

## ARTICLE

# Combining mesocosms with models reveals effects of global warming and ocean acidification on a temperate marine ecosystem

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## Funding information

Australian Research Council,

Grant/Award Number: FT120100183

**Handling Editor:** Éva E. Plagányi

## Abstract

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. We combined a time-dynamic integrated food web modeling approach (Ecosim) with previous data from community-level mesocosm experiments to determine the independent and combined effects of ocean warming, ocean acidification and fisheries exploitation on a well-managed temperate coastal ecosystem. The mesocosm parameters enabled important physiological and behavioral responses to climate stressors to be projected for trophic levels ranging from primary producers to top predators, including sharks. Through model simulations, we show that under sustainable rates of fisheries exploitation, near-future warming or ocean acidification in isolation could benefit species biomass at higher trophic levels (e.g., mammals, birds, and demersal finfish) in their current climate ranges, with the exception of small pelagic fishes. However, under warming and acidification combined, biomass increases at higher trophic levels will be lower or absent, while in the longer term reduced productivity of prey species is unlikely to support the increased biomass at the top of the food web. We also show that increases in exploitation will suppress any positive effects of human-driven climate change, causing individual species biomass to decrease at higher trophic levels. Nevertheless, total future potential biomass of some fisheries species in temperate areas might remain high, particularly under acidification, because unharvested opportunistic species will likely benefit from decreased competition and show an increase in biomass. Ecological indicators of species composition such as the Shannon diversity index decline under all climate change scenarios, suggesting a trade-off between biomass gain and functional diversity. By coupling parameters from multilevel mesocosm food web experiments with dynamic food web models, we were

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able to simulate the generative mechanisms that drive complex responses of temperate marine ecosystems to global change. This approach, which blends theory with experimental data, provides new prospects for forecasting climate-driven biodiversity change and its effects on ecosystem processes.

#### KEYWORDS

biodiversity change, climate change, fisheries exploitation, food web models, multiple stressors, species interactions, trophic modeling

## 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 (OA) (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.

Most 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 biogeochemical models (Olsen et al., 2018), and species distribution models (Cheung et al., 2011; Peterson et al., 2002). Most of these projections, however, are predominantly based on species thermal niches or ecological proxies that lack consideration of real-time observations from natural systems 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 OA) on model outcomes. Aside from thermal niches, the occurrence and abundance of species are also heavily regulated by biotic interactions (Fordham et al., 2013; Mellin et al., 2016). While modeling 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 & Gorton, 2014; Kaplan et al., 2010; Koenigstein et al., 2018), accounting for complex biotic responses to multiple stressors in food webs 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 enable 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).

Previous dynamic food web simulation models have shown that scenarios of increased temperature or acidification, modeled in isolation, could either 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 & Kingsford, 2009). Furthermore, food chain length may alter community responses to global change in aquatic systems, although this has hardly been studied, especially at higher trophic levels (Alsterberg et al., 2013; Hansson et al., 2013). Species that occupy the fourth trophic level of food chains, such as birds, mammals, or large sharks, are therefore of particular interest. Using an experimental mesocosm food web, Nagelkerken et al. (2020) predicted that climate change would eventually result in bottom-heavy food webs that will also experience collapse at the higher trophic levels. A combination of climate change impacts and overfishing may further exacerbate the decline of ocean health and societal benefits (Sumaila & Tai, 2020).

We combined empirical data from mesocosm experiments with dynamic food web models to test whether (1) the combination of ocean warming and acidification

was likely to exert synergistic, additive, or antagonistic effects on food web structure and function in a temperate coastal ecosystem and (2) whether increased exploitation would amplify these projected responses to increased greenhouse gas emissions. We used data from some of our previous mesocosm experiments to integrate physiological and behavioral responses of a wide range 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). Model results suggested that integrating mesocosm experiments with dynamic food web models could 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 into an existing food web model for the Port Phillip Bay (PPB) temperate coastal marine ecosystem (Victoria, Australia) (Koopman, 2005) using Ecopath with Ecosim (EwE) (Christensen et al., 2008). Additionally, we made substantial updates and changes to the existing model by incorporating several additional functional groups with higher taxonomic resolution, including multistanza groups. EwE applications that account for uncertainty and are based on good data points can improve fisheries management advice (Plaganyi & Butterworth, 2004). PPB is regarded as a sustainably managed ecosystem in terms of its fisheries exploitation (Flood et al., 2014). We calibrated the PPB food web model with fish biomass, fisheries catches and effort, and seawater temperature data (years 1990–2015) and carried out a retrospective test to assess the quality of the model transferability (mesocosms to open water food web model) and then simulated likely future community-level changes for the PPB ecosystem (Figure 1). The entire methodological approach can be explained in two steps. First, in Step A, we presented the mesocosm study and how we estimated the parameters from the experiments to use in the model. Then, in Step B, we provided the details of how we used these estimated parameters into the food web model.

### Mesocosm experiments

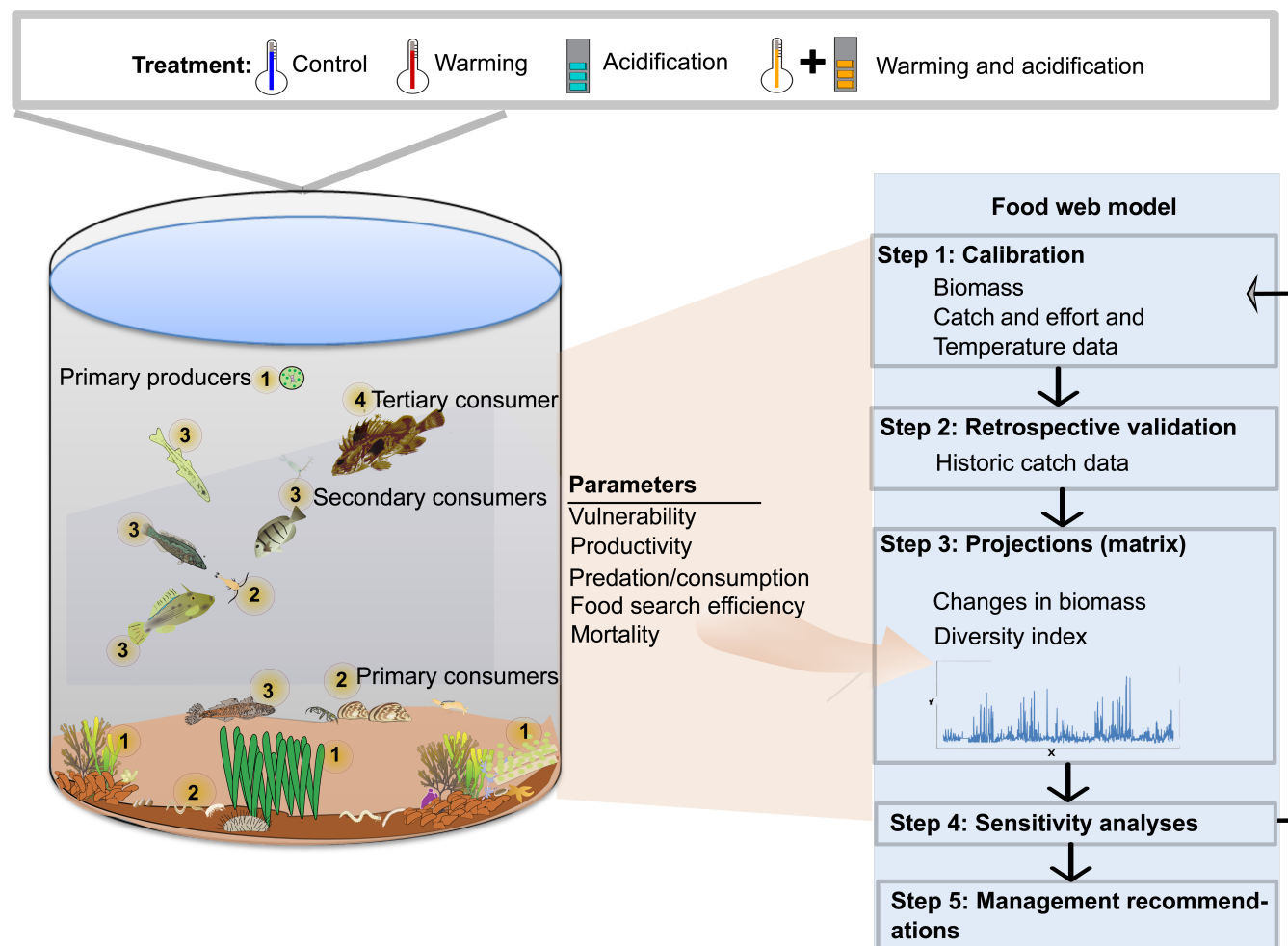
#### Experimental design and seawater manipulation

We used two of our own, previously published, species-rich multilevel mesocosm food web experiments that

included live habitats and natural abiotic variability (Appendix S1: Figure S1) to explore future changes in marine food webs (mesocosm designs provided in: Pistevo et al., 2015; Ullah et al., 2018). Due to the intricacies of the food webs, housing chondrichthyans and fish together for climate change response experiments was impractical. Specifically, measuring the prey consumption capacity of chondrichthyans in a single experiment is challenging, considering their size, habitat, and feeding patterns. While we combined data from two distinct experiments, we ensured consistency in both mesocosm studies by maintaining a uniform design with elevated CO<sub>2</sub> and temperature, with three replicate mesocosms per treatment combination: both mesocosm systems (1) assumed and simulated an increase in future temperature of approximately +2.8 °C (exposed to the climate treatments for ≥4 months), (2) were multitrophic from primary producers (e.g., algae) through primary consumers (e.g., amphipods) to predators (e.g., either sharks or carnivorous fishes), (3) included a total habitat volume of ~1800 L, (4) were supplied by a flow-through of seawater from the same source ensuring comparable nutrient levels, and (5) replicated a similar ecosystem using the same source of water. The similarity between the two mesocosm systems is critical as geographical variation and experimental contexts can alter the effect of climate change on consumer–resource interactions and lead to additional sources of variability (Marino et al., 2018).

Model parameters for various functional groups, with the exception of chondrichthyans, were derived from the mesocosm study conducted by Ullah et al. (2018). Consequently, we provide a summarized version of the experimental design and seawater manipulation below.

To simulate shallow temperate coastal ecosystems typical of PPB, 12 circular mesocosms, each containing 1800 L water, were set up in a temperature-controlled room and ran for 4.5 months. We collected habitats and organisms from a depth of 1–5 m within 60 km of the mesocosm facility. In each mesocosm, three primary local habitats were replicated (two patches of each habitat per mesocosm): rocky reef, seagrass, and open sand. Rocky reefs comprised natural rocks collected in situ, with attached macrophytes dominated by fucoid algae and benthic invertebrates. We created artificial seagrass habitats with green polypropylene ribbons attached with epiphytes resembling the habitat of abundant local *Posidonia* seagrass species. Mimicking natural seagrass using green polypropylene ribbons is a common practice in experimental studies (Bostrom & Mattila, 1999; Freestone et al., 2020) because it is exceedingly challenging to maintain seagrasses in long-term mesocosm experiments. To replicate natural seagrass communities that



**FIGURE 1** Conceptual representation of how different food web parameters from mesocosm experiments can be integrated with dynamic modeling approaches to project the state of future ecosystems. Several trophic-level groups are illustrated, for example, (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, carnivorous (benthic) fish; (4) tertiary consumer: scorpionfish (behavioral experiment). Organism symbols were drawn by the authors or were courtesy (free to use) of the Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)), and partly redrawn by the first author.

harbor existing epiphytic communities, we placed all the artificial seagrass habitats in situ for 2 weeks to allow for epiphytic colonization before planting them into fine silica sand. The artificial seagrasses mimicked *Posidonia* spp., which are the most dominant seagrass in South Australian Gulfs. There was open sand habitat in the area between and around these patches. Additionally, 0.025 m<sup>3</sup> of natural sediment collected between patches of live seagrass was added to the open sand and sand within seagrass patches in the mesocosm. Fish and invertebrates were introduced into all mesocosms and distributed evenly.

A continuous flow-through system was used to supply each mesocosm with 2300 L day<sup>-1</sup> of unfiltered seawater that contained nutrients and planktonic propagules. By

using a diffuser, we created a light circular current in the mesocosms to simulate tidal water movement in alternating directions every 6 h. Each mesocosm was equipped with a lamp whose spectrum was close to sunlight (72.83 ± 24.78 μmoles/m<sup>2</sup>/s photon flux) and represents a local water depth of 6 m. The control temperature in our mesocosm experiment corresponded to 21°C, the local average summer temperature. A header tank preconditioned to elevated pCO<sub>2</sub> levels was used for each mesocosm to achieve the target OA (control system ACQ110 Aquatronica, Italy). Submersible titanium heaters were used inside 60-L bins to supply water for future warming treatments. We monitored temperature and pH daily and measured salinity fortnightly. We also measured total alkalinity fortnightly via Gran titration from samples of water

(888 Titrand, Metrohm, Switzerland). Our mesocosms are considered autonomous systems that replicate natural day-night fluctuations in pH. For further details of the experimental design, seawater manipulation, and associated output see Ullah et al. (2018).

### Consumer composition in mesocosms

Our research centered on a group of highly mobile omnivorous and carnivorous consumers that comprised juvenile forms of six different fish species and two shrimp species from the same genus. Initially, each mesocosm was populated with seven to 10 specimens of each fish type and 10 shrimps, totaling 55 individuals per mesocosm, all between 10 and 40 mm in size. These mesocosms underwent climate treatments for a time span of 4.5 months. Such prolonged exposure played a dual role: It promoted a profound acclimatization in the consumers and also permitted both trophic and competitive interactions to influence this consumer composition. Consequently, as the consumers adapted to the unique conditions of their environment through growth and survival, their numbers averaged  $25.1 \pm 4.4$  ( $\pm$ SD) per mesocosm at the end of the experiment (Appendix S1: Table S1).

### Species interaction under future climate change

We used data from our previously published mesocosm experiments to estimate predator–prey interactions within the food web models (Pistevos et al., 2015; Ullah et al., 2018). We derived values from the mesocosm experiments to particularly estimate the vulnerability of prey to predators, the effective search rate of predators for their prey, and mortality for some groups as a function of biomass.

Here, prey is classified as “vulnerable” or “invulnerable,” with “vulnerability” determining the speed of their transition between these groups. Effective search indicates how swiftly predators locate and consume prey, taking into account prey handling time. We calculated the vulnerability of lower trophic level (trophic level  $\leq 2$ ) species/functional groups to their predators using data from stomach content analysis of fishes (referred to as a direct approach) used in the mesocosm experiments through in situ feeding trials. Fish were first starved for 20 h (i.e., gastric evacuation), allowed to freely feed for 4 h, and then captured and frozen using a liquid nitrogen Dewar ( $-196$  °C). Stomach contents were examined under a microscope to identify and count different prey items at the level of individual taxa (e.g., tanaid shrimps,

annelids). Prey weight was calculated by multiplying the average mass of each prey item by its count, and the relative weight of different prey groups was determined based on their contribution to the total prey weight. This information was then assigned to individual fish species. Finally, this diet information (consumption rate as milligrams per 4 hours per individual) was used to calculate the relative predation pressure on species occupying at trophic level  $< 2$  by the species occupying a trophic level of  $\geq 2$  in each of the three climate treatments relative to that of the controls in the mesocosm.

The estimation of prey vulnerability through in situ feeding trials in mesocosms is robust because feeding at the community level incorporates the complex interplay between morphology, physiology, behavior, population dynamics, and predator–prey interactions (Brodeur et al., 2017). For more details about the stomach content analysis see Ullah et al. (2018).

We applied an indirect approach to estimate the vulnerability of prey groups (trophic level  $\geq 2$ ) for higher-order carnivorous trophic groups (i.e., for which omnivorous and carnivorous fishes in the mesocosms acted as their prey) under warming and acidification. The indirect approach was based on behavioral experiments related to the foraging behavior of omnivorous and carnivorous fishes in the mesocosms, where degree of risk taking was used as a proxy for prey vulnerability to their predator (Goldenberg et al., 2018). Briefly, after 2.5 months of exposure to the climate treatments, five species of prey fish (*Neodax balteatus*, *Haletta semifasciata*, *Favonigobius lateralis*, *Girella zebra*, and *Acanthaluteres vittiger*) were exposed to a fish predator (*Gymnapistes marmoratus*) as part of a behavioral test. The predator was caged, and a small container in front of the cage emitted food cues to attract the prey fish to the general area and encourage risk-taking behaviors.

In each mesocosm, a total of three behavioral trials lasting 7 min each were conducted. Using video recordings, the position of the individual prey fishes throughout the trial was assessed through manual tracking using the software Solomon Coder. The field of view of the camera was subdivided into an area distant from the food cue, which also provided shelter habitat and the area close to the food cue, which was unsheltered and faced the predator cage. The area close to the food cue was further subdivided into the side directly in front of the predator cage, where predation risk was highest and the side farther away.

Three response variables that represent prey vulnerability were derived: (1) “Prey attraction” was calculated as the percentage of time spent in the open area close to a food cue relative to the time spent in the entire field of view, (2) “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, and (3) “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. The three response variables were averaged across treatments and given equal weighting to derive a composite vulnerability index of prey to its predator, which was then used as a forcing function in the model.

Effective search rates for Port Jackson sharks were determined by the time taken to locate hidden prey in the sand. Data on sharks’ hunting abilities, primarily through olfaction under varying climate conditions, were sourced from Pistevos et al. (2015). Briefly, sharks, after an average 36-day exposure to experimental conditions and without prior feeding, were tested for their ability to distinguish between two sand-filled trays. One tray had a mix of prawn meat and fresh cockles, while the other, a control, contained only empty cockle shells. With an average separation of 5 cm between trays, sharks’ success in locating prey was observed for 40 min. The time each shark took to find the hidden food was then recorded to calculate the relative effect size under different climatic conditions.

Primary producer groups, including phytoplankton, phytobenthos, mat-forming algae, and macrophytes, were assessed for their biomass in mesocosms. Phytoplankton biomass (4 L/mesocosm) was estimated by filtering water with specific fiber filters (Whatman GF/C filters of 4.7 cm diameter), while phytobenthos samples were collected using benthic samplers. Biomass was measured using chlorophyll *a* (chl *a*) and converted to wet weight through two established conversion factors: transforming chl *a* to carbon (40:1-carbon to chl *a* ratio) and then carbon to wet weight (Wet weight = Carbon × 10) (Jones, 1979). Macrophytes and mat-forming algae were sampled from various habitats and dried (65 °C for 24–48 h), and their dry weight was converted to wet weight using a factor of 10. The production/biomass (*P/B*) ratios of these producers were determined using community photosynthesis measurements and the standard average *P/B* ratio for primary producer groups published for related marine ecosystems (Bozec et al., 2004; Murray & Parslow, 1997; Pinkerton et al., 2008; Wabnitz et al., 2010). We then used these ratios to calculate the relative production rate for each functional group based on in situ community photosynthesis for each mesocosm:

$$P_{/Bi} = \left\{ \frac{(a^{P_{/Bi}} \times B_i) \times 100}{\sum a^{P_{/Bi}} \times B_i} \times \frac{CM}{100} \right\} / B_i,$$

where  $P_{/Bi}$  is turnover rate calculated for group *i* as model input,  $a^{P_{/Bi}}$  is the standard average turnover rate assigned for group *i*,  $B_i$  is the biomass of group *i* sampled from

each mesocosm,  $\sum a^{P_{/Bi}} \times B_i$  is the total theoretical production for all functional groups, *CM* is the community photosynthesis measured in situ from the mesocosm, and  $\left\{ \frac{(a^{P_{/Bi}} \times B_i) \times 100}{\sum a^{P_{/Bi}} \times B_i} \times \frac{CM}{100} \right\}$  is the calculated production of functional group *i* to total community production measured in each mesocosm. These values were later used to calculate the difference in productivity of different functional groups under different treatments.

The methods for calculating the effect size as a model input (Ecosim) for all these parameters, derived from mesocosm data, are provided in the next section, “Food Web Model” (“Estimation of model parameters for present day and future scenarios”).

## PPB food web model

The PPB food web model was developed using the Ecopath food web modeling approach to create a baseline snapshot (static model) of the ecosystem for the year 1990 and then extended to a time-dynamic (1990–2015) simulation model (Ecosim) to quantify the flow of energy between functional groups (Christensen et al., 2008). We chose this hindcast simulation period based on the available time series data. The PPB food web model has 53 functional groups. The model requires four key primary input variables: biomass (*B*), *P/B* ratio, consumption/biomass ratio (*Q/B*), and diet composition.

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).

Following foraging arena theory, predator consumption rates ( $Q_{ij}$ ) are quantified using a nonlinear relationship between prey and predator (Equation 1), which assumes that only a portion of the biomass of the prey is available to a predator. This means that the biomass of prey *i* is divided between a vulnerable and a nonvulnerable state. The vulnerability concept incorporates density dependency and expresses how far a group is from its carrying capacity (Christensen & Walters 2004; Christensen et al., 2008). The vulnerability parameter (rate) can be modeled both as top-down and bottom-up controls of the predator–prey interactions. For example, vulnerabilities >2 describe top-down control of the predator–prey relationship, where the predator biomass drives the prey mortalities, while vulnerabilities <2 define bottom-up control, where the biomass of the predator has little effect on the predation mortality of that prey. For each predator–prey interaction, we calculated  $Q_{ij}$  at time *t* as

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

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  $Q_{ij}$ . The details of the modeling approach are described in Appendix S1.

## Simulating climate and fishing scenarios in food web models

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 & Eddy, 2015) based on observations from the mesocosm experiments. Specifically, we used the estimated mean (across species and treatments) effects of warming, acidification, and their combination on prey vulnerability, food search activity (higher-level consumer), mortality, and productivity (primary producers) of trophic groups to alter modeled consumption ( $Q/B_i$ ) and production ( $P/B_i$ ) rate.

The model's initial conditions for simulations reflect a stable exploited system, with biomass levels and level of fishing effort focused on the year 2015. We used a burn-in period (focused on 2015 conditions), to ensure that the food web model was in equilibrium, and then projected annual ecosystem change for 85 years under a set of scenarios: no-climate-change (NC) (baseline), ocean warming (T), OA, and their combination (OAT). With +2.8 °C warming and a  $p\text{CO}_2$  of 900 ppm (pH = 7.89), we simulated climate conditions predicted for the end of this century following a business-as-usual emission scenario (Representative Concentration Pathway 8.5, Bopp et al., 2013). For the PPB region specifically, a 1.9–3.8 °C increase from a 1995 baseline is forecast (Clarke et al., 2011). The average temperature in PPB in the warmest month (February) was 20.5 °C between 2010 and 2015, which is close to the ambient summer temperature of 21 °C applied in our mesocosm experiment, which in turn was based on a 5-year data set of two local loggers (5 m depth, 2010–2015, SA Water). Given the fully crossed two-factor design and high cost per mesocosm unit, only one emission scenario could be tested. The uncertainty in biomass ( $B$ ), production ( $P/B$ ), and consumption ( $Q/B$ ) rates and ecotrophic efficiency (EE) parameters was explored through 100 simulations, with these parameters being randomly varied (in combination) within bounds of a  $\pm 20\%$  coefficient of variation and thus made it possible

to examine the more influential parameters in model predictions (Essington, 2007).

The NC scenario assumes that model parameters will 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, the mortality of trophic functional groups, and productivity of primary producers 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. As an additional driver, fisheries exploitation has the capacity to alter how fish respond to climate on a physiological level (Duncan et al., 2019). However, little is known about how exploitation rates are likely to change by the end of the century because fisheries management is generally done at decadal temporal resolutions or finer (Fulton et al., 2018). Therefore, exploitation was initially held constant at 2015 levels for all 21st-century climate change scenarios. Afterward, we ran additional scenarios to test the response of future food webs to increased exploitation. We did this using a scenario approach that increased exploitation by 1.5-, two-, and five-fold compared to present-day fishing pressure for all target species. Even though fishing pressure had decreased and is relatively low in our model system, we included increased fishing pressure as a stressor as fisheries (over)exploitation is a major issue across marine ecosystems globally, and many of these systems will be subjected to fishing pressure as well as climate stressors.

## Estimation of model parameters for present-day and future scenarios

Experimental data from the two mesocosms and published field data were used to calculate the model input variables (Appendix S1: Tables S2, S5, and S6). Food web models that considered climate change scenarios used experimentally derived vulnerability parameters, while models without climate change scenarios used model-fitted vulnerability parameters to simulate future food web change.

We calculated the effect sizes (mean) of the climate change treatments relative to the present-day control for prey vulnerability, search activity, mortality, and productivity using the absolute values. These effect sizes were used to derive the model forcing functions for different climate change scenarios (OA, T, and OAT). The effect sizes for a given parameter were standardized to the baseline scenario (no change) by dividing the response value of each scenario by the corresponding baseline value for

that parameter. This resulted in a consistent baseline value of 1. We then used linear interpolation to generate an annual time series for each of the parameters under different climate scenarios to use as forcing functions from 2015 to 2100. Forcing functions were used on specific species in the model as detailed in Appendix S1: Table S2. For instance, time series generated from the vulnerability index of carnivorous fish were applied (as forcing functions) to higher-trophic-level predator groups that potentially prey on them. Similarly, time series created from the vulnerability index of zooplankton were applied to all predator groups that feed on them. The feeding categories of the model groups can be found in Appendix S1: Table S3.

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 focused on the year 2100. We used community-level groups because indicators at the community level are reliable for detecting the effects of perturbations on marine ecosystems (Fulton et al., 2005).

## Analysis of model outputs

We pooled food web functional groups into 10 community levels, including pelagic groups (mammals, birds, cephalopods, and pelagic finfish), demersal groups (chondrichthyans and demersal finfish), and their prey (benthic crustaceans, invertebrates, small pelagic crustaceans, primary producers) (Appendix S1: Table S3). 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 & Weaver, 1963) and Kempton's  $Q$  index (Ainsworth & Pitcher, 2006). The Shannon diversity index captures changes in evenness, whereas Kempton's  $Q$  index captures changes in both evenness and richness at the level of functional groups (Appendix S1: Section S3.1).

## Model validation

We evaluated the quality of input data for the PPB model using food web diagnostics (Link, 2010), performed calibration of the time dynamic Ecosim module (see Appendix S1), assessed model transferability using independent validation data, and conducted both an ecosystem model skill assessment (Olsen et al., 2016) and a global sensitivity analysis (Fordham et al., 2016).

To verify that parameters from our mesocosm were transferrable to the PPB coastal marine system, we performed retrospective tests (Appendix S1: Section S4.2). For this purpose, we simulated historical abundances (1993 and 2011) using a mesocosm model and a PPB submodel (simplified) that only included functional groups that were in the mesocosm experiment. The PPB submodel was developed based on field data, whereas data for the mesocosm model were derived primarily from mesocosm experiments. We ran hindcast simulations and validated them using independent catch data (VFA, 2016) (Appendix S1: Table S4).

To assess the skill of the PPB model (full), we used independent observation data for two model functional groups (Appendix S1: Table S4) and calculated six model skill assessment metrics as has been recommended for ecosystem model assessments (Olsen et al., 2016; Stow et al., 2009). These model skill assessment metrics were root mean square error (RMSE), average error (AE), average absolute error (AAE), Pearson ( $P$ ) and Spearman ( $S$ ) correlation, and modeling efficiency (MEF).

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 perform these tests, we used the built-in Monte Carlo routine within the Ecosim module, which allows model input parameters to be varied (Coll & Steenbeek, 2017; Heymans et al., 2016). Specifically, we ran 100 Monte Carlo simulations with  $B$ ,  $P/B$ ,  $Q/B$ , and EE varying randomly within bounds of  $\pm 20\%$  CV. Initial and projected future biomass for three community groups (cephalopods, pelagic finfish, and invertebrates) representing three trophic levels were recorded for the year 2100. We used generalized linear models (GLMs) 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 (SRCs), along with the coefficients and their confidence intervals. Furthermore, we also showed the effects of parameter uncertainty on model outputs for some of the major species of the PPB model.

## RESULTS

### Biomass changes under future climate change

Model simulations show that the total biomass of most higher-trophic-level community groups (mammals, birds,

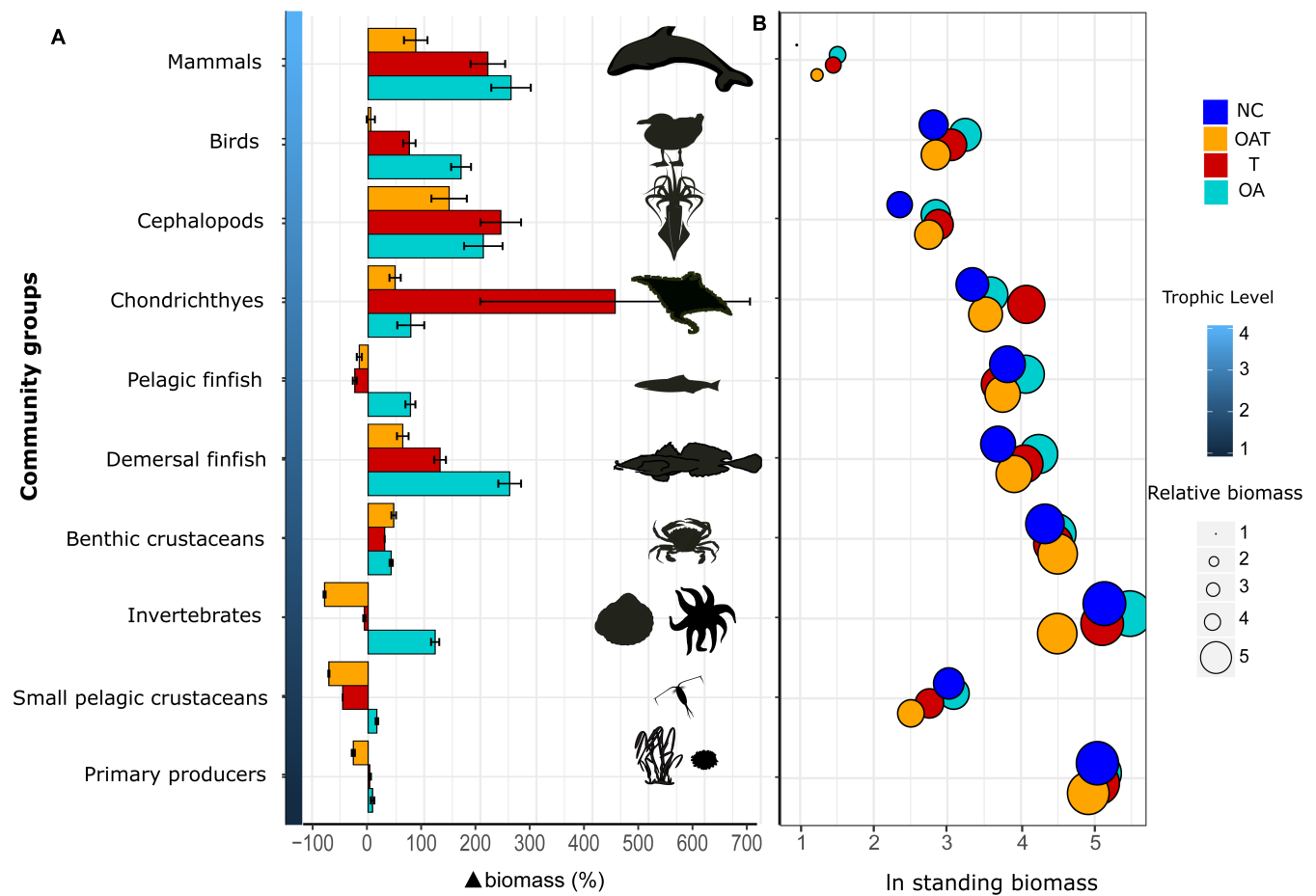


cephalopods, chondrichthyans, and demersal finfish) is likely to benefit from ocean warming (T) or acidification (OA) when modeled separately (Figure 2; Appendix S1: Figure S2). However, the combination of the two stressors has an antagonistic effect on biomass increase. At the level of individual species or functional groups, the positive effects on biomass are more disparate. Some species or functional groups declined considerably, others increased, while only a few increased dramatically, causing an overall large biomass increase at higher trophic levels (Appendix S1: Figures S3 and S4).

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 NC and under current (low) levels of fish exploitation (“no change” scenario) (Figure 2A). Modeling 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 236% 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 166%, respectively), with a smaller increase under T (128% and 73%, respectively). Pelagic finfish showed a negative response to warming (−24%), irrespective of acidification, with small pelagic functional group (mostly planktivores) showing severe depletions (>70%) under both T and OAT (Appendix S1: Figure S3).

Conversely, model simulations show that ocean warming, either alone or in combination with OA, is projected to exert a negative effect on lower-trophic-level faunal groups, with the exception of benthic crustaceans (Figure 2A). Invertebrates (predominantly mollusks and other invertebrates that do not possess a chitinous



**FIGURE 2** (A) Mean ( $\pm 95\%$  CI) relative change in biomass ( $\Delta$  %) 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; OAT, combined ocean acidification and warming. Functional groups of food web models are aggregated to community groups for clarity. (B) The future standing biomass (in kilograms per square kilometer; ln-transformed) estimates for each community group. The bubble size is proportional to its biomass. Exploitation rates for all scenarios are modeled at present-day rates. Silhouettes used in this figure created by the first author.

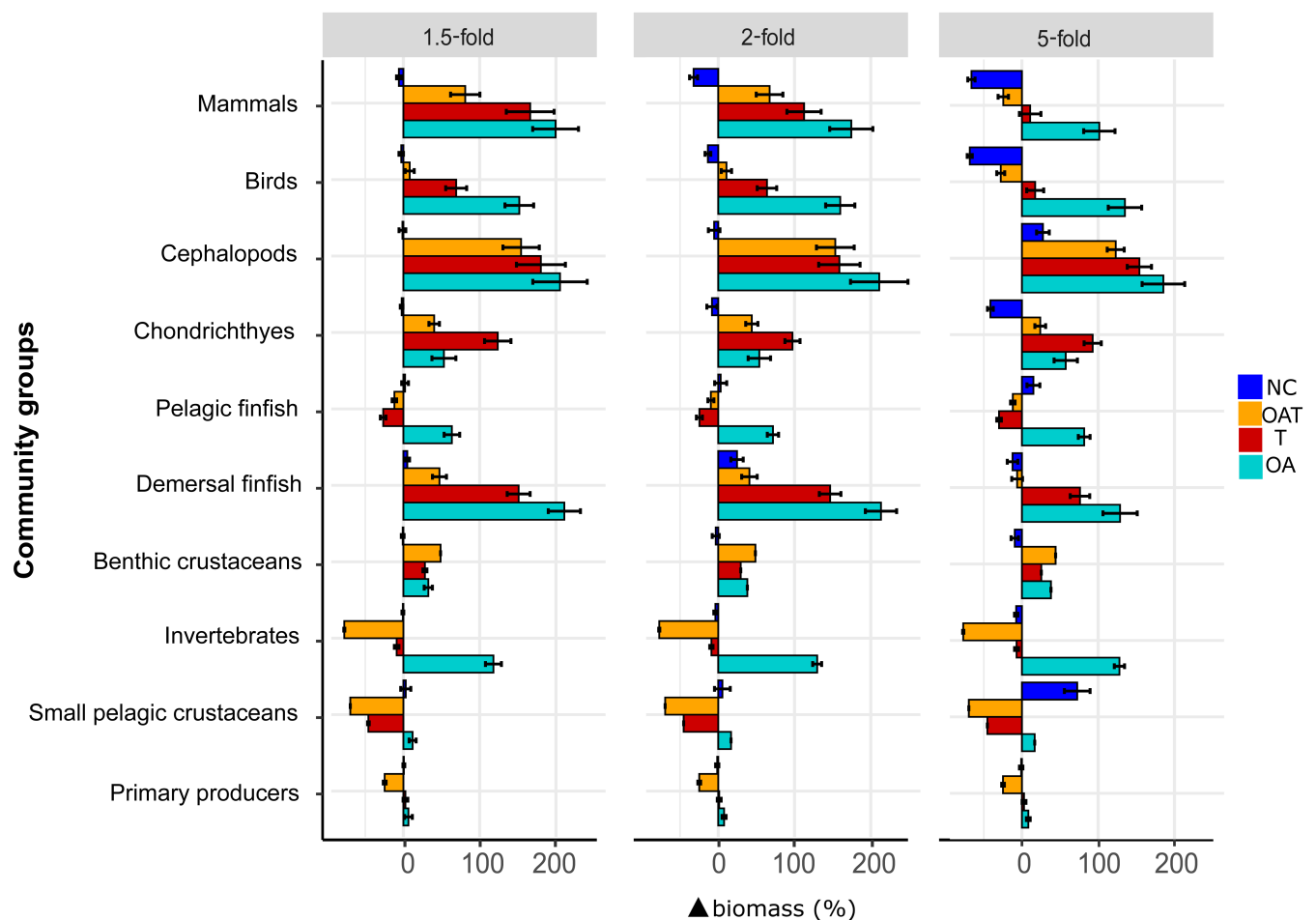
exoskeleton; Appendix S1: Table S6), and small pelagic crustaceans (zooplankton) are projected to experience biomass declines of 7%–78% and 45%–70%, respectively, under T or OAT (Figure 2).

The standing biomass of primary producers increased slightly under OA (8%) and T (3%) but decreased by ~26% under OAT (Figure 2A), largely driven by a reduction of phytoplankton, micro-phytobenthos and macro-algal biomass (Appendix S1: Figure S4). Turf algae, in contrast, experienced a large increase in biomass (Appendix S1: Figure S4).

### Climate change effects under different fishing exploitation scenarios

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 two-fold increase in exploitation rate (Figure 3). Further increases in exploitation (up to five-fold) exacerbated this declining trend (by 41%–66%) for mammals, birds (due to reduced prey), and chondrichthyans. Negative effects of up to a two-fold increase in exploitation were suppressed at higher trophic levels (except for pelagic finfish) under modeled climate change (OA, T, and OAT), due to greater top-down control of consumers over prey resources (Figure 2). However, a five-fold increase in exploitation caused the biomass of mammals and birds to collapse under warming scenarios, whereas opportunistic groups such as cephalopods remained abundant (T: 178%; OAT: 144%) (Appendix S1: Figure S5). While both T and OA scenarios positively affected higher trophic levels in the face of medium to large increases in exploitation, their largely negative effects on lower trophic levels (primary producers, small pelagic crustaceans, and invertebrates) were not decreased by increased exploitation (Figure 3; Appendix S1: Figure S6).



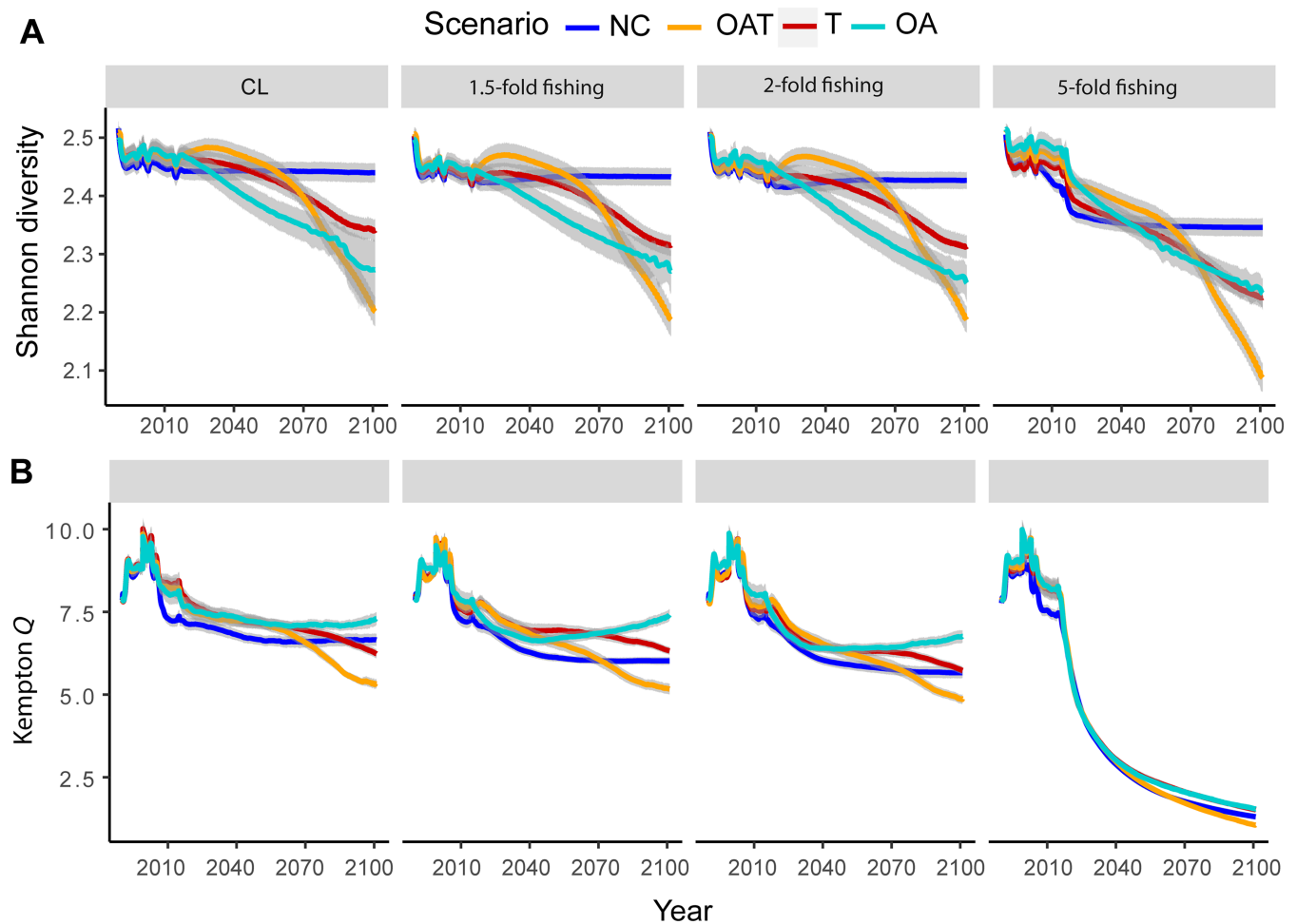
**FIGURE 3** Mean ( $\pm 95\%$  CI) change in food web biomass ( $\Delta\%$ ) in year 2100 under different fishing pressure and climate scenarios. Responses are relative to the scenario of no change in climate and fishing (NC). OA, ocean acidification; T, ocean warming; OAT, combined ocean acidification and warming. Functional groups are aggregated into community groups for clarity. Number of “folds” equals the magnitude of increase in fishing pressure starting in 2015.

Under the no change in climate and fishing (NC) scenario, the Shannon diversity index remained relatively stable in the future under 1.5- and two-fold increases in exploitation, while it decreased by ~4% under a five-fold increase in exploitation (Figure 4A). In contrast, the Shannon diversity index declined under all global change scenarios with the largest declines projected for OAT under a five-fold increase in exploitation (Figure 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 (Figure 4B). A five-fold increase in exploitation resulted in a steep and immediate decline in the Kempton Q index regardless of the climate change scenario.

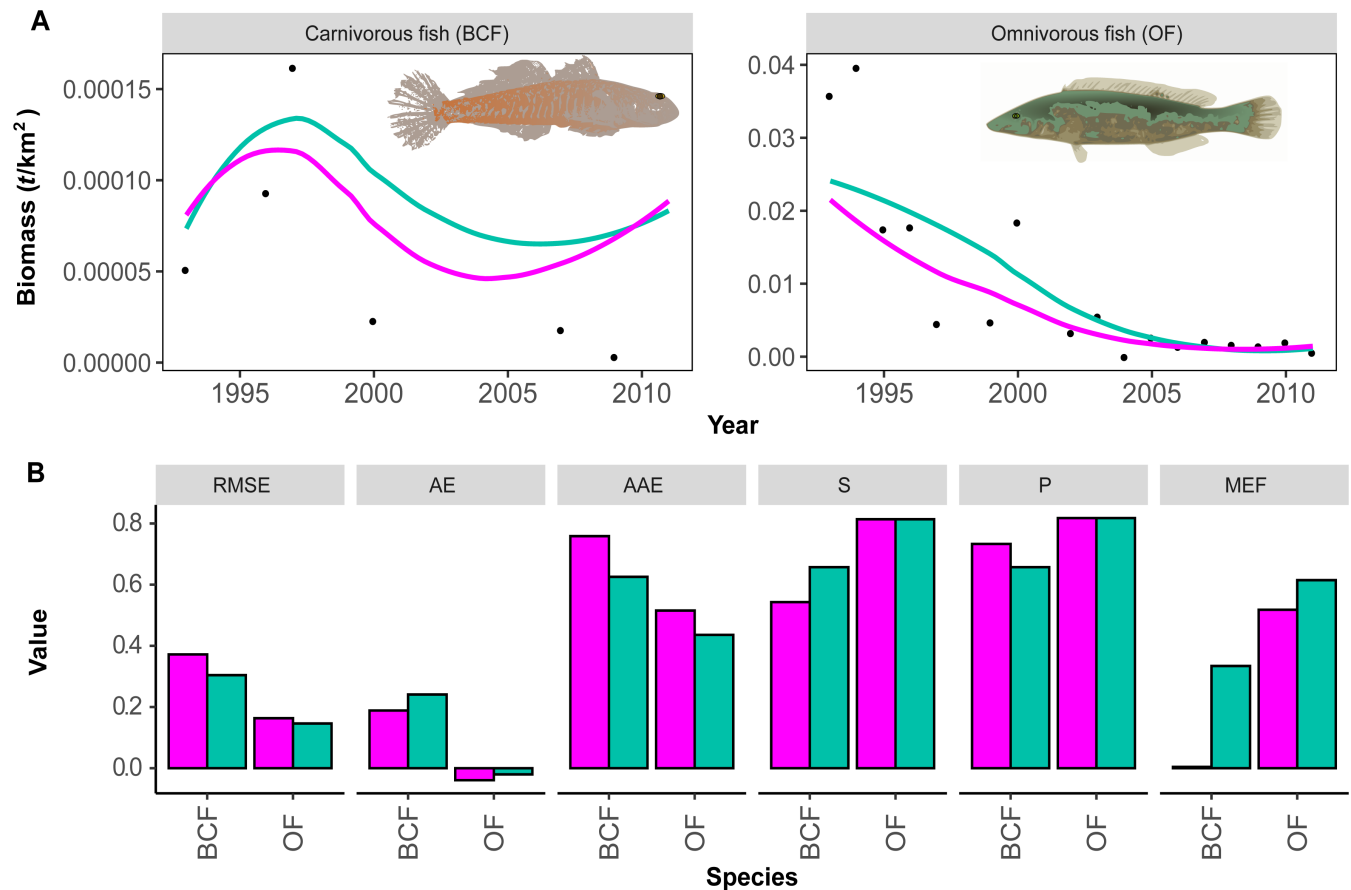
### Model validation and sensitivity

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 parameterized with mesocosm data are generally as skillful at projecting changes in biomass as models parameterized with field data (Figure 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  $\leq 0.0001$ ;  $r = 0.82$ , RMSE = 0.007, respectively) or mesocosm data ( $r = 0.69$ , RMSE  $\leq 0.0001$ ;  $r = 0.82$ , RMSE = 0.007, respectively). 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 modeling 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



**FIGURE 4** Ecological indicators of change in community composition, showing (A) Shannon diversity index and (B) Kempton Q index. Gray shadows represent the 95th and 5th percentiles. NC, no change in climate from present-day levels; OA, ocean acidification; T, ocean warming; 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.



**FIGURE 5** Validation of Port Phillip Bay model for two major functional groups (multiple species combined in each group) built with field (pink) and mesocosms data (green) between years 1993 and 2011. (A) Mesocosm transferability by comparison with actual standing catch biomass (black dots). (B) Ecosystem model skill assessment: root mean squared error (RMSE), average error (AE), average absolute error (AAE), Spearman rank (*S*) and Pearson (*P*) correlation, and modeling efficiency (MEF). Y-axis is limited to values between  $-0.05$  and  $0.80$ . Fish images used in this figure were created by the first author.

(Appendix S1: Figure S7). Importantly, bias (AE) in projections of biomass 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 (Appendix S1: Table S7) 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 relationships remained the same regardless of whether or not exploitation was modeled. The effects of parameter uncertainty on outputs for some of the important species in the PPB model showed that generally pelagic fish species and those at the top of the food web (such as mammals and birds) were the most sensitive to changes in model input parameters (Appendix S1: Figure S10).

## DISCUSSION

By integrating empirical data on species' physiological and behavioral performance from two large-scale mesocosm experiments into dynamic food web models and accounting for historical exploitation rates, we found that near future climate change (i.e., next few decades, up until the year 2100) was likely to benefit the biomass of some animal species at higher trophic levels in a temperate marine ecosystem experiencing sustainable fisheries exploitation rates, albeit at a potential cost to biodiversity. Model results suggested that under future scenarios of warming, the biomass of higher-order consumers and apex predators (species of mammals, birds, cephalopods, chondrichthyans, and demersal finfish) is likely to increase in some temperate systems 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). Accordingly, the changing structure of temperate marine food webs under climate change 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 just an increased bottom-up forcing as expected with OA as a sole climate stressor (Nagelkerken et al., 2020; Sswat et al., 2018).

Organisms at higher trophic levels are likely to increase their top-down control over their prey, and therefore increase in biomass, in response to temperature-driven increases in their metabolic rates (Brown et al., 2010). Such increased top-down control by consumers in response to warming has been experimentally shown for a three-trophic-level food web (Goldenberg et al., 2017; Marino et al., 2018), but insights for more complex food chains (e.g., four trophic levels) are lacking. A recent meta-analysis carried out from primary producers to top predators revealed that higher trophic levels showed stronger tolerance to climatic stressors (Hu et al., 2022). This meta-analysis showed a positive, but nonsignificant, effect of warming on marine species when all response variables (on survival, growth, reproduction, development, and calcification) were pooled. Studies, however, have also suggested that the top trophic level and every second level below in a food web could benefit from climate change, whereas the levels in between will suffer (Hansson et al., 2013). The latter study showed that in three-trophic-level systems, phytoplankton and planktivorous fish (i.e., every second level) benefited from climate change, while elevated temperatures in the absence of fish increased zooplankton abundance but adversely affected phytoplankton biomass. A more complex food web structure was experimentally studied by Nagelkerken et al. (2020), who showed that under warming combined with acidification, biomass expanded at the base and the top of the food web but contracted at the center. However, they argued that this represented a transitional state over the shorter term of climate change, with forecasts of an eventual food web collapse into shortened, bottom-heavy, and top-eroded food webs over the long term (Nagelkerken et al., 2020). Hence, our observed food web response with a biomass expansion at the top and a gradual compression toward the bottom likely also represents a transitional food web structure under near-future climate change. In the longer term, however, a collapse at the top is likely to ensue as diminishing lower trophic levels will be unable to continue to support increased biomass at the top. Such negative cascading effects in natural food webs have been shown, for example, in tropical reef ecosystems where simultaneous declines in algal turfs and herbivore fish biomass have negatively impacted species at higher levels in the food chain (Capitani et al., 2021).

Responses to climate change can be significantly mediated by food availability. Higher metabolic rates due to warming might be beneficial to organisms when food is plentiful but stressful when food is scarce (Auer et al., 2016; Zeng et al., 2017). In some cases, larger mobile organisms such as teleost fishes, crustaceans, and some mollusks, with relatively high metabolic rates, may be better at adjusting to environmental stress in terms of growth rates than inactive, sessile groups (e.g., echinoderms and bivalve mollusks) that have a lower ability to regulate their physiology (Melzner et al., 2009; Pörtner et al., 2005). A recent study by Lindmark et al. (2022) suggests that under natural feeding conditions, the growth of fish may differ from those observed in experimental studies under food satiation. This suggests that changes in fish growth are caused not only by direct physiological responses to increased temperatures but also by changes in resource availability caused by warming.

Acidification alone is not expected to enhance top-down control by consumers because elevated  $\text{CO}_2$  tends not to increase the metabolism of consumers (Carter et al., 2013; Kroeker et al., 2013). Recent food web studies showed that enhanced primary production can increase prey availability (i.e., herbivores), which can boost the growth of their consumers under acidification (Nagelkerken et al., 2017; Sswat et al., 2018). This was true for all higher-order predators in our study, although for chondrichthyans the biomass increase was weak. Elevated  $\text{CO}_2$  is known to affect the foraging behavior (e.g., reduced prey search efficiency and impaired odor tracking) of both juvenile and adult chondrichthyans, which might explain the reduced increase in biomass for this group (Dixon et al., 2015; Pistevos et al., 2015). Because of their different physiology, highly active predators, such as marine mammals, birds, and nonbony animals like 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 showed that warming and acidification could 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. Chondrichthyans, for instance, exhibited a notable biomass reduction under the combined impacts of warming and acidification, primarily because of a significant decrease in their main prey group: filter-feeding mollusks.

In contrast to other invertebrates, benthic crustaceans sustained a biomass increase under all modeled climate scenarios, enabling an increase in the biomass of their consumers (e.g., of demersal finfish, and consequently of 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 in this study, 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 and small and large fish to sharks) at high latitudes 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 the 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). However, using a mechanistic population dynamics model, a recent study revealed that ocean temperature had a notable negative effect on the productivity of commercially and ecologically important fish families such as codfishes and sand eels (Free et al., 2019). While these studies modeled food web responses or fisheries productivity through a population model, they used relatively simplified approaches, 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 modeling approach, model results suggested that opportunistic and less-targeted groups such as cephalopods continued to flourish in their biomass irrespective of exploitation rates, although demersal finfish, which were the major fishery of the system, are likely to decline at higher fishing levels ( $\geq$ two-fold). Overfishing is widespread in

many oceanic regions, and a five-fold fishing increase is unlikely, unless there is a pristine fish stocks and a high demand for harvest. Yet, studying how well-managed or pristine fisheries stock respond to intense stressors is insightful. Overall, model results suggested that the greatest effects of exploitation on some of the future temperate 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 some primary producers (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 & Connell, 2015). Together, global warming and fishing will likely shift the distribution of biomass within the community and reduce species 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 to mitigate the impact of climate change on fisheries productivity. Blending mesocosm experiments with “real-world” ecological models has been questioned on the grounds that they are unlikely to attain realistic projections (Carpenter, 1996). One reason is that experimental outcomes can be swayed by community structure, ecological complexity, and trophic levels considered within mesocosms. Even the most complex mesocosm food web is likely to exhibit lower functional redundancy than natural food webs, as evidenced by our mesocosm and PPB model. Also, mesocosms can inadvertently boost weedy species growth, such as turf algae, adding uncertainty to future ecosystem predictions, as observed in our mesocosm experiments. While the value of mesocosm data in enhancing ecosystem model projections are clear, it is beneficial to test parameter transferability with simpler models before integration. We demonstrate that the mesocosm model does a fair to good job replicating historical biomass trends for selected groups, consistent with the simple PPB model that is built with similar

numbers of functional groups. We advise modelers to adjust parameters judiciously during these retrospective tests, given the multitude of variables available to tailor the model.

Our modeling approach, like other modeling 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 & Hobday, 2011). These fine-temporal-scale climate dynamics could not be captured in the mesocosm experiment and, therefore, the food web model. This could affect our modeled trajectories of biomass and community composition. To calculate the vulnerability of fish to their consumers, all fish species were classified into two major categories, carnivores and omnivores (feeding guilds). Although evidence suggests that OA negatively affects the ability of some sharks to detect or perceive food olfactory cues, thereby reducing their feeding ability under a changing climate (Pistevos et al., 2015), our results for chondrichthyans should be interpreted with caution. The somewhat poor fit of modeled projections to observed data for Port Jackson shark is likely to reflect an oversimplification of the food web structure for the validation exercise (see Appendix S1). 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-Aroita, 2017). Our results for mammals (endothermic) and birds require careful interpretation since climate change impacts were not directly accounted for in model parameters for these groups but rather by changes in prey availability and trophic cascades due to a changing climate. Furthermore, even though large mesocosms are close representations of nature (Stewart et al., 2013), in natural systems, food web responses to climate change are influenced by the community structure, ecological complexity, and number of trophic levels included. Despite these limitations, our study included the best available historical data and the most robust estimates of physiology and behavior responses to global warming for a four-trophic-level natural temperate benthic food web system.

The study has practical applications and offers valuable insights into the decision-making process for marine ecosystem management in the context of climate change. The findings shed light on the intricate responses of marine ecosystems to global change, emphasizing the necessity for comprehensive and multidimensional approaches to ecosystem management. For example, the study provides valuable insights into the potential impacts of combined warming and acidification on marine food webs where biomass at higher trophic levels under individual stressors may diminish or even disappear when these stressors act together, with the potential consequence of cascading

impacts and a simplified ecosystem. Consequently, this information underscores the importance of adopting a holistic management approach that considers multiple variables and potential threats, as managing these factors in isolation is unlikely to yield positive outcomes. Policymakers can harness this knowledge to craft conservation measures considering various stressors and their combined effects. The study also highlights the significance of considering functional diversity and evenness within food webs when formulating policy guidelines. It reveals that ocean warming and acidification may have more pronounced negative effect on functional diversity compared to overexploitation in some ecosystems. Thus, conservation strategies should prioritize maintaining this diversity for stable food webs, rather than just focusing on overall ecosystem throughput. One key advantage of the study is its use of mesocosms to bridge theoretical and experimental models. This method closely replicates real-world interactions, providing a realistic and reliable representation of natural environments within controlled settings, enhancing the reliability and applicability of the study’s output.

## CONCLUSIONS

Here we used a novel approach to simulate the effects of global warming, OA, and fishing on the biomass and diversity of species in a temperate coastal ecosystem, using experimental data on the effects of ocean warming and OA 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 showed that the structure and function of some future temperate marine food webs under warming and acidification could 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 in the near future from ocean warming and acidification in some temperate systems, albeit at a potential cost to functional diversity. These potential benefits will be reduced or lost when these stressors co-occur and are likely to diminish over longer time scales. More importantly, model results suggested that mesocosm experiments could be integrated with food web models to better model marine biodiversity and productivity in response to 21st-century climate change.

## AUTHOR CONTRIBUTIONS

Hadayet Ullah, Ivan Nagelkerken and Damien A. Fordham conceived the research. Hadayet Ullah and Silvan U. Goldenberg collected the data. Hadayet Ullah developed

the methods and analyzed the data. Hadayet Ullah, Ivan Nagelkerken and Damien A. Fordham wrote the manuscript. All authors contributed to revisions and approved the final submission.

## ACKNOWLEDGMENTS

This study was financially supported by an Australian Research Council Future Fellowship Grant to Ivan Nagelkerken (FT120100183) and a grant from The Environment Institute (University of Adelaide) to Ivan Nagelkerken. Hadayet Ullah was supported by an International Postgraduate Research Scholarships (IPRS) scholarship program funded by the Australian Government. Greg Perry and Simon Conron provided historical fish biomass data for PPB. We acknowledge W. Hutchinson and M. Gluis for their technical assistance in setting up the mesocosm experiment at the South Australian Research and Development Institute (SARDI) facilities. We would also like to gratefully acknowledge the effort of all lab members, with special thanks to Camilo Ferreira and Georgia Walden, Emma Marangon, and Angélique Bonnet to help set up and maintain the mesocosm experiment. Open access publishing facilitated by The University of Adelaide, as part of the Wiley - The University of Adelaide agreement via the Council of Australian University Librarians.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Ullah et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.jwstjqgk>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Ullah, Hadayet, Damien A. Fordham, Silvan U. Goldenberg, and Ivan Nagelkerken. 2024. "Combining Mesocosms with Models Reveals Effects of Global Warming and Ocean Acidification on a Temperate Marine Ecosystem." *Ecological Applications* e2977. <https://doi.org/10.1002/eap.2977>