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Metabolic impacts of climate change on marine ecosystems: implications for fish communities and fisheries

Short running title: Climate and marine ecosystem metabolism

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Abstract

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

Location: Global ocean.

Time period: 1950-2100.

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

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

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

The climate impacts are similar across the range of conservation scenarios, but are slightly amplified in the strong conservation scenarios due to the greater role of natural mortality.

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

Keywords

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

Introduction

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

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

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

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

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

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

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

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

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

Methods

Macroecological model

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

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

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

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

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

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

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

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

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

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

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

Simulation strategy

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

1. **NPP**. Isolates the effects of changes in the input of energy to the base of the food web by photosynthesis. In the model, an individual fish of size m is limited by the proportion of NPP that is transferred to all fish of size m through the local food web, divided by the number of fish in that size class. Because this energy is partitioned uniformly among all fish of size m, the individual growth rate will increase (up to a maximum physiological rate) when NPP increases and/or the number of fish decreases. The fraction of NPP that can reach size m depends on the trophic efficiency and the predator to prey mass ratio, both of which are global constants that differ for each ensemble member. Greater NPP also improves larval survival by increasing the flux of biomass from mature individuals that enters the smallest size classes (recruitment).

2. **PhytoSize**. Isolates the effects of changes in phytoplankton size structure on fish growth rates. The transfer of energy from NPP to fish of size m depends on phytoplankton cell size, since this contributes to determining the trophic distance (Ryther, 1969; Woodworth-Jefcoats et al., 2012; Stock et al., 2017).

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

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

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

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

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

Simulation design

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

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

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

Results

Global changes of total biomass

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

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

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

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

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

Spatial patterns of change

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

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

regional contrasts but a more significant negative global impact.

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Data Availability Statement

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

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

Biosketch

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

Supporting Information

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

Appendix S2: Ensemble member characteristics.

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

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

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

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

Appendix S7: Globally-integrated fish catch change, relative to the constant climate 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

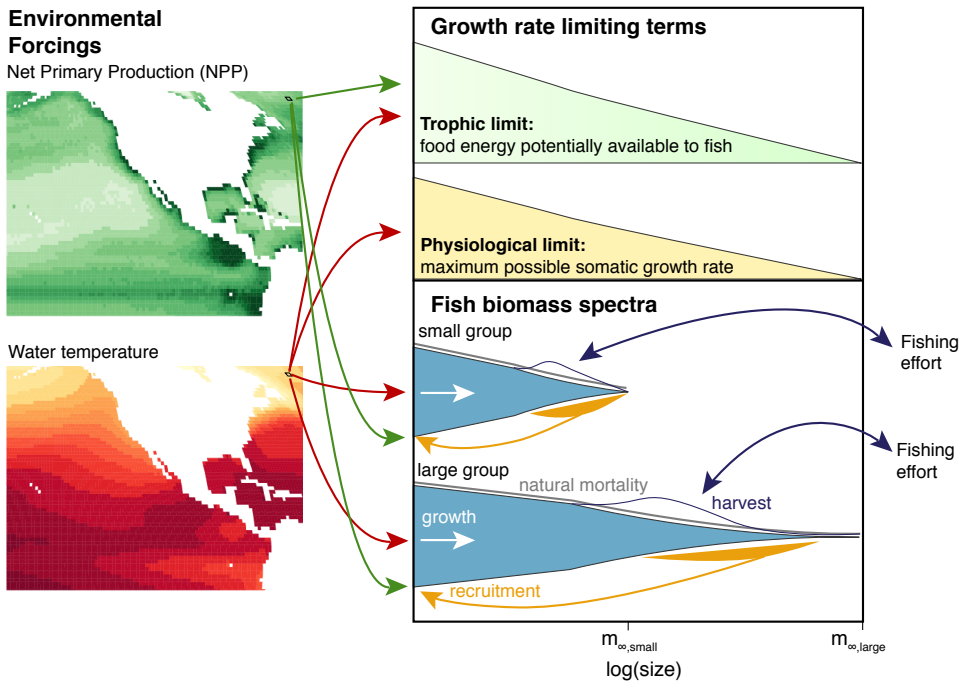

Figure 1: Schematic overview of the BOATS model. The red, green, and black arrows indicate dependencies of model components on external forcings (left panel). The top-right panel indicates the energetic limits of growth as a function of fish size, whereas the bottom-right panel illustrates the size spectra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

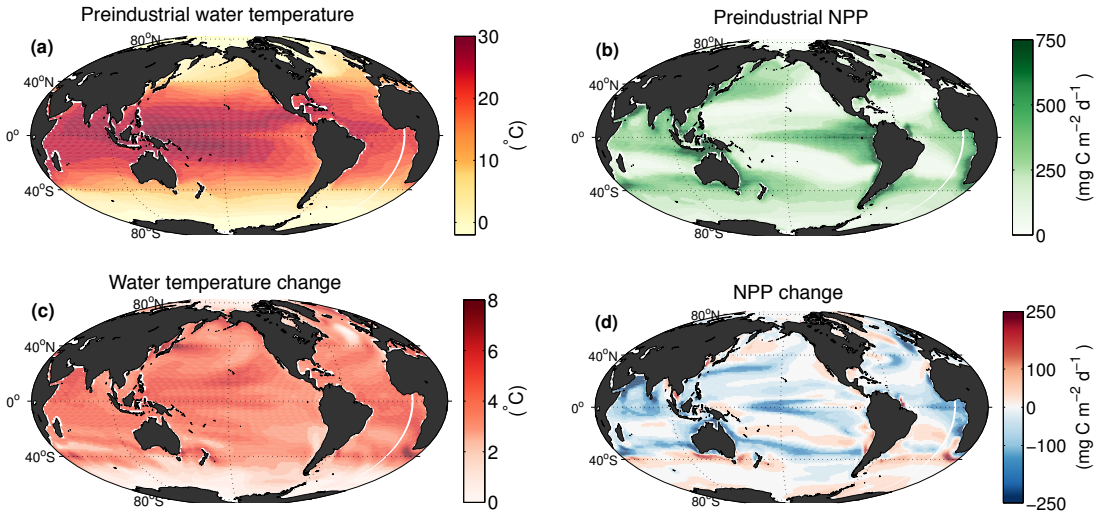

Figure 2: Preindustrial climate forcing variables and change in those variables due to climate change in the IPSL-CM5A-LR global climate model used to force BOATS. (a) Preindustrial water temperature. (b) Preindustrial net primary production (NPP). (c) Water temperature change. (d) Net primary production 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.

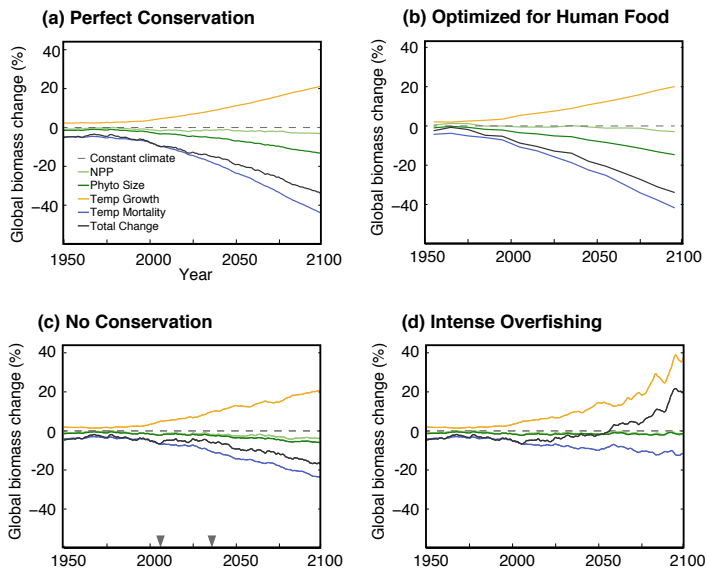

Figure 3: Globally-integrated fish biomass change, relative to the constant climate simulation. Each panel shows the six metabolic simulations (colour-coded), for one conservation scenario. Normalized quantities for each simulation are expressed in terms of the % change relative to the constant climate 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.

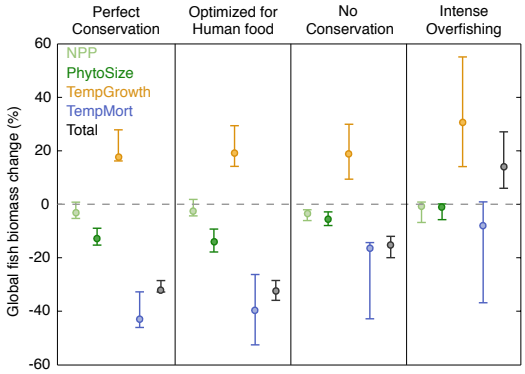

Figure 4: Globally-integrated fish biomass change relative to the constant climate scenario from 2081 to 2100. Circles represent the median over the 6 ensemble members, whereas the lower and upper bars represent the 5th and 95th percentiles over the 6 ensemble members, respectively.

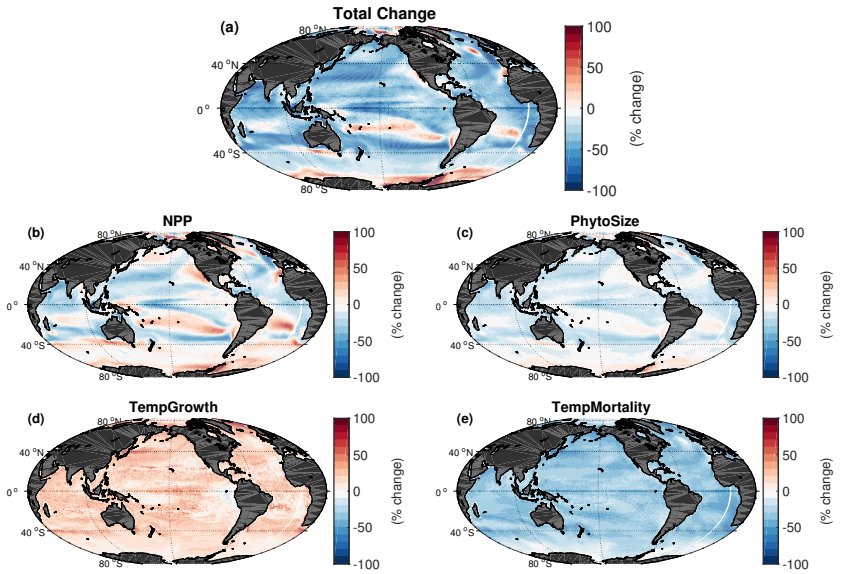

Figure 5: Maps of median normalized change in biomass due to the impacts of climate change on the metabolic model components for the Optimized for Human Food scenario over 2081-2100. (a) All combined effects (Total). (b) Growth rate dependence on net primary production (NPP). (c) Growth rate dependence 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.