Combining mesocosms with models to unravel the effects of global warming and ocean acidification on temperate marine ecosystems

Running title: Mesocosm data improves biodiversity forecasts

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Abstract

1. Ocean warming and species exploitation have already caused large-scale reorganization of biological communities across the world. Accurate projections of future biodiversity change require a comprehensive understanding of how entire communities respond to global change.
2. We combined a time-dynamic integrated food web modelling approach (Ecosim) with a community-level mesocosm experiment to determine the independent and combined effects of ocean warming and acidification, and fisheries exploitation, on a temperate coastal ecosystem. The mesocosm enabled important physiological and behavioural responses to climate stressors to be projected for trophic levels ranging from primary producers to top predators, including sharks.
3. We show that under current-day rates of exploitation, warming and ocean acidification will benefit most species in higher trophic levels (e.g. mammals, birds, demersal finfish) in their current climate ranges, with the exception of small pelagic fish, but these benefits will be reduced or lost when these physical stressors co-occur.
4. We show that increases in exploitation will, in most instances, suppress any positive effects of human-driven climate change, causing individual species biomass to decrease at high-trophic levels. Species diversity at the trailing edges of species distributions is likely to decline in the face of ocean warming, acidification and exploitation.
5. Synthesis and applications. We showcase how multi-level mesocosm food web experiments can be used to directly inform dynamic food web models, enabling the ecological processes that drive the responses of marine ecosystems to scenarios of global change to be captured in model projections and their individual and combined effects to be teased apart. Our approach for blending theoretical and empirical results

from mesocosm experiments with computational models will provide resource managers and conservation biologists with improved tools for forecasting biodiversity change and altered ecosystem processes due to climate change.

Keywords: biodiversity change, fisheries exploitation, food web models, climate change, multiple stressors, species interactions, trophic modelling

INTRODUCTION

Marine ecosystems and resources are facing significant challenges due to the cumulative effects of multiple global and local stressors, including overfishing, eutrophication, pollution, habitat destruction, climate change, and ocean acidification (Cheung, 2018; Halpern et al., 2015). Hence, significant effort is needed to generate reliable projections of future changes in marine food webs and fisheries productivity.

Past attempts to forecast climate-driven changes in populations of fisheries species have incorporated the direct impact of temperature on species physiology using deterministic food web models (Blanchard et al., 2012; Brown et al., 2010), end-to-end climate models (Olsen et al., 2018), and species distribution models (Cheung et al., 2011; Peterson et al., 2002). Most of these projections, however, are based on species thermal niches or ecological proxies that do not consider real time observations from the natural system or experimental settings. Thus, they ignore the potentially large role of indirect (e.g. shifting predator-prey relationships) and interactive drivers of change (e.g., with ocean acidification) on model outcomes. Although thermal niches play an important role in governing species distributions and their population sizes, the occurrence and abundance of species is also heavily regulated by life-history traits, metapopulation processes and biotic interactions (Fordham et al., 2013; Mellin et al., 2016). While modelling architectures have been developed to improve our understanding of how multiple drivers of global change (including warming, acidification and exploitation) interact and affect marine communities (Fulton and Gorton, 2014; Kaplan et al., 2010; Koenigstein et al., 2018), accounting for complex biotic responses to multiple stressors at the level of the food web has proved difficult.

The role of indirect effects of climate change (e.g. shifting predator-prey relationships) on marine communities has received less attention than direct effects, even though they are likely to strongly shape future marine communities (Lord et al., 2017; Nagelkerken et al., 2017). Empirical data that enables biotic interactions to be quantified under near-future climate change scenarios is urgently needed to better project and understand the role of direct and indirect drivers of climate change on biological systems. A promising avenue is to use large-scale mesocosm experiments to quantify the potential effect of global warming on the strength of biotic interactions, rates of species turnover and composition, along with many other key ecological processes that drive population- and community-level responses to climate change (Fordham, 2015; Nagelkerken et al., 2020). Although scale, closed boundaries, simplified ecological communities, and replication can impose challenges for researchers using mesocosm experiments, they have the potential to quantify community-to-ecosystem level responses to scenarios of global warming (Sagarin et al., 2016), particularly if climate change mesocosm experiments align with regional climate projections for their study system (Korell et al., 2020).

Dynamic food web simulation models have shown that scenarios of increased temperature or acidification, modelled in isolation, could positively or negatively affect future fisheries through increased primary productivity (Brown et al., 2010) or higher mortality of invertebrates (Griffith et al., 2011; Marshall et al., 2017), respectively. However, the cumulative effects of ocean warming and acidification on complex natural food webs remain largely unknown, despite both stressors being a consequence of human-induced greenhouse gas emissions, affecting marine systems in unison (Brierley and Kingsford, 2009).

We combined empirical data from mesocosm experiments with dynamic food web models to test whether: (1) the combination of ocean warming and acidification is likely to exert synergistic, additive or antagonistic effects on food web structure and function for a temperate coastal ecosystem, and (2) whether increased exploitation will amplify these projected responses to increased greenhouse gas emissions. We use the mesocosm experiments to integrate physiological and behavioral responses of organisms to different scenarios of warming and/or acidification into the food web model, based on observations at trophic levels ranging from primary producers to top predators (including sharks). We show that integrating mesocosm experiments with dynamic food web models can provide ecologically robust frameworks for exploring the consequences of climate change on the structure and function of future food webs and their production capacity.

MATERIALS AND METHODS

We integrated empirical data from two food-web-level mesocosm studies (and other sources) into an existing food web model for the Port Philip Bay (PPB) temperate coastal marine ecosystem (Victoria, Australia) (Koopman, 2005) using Ecopath (Christensen et al., 2008). We validated the food web model retrospectively, using hindcast validation and then simulated likely future community-level changes for the PPB ecosystem (Fig 1).

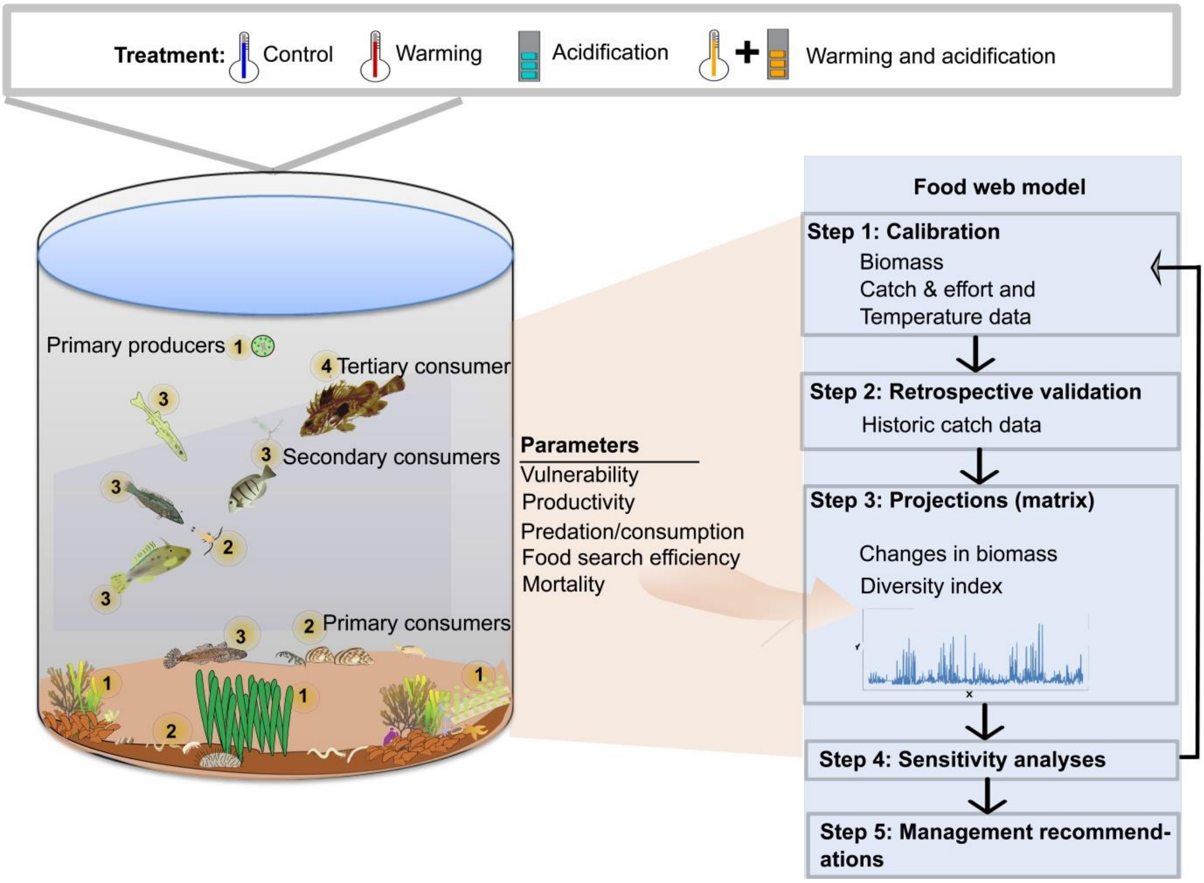

Figure 1: Conceptual representation of how different food web parameters from mesocosm experiments can be integrated with dynamic modelling approaches to project the state of future ecosystems. Several trophic level groups are illustrated e.g.: 1) primary producers: phytoplankton, macroalgae, seagrass, algal turf, microphytobenthos; 2) primary consumers: gastropods, shrimps, copepods, bivalves, polychaetes, sea urchins, sea stars, sponges, ascidians, tanaids; 3) secondary consumers: carnivorous (pelagic) fish, omnivorous fish, herbivorous fish, carnivorous (benthic) fish; 4) tertiary consumer: scorpionfish (behavioural experiment). Organism symbols were drawn by the authors or were courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

Food web model and scenarios

Ecopath is a mass-balance food-web modelling approach used to create a baseline snapshot of the ecosystem and quantify the flow of energy between food web functional groups (Christensen et al., 2008). The model requires four primary input variables: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), and diet composition. Experimental data from two large-scale mesocosms (Pistevos et al., 2015; Ullah et al., 2018), and field data published elsewhere, were used to calculate these input variables (see Supporting Information).

Differential equations were used to estimate biomass fluxes for each species and/or functional group within the food web using foraging arena theory (Ahrens et al., 2012). Vulnerability parameters were used to define predator consumption rates (Q_{ij}) (Equation 1) (see Supporting Information). For each predator-prey interaction, we calculated Q_{ij} at time t as,

$$Q_{ij}(t) = \frac{a_{ij} \times v_{ij} \times B_i(t) \times B_j\,(t) \times f(t)}{2 \times v_{ij} \times a_{ij} \times B_j(t)} \qquad \text{(Eq. 1)}$$

where a_{ij} is the effective search rate of predator j feeding on prey i, B_i is the biomass of the prey, B_j is the predator biomass, and v_{ij} is the vulnerability of prey i to predator j (Christensen et al., 2008). The forcing function $f\,(t)$ was used to account for external drivers changing through time affecting Q_{ij}.

Climate change was incorporated into model projections using forcing functions that temporally affect the consumption and production of functional groups (Ainsworth et al., 2011; Cornwall and Eddy, 2015) based on observations from the mesocosm experiments (see below). Specifically, we used the estimated effects of warming, acidification and their combination on prey vulnerability, search activity (higher trophic levels), mortality and productivity (primary producers) of trophic groups to alter modelled consumption (Q/B_i) and production (P/B_i) rate.

We developed four 85-year simulations (2015-2100): a no-climate-change scenario (baseline), ocean warming (T), ocean acidification (OA) and their combination (OAT). The climate change scenarios assumed a 2.8 °C increase in warming by 2100, representing a high representative concentration pathway scenario (RCP 8.5) for the Port Phillip Bay region (1.9

to 3.8 °C increase from a 20-year baseline focused on 1995 (Clarke et al., 2011)). We considered only RCP 8.5 because it was feasible to do the mesocosm experiment under only one RCP scenario. Uncertainty in parameter estimates for biomass (B), production (P/B) and consumption (Q/B) rates, and ecotrophic efficiency (EE) was simulated by varying these parameters randomly within bounds of ± 20% coefficient of variation.

The no-climate-change scenario (NC) assumes that model parameters do not change in the future, with model drivers, including fishing effort, set to the last year of the historical observation data (2015). For the three climate change scenarios (T, OA, and OAT), we incorporated direct and indirect climate-driven changes in species interactions and mortality of trophic functional groups in the food web. The effects of climate change were assessed by comparing biomasses and ecological indicators observed under the NC scenario with that of the climate change scenarios. Exploitation was initially held constant at 2015 levels for 21st Century climate change scenarios because fisheries management is generally done at decadal temporal resolutions, or finer (Fulton et al., 2018), meaning little is known about how exploitation rates are likely to change by the end of the century. However, we did run further scenarios to test the response of future food webs to increased exploitation. We did this by increasing exploitation by 1.5, 2 and 5-fold compared to present-day fishing pressure.

Mesocosm experiment

Empirical data from the mesocosm experiments were used to quantify the effects of climate change on food web structure and function, including trophic level biomass and diversity (Fig. 1; Supporting Information). Three response variables were derived and combined to estimate prey vulnerability to higher order trophic levels (trophic level ≥ 2) using behavioural experiments under the different mesocosm treatments (NC, T, OA, OAT). I) “prey attraction” was calculated as the percentage of time spent in the area close to a food cue relative to the time spent in the entire field of view (Goldenberg et al., 2018). II) ‘food search activity’ was given as the number of position changes in the area close to a food cue relative to the time spent in this area (Goldenberg et al., 2017). III) ‘boldness’ was measured as the percentage of time spent directly in front of a predator within the area close to a food cue relative to the time spent in the entire area close to the food cue. We averaged across the three response variables, weighting each variable equally, to obtain a composite vulnerability index of prey to its predator. For chondrichthyans, we calculated effective search activity as the total time taken by Port Jackson sharks (*Heterodontus portusjacksoni*) to successfully locate prey hidden in the sand using olfactory cues (see methods in (Pistevos et al., 2015) for details). Mortality as a direct function of biomass decline was quantified for functional groups not predated in the system. Primary productivity was measured from community metabolism as gross oxygen production (mg $O_2/m^3/min^1$) once per mesocosm at the end of the experiment. See Supporting Information for more details.

We calculated relative effect sizes for prey vulnerability, search activity, mortality and productivity by comparing the NC (control) scenarios with climate change treatments. These effect sizes were used to derive the model forcing functions for different climate change scenarios (OA, T, and OAT) (Table S1). The forcing function (input) and responses (biomass) were standardized to the base scenario by dividing the response value by the base values under a particular scenario. We used linear interpolation to construct a time series for all the forcing function parameters between 2015 and 2100. While it is common practice in climate change ecology to interpolate temporally between climate snapshots (Fordham et al., 2012), doing so can potentially mask important decadal variation (Fordham et al., 2018). We were limited to this approach because the mesocosm experiments were snapshots focussed on year 2100. The forcing functions were applied to appropriate functional groups in the model (Table

S1). We provide a more detailed explanation of the estimation of different forcing function parameters in the Supporting Information.

Analysis and model validation

We pooled food web functional groups into 10 community levels, including pelagic groups (mammals, birds, cephalopods, pelagic finfish), demersal groups (chondrichthians and demersal finfish) and their prey (benthic crustaceans, invertebrates, small pelagic crustaceans, primary producers) (Table S2). We calculated effect sizes for changes in biomass under different model scenarios using Hedges' *g* (Lakens, 2013). We calculated and compared key biodiversity indicators under different model scenarios, including the Shannon index (Shannon and Weaver, 1963) and Kempton's Q index (Ainsworth and Pitcher, 2006). The Shannon diversity index captures changes in evenness, whereas the Kempton's Q index captures changes in both evenness and richness at the level of functional groups (see Supporting Information for details).

We did an ecosystem model skill assessment (Olsen et al., 2016) and a global sensitivity analysis (Fordham et al., 2016) to determine the influence of input parameters on model results (see Supporting Information). To assess ecosystem model skill for our PBB model — and verify that parameters from our mesocosm were transferrable to the PPB coastal marine system — we validated hindcast simulations using independent catch-data (Table S3). Historical abundances (1993 and 2011) were simulated using the full-PBB model and sub-models with only functional groups in the mesocosm experiment. We assessed model-skill using a wide range of metrics (Olsen et al., 2016; Stow et al., 2009): root mean squared error (RMSE), average error (AE), average absolute error (AAE), modelling efficiency (MEF), and Pearson (*P*) and Spearman (*S*) correlation.

We determined the sensitivity of Ecopath input parameters — biomass (B), production (P/B) and consumption (Q/B) rates, and ecotrophic efficiency (EE) — on estimates of change in biomass under a scenario of projected ocean warming and acidification (OAT) and a scenario that included a moderate level of exploitation as well as OAT. To do this we used the built-in Monte Carlo routine within Ecosim module, which allows model input parameters to be varied (Coll and Steenbeek, 2017; Heymans et al., 2016). Specifically, we ran 100 Monte Carlo simulations with B, P/B and Q/B and EE varying randomly within bounds of ± 20% coefficient of variation. Initial and projected future biomass for 3 community groups (cephalopods, pelagic finfish and invertebrates) were recorded for the year 2100. We used generalized linear models (GLM) to explore the relative importance of different model input parameters on projected changes in future biomass (Fordham et al., 2016). We did this by calculating standardized regression coefficients (SRC) along with the coefficients and their confidence intervals. Furthermore, we assessed the quality of input data for the PPB model using food web diagnostics (Link, 2010) and explored the effects of parameter uncertainty on model outputs using sensitivity analysis. See Supplementary Information for more details.

RESULTS

Biomass changes under future climate change

Model simulations show that the total biomass of most higher-trophic-order community groups (mammals, cephalopods, chondrichthians, and demersal finfish) is likely to benefit from ocean warming (T) or acidification (OA), when modelled separately (Fig. 2, Fig S1). However, the combination of the two stressors has an antagonistic effect on biomass increase. At the level of individual species or functional group the positive effects on biomass are more disparate (Figs. S2, S3).

Our models project an average increase in marine mammal biomass of 85% by the end of the 21st Century under the combined effect of acidification and warming (OAT) compared to no-climate-change and current levels of fish exploitation (‘no change’ scenario) (Fig. 2A). Modelling acidification (OA) and warming (T) separately resulted in even higher average increases in marine mammal biomass: 254% and 213%, respectively. Cephalopod biomass is projected to increase by 144% under OAT, while warming and acidification in isolation likely boost biomass by 237% and 205%, respectively. Although chondrichthyans showed the largest increase in their biomass under warming, this increase in biomass was affected by parameter uncertainty. Demersal finfish and seabirds are projected to increase their biomass the most in response to OA (252% and 165%, respectively), with a smaller increase under T. Pelagic finfish showed a negative response to warming, irrespective of acidification, with small pelagics (mostly planktivores) showing severe depletions (>70%) under both under T and OAT (Fig. S2).

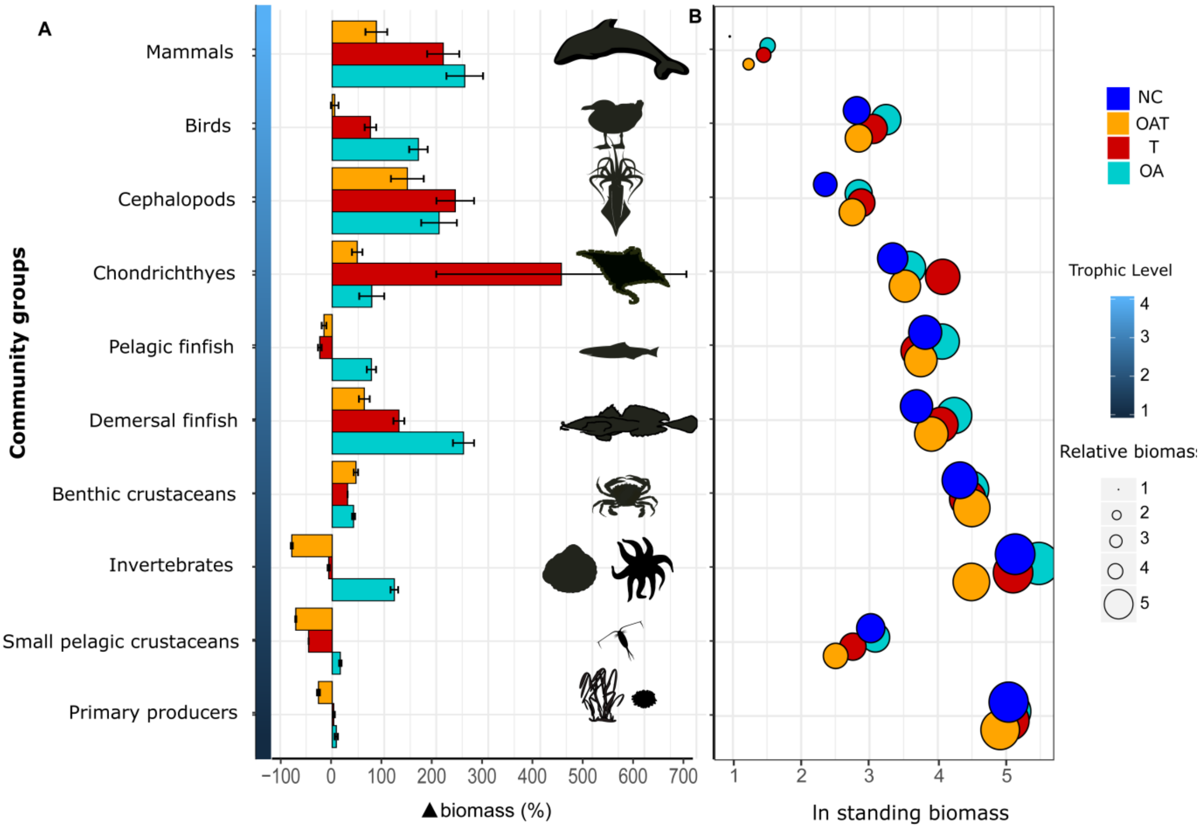

FIGURE 2:: A) Mean (± 95% confidence interval) relative change in biomass (Δ %) in year 2100 for different food web community groups under three climate change scenarios relative to a no-climate-change (NC) scenario. OA = ocean acidification, T = ocean warming, and OAT = combined ocean acidification and warming. Functional groups of food web models are aggregated to community groups (CGs) for better representation and clarity. The order of CGs is based on the mean trophic level (shown in blue). B) The future standing biomass (kg/km^2; ln- transformed) estimates for each CG. The bubble size is proportional to its biomass. Exploitation rates for all scenarios are modelled at present-day rates.

Conversely, ocean warming – either alone or in combination with ocean acidification – is projected to exert a negative effect on lower trophic-level faunal groups, with the exception of benthic crustaceans (Fig. 2A). Invertebrates (predominantly molluscs and invertebrates that do not possess a chitinous exoskeleton; Table S5), and small pelagic crustaceans (zooplankton) are projected to experience biomass declines of 7-78% and 45-70%, respectively, under T or OAT (Fig. 2).

The standing biomass of primary producers increased under OA and T, but decreased by ~ 26% under OAT (Fig. 1A), largely driven by a reduction of phytoplankton, micro-phytobenthos and macro-algal biomass (Fig. S3). Turf algae, in contrast, experienced a large increase in biomass (Fig. S3).

The combined effect of warming, acidification and exploitation

In the absence of ocean warming and acidification, exploitation reduced (by 1-32%) projected biomass in the year 2100 for most higher-order community groups under a 1.5- to 2-fold increase in exploitation rate (Fig. 3). Further increases in exploitation (up to 5-fold) exacerbated this declining trend (by 41-66%) for mammals, birds (due to reduced prey) and chondrichthians. Negative effects of up to a 2-fold increase in exploitation were suppressed at higher trophic levels (except for pelagic finfish) under modelled climate change (OA, T and OAT), due to greater top-down control of consumers on prey resources (Fig. 2). However, a 5-fold increase in exploitation caused the biomass of mammals and birds to collapse under warming scenarios, causing some functional groups for example cephalopods to increase in biomass (T: 178%; OAT: 144%) (Fig. S4). Whilst both T and OA scenarios positively affected higher trophic levels in the face of medium-to-high increases in exploitation, their largely negative effects on lower trophic levels (primary producers, small pelagic crustaceans and invertebrates) were not decreased by increased exploitation (Fig. 3; Fig. S5).

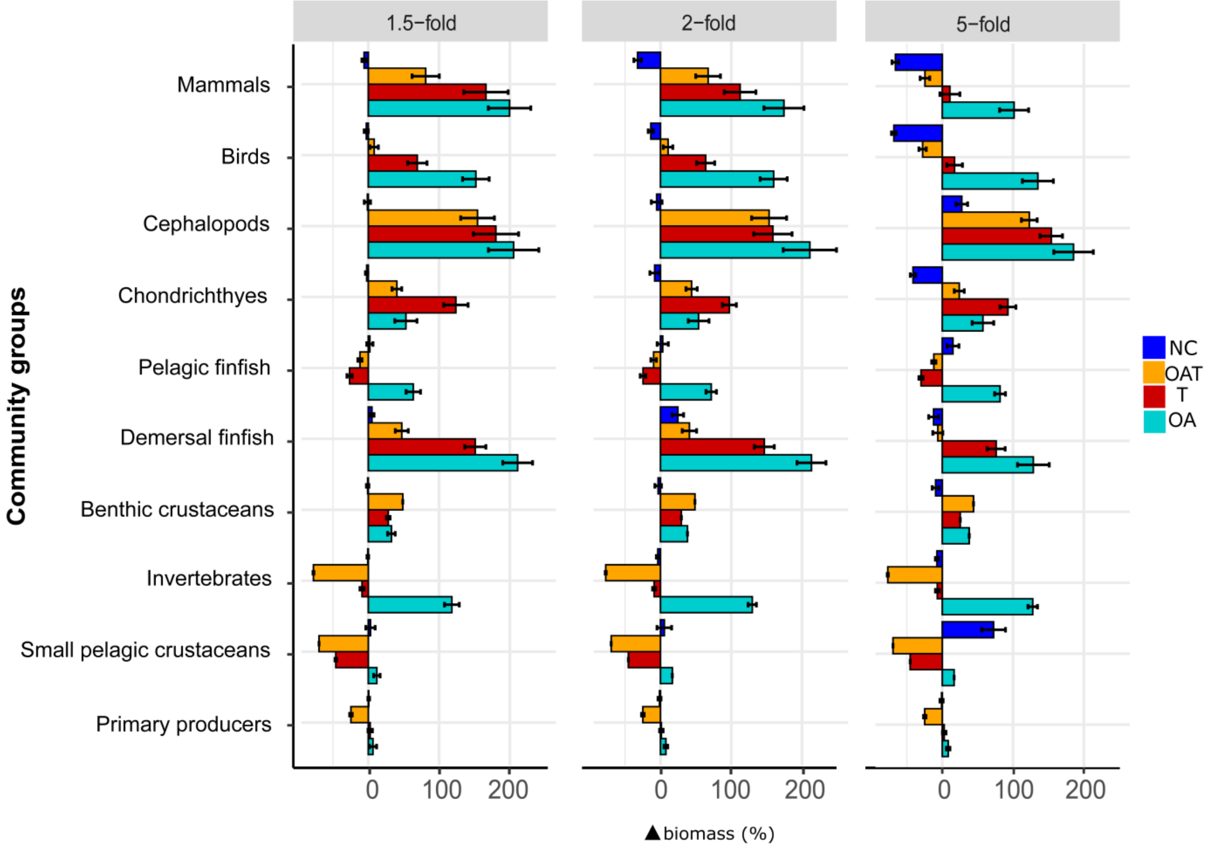

FIGURE 3: Mean (± 95% confidence interval) relative change in biomass (Δ %) in year 2100 compared to no change in climate and fishing from present-day levels (NC). OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. Functional groups are aggregated to community groups (CGs) for better representation and clarity. Number of 'folds' equals the magnitude of increase in fishing pressure starting in 2015.

Under the NC scenario, the Shannon diversity index remained relatively stable in the future under 1.5- and 2- fold increases in exploitation, whilst it decreased by ~ 4% under a 5-fold increase in exploitation (Fig. 4A). In contrast, the Shannon diversity index declined under all global change scenarios with the largest declines projected for OAT, under a 5-fold increase in exploitation (Fig. 4A). The Kempton Q metric for higher trophic levels showed a stronger decline (after year 2070) under OAT compared to the other climate change scenarios (Fig. 4B). A 5-fold increase in exploitation resulted in a steep and immediate decline in the Kempton Q index regardless of the climate change scenario.

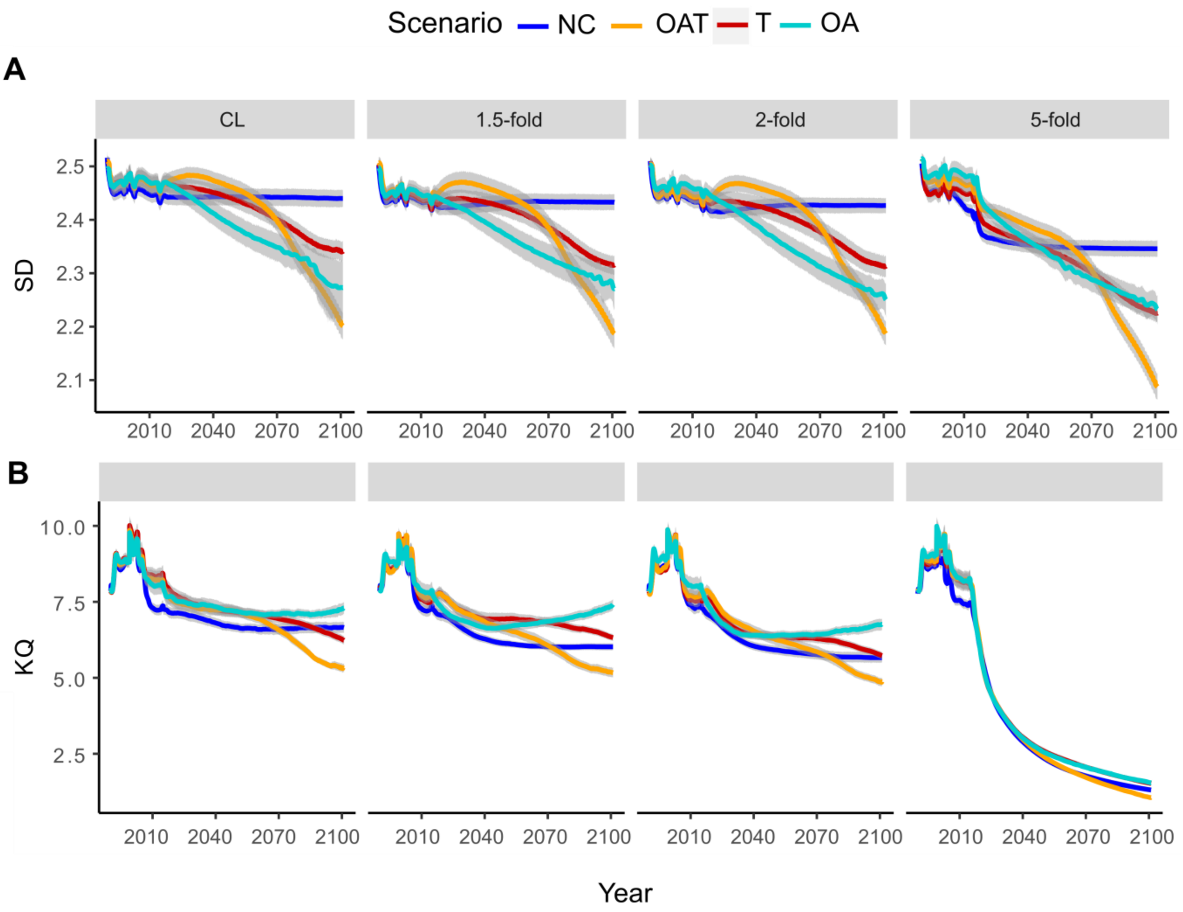

FIGURE 4: Ecological indicators of change in community composition, showing A) Shannon diversity index and B) Kempton Q index. The grey shadows represent the 95% percentile and 5% percentile. NC = no change in climate from present-day levels, OA = ocean acidification,

T = ocean warming, and OAT = combined ocean acidification and warming. CL= current level of fishing effort. Number of ‘folds’ equals the magnitude of increase in fishing pressure starting in 2015.

Model validation and sensitivity

Hindcasts of biomass from models parameterized using mesocosm data were correlated with empirical field data for carnivorous fish and omnivorous fish (correlation coefficient [r] = 0.54-0.82). The food web model skill assessment showed that models parametrized with mesocosm data are generally as skillful at projecting changes in biomass as models parameterized with field data (Fig. 5). Model projections for carnivorous and omnivorous fish biomass were relatively synchronous with independent biomass (survey) data, regardless of whether the models were parameterized using empirical data from the field ($r = 0.73$, RMSE ≤ 0.0001; $r = 0.82$, RMSE = 0.007, respectively) or mesocosm ($r = 0.69$, RMSE ≤ 0.0001; $r = 0.82$, RMSE = 0.007, respectively) data. Models parameterized with either field or mesocosm data did worse at projecting observed temporal variability in biomass for Port Jackson shark ($r = 0.12$, RSME = 0.011, $r = 0.29$, RSME = 0.011, respectively). Estimates of modelling efficiency (MEF) suggest that models for omnivorous fish and carnivorous fish do better than random (MEF > 0). This was not the case for Port Jackson sharks (Fig. S6). Importantly, bias (average error) in model projections remained low for all functional groups for models calibrated with field (carnivorous fish: + 0.24 g; omnivorous fish: - 0.02 g; Port Jackson shark: -0.12 g) or mesocosm data (carnivorous fish: + 0.18 g; omnivorous fish: -0.03 g; Port Jackson shark: -0.09 g).

The global sensitivity analysis (Table S6) showed that estimates of change in biomass (years 2015 to 2100) under an OAT scenario for pelagic finfish and invertebrates are most sensitive to changes in the Ecopath input parameter B followed by PB. For cephalopods, estimates of change in biomass were most sensitive to changes in QB, followed by PB. The most important parameter for each community remained the same regardless of whether exploitation was modelled or not.

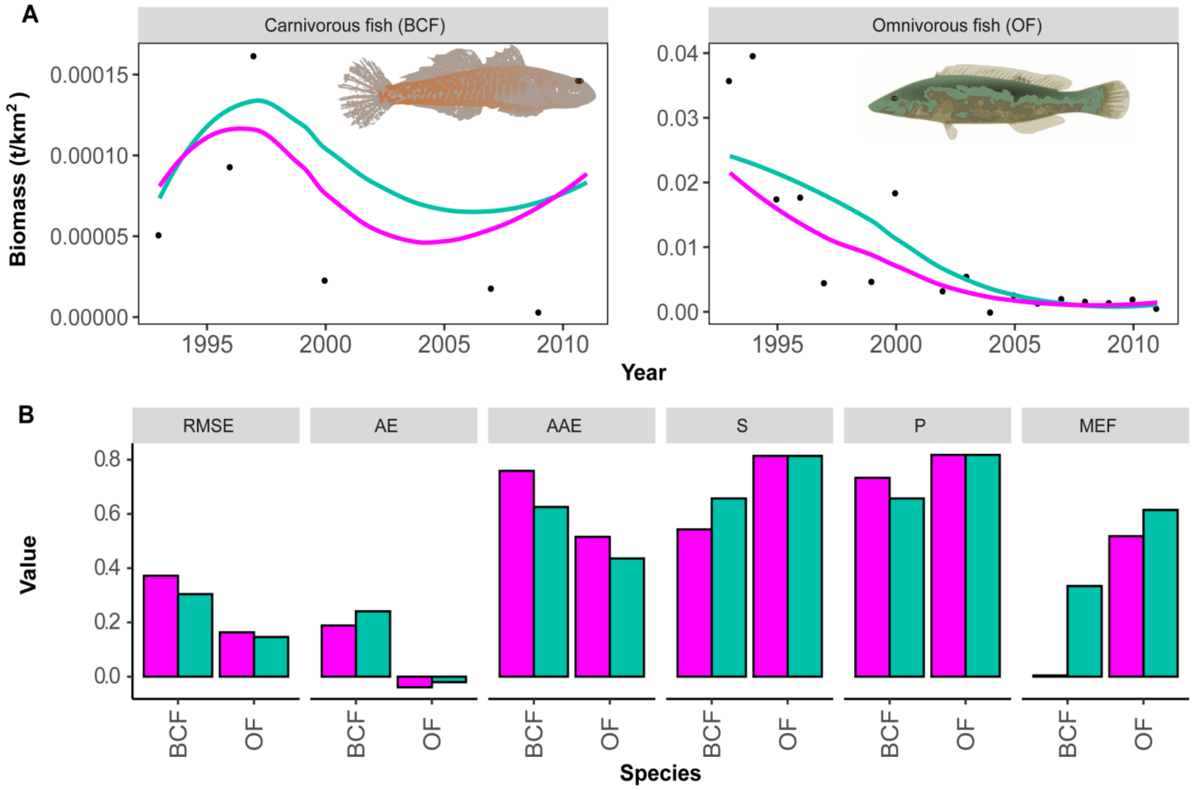

FIGURE 5: A) Mesocosm transferability. Comparison of the Port Phillip Bay (PPB) model built with the field (pink) and experimental data from the mesocosms (green) to standing catch biomass (tonnes per km^2; solid black dots) for two major functional groups between years 1993 and 2011. BCF = benthic carnivorous fish and OF = omnivorous fish.
B) Ecosystem model skill assessment for models built using empirical field (pink) and experimental mesocosm data (green) for Port Phillip Bay (between 1993 and 2011): root mean squared error (RMSE), average error (AE), average absolute error (AAE), Spearman rank (S) and Pearson (P) correlation, and modelling efficiency (MEF) for 2 species. Y-axis limited to show values between -0.05 and 1.00.

DISCUSSION

By integrating empirical data on species physiological and behavioural performance from two large-scale mesocosm experiments into dynamic food web models, accounting for historical exploitation rates, we show that climate change is likely to benefit the biomass of animals at higher trophic levels in some temperate marine ecosystems, albeit at a potential cost to biodiversity. Increased biomass under warming results from strengthened top-down control of consumers that occupy higher trophic levels, supported by a positive biomass response of some of their prey groups. Accordingly, the structure of future temperate marine food webs appears to be shaped by altered predator-prey dynamics, resulting from a reshuffling of predatory and prey species abundances in response to warming, and not a continuous fuelling of the food web from the bottom up as would be the case if ocean acidification was the dominant climate stressor (Nagelkerken et al., 2020; Sswat et al., 2018).

Organisms at higher trophic levels are likely to increase their top-down control on their prey, and therefore increase in biomass, in response to temperature-driven enhancements in their metabolic rates (Brown et al., 2010). Although an increase in top-down control by consumers has been previously suggested as a response to ocean warming for simplified (three-trophic- level) food webs (Goldenberg et al., 2017; Marino et al., 2018), a robust understanding of how higher-order consumers or apex predators will respond to global warming, and the subsequent effects for lower-order trophic levels, has until now been lacking. We show that under future scenarios of warming, the biomass of all higher-order consumers and apex predators (mammals, birds, cephalopods, chondrichthians, and demersal finfish) is likely to increase compared to a no-warming scenario due to amplified rates of prey consumption (pelagic finfish, invertebrates and small pelagic crustaceans), driven, in part, by increases in biomass of benthic crustaceans (major prey group in the system). Our new results, for a temperate marine ecosystem, suggest that the benefit of warming for higher trophic levels is likely to be universal, with associated negative effects for their prey at lower trophic levels.

Acidification alone is not expected to enhance top-down control by consumers because elevated CO_2 tends not to positively affect the metabolism of consumers (Carter et al., 2013; Kroeker et al., 2013). Recent food web studies showed that enhanced primary production can enlarge available prey resources, which can boost the growth of consumers under acidification (Nagelkerken et al., 2017; Sswat et al., 2018). This was true for all higher-order predators in our study, although for chondrichthians the biomass increase was weak. Elevated CO_2 is known to affect the foraging behaviour (e.g. reduced prey search efficiency and impaired odour tracking) of chondrichthians which might explain the reduced increase in biomass for this group (Pistevos et al., 2015). Because of their different physiology, highly active predators such as marine mammals, birds, and non-bony animals such as cephalopods tend to be more tolerant to increasingly acidic environmental conditions (Melzner et al., 2009). They benefit from amplified acidification only if increased resource availability at the bottom of the food web is transferred up the food web.

Although warming and acidification in isolation showed striking positive effects on the biomass of predators, their combined effect was antagonistic for many of the top consumers in the food web and caused a decline in the biomass of many lower-order consumers. Previous studies have shown that warming and acidification can antagonistically affect the growth of carnivores such as sharks by affecting prey search time (Pistevos et al., 2015), and of herbivores by increasing the degree of unpalatable or poor-quality food (Poore et al., 2013). Two of the major prey groups in our model (small pelagic crustaceans and invertebrates) experienced collapses in their biomass under the combined effect of warming and acidification, reducing the availability of resources for higher level consumers, resulting in reduced rates of change in consumer biomass under this scenario.

In contrast to other invertebrates, benthic crustaceans sustained a biomass increase under all modelled climate scenarios, enabling an increase in the biomass of their consumers (e.g. demersal finish, and consecutively some higher-order predators). Benthic crustaceans (e.g. lobsters, crabs, and shrimp) are generally considered to have a higher tolerance to acidification than other invertebrates (Kroeker et al., 2013) and show, in some cases, positive responses to warming (Faulkner et al., 2014). These observations could explain their successful propagation under scenarios of global warming.

Exploitation is a local stressor that negatively affected the biomass of all higher order community groups, except pelagic finfish. However, warming and acidification negated these negative effects, boosting the biomass of top predators at exploitation intensities equal to or smaller than a two-fold increase. Global-scale models, with static fishing rates, suggest that some commercial fisheries (ranging from crustaceans, small and large fish, to sharks) in high-latitude regions could experience an increase in future catches, owing to temperature-driven shifts in species distributional ranges (Cheung et al., 2010). However, we here limited our findings to changes in food webs based on current species distributions (i.e. at their climate trailing edges). Dynamic food web approaches also project a productivity increase in pelagic fisheries in response to forecast warming of oceans (Blanchard et al., 2012), and increased yields of commercially valuable fish stocks by 2050 under future warming (Merino et al., 2012). While the latter studies modelled food web responses, they used a simplified approach, with phytoplankton productivity as the only primary source of energy input, exploited species as the primary elements of the food web, and ocean warming as a single stressor. Here, using a more inclusive dynamic food web modelling approach, we show that opportunistic and less-targeted groups such as cephalopods are likely to flourish in their biomass at higher fisheries exploitation (≥ two-fold) rates due to a decrease in the biomass of major commercial species such as demersal finfish irrespective of climate change. Overall, we show that the greatest effects on future marine food webs are likely to arise at the top of the food web when overexploitation coincides with the combined effect of warming and acidification.

Ocean warming and acidification have a much greater negative effect on functional diversity in food webs than overexploitation. Future ocean warming and acidification can significantly reduce diversity (i.e., Shannon diversity) within temperate coastal food webs even under present-day exploitation levels, owing to declines in the biomass of primary producers (i.e. non-weedy species such as macrophytes and certain species of phytoplankton), small pelagic crustaceans, invertebrates, and pelagic fish species. Moreover, it can cause a reduction in evenness (Kempton Q index) for higher-order groups in the food web. These changes in diversity and evenness are likely to enable ecological opportunistic species to flourish (Woodruff, 2001), such as high-order cephalopods and lower-order “weedy” turf algae, leading to further simplification of community structure (Nagelkerken and Connell, 2015). Together, global warming and fishing will likely shift the distribution of biomass within the community and reduced diversity of future food webs.

By combining empirical data on species response to climate change from large mesocosms with historical population data (from scientific surveys and fisheries landings) in a dynamic food web model, we moved from experimental ecology to making projections and management recommendations aimed at safeguarding marine biodiversity under climate change. Blending mesocosm experiments with “real world” ecological models has been questioned on the grounds that they are unlikely to attain realistic projections (Carpenter, 1996). By independently validating our model projections against historical population data (trawl surveys), we not only show that our dynamic food web model does a fair to good job at reconstructing observed historical trends in biomass (particularly for selected functional groups), but that models based on mesocosm experiments provide a relatively close representation of ‘real world’ food webs. Therefore, mesocosms with realistic multifactorial experiments that capture food web complexity can indeed be used with confidence to parameterize ecosystem models and help to bridge the gap between simplified experimental conditions and the real world.

Our modelling approach, like other modelling techniques, has its own caveats. El Niño–Southern Oscillation (ENSO) is known to influence Australia’s marine ecosystem through its year-to-year dynamics in climate variability (Lough and Hobday, 2011). These fine temporal scale climate dynamics could not be captured in the mesocosm experiment and therefore the food web model. This could, potentially, affect our modelled trajectories of biomass and community composition. To calculate the vulnerability of fish to their consumers, all fish species were considered into two major categories, namely carnivores and omnivores (feeding guilds). The somewhat poor fit of modelled projections to observed data for Port Jackson shark is likely to reflect an over-simplification of food web structure for the validation exercise (see Supplementary Information). Likewise, important and unaccounted uncertainties in the validation data (i.e., detection probability) could partly explain the difference between predicted and observed patterns of temporal variability in biomass (Guillera-Arroita, 2017). Despite these limitations, our study included the best available historical data and the most robust estimates of physiology and behaviour responses to global warming for a 4-trophic level temperate food web system.

CONCLUSIONS

Here we used a novel approach to simulate the effects of global warming, ocean acidification, and fishing on the biomass and diversity of species in a temperate coastal ecosystem, using experimental data on the effects of ocean warming and ocean acidification on species interactions and physiology, and historical fisheries (survey and catch) data. By simulating the potential magnitude and direction of biomass changes for different functional groups, we show that the structure and function of future temperate marine food webs under ocean warming is likely to be altered by predator-prey dynamics at the top of the food web rather than changes from the bottom up. Consumers at higher trophic levels are likely to benefit from ocean warming and acidification, but these benefits will be reduced or lost when these stressors co-occur. More generally, we show that mesocosm experiments can be integrated with food web models to better manage marine biodiversity in response to 21st century climate change.

DECLARATION OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

HU, IN and DF conceived the research; HU and SG collected the data; HU developed the methods; HU analysed the data; HU, IN and DF wrote the manuscript; All authors contributed to revisions and approved the final submission.

DATA AVAILABILITY STATEMENT

Data will be available via the Dryad Digital Repository upon the acceptance of the article.

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Appendix A. Supporting Information

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