much more homogeneous warming, suggests that the dominance  
426 of NPP in determining spatial patterns is a robust result.

427 Our results in the Perfect Conservation set of simulations are generally consistent  
428 with those simulated by Lefort et al. (2014), despite important structural differences  
429 between the models employed. Simulated biomass in BOATS falls nonlinearly with  
430 decreases in the fraction of large phytoplankton, with a global spatially-weighted  
431 average decrease of 3% in the large fraction (Supporting Information Appendix S3)  
432 resulting in a median biomass decrease of 13%. This is a much greater sensitiv-  
433 ity to the phytoplankton size than that presented by Blanchard et al. (2012) and  
434 Woodworth-Jefcoats et al. (2012), in which fish biomass varied linearly with phy-  
435 toplankton size, and points to the important uncertainty regarding the response of  
436 trophic efficiency to climate change.

437 Our simulations also agree with Cheung et al. (2010) in many parts of the world,

438 but whereas those authors estimated that fish would increase in high northern lati-  
439 tudes, we find decreases over much of the high northern latitudes by 2100, in agree-  
440 ment with Lefort et al. (2014). This contrast likely reflects the fact that the biocli-  
441 mate envelope approach applied by Cheung et al. (2010) is designed to estimate catch  
442 potential for particular species based on environmental factors such as temperature,  
443 but does not explicitly simulate the metabolic effect of temperature on growth and  
444 mortality. Given that these aspects produce the largest climate impact on BOATS,  
445 it is not surprising that Cheung et al. (2010) simulate a different spatial pattern of  
446 change, as well as a weaker globally-averaged response to climate.

447 One potentially-surprising aspect of the simulations is a reduction in the negative  
448 impact of climate change in the total absence of fishery regulation, as fishing pressure  
449 increases to extremely high levels. This reduction is mainly due to a reduction of  
450 the temperature impact on natural mortality, with further important contributions  
451 from temperature-dependent growth and phytoplankton size effects (Figure 4). In a  
452 hypothetical future with Perfect Conservation, biomass is large and growth is there-  
453 fore significantly limited by NPP, while increasing temperature tends to have a net  
454 negative effect since the natural mortality effect is larger than the growth rate effect.  
455 Essentially, if primary production is the limiting factor for growth of the overall com-  
456 munity, then NPP changes are important for determining total biomass. Similarly,  
457 if biomass production is balanced only by natural mortality, then the temperature  
458 effect on mortality is important. In contrast, under Intense Overfishing, the reduc-  
459 tion of fish biomass results in more energy availability per individual fish, and so  
460 somatic growth becomes less dependent on NPP and the phytoplankton community  
461 size structure.

462 In addition, as fishing becomes a major loss term for biomass, it reduces the  
463 impact of natural mortality relative to the case without harvest. Instead, the impor-  
464 tance shifts to the rate at which fish can grow from juveniles to adulthood, which  
465 limits the replacement rate of harvested fish. As a result, the positive impact of  
466 warmer temperatures on growth rates becomes increasingly significant as fishing in-  
467 tensifies, counterbalancing the negative impacts of NPP and natural mortality.

468 The real world outcomes would undoubtedly be more nuanced than in this simple  
469 model framework, but we hypothesize that the general weakening of climate-driven  
470 bioenergetic impacts under intense fishing is likely to be a robust feature of marine  
471 ecosystems. If true, this metabolic effect would be expected to reduce the relative  
472 impact of climate change on biomass in heavily exploited ecosystems, all else being  
473 equal. At the same time, it may offset some gains to be made from future conservation  
474 efforts, as accelerated natural mortality may consume a significant portion of the  
475 biomass saved from fishing. We would caution that this implied trade-off refers only  
476 to the biomass, and does not consider the impacts on other aspects of the community  
477 such as species diversity. In addition, the model does not include other impacts of  
478 climate change, such as ocean deoxygenation, which may interact differently with  
479 fishing pressure.

480 At the same time, it is important to emphasize that overfishing could have a  
481 significantly more deleterious impact on the evolution of 21st century biomass than  
482 climate change (Galbraith et al., 2017). In the Intense Overfishing scenario, biomass  
483 is reduced by  $> 90$  % by relative to that of Perfect Conservation (Supporting Infor-  
484 mation Appendix S4), as opposed to an average climate-change-induced reduction of  
485 30 % (Figure 3a). Thus, although the metabolic impacts of climate change may be

486 stronger for an ecosystem protected by effective conservation, this effect is dwarfed by  
487 the much larger overall benefits to be achieved through conservation. It is also pos-  
488 sible that additional ecosystem resilience may be provided by conservation measures  
489 (Loreau et al., 2001), which could counteract the metabolic trade-off.

490 Finally we point out that, within our observationally-calibrated macroecological  
491 model, the dominant effects of temperature on ecosystem metabolism are via growth  
492 and natural mortality. Thus, if other unresolved temperature-dependences affect ma-  
493 rine fish communities, we expect they would have biased the parameter selection by  
494 masquerading as the temperature sensitivities of growth and mortality. For example,  
495 it has been suggested that trophic efficiency varies with temperature (Stock et al.,  
496 2017), which would cause harvests to vary with temperature in a way not explic-  
497 itly simulated by the model. Our parameter selection would implicitly ‘correct’ for  
498 this by including the trophic efficiency contribution in one of the other temperature  
499 dependences. Similarly, ‘natural mortality’ is a simplification of a complex web of  
500 processes that ultimately results in the removal of biomass from the spectrum of up-  
501 per trophic level organisms; explicit representation of these processes could modify  
502 their environmental sensitivities to some degree. These are important uncertainties  
503 that could be addressed in future work.

504 In summary, our model predicts that climate change will reduce the total supply  
505 of energy to upper trophic levels, and will accelerate the rate at which energy flows  
506 through ecosystems. These changes result in a large decrease of total fish abundance  
507 under the strong warming of the RCP8.5 emissions scenario. The overall negative  
508 impact reflects the net outcome of opposed, nearly-compensating accelerations of  
509 mortality and growth rates under warming, coupled with a shrinking of phytoplank-

510 ton cells that lengthens trophic chains. Meanwhile, changes in primary production  
511 determine the spatial patterns of simulated climate impacts but have relatively little  
512 effect on globally-integrated responses, particularly under Intense Overfishing. Fur-  
513 ther work should focus on improving the quantitative, mechanistic understanding  
514 of the ecological processes behind this response, particularly the poorly-constrained  
515 variations in natural mortality due to rising temperatures, and the impacts of com-  
516 munity structure on the transfer of energy from producers to consumers. Our results  
517 also emphasize the importance of preventing overfishing through effective regula-  
518 tions, with or without climate change (Worm, B et al., 2009; Galbraith et al., 2017),  
519 if further loss of wild fish abundance is to be prevented.

## 520 **References**

- 521 Andersen, K. H. and Beyer, J. E. (2015). Size structure, not metabolic scaling rules,  
522 determines fisheries reference points. *Fish and Fisheries*, 16:1–22.
- 523 Asch, R. G. (2015). Climate change and decadal shifts in the phenology of larval  
524 fishes in the california current ecosystem. *Proceedings of the National Academy of*  
525 *Sciences*, 112:E4065–E4074.
- 526 Aumont, O. and Bopp, L. (2006). Globalizing results from ocean in situ iron fertil-  
527 ization studies. *Global Biogeochemical Cycles*, 20:GB2017.
- 528 Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J.,  
529 Dulvy, N. K., and Barange, M. (2012). Potential consequences of climate change for



- 530 primary production and fish production in large marine ecosystems. *Philosophical*  
531 *Transactions of the Royal Society B: Biological Sciences*, 367(1605):2979–2989.
- 532 Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran,  
533 P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., and Vichi, M. (2013). Multiple  
534 stressors of ocean ecosystems in the 21st century: projections with CMIP5 models.  
535 *Biogeosciences*, 10(10):6225–6245.
- 536 Briffa, M., de la Haye, K., and Munday, P. L. (2012). High CO<sub>2</sub> and marine animal  
537 behaviour: Potential mechanisms and ecological consequences. *Marine Pollution*  
538 *Bulletin*, 64(8):1519–1528.
- 539 Brown, J., Gillooly, J., Allen, A., Savage, V., and West, G. (2004). Toward a  
540 metabolic theory of ecology. *Ecology*, 85(7):1771–1789.
- 541 Carozza, D. A., Bianchi, D., and Galbraith, E. D. (2016). The ecological module  
542 of boats-1.0: a bioenergetically constrained model of marine upper trophic levels  
543 suitable for studies of fisheries and ocean biogeochemistry. *Geoscientific Model*  
544 *Development*, 9(4):1545–1565.
- 545 Carozza, D. A., Bianchi, D., and Galbraith, E. D. (2017). Formulation, general fea-  
546 tures and global calibration of a bioenergetically-constrained fishery model. *PLOS*  
547 *ONE*, 12:1–28.
- 548 Chassot, E., Bonhommeau, S., and Dulvy, N. (2010). Global marine primary pro-  
549 duction constrains fisheries catches. *Ecology Letters*, 13:495–505.
- 550 Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R.,  
551 Zeller, D., and Pauly, D. (2010). Large-scale redistribution of maximum fisheries

552 catch potential in the global ocean under climate change. *Global Change Biology*,  
553 16(1):24–35.

554 Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y.,  
555 Deng Palomares, M. L., Watson, R., and Pauly, D. (2013). Shrinking of fishes  
556 exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate*  
557 *Change*, 3:254–258.

558 Clarke, A. and Fraser, K. P. P. (2004). Why does metabolism scale with temperature?  
559 *Functional Ecology*, 18(2):243–251.

560 Csillry, K., Blum, M. G., Gaggiotti, O. E., and Franois, O. (2010). Approxi-  
561 mate Bayesian Computation (ABC) in practice. *Trends in Ecology & Evolution*,  
562 25(7):410 – 418.

563 Darimont, C. T., Fox, C. H., Bryan, H. M., and Reimchen, T. E. (2015). The unique  
564 ecology of human predators. *Science*, 349(6250):858–860.

565 Daufresne, M., Lengfellner, K., and Sommer, U. (2009). Global warming benefits  
566 the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*,  
567 106(31):12788–12793.

568 Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H., and Huey, R. (2015). Climate change  
569 tightens a metabolic constraint on marine habitats. *Science*, 348:1132–1135.

570 Dufresne, et al. (2013). Climate change projections using the IPSL-CM5 Earth  
571 System Model: from CMIP3 to CMIP5. *Climate Dynamics*, 40(9-10):2123–2165.

- 572 Dunne, J., Armstrong, R., Gnanadesikan, A., and Sarmiento, J. (2005). Empirical  
573 and mechanistic models for the particle export ratio. *Global Biogeochemical Cycles*,  
574 19(4).
- 575 Dutkiewicz, S., Scott, J. R., and Follows, M. J. (2004). Winners and losers: Ecological  
576 and biogeochemical changes in a warming ocean. *Global Biogeochemical Cycles*,  
577 27(2):463–477.
- 578 Fabry, V. J., Seibel, B. A., Feely, R. A., and Orr, J. C. (2008). Impacts of ocean  
579 acidification on marine fauna and ecosystem processes. *ICES Journal of Marine*  
580 *Science*, 65(3):414–432.
- 581 Galbraith, E. D., Carozza, D. A., and Bianchi, D. (2017). A coupled human-Earth  
582 model perspective on long-term trends in the global marine fishery. *Nature Com-*  
583 *munications*, 8:14884.
- 584 Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. (2001).  
585 Effects of size and temperature on metabolic rate. *Science*, 293(5538):2248–2251.
- 586 Gislason, H., Daan, N., Rice, J. C., and Pope, J. G. (2010). Size, growth, temperature  
587 and the natural mortality of marine fish. *Fish and Fisheries*, 11(2):149–158.
- 588 Hartvig, M., Andersen, K. H., and Beyer, J. E. (2011). Food web framework for  
589 size-structured populations. *Journal of theoretical Biology*, 272(1):113–122.
- 590 Kooijmann, S. A. L. M. (2000). *Dynamic Energy Mass Budgets in Biological Systems*.  
591 Cambridge: Cambridge University Press.

592 Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti,  
593 F., Wilson, A., Bergman, B., White, T. D., Block, B. A., Woods, P., Sullivan,  
594 B., Costello, C., and Worm, B. (2018). Tracking the global footprint of fisheries.  
595 *Science*, 359(6378):904–908.

596 Lefort, S., Aumont, O., Bopp, L., Arsouze, T., Gehlen, M., and Maury, O. (2014).  
597 Spatial and body-size dependent response of marine pelagic communities to pro-  
598 jected global climate change. *Global Change Biology*, 21(1):154–164.

599 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper,  
600 D., Huston, M., Raffaelli, D., Schmid, B., et al. (2001). Biodiversity and ecosystem  
601 functioning: current knowledge and future challenges. *science*, 294(5543):804–808.

602 Moore, C. M., Mills, M. M., Arrigo, K. R., Berman-Frank, I., Bopp, L., Boyd,  
603 P. W., Galbraith, E. D., Geider, R. J., Guieu, C., Jaccard, S. L., Jickells, T. D.,  
604 La Roche, J., Lenton, T. M., Mahowald, N. M., Maran, E., Marinov, I., Moore,  
605 J. K., Nakatsuka, T., Oschlies, A., Saito, M. A., Thingstad, T. F., Tsuda, A., and  
606 Ulloa, O. (2013). Processes and patterns of oceanic nutrient limitation. *Nature*  
607 *Geoscience*, 6:701–710.

608 Moss, et al. (2010). The next generation of scenarios for climate change research and  
609 assessment. *Nature*, 463(7282):747–756.

610 Pauly, D. and Zeller, D. (2016). Catch reconstructions reveal that global marine  
611 fisheries catches are higher than reported and declining. *Nature Communications*,  
612 7:10244.

613 Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C.,  
614 Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., et al. (2017). Biodiversity  
615 redistribution under climate change: Impacts on ecosystems and human well-being.  
616 *Science*, 355(6332):eaai9214.

617 Pepin, P. (1991). Effect of temperature and size on development, mortality, and  
618 survival rates of the pelagic early life history stages of marine fish. *Canadian*  
619 *Journal of Fisheries and Aquatic Sciences*, 48(3):503–518.

620 Pörtner, H.-O. (2002). Climate variations and the physiological basis of temperature  
621 dependent biogeography: systemic to molecular hierarchy of thermal tolerance in  
622 animals. *Comparative Biochemistry and Physiology Part A: Molecular & Integra-*  
623 *tive Physiology*, 132(4):739–761.

624 Puig, P., Canals, M., Company, J. B., Martn, J., Amblas, D., Lastras, G., Palan-  
625 ques, A., and Calafat, A. M. (2012). Ploughing the deep sea floor. *Nature*,  
626 489(7415):286–289.

627 Pörtner, H.-O., Karl, D., Boyd, P., Cheung, W., Lluçh-Cota, S., Nojiri, Y., Schmidt,  
628 D., and PO, Z. (2014). Ocean systems. In Field, C., Barros, V., Dokken, D., Mach,  
629 K., Mastrandrea, M., Bilir, T., Chatterjee, M., Ebi, K., Estrada, Y., Genova, R.,  
630 Girma, B., Kissel, E., Levy, A., MacCracken, S., Mastrandrea, P., and White,  
631 L., editors, *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part*  
632 *A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth*  
633 *Assessment Report of the Intergovernmental Panel on Climate Change*, chapter 6,  
634 pages 411–484. Cambridge University Press, Cambridge, UK and New York, USA.

635 Prtner, H. O. and Peck, M. A. (2010). Climate change effects on fishes and fisheries:  
636 towards a cause-and-effect understanding. *Journal of Fish Biology*, 77(8):1745–  
637 1779.

638 Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmuller, F., Vucic-Pestic,  
639 O., and Petchey, O. L. (2012). Universal temperature and body-mass scaling  
640 of feeding rates. *Philosophical Transactions of the Royal Society B: Biological*  
641 *Sciences*, 367(1605):2923–2934.

642 Ricard, D., Minto, C., Jensen, O. P., and Baum, J. K. (2011). Examining the  
643 knowledge base and status of commercially exploited marine species with the RAM  
644 Legacy Stock Assessment Database. *Fish and Fisheries*, 13(4):380–398.

645 Ryther, J. H. (1969). Photosynthesis and fish production in the sea. *Science*,  
646 166(3901):72–76.

647 Schulte, P. M. (2015). The effects of temperature on aerobic metabolism: towards a  
648 mechanistic understanding of the responses of ectotherms to a changing environ-  
649 ment. *Journal of Experimental Biology*, 218(12):1856–1866.

650 Seebacher, F., White, C. R., and Franklin, C. E. (2014). Physiological plasticity  
651 increases resilience of ectothermic animals to climate change. *Nature Climate*  
652 *Change*, 5(1):61–66.

653 Stock, C. A., John, J. G., Rykaczewski, R. R., Asch, R. G., Cheung, W. W. L.,  
654 Dunne, J. P., Friedland, K. D., Lam, V. W. Y., Sarmiento, J. L., and Watson,  
655 R. A. (2017). Reconciling fisheries catch and ocean productivity. *Proceedings of*  
656 *the National Academy of Sciences*, 114(8):E1441–E1449.

- 657 Sunday, J. M., Bates, A. E., and Dulvy, N. K. (2012). Thermal tolerance and the  
658 global redistribution of animals. *Nature Climate Change*, 2:686–690.
- 659 von Bertalanffy, L. (1949). Problems of Organic Growth. *Nature*, 163(4135):156–158.
- 660 Ware, D. M. and Thomson, R. E. (2005). Bottom-up ecosystem trophic dynamics  
661 determine fish production in the northeast pacific. *Science*, 308(5726):1280–1284.
- 662 Watson, J. R., Stock, C. A., and Sarmiento, J. L. (2015). Exploring the role of  
663 movement in determining the global distribution of marine biomass using a coupled  
664 hydrodynamic size-based ecosystem model. *Progress in Oceanography*, 138, Part  
665 B:521 – 532.
- 666 Woodworth-Jefcoats, P. A., Polovina, J. J., Dunne, J. P., and Blanchard, J. L. (2012).  
667 Ecosystem size structure response to 21st century climate projection: large fish  
668 abundance decreases in the central North Pacific and increases in the California  
669 Current. *Global Change Biology*, 19(3):724–733.
- 670 Worm, B et al. (2009). Rebuilding global fisheries. *Science*, 325(5940):578–585.

## 671 **Data Availability Statement**

672 The BOATS model was written in MATLAB version R2012a and was also tested  
673 in version R2010b. BOATS for a single patch of ocean, which includes the model  
674 run script, required functions, and forcing data, is archived and available for down-  
675 load under the reference Carozza, David A, Bianchi, Daniele, & Galbraith, Eric D.  
676 (2015). 0-D BiOeconomic mArine Trophic Size-spectrum (BOATS) model (Version

677 v1.0) [Data set]. Zenodo. <http://doi.org/10.5281/zenodo.27700>, and is additionally  
678 available at <https://github.com/davidcarozza/boats0d-review>. Supporting Informa-  
679 tion Appendix S1 provides a descriptive example for the use of the model. The  
680 model output and all MATLAB scripts required to reproduce the figures in this ar-  
681 ticle have been archived and are available for download under the reference Carozza,  
682 David A, Bianchi, Daniele, and Galbraith, Eric D. (2017). Metabolic impacts of  
683 climate change on marine fish communities and fisheries - Dataset and figure plot  
684 script [Data set]. Zenodo. <http://doi.org/10.5281/zenodo.495487>.

## 685 **Biosketch**

686 David A. Carozza has a background in mathematics, economics and climate science,  
687 and led the development of the BOATS model as a PhD student. He is currently  
688 a Postdoctoral Fellow at the University of Quebec at Montreal studying economic  
689 vulnerability and climate change. Daniele Bianchi is an Assistant Professor at the  
690 University of California, Los Angeles, where he studies ocean biogeochemistry and  
691 marine ecosystems. Eric Galbraith is an ICREA Research Professor based at the  
692 Autonomous University of Barcelona, where he is focused on improving the large-  
693 scale understanding of coupling between global ecosystems and human activity.



## 694 **Supporting Information**

695 **Appendix S1:** Simulation methods detailing parameter optimization, experimental  
696 design; choice of IPSL model; simulation protocol; analyses; BOATS example use  
697 instructions.

698 **Appendix S2:** Ensemble member characteristics.

699 **Appendix S3:** Maps of preindustrial values of the large phytoplankton fraction  
700 (average of 1851-1900) and its change between 2081-2100 and 1851-1900.

701 **Appendix S4:** Globally-integrated nonnormalized biomass and fish catch.

702 **Appendix S5:** Maps of median normalized change in biomass due to the impact of  
703 climate change on metabolism for the Perfect Conservation scenario.

704 **Appendix S6:** Maps of median normalized change in biomass due to the impact of  
705 climate change on metabolism for the No Conservation scenario.

706 **Appendix S7:** Globally-integrated fish catch change, relative to the constant cli-  
707 mate simulation.

Table 1: Metabolic simulations and conservation scenarios. Each metabolic simulation was conducted with all conservation scenarios, for each of the six model ensemble members, leading to a total of 144 simulations.

Metabolic Simulation	Input(s) from warming scenario	Resulting impacts on fish
NPP	NPP	Trophic growth limit, recruitment
PhytoSize	NPP and water temperature	Trophic growth limit, recruitment
TempGrowth	Water temperature	Physiological growth limit
TempMortality	Water temperature	Natural mortality rate
Total	NPP and Water temperature	All
Clim	None	None

---

Conservation Scenario	Characteristics
Perfect Conservation	Zero fishing effort everywhere
Optimized for Human Food	Maximum stable fish catch everywhere
No Conservation	Open access, stabilizing by 2036
Intense Overfishing	Open access, increasing continuously

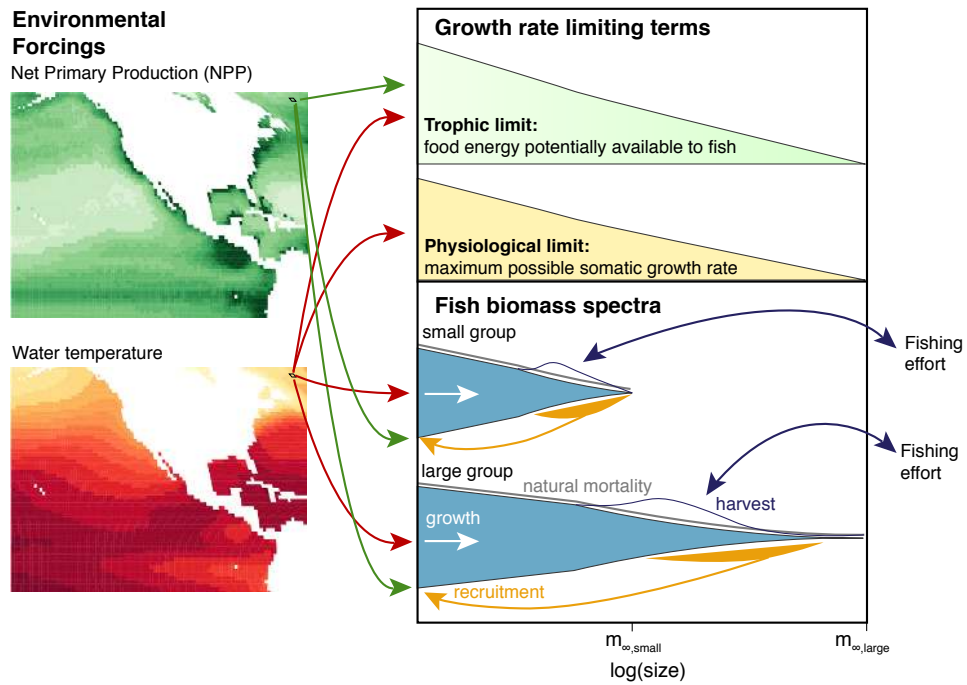


Figure 1: Schematic overview of the BOATS model. The red, green, and black arrows indicate dependencies of model components on external forcings (left panel). The top-right panel indicates the energetic limits of growth as a function of fish size, whereas the bottom-right panel illustrates the size spectra of fish groups, their internal dynamics, and link to economics via fish catch and the interactive effort.

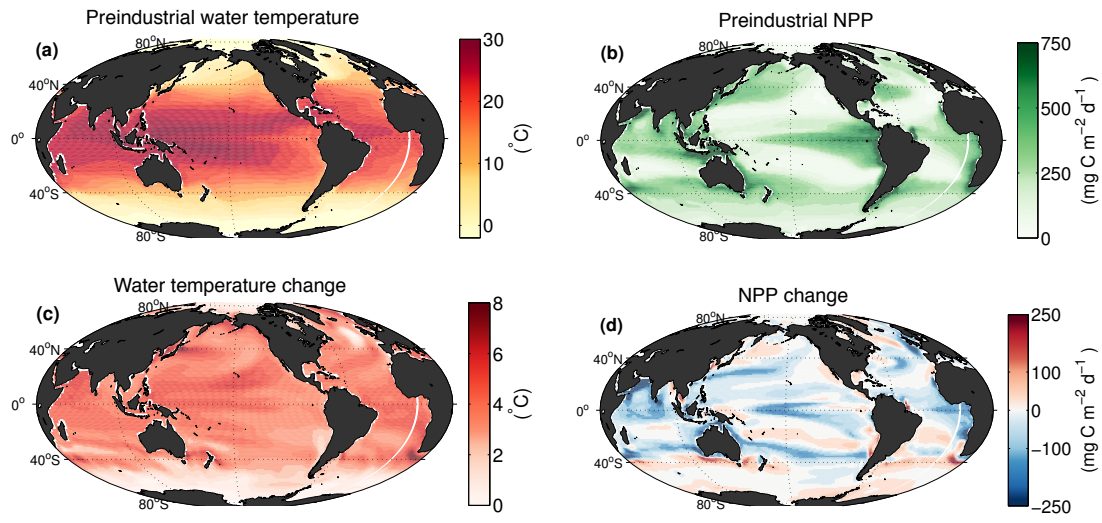


Figure 2: Preindustrial climate forcing variables and change in those variables due to climate change in the IPSL-CM5A-LR global climate model used to force BOATS. (a) Preindustrial water temperature. (b) Preindustrial net primary production (NPP). (c) Water temperature change. (d) Net primary production change. Water temperature is averaged over the upper 75 meters of the ocean, while NPP is vertically-integrated. Preindustrial climate variables are the average over 1851-1900, whereas change is measured as the average over 2081-2100 less the average over 1851-1900. The constant climate scenario employs the preindustrial climate variables.

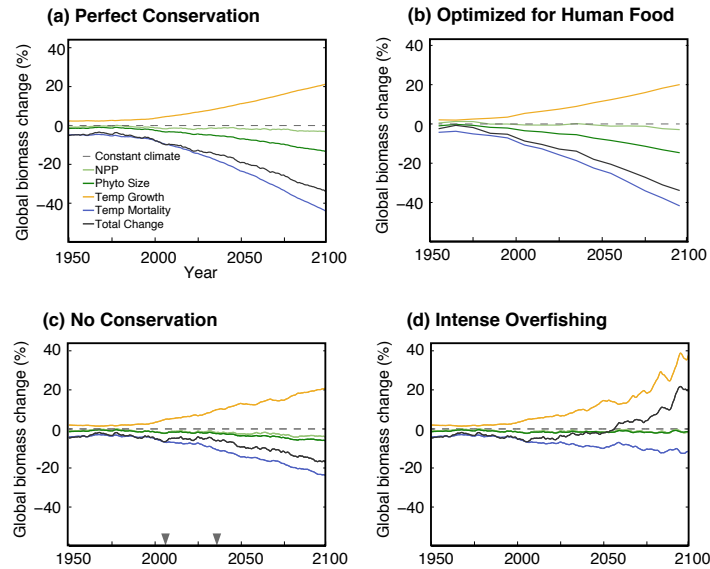


Figure 3: Globally-integrated fish biomass change, relative to the constant climate simulation. Each panel shows the six metabolic simulations (colour-coded), for one conservation scenario. Normalized quantities for each simulation are expressed in terms of the % change relative to the constant climate biomass for that simulation by taking the mean over the 6 ensemble members. Grey vertical triangles at years 2006 and 2036 in (c) represent years where the increase in fishing technology begins to slow and stops, respectively.

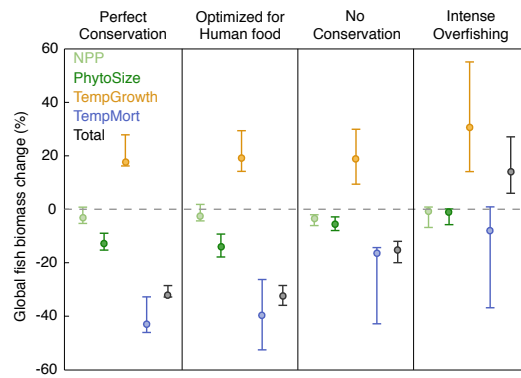


Figure 4: Globally-integrated fish biomass <sup>38</sup> change relative to the constant climate scenario from 2081 to 2100. Circles represent the median over the 6 ensemble members, whereas the lower and upper bars represent the 5th and 95th percentiles over the 6 ensemble members, respectively.

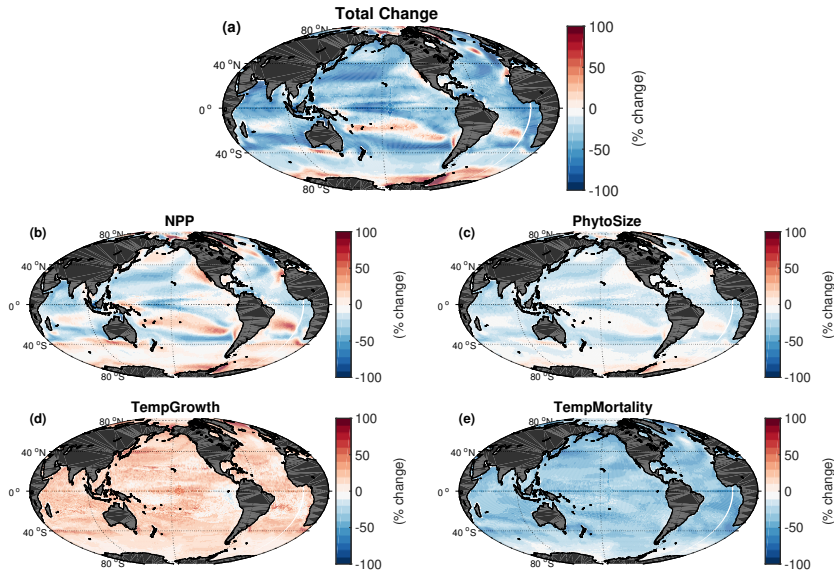


Figure 5: Maps of median normalized change in biomass due to the impacts of climate change on the metabolic model components for the Optimized for Human Food scenario over 2081-2100. (a) All combined effects (Total). (b) Growth rate dependence on net primary production (NPP). (c) Growth rate dependence on phytoplankton size structure (PhytoSize). (d) Growth rate upper limit temperature dependence (TempGrowth). (e) Natural mortality rate temperature dependence (TempMortality). For each metabolic simulation and set of ensemble members, changes are calculated relative to the constant climate forcing scenario. For each scenario, we calculate the median change over the 6 ensemble members of the temporal average of the normalized biomass over 2081-2100. Biomass change in the Perfect Conservation scenario is presented in Supporting Information Appendix S5, whereas biomass change in the No Conservation scenario is detailed in Supporting Information Appendix S6.