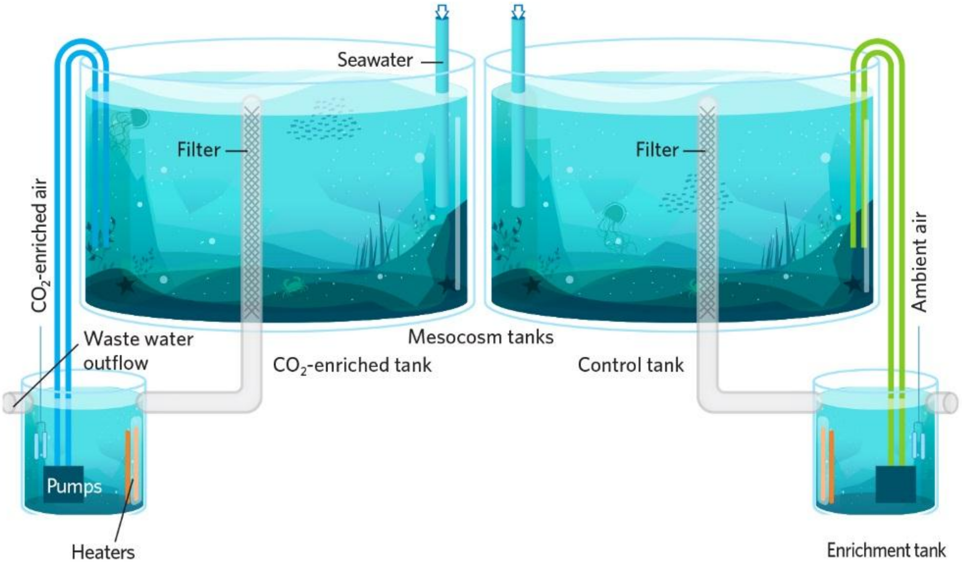
RESPONSE OF TEMPERATE MARINE FOOD WEBS TO CLIMATE CHANGE AND OCEAN ACIDIFICATION: BRIDGING THE GAP BETWEEN EXPERIMENTAL MANIPULATION AND COMPLEX FOODWEBS



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THE UNIVERSITY
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Md. Hadayet Ullah

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Chapter III

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ABSTRACT

Global warming and ocean acidification are forecast to exert significant impacts on marine ecosystems, while intensive exploitation of commercial marine species has already caused large-scale reorganizations of biological communities in many of the world's marine ecosystems. Whilst our understanding on the impact of warming and acidification in isolation on individual species has steadily increased, we still know little on the combined effect of these two global stressors on marine food webs, especially under realistic experimental settings or real-world systems. We particularly lack evidence of how the top of the food web (piscivores and apex predators) will respond to future climate change (ocean warming and acidification) because responses of ecological communities could vary with increasing trophic level. The picture is further complicated by the interaction of global and local stressors that affect our oceans, such as fishing pressure. Accurate predictions of the potential effects of these global and local stressors at ecosystem-levels require a comprehensive understanding of how entire communities of species respond to climate change. Mechanistic insights revealed by a combination of different approaches such as experimental manipulation of food webs, and integrated with ecosystem modelling approaches provide a way forward to improve our understanding of the functioning of future food webs. In this thesis, I show how the combined effect of such global and local stressors could affect a three trophic level temperate marine mesocosm food web and how these outcomes could be translated to predict the response of ecological communities in a four trophic level natural food web. Using a sophisticated mesocosm experiment (elevated $p\mathrm{CO}_2$ of approximately 900 ppm and warming of +2.8°C), I first modelled how energy fluxes are likely to change in marine food webs in response to future climate. I experimentally show that the combined stress of acidification and warming could reduce energy flows from the first trophic level (primary producers and detritus) to the second (herbivores) and from the second to the third trophic level (carnivores). Although warming and acidification jointly boosted primary producer biomass, most of it was constrained to the base of the food web as consumers were unable to transfer unpalatable cyanobacterial production up the food web. In contrast, ocean acidification affected the food web positively by increasing the biomass from producers to carnivores. I then developed a unique approach that combines the empirical data on species response to climate change from our mesocosms experiments with historical population data (fisheries biomass and catch data) to predict future changes in a natural food web. I incorporated physiological and behavioural responses (complex species-interactions) of species from primary producers to top predators such as sharks within a time-dynamic integrated ecosystem modelling approach (Ecosim). I show that under continuation of the present-day fishing regime, warming and ocean acidification will benefit most of the higher trophic level community groups (e.g. mammals, birds, demersal finfish). The positive effects of warming and acidification in isolation will likely be reduced under their combined effect (antagonistic interaction) which is likely to be further negated under increased fishing pressure, decreasing the individual biomass of consumers. The total future fisheries biomass, however, will likely still remain high compared to the present-day scenario. This is because unharvested species in present day fishery will likely benefit from decreased competition and an increase in biomass. Nevertheless, ecological indicator such as the Shannon diversity index suggests a trade-off between biomass gain and loss of functional diversity within food webs. The mechanisms behind the increase in biomass at higher trophic level consumers and a decrease in the biomass of lower trophic levels is mostly driven by the increasing top down control by consumers on their prey through increasing trophic interaction strength and a positive response of some of the prey groups under warming irrespective of acidification. I show that in a future food web, temperature-driven changes in direct trophic interactions strength (feeding and competition) will largely determine the direction of biomass change (increase or decrease) of consumers due to higher mean interaction strength (magnitude of change). In contrast, although acidification induces a relatively small increase in trophic interaction strength it shows a much larger change in the percent interactions altered for indirect interactions. Hence, ocean acidification is likely to propagate boosted primary consumer biomass to higher trophic levels. The findings of this thesis reveal that warming in combination with acidification can increase trophic interaction strengths (top down control), resulting in a reorganization of community biomass structure by reducing or increasing the biomass of resources and consumers and a loss of functional diversity within the food web. Also, the degree to which warming and acidification will be beneficial or detrimental to functional groups in future food webs will largely depend on how interaction strengths affects individual consumers or resource groups due to multi-trophic species interaction, the availability of prey resources and the complexity of the food web considered (e.g. three or four trophic level and more diverse ecological communities).

CHAPTER I

CHAPTER I

GENERAL INTRODUCTION

1. Global Ocean in the Anthropocene

The global ocean covers 71% of Earth’s surface and makes up 97% of the Earth's water, making Earth unique and unusual among planets (Bounama *et al.*, 2007) Global oceans have an important role in regulating climate and life on our planet (Hoegh-Guldberg & Bruno, 2010). However, growing human pressures are having profound and diverse consequences for the global ocean. Starting with the Industrial Revolution (c.1750), atmospheric carbon dioxide (CO_2) has been increasing at an unprecedented rate, predominantly driven by fossil fuel combustion and deforestation (Doney *et al.*, 2009). Anthropogenic greenhouse gas emissions have resulted in significant changes in the physical and chemical properties of the ocean (Barros *et al.*, 2014, Hartmann *et al.*, 2013). By absorbing approximately 93% of the extra energy arising from anthropogenic greenhouse gas emissions, global oceans to some extent temper global warming. However, global oceans have experienced an average increase of approximately 1 °C (0.89 °C from 1901–2012) in global sea surface temperatures (Stocker, 2014). While atmospheric CO_2 levels have risen by approximately 40% within the last two centuries (reaching 400 ppm in 2014) (Blunden & Arndt, 2016), global oceans have absorbed approximately 30% of this, resulting in decreasing ocean pH and fundamental changes in ocean carbonate chemistry (Stocker, 2014). Thus, rising atmospheric CO_2 has been considered one of the most critical problems that humanity faces today because of its pervasive and irreversible effects globally on ecological timescales (Council, 2011). While other chemical and physical changes occur in the oceans due to anthropogenic forcing, such as decrease in dissolved oxygen concentrations (Andrews *et al.*, 2012) and alteration of ocean circulation, the primary direct consequence of rising atmospheric CO_2 is ocean warming (Bindoff *et al.*, 2007) and ocean acidification (Doney *et al.*, 2009). Here after climate change refers both ocean warming and ocean acidification. The widespread ecological impacts of these two global stressors, from polar terrestrial to tropical marine environments, present increasing risks to marine life and ecosystems (Gattuso *et al.*, 2015, Nagelkerken & Connell, 2015, Poloczanska *et al.*, 2013).

1.2 Ocean warming

The consequences of ocean warming are diverse and include changes in physical, chemical, and biological aspects of the ocean. Some of the physical and chemical changes in ocean condition include sea ice melting, sea level rise, decreased solubility of oxygen, and changes in the frequency of regional climate anomalies (Kim *et al.*, 2009). Growing evidence undoubtedly indicates that warming causes diverse biological effects on ocean ecosystems and its life from microorganisms to algae to top predators (Brierley & Kingsford, 2009).

Ocean warming influences the ecophysiology (Pörtner, 2010), distribution (Perry *et al.*, 2005), phenology (Edwards & Richardson, 2004), productivity (Cheung *et al.*, 2011, Cheung *et al.*, 2010, Cheung *et al.*, 2013, Fernandes *et al.*, 2013), and diversity across many marine taxa (Beaugrand *et al.*, 2015, Harley, 2011, Tittensor *et al.*, 2010). While many of the above studies conducted to date help improve our understanding of how climate change can influence marine organisms in the global ocean, we are still deepening our understanding of how ocean warming will affect top predators, such as certain species of fish. Detecting similarities among fish populations in response to climate change is difficult as individual species tend to differ widely in their response (Rijnsdorp *et al.*, 2009).

Most fish are ectotherms and thus fishes have relatively low energetic expenditures. The low energetic demand, however, comes at the expense of temperature-dependent metabolic and physiological performance (Angilletta *et al.*, 2004, Griffen, 2017). Temperature has a strong and direct influence on metabolic processes by changing digestion and physical performance of marine ectotherms. Thus, metabolic rate is expected to increase with increasing temperature (Clarke & Fraser, 2004, Ege & Krogh, 1914, Hans O. Pörtner *et al.*, 2006). Since the biological performance of species is extremely sensitive to temperature, most of the species cannot perform well outside their natural thermal window (Angilletta Jr & Angilletta, 2009, Kearney & Porter, 2009). This may result in reduced somatic growth and reproduction (Pörtner *et al.*, 2001), and considerably influences their biology and geographical distribution depending on their realized thermal niches (Bozinovic *et al.*, 2011, Hans O. Pörtner *et al.*, 2006, Stuart-Smith *et al.*, 2017).

1.3 Ocean acidification

The study of how ocean acidification affects marine biota has attracted considerable attention in the last decade. There have been tremendous efforts during this period to increase our understanding of how ocean acidification may affect individual organisms and communities. It is widely recognised that ocean acidification lowers pH levels, potentially exerting significant impacts on many calcifying organisms (Hofmann *et al.*, 2010). On the other hand, although recent progress on the potential effect of acidification on other taxa, such as fishes is promising; we are still unable to make any generalization out of it due to the fact that the effects of acidification are not consistent among fish species (Kroeker *et al.*, 2013). Ocean acidification can raise the energetic costs involved with calcification and acid-base regulation (Kroeker *et al.*, 2013, Pörtner, 2008). Acidification lowers the saturation state of calcium carbonate which makes the production of hard calcified parts difficult for species like corals and shellfish, thus affecting their growth and survival (Hoegh-Guldberg *et al.*, 2007, Orr *et al.*, 2005). Therefore, it is not surprising that most of the earlier studies of ocean acidification have focused on calcifiers. However, recent efforts suggest that ocean acidification can exert significant negative effects on other organisms as well, including fishes, by affecting embryonic development (Tseng *et al.*, 2013), tissue/organ health (Frommel *et al.*, 2011), larval and juvenile growth (Baumann *et al.*, 2011), metabolism (Franke & Clemmesen, 2011, Miller *et al.*, 2012), fitness (Franke & Clemmesen, 2011), behaviour (Devine *et al.*, 2012, Dixson *et al.*, 2010, Domenici *et al.*, 2012, Ferrari *et al.*, 2012, Munday *et al.*, 2009, Simpson *et al.*, 2011), capability of successful settlement of larval fish (Rossi *et al.*, 2015), and reducing the ability of food search efficiency for predatory sharks (Pistevos *et al.*, 2015). Many of the changes driven by ocean acidification are related to alterations of species behavior, as organisms fail to respond appropriately to homing cues (Munday *et al.*, 2009, Rossi *et al.*, 2018) and predatory and alarm cues (Dixson *et al.*, 2010, Ferrari *et al.*, 2017). While there is ample evidence that ocean acidification can negatively affect the growth of calcifying taxa, the growth of opportunistic species such as diatoms and fleshy algae can be boosted (Kroeker *et al.*, 2013). These studies highlight a pressing need for a greater understanding on the effect of acidification at the population (across different life history stages) and the community level.

1.4 Influence of combined climate stressors on marine organisms

While there is evidence that ocean warming and ocean acidification in isolation can greatly influence marine biota, we are yet to develop a comprehensive understanding on the combined effect of these two co-occurring global stressors. Studies suggested that the impact on organisms varies in direction and magnitude depending on whether stressors were tested in isolation or in combination (Ferrari *et al.*, 2015, Kroeker *et al.*, 2013, Nowicki *et al.*, 2012). In the natural environment, organisms are subjected to the multi-stressor effect of human-induced global change. The response of species to these effects may be synergistic, additive or even antagonistic depending on species-specific sensitivities and related ecological processes (Fulton, 2011, Seabra *et al.*, 2015).

Therefore, it is increasingly important to account for warming and acidification on the future of marine biota. In fact, an increasing number of studies indicate that warming and acidification together can influence a diverse range of marine organisms by affecting their survival, calcification, growth and abundance (Byrne & Przeslawski, 2013, Crain *et al.*, 2008, Garzke *et al.*, 2016, Paul *et al.*, 2015, Przeslawski *et al.*, 2015), body size, and fatty acid composition (Garzke *et al.*, 2016). Warming and acidification together can also influence metabolic and foraging rate, and thus primary and secondary production (Nagelkerken & Connell, 2015). Warming and acidification also interactively affect marine organisms by changing their energy budgets (Bozinovic & Pörtner, 2015).

In spite of all these efforts, our understanding of the combined effects of warming and acidification has been largely hindered by a lack of experiments that are conducted at the food-web level and incorporating higher-trophic level species. This is important because experiments on the level of food webs with representative ecological complexity has the potential to capture both direct and indirect effects of altered consumer–resource interactions which could play a pivotal role in influencing species response and shaping the overall community structure. Most of the studies on the combined effect of warming and acidification have targeted invertebrates, or the egg and larval stages of fishes, but have not considered food web that comprised several trophic levels and a diversified food web community. Therefore, experiments that include multiple stressors, multi-trophic levels, and diversified communities should be at the frontline of future research to test the response of organisms and communities to climate change in the 21st century.

1.5 Food-webs in the context of climate change

1.5.1 Direct negative effect of ocean warming

The responses of species to global change are not individual-based; they are connected through a network of trophic relationships within and across trophic levels (Van der Putten *et al.*, 2010, Walther, 2010). The flow of energy in a food web from lower trophic level to higher trophic levels is determined by various biological interactions (e.g., predator-prey relationships, competition, facilitation, and mutualism) of species that are directly or indirectly linked to adjacent trophic levels (Doney *et al.*, 2012, Woodward *et al.*, 2010). The sensitivity and response of individual species under climate change could be influenced by these biological interactions and could have cascading effects on other species at the same trophic level or the next trophic levels above or below. Thus, the response of individual organisms or functional groups could differ significantly when considered at a food web level.

Climate change can have a diverse and contrasting impact on the different trophic levels of a food web. For example, one of the prevailing concepts of our understanding of the effects of increasing temperature on food webs is that consumer production is predominantly controlled indirectly by temperature effects on primary production through boosted productivity that propagates up the food web (Cushing, 1982). However, metabolic theory of ecology (Brown *et al.*, 2004) suggests that strong top-down control by consumers could be more important under warming, as heterotrophic (respiration-limited) metabolism is more sensitive to warming than autotrophic (photosynthesis-limited) metabolism and production. This metabolism driven difference can induce mismatches between resource supply and consumer demand between two successive trophic levels (López-Urrutia *et al.*, 2006). This may have far-reaching consequences when we consider three- or more trophic-level food chains because food chain length can alter the response of organisms at different trophic levels (Hansson *et al.*, 2013).

Climate change can independently affect, or synergistically amplify, the effect of other disturbances such as habitat modification and decouple, alter, or concentrate energy flows towards a smaller number of species, removing alternative feeding pathways in the food web (Brook *et al.*, 2008, Tylianakis *et al.*, 2008). Although, studies suggest that synergies among the multiple ecosystem stressors are not the most common, and other interaction types such as antagonistic and additive effects should also be considered in ecosystem studies (Côté *et al.*, 2016). The different types of interactions between multiple ecosystem stressors could result in a modified food web through major structural changes such as shifts in the number of trophic groups and links within a food web or a major change in the energy flow and shifts in the biomass of functional groups, affecting ecosystem functioning (Yvon-Durocher *et al.*, 2015).

Besides reducing the net energy flow to the next trophic level within a food web, climate change can also weaken the energy transfer efficiency between primary producers and consumers by weakening or decoupling trophic linkages (Sommer & Lengfellner, 2008). Climate change driven boosts in productivity may therefore not necessarily transfer to higher trophic levels or be converted to an increase in productivity for the species at the next trophic level (Goldenberg *et al.*, 2017). An increase in dominance of herbivory-resistant primary producers, such as some species of the cyanobacteria, can also potentially divert productivity into alternate food web pathways, which are unavailable to higher trophic levels (Davis *et al.*, 2010, Diaz & Rosenberg, 2008). Cyanobacteria, and other less desirable weedy species such as turf algae, have been forecast to increase in dominance due to global warming (Hansson *et al.*, 2013, Paul, 2008). This increase in the dominance of undesirable weedy species at the bottom of the food web combined with the higher energetic demand of the predators (metabolism driven) can jeopardise intermediate trophic levels, with unknown consequences for the higher order trophic levels of the food web. Alternatively, collapse in the biomass of important food web species at intermediate or higher trophic levels could also open a window of opportunity for highly voracious, short-lived predatory species at higher trophic levels (e.g. cephalopods), which can reshuffle overall community structure of the food web.

1.5.2 Accounting for species interactions within food webs

Ecological communities consist of many species that frequently interact with each other. These consumer-resource interactions are particularly important in food web dynamics since they determine the majority of energy fluxes between individuals, and through ecological communities and ecosystems (Dell *et al.*, 2014). Climate change can profoundly affect species interactions (Tylianakis *et al.*, 2008) and can strengthen top down control within food web (Marino *et al.*, 2018). However, most of the predictive models ignore important biotic interactions when forecasting climate change effects on biota.

The effect of direct and indirect biotic interactions is further exemplified via its potential upward or downward cascading effect within the food webs. For example, a prey which is directly linked to its predator through feeding interactions may also be involved in direct interference as a competitor if it shares a prey species with its predator. Species at different trophic levels also vary in their sensitivity to warming due to differences in metabolic rates (Allen *et al.*, 2005). Therefore considering ecological complexity in addition to species physiological response to external perturbation is important to predict the consequences of climate change (warming and acidification) induced cascading effects on future food webs. For example, the direct negative effect of a global stressor (e.g. acidification) could be dampened by an indirect positive effect (e.g. mediated by changes in food availability), meaning it is important to consider complex ecological responses across the food web (Goldenberg *et al.*, 2018, Sswat *et al.*, 2018).

Even though direct negative effects of global stressors are predicted for organisms, including fish, crustaceans, and calcifying herbivores, some species have been observed to increase in density at natural analogs of ocean acidification representing near-future CO_2 levels (Connell *et al.*, 2017, Nagelkerken *et al.*, 2017). A similarly positive response, such as an increase in growth in some species, has been observed under warming when food (prey resources) is not a limiting factor (Pistevos *et al.*, 2015).

Crustaceans can serve as an important link (as prey) between benthic primary production, benthic predators as well as for pelagic environments, and are often less sensitive than many other invertebrates to acidification (Wittmann & Pörtner, 2013). Such resilience in lower-trophic-level prey species could be important for food webs facing external perturbations. Prey species which can maintain their abundance (e.g. via a high reproductive rate) in the face of increased predation due to warming, can positively affect community structure by sustaining the densities of predators.

1.5.3 Adaptation and plasticity in species

Species are always not uniform in their entities, but are composed of different populations that vary in phenotypic plasticity and their thermal niches, and thus can be adapted to local conditions (Valladares *et al.*, 2014). The plasticity and potential adaptation may affect species production and distributions in a warming climate. Particularly actively foraging animals such as fish could pose greater plasticity because of their diversified diet (Duffy *et al.*, 2007), capability of reacting quickly to external perturbation through their mobility, and complex behaviour (Goldenberg *et al.*, 2018, Tuomainen & Candolin, 2011), and have remarkable capacity in using the complexity of their environment to adjust to abiotic stress (Schmidt *et al.*, 2010). Therefore, understanding the response of species community characterized by such capacity (plasticity) to global change is particularly challenging. Additionally, some species such as those living in shallow coastal areas could experience a wide range of environmental variability that overlap in their thermal tolerance and thus may be more adapted to local conditions. For example, recent study (Goldenberg *et al.*, 2018) showed that the realised thermal niche of many shallow-water coastal species in temperate South Australia is warmer than the mean average summer temperature of the coast. This suggests that higher thermal tolerances would not be unexpected for some of the temperate fish species. On the contrary, several earlier studies indicated that tropical species have narrower thermal niches than temperate species (Araújo *et al.*, 2013, Pörtner & Farrell, 2008, Sunday *et al.*, 2011).

The potentially diverse response of species to global stressors implicates that predicting the impact of climate change on future food webs is not straightforward. The response of organisms and communities to ocean warming is likely to be largely influenced by the trophic structure, availability of prey resources, predator behaviour, species interaction, trophic strengthening, diversity, plasticity, local adaptation the emergence of alien species and geographical distribution. The picture is further complicated by the interaction of global and local stressors that affect our oceans, such as fishing pressure, eutrophication, and habitat modification (Halpern *et al.*, 2008). Fishing can also induce greater variability in the ecosystem by cascading effects where top predators are selectively removed from the system and short-lived opportunistic groups flourish. Thus, the interactive effects of global and local stressors make it more difficult for fisheries managers to formulate fixed management guidelines.

1.6 Thesis aim and approach

Whilst our understanding of the impact of warming and acidification in isolation on species has steadily increased, we still know little of the combined effect of these two global stressors on marine food webs, studied in ecologically more realistic experimental setting or real-world systems (field experiments). Since warming and acidification co-occur and will be doing so in the future it is important to investigate their potential combined role in shaping future marine communities and ecosystem function. Although meta-analysis reveals some potential impact of these two stressors on various organisms, the effects at ecosystem level can only be inferred from this. Most studies have been conducted either on a single species, with stressors in isolation, over short time scales (typically days to weeks), or in microcosm studies, and are therefore unable to capture the complexity of whole food webs.

A range of modelling approach have been developed to project future changes in populations of fisheries and food web under ongoing climate change (Brown *et al.*, 2010, Fulton, 2011, Griffith *et al.*, 2012, Griffith *et al.*, 2011, Olsen *et al.*, 2018, Ortega-Cisneros *et al.*, 2018, Weijerman *et al.*, 2015). Most of these projections, however, are based on species thermal niches, ignoring the potentially large role of indirect (e.g. shifting predator-prey relationships) and interactive stressor effects (e.g., with ocean acidification) on model outcomes. Although a few studies have been taken a step forward to improve our understanding of how multiple stressors such as warming, acidification, and fishing interact and affect marine community (Griffith *et al.*, 2012, Koenigstein *et al.*, 2016), they lack incorporation of realistic, opposite of theoretical, biotic interaction in response to future climate change.

Food webs can provide complex yet tractable descriptions of species interactions, biodiversity and ecosystem structure (Dunne *et al.*, 2002). A recent study, using a representative food web experiments, showed that ecological complexity can buffer many of the impacts of future climate change (warming and acidification) on marine consumers (Goldenberg *et al.*, 2018). We particularly lack evidence of how the top of the food web (piscivores and apex predators) will respond to future climate change. This is challenging because piscivores and apex predators are difficult to study in experimental approaches within a food web context and therefore it is challenging to gather these data experimentally. Mechanistic insights into the responses of future food webs to global and local stressors requires a combination of different approaches such as experimental manipulation of food webs, integrated with ecosystem modeling approaches (Stewart *et al.*, 2013).

By combining large-scale multi-level mesocosm food web experiments and food web modelling tools, both static as well as dynamic (Ecopath with Ecosim), my thesis provides a better understanding of the response of future marine food webs to the combined effects of ocean warming and ocean acidification. Additionally, this study to the best of my knowledge, for the first time models marine food webs under two global stressors in conjunction with local stressors such as fishing.

This thesis assessed the following specific aims:

1. Examine whether global warming and ocean acidification enhance energy fluxes through bottom-up effects that stimulate primary productivity (Chapter 2).
2. Determine whether biomass of lower trophic levels will dominate the future structure of marine food webs or allow opportunistic groups to divert productivity to alternative pathways (Chapter 2).
3. Show how the interaction between two global stressors (ocean acidification and warming) potentially affects future food webs and fisheries stocks of a temperate coastal ecosystem (Chapter 3).
4. Verify whether fishing effort as an additional local stressor amplifies or lessen the response of these two global stressors (ocean acidification and warming) (Chapter 3).
5. Predict how the change in relative trophic interactions strength (change in magnitude) of direct and indirect interactions alter (increase or reduce) the direction of biomass change for different food web groups under future global change (Chapter 4).

1.7 Thesis outline

Each thesis chapter is outlined below.

Chapter 1

In chapter 1, I provide a general introduction to climate change research in marine ecosystems and identify existing knowledge gaps that need to be addressed to improve our understanding of the response of future food webs to global change.

Chapter 2

Marine ecosystem functioning is maintained by the flow of energy from primary producers to predators which could be seriously hampered by perturbations. Disturbances can decouple, alter, or concentrate energy flows towards a smaller number of species or remove alternative feeding pathways in the food web. This can open the window for opportunistic species to flourish and shift ecosystems to a different state. In chapter 2, I examine the combined effect of global warming and ocean acidification on the energy fluxes through a marine food web. Using a sophisticated mesocosm experiment that mimics temperate rocky reefs, I model energy flows through a species-rich multi-level food web, with live habitats and natural abiotic variability. I show how future climate change can potentially weaken marine food webs through reduced energy flow to higher trophic levels and a shift towards a more detritus-based system, leading to food web simplification.

Chapter 3

Marine ecosystems and fisheries stocks are facing significant challenges due to the cumulative (and potentially synergistic) effects of multiple global and local stressors such as overfishing. Past attempts to project future changes in communities and food webs under climate change incorporated the direct impact of temperature on species physiology but largely ignored in-situ responses of species interaction to climate change. Species interactions have the potential to affect predator-prey relationships and thus shape future marine communities. In chapter 3, I examine how the combinations of two global stressors (ocean acidification and warming) affect future food webs and fisheries stocks. This was achieved through an integration of experimental data that includes species physiology and species interactions to global warming within an ecosystem modelling approach. I used a time dynamic Ecosim model simulation approach to predict the future state of fisheries and food web of a temperate marine food web at 2100. The climate models were manipulated based on the experimental data compared to the base model (no change scenario at 2100) Additionally, I examined how fishing effort as an additional local stressor affect the response of these two global stressors.

Chapter 4

Consumer-resource interactions are of particular importance in food web dynamics since they determine the majority of energy fluxes between individuals and communities within the food web.

Quantifying the strength of consumer-resource interactions, both direct and indirect, is essential for understanding how ecological communities are organized and how they respond to any internal or external perturbations. In the previous chapter (chapter 3), I showed the potential future state for fisheries and food web in response to 21^{st} century climate change. In this chapter (chapter 4), I explain the underlying mechanisms that drive such changes in the future food web. Specifically, I examine and show how changes in relative trophic interaction strength (change in magnitude) of direct and indirect species interactions are likely to alter (increase or reduce) the direction of biomass change for different food web groups under future global change.

Chapter 5

In chapter 5, I discuss the overall significance of this study and the advances it has made to the field of climate change research. Whilst our understanding on the impact of warming and acidification in isolation on species has steadily increased, we still know little on the combined effect of these two global stressors on marine food webs, studied in an ecologically more realistic experimental setting or real-world systems. However, even the more complex and realistic experimental setting is not good enough to directly simulate the potential future state of a natural food web and fisheries due to its scale limitation. Therefore, a holistic approach that considers a combination of different approaches such as experimental manipulation of food webs, and integrated with ecosystem modelling approaches could be a way forward to improve our understanding of the functioning of future food webs. In the first chapter, I show the potential future state of a marine mesocosm food web and then used the information from mesocosm experiment to build dynamic food web models and predict the future state of a four trophic level natural food web. I also describe the mechanism behind the dynamic response of the food web at different scale and trophic levels. Finally, I outline the strengths and weaknesses of the approaches used in this thesis with possible directions for future research.

Thesis

Each data chapter (2 - 4) has been written in the form of an individual scientific paper and therefore uses article formatting. A list of co-authors and their contributions to the paper has been highlighted in the statement of authorship for each data chapter. A comprehensive reference list is included at the end of each chapter. Chapter 2 has already been published in a peer-reviewed journal.

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CHAPTER II

CHAPTER II

Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation

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Name of Principal Author (Candidate)	Hadayet Ullah		
Contribution to the Paper	Study design, data collection, data analysis, writing		
Overall percentage (%)	85		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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RESEARCH ARTICLE

Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation

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Abstract

Global warming and ocean acidification are forecast to exert significant impacts on marine ecosystems worldwide. However, most of these projections are based on ecological proxies or experiments on single species or simplified food webs. How energy fluxes are likely to change in marine food webs in response to future climates remains unclear, hampering forecasts of ecosystem functioning. Using a sophisticated mesocosm experiment, we model energy flows through a species-rich multilevel food web, with live habitats, natural abiotic variability, and the potential for intra- and intergenerational adaptation. We show experimentally that the combined stress of acidification and warming reduced energy flows from the first trophic level (primary producers and detritus) to the second (herbivores), and from the second to the third trophic level (carnivores). Warming in isolation also reduced the energy flow from herbivores to carnivores, the efficiency of energy transfer from primary producers and detritus to herbivores and detritivores, and the living biomass of detritivores, herbivores, and carnivores. Whilst warming and acidification jointly boosted primary producer biomass through an expansion of cyanobacteria, this biomass was converted to detritus rather than to biomass at higher trophic levels—i.e., production was constrained to the base of the food web. In contrast, ocean acidification affected the food web positively by enhancing trophic flow from detritus and primary producers to herbivores, and by increasing the biomass of carnivores. Our results show how future climate change can potentially weaken marine food webs through reduced energy flow to higher trophic levels and a shift towards a more detritus-based system, leading to food web simplification and altered producer–consumer dynamics, both of which have important implications for the structuring of benthic communities.

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Author summary

Healthy marine ecosystems are crucial for people's livelihoods and food production. Global climate stressors, such as warming and ocean acidification, can drastically impact the structure and function of marine food webs, diminishing the production of goods and

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Abbreviations: MTE, metabolic theory of ecology; *OA*, elevated CO_2; *OAT*, elevated CO_2 and temperature; *T*, elevated temperature.

services. Our ability to predict how future food webs will respond to a changing environment is limited by our understanding of species responses to climate change, which are often tested in isolation or in simplified experimental designs. More realistic predictions of the impacts of climate change on ecosystems requires consideration of entire species communities, including the species interactions that can buffer or exacerbate these impacts. We experimentally tested the effects of warming and acidification, both individually and in combination, on a benthic marine food web in a near-natural ecological setting. Energy flow from the first trophic level (primary producers and detritus) to the second (herbivores), and from the second to the third trophic level (carnivores) was quantified under these different regimes. We show that warming, either alone or in combination with acidification, can constrain productivity to the bottom of the food web by enhancing cyanobacterial biomass and reducing energy flow to higher trophic levels, thus lowering energy transfer efficiency between producers and consumers. In contrast, increased ocean acidification alone showed a positive effect on herbivores and carnivores. Our finding is important because it demonstrates that future warming could drive marine food web collapses to potentially simplified and less productive coastal systems.

Introduction

Forecasting the effect of global change on ecosystem functioning is a major challenge in ecology [1], partly because future climate shifts are likely to reorganize complex food webs, generating novel communities composed of new combinations of species [2]. In marine ecosystems, multiple anthropogenic stressors are already eroding biodiversity by changing the composition of species [3] and affecting rates of biomass transfer through ecological networks, resulting in altered food web organisation and dynamics [4,5]. While overexploitation is largely responsible for altering the structure and functioning of many ecosystems [6], global warming is forecast to amplify these effects, having serious consequences for the health and sustainability of marine ecosystems [7]. Despite many studies showing a potential detrimental effect of climate change on biodiversity [2], we still lack a strong and coherent theoretical and empirical foundation for understanding how species communities are likely to respond to global change [8].

Marine ecosystem functioning is maintained by the flow of energy from primary producers at the base of food webs through intermediate consumers to top predators, as well as via cycling of materials such as nutrients within the ecosystem [7,9]. Disturbances such as habitat modification can decouple, alter, or concentrate energy flows towards a smaller number of species and erode resilience by removing alternative feeding pathways in the food web [10]. This can drive trophic food webs to shift states and potentially collapse [11]. In this context, climate change can independently affect, or synergistically amplify, the effect of other disturbances such as habitat degradation, species overexploitation, and species invasions [12]. This can reconfigure future food webs through major structural changes, like shifts in the number of trophic groups and links that connect species at the top of the food chain to basal species, which can result in altered flows of energy and shifts in the biomass of key functional groups, leading to biodiversity loss, with potentially serious implications for ecosystem functioning [13].

Global warming and ocean acidification are already affecting the physiology, behaviour, phenology, demography, abundance, and distribution of many marine species [14]. Elevated temperature (*T*) affects fish performance and growth through increasing metabolic rates and respiratory demands, leading to a reduced aerobic scope for important life-supporting activities such as feeding, somatic growth, maturation, and predator avoidance [15–17]. Ocean acidification raises the energetic costs involved with calcification and acid-base regulation [18,19] and can impair neural functioning [20]. Besides such direct effects, there is a suite of indirect effects that can impact species persistence and diversity under global change [21].

The survival of a species or a group of species in an ecosystem depends on how well they respond to dynamic changes in productivity, in terms of direction (i.e., positive or negative) and strength. However, the responses of species to global change are not individual-based; they are connected through biotic interactions within and across trophic levels [22,23]. Importantly, the energy flow (biomass fluxes) to higher trophic levels is determined by various biological interactions (e.g., predator–prey relationships, competition, facilitation, and mutualism) of species that are directly or indirectly linked to proximate trophic levels [7,24]. For example, climate change can weaken the energy transfer efficiency between primary producers and consumers by reducing feeding performance with potential impacts further up the food chain [25]. Although ocean warming and acidification can boost basal productivity [26,27], it does not necessarily result in an increase in secondary productivity [28]. The propagation of production through trophic levels could be modified by food chain length [29] or with an increase in the dominance of herbivory-resistant primary producers [30,31]. Cyanobacteria, in the form of toxin-producing deleterious phytoplankton, can potentially divert productivity into alternate food web pathways, which are unavailable to higher trophic levels. Cyanobacteria have been forecast to increase in dominance as a result of global warming [29]. Conversely, in line with metabolic theory [32], increased food demand in predators can intensify top-down control of their prey populations [16], influencing body size-driven metabolic differences in food web structure [33]. Thus, a dichotomy between enhanced bottom up control through an increase in herbivory-resistant primary producers and enhanced top-down control due to higher metabolism-driven energetic demand in predators can jeopardise intermediate trophic levels and weaken food web stability. Such a mismatch can alter trophic energy flow dynamics [25,34], with the consequences expected to be greater in food webs with three trophic levels or more [29].

Forecasting the effects of climate change at the ecosystem level requires holistic approaches that consider complex ecological communities with multiple functional groups or species of different trophic levels [35]. Large-scale mesocosm experiments are ideal for such approaches and have the potential to enhance our understanding of the ecological consequences of climate change on the sudden expansion of opportunistic species, species extinction risk, community structure, and ecosystem functions [36].

We did a community-level manipulation of a temperate marine food web, consisting of 17 functional groups (ranging from primary producers to herbivores to carnivores across 3 broad trophic levels). We maintained these groups in an indoor mesocosm experiment divided into 4 treatments: elevated CO_2 (*OA*), elevated temperature (*T*), elevated CO_2 and temperature (*OAT*), and ambient controls (present-day levels of pCO_2 and temperature), each with 3 replicate mesocosms per treatment. We achieved an elevated pCO_2 of approximately 900 ppm (pH = 7.89) and warming of +2.8˚C, which represent the conditions predicted for the end of this century, following a business-as-usual emission scenario (RCP8.5) [37]. We used an ecosystem modelling tool (Ecopath) widely used to characterise quantitative food web structures and pathways of energy flows in aquatic ecosystems [38]. The Ecopath model is built on a system of linear equations and creates a static mass-balanced snapshot of the resources in a given ecosystem according to biomass estimates and food consumption relationships of functional groups that represent the organisms in a food web. The quantitative description of food web properties is essential to advance our understanding of ecosystem structure and functioning at a community level [39]. Using the Ecopath approach, we tested whether: (1) global warming and ocean acidification enhance energy fluxes through bottom-up effects that stimulate primary productivity, or (2) global warming and ocean acidification allow opportunistc groups to proliferate and divert productivity into alternative pathways, as well as (3) biomass of lower trophic levels and detritus will dominate the future structure of marine food webs due to reduced energy transfer efficiencies to higher trophic levels. We also test whether synergies between ocean acidification and increasing temperature are likely to amplify the effect of global warming on marine ecosystems. Thus, through a combination of experimental and modelling approaches, we provide new evidence for altered energy flow (biomass fluxes) and transfer efficiency through food webs due to global change stressors, which is crucial for understanding the potential effects of climate change on marine food web structure and functioning.

Results

Neither warming nor acidification affected the energy flow originating from primary producers and detritus at trophic level 1 (Fig 1; S1 Table). The combined effect of warming and acidification (*OAT*) ($p = 0.003$; post hoc energy flow: *OAT* < control) reduced the energy flow from trophic level 1 to trophic level 2. In contrast, energy flow was higher in the *OA*-only treatment compared to the controls ($p = 0.011$; post hoc energy flow: high CO_2 > control). Warming (*T* and *OAT*) also reduced the energy flows from trophic level 2 to trophic level 3 (ANOVA, $F_{1,8} = 43.06$, $p < 0.001$).

The individual functional groups at trophic level 2 and trophic level 3 showed variable responses to warming and acidification. For example, functional groups such as meiobenthos, copepods, small epifaunal invertebrates, and filter feeders experienced significantly lower energy flow from trophic level 1 to trophic level 2 under warming (*T*), while macroinvertebrates experienced reduced flow under the combination of warming and acidification (*OAT*) (S1 Fig; S4 Table). Furthermore, warming significantly reduced the capacity of transferring energy flows of omnivorous, filter feeding, and benthic carnivorous fish, while benthic carnivorous and carnivorous fish experienced an increase in flow under acidification from trophic level 2 to trophic level 3 (S2 Fig, S5 Table).

The reduced energy flow from trophic levels 1 to 2 under the combined warming-acidification treatment (*OAT*) coincided with a negative effect of warming (*T* and *OAT*) on energy transfer efficiency between levels 1 and 2 (ANOVA, $F_{1,8} = 11.22$, $p = 0.010$) (Fig 1; S1 Table). In contrast, *OA* had no effect on energy transfer efficiency between these levels. Energy transfer efficiency between trophic levels 2 to 3 was not affected by either warming or acidification.

Whilst the combined effect of warming and acidification enhanced the biomass of primary producers ($p = 0.001$; post hoc living biomass: *OAT* > control) and acidification enhanced secondary consumer biomass ($p = 0.034$; post hoc living biomass: *OA* > control), warming (*T* and *OAT*), irrespective of ocean acidification, caused a decrease in living biomass at trophic levels 2 and 3 (Fig 2; S2 Table). Warming (*T* and *OAT*) induced higher cyanobacterial biomass (ANOVA, $F_{1,8} = 19.90$, $p = 0.002$), replacing palatable turf algae at trophic level 1 (Fig 3a, S3a Table). Consequently, energy was not transferred to successive trophic levels through consumption but accumulated as detrital biomass (ANOVA, $F_{1,8} = 9.12$, $p = 0.017$) (Fig 3b; S3b Table) at the bottom of the food web. The system became less efficient in recycling the accumulated detrital biomass under warming (S3 Fig; S3c Table; ANOVA, $F_{1,8} = 9.31$, $p = 0.016$), suggesting a collapse at the base of the food web.

Discussion

Our study provides strong empirical evidence that global warming has the capacity to drive a collapse in marine food webs by altering energy flows between successive trophic levels. In our

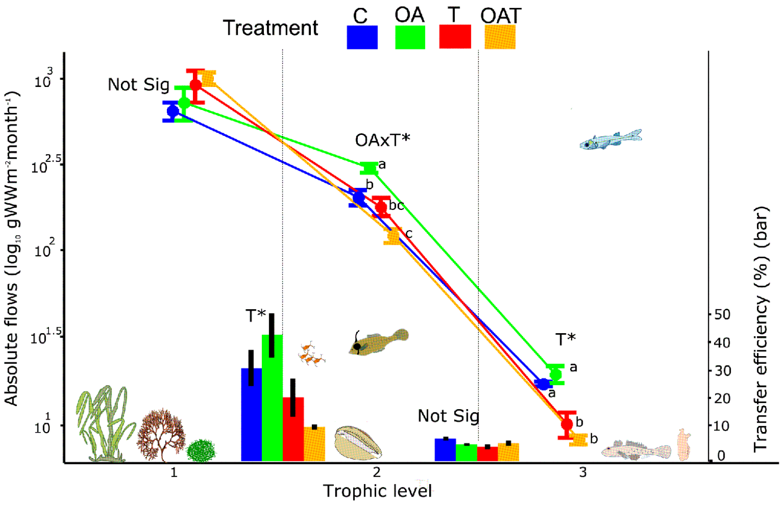

Fig 1. The effects of future climate on absolute flows and transfer efficiency between successive trophic levels of the mesocosm food web. Absolute flows, shown as line diagrams, refer to the total amount of energy that flows to higher trophic levels through consumption (log10 g Wet Weight/m^2/month) aggregated by trophic level. The first trophic level shows flows originating from both the primary producers and detritus, which are transferred to the second and third trophic level through consumption by herbivores and carnivores, respectively. Transfer efficiency, presented as bar charts, refer to the ratio at which absolute flows are transferred from one trophic level to the next. Mean ± SE are based on $n = 3$ mesocosms. Significant effects ($p < 0.05$) within trophic levels are based on two-way ANOVAs (df = 1,8) and are indicated with asterisks. See S1 Table for statistical test outcomes. Means with different lower-case letters indicate significant differences among treatments based on posthoc tests corrected for false discovery rate and done separately for different trophic levels. The distribution of organisms within the mesocosms is reflected as their vertical position inside the graph (ranging from the bottom of the mesocosm to the surface of the water column). Species cliparts were obtained or modified from Openclipart (https://openclipart.org/). C, control; not sig, not significantly different; OA, elevated CO_2; OAT, elevated CO_2 and temperature; T, elevated temperature.

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ecologically complex benthic mesocosm experiment, the combination of warming and acidification enhanced the biomass of primary producers, but reduced energy flow to herbivores, while warming (irrespective of acidification) reduced energy flow to carnivores at higher trophic levels. Warming also decreased the trophic transfer efficiency between primary producers and herbivores, consequently reducing standing biomass of herbivores and carnivores. Other studies based on the metabolic theory of ecology (MTE) [32], however, suggest that temperature-driven increased primary production is likely to propagate through food webs via strong top-down control [40,41], resulting in greater levels of heterotrophic biomass, relative to autotrophic biomass [4]. In our case, the combination of warming and acidification decoupled increased basal productivity from herbivore production, while warming in isolation reduced predator production, making most of the primary production unavailable further up the food chain. Thus, energy from enhanced primary producer biomass under future climate conditions may not always transfer through to successive trophic levels, but instead can decouple food demand and supply. Such a decoupling may alter dietary preferences of consumers, modifying consumer–prey relationships within food webs.

Our current inability to capture more realistic features of food web responses to global climate change is mostly due to a reliance on short-term, small-scale experiments harbouring single species and lower trophic levels, which provide an ambiguous approximation of

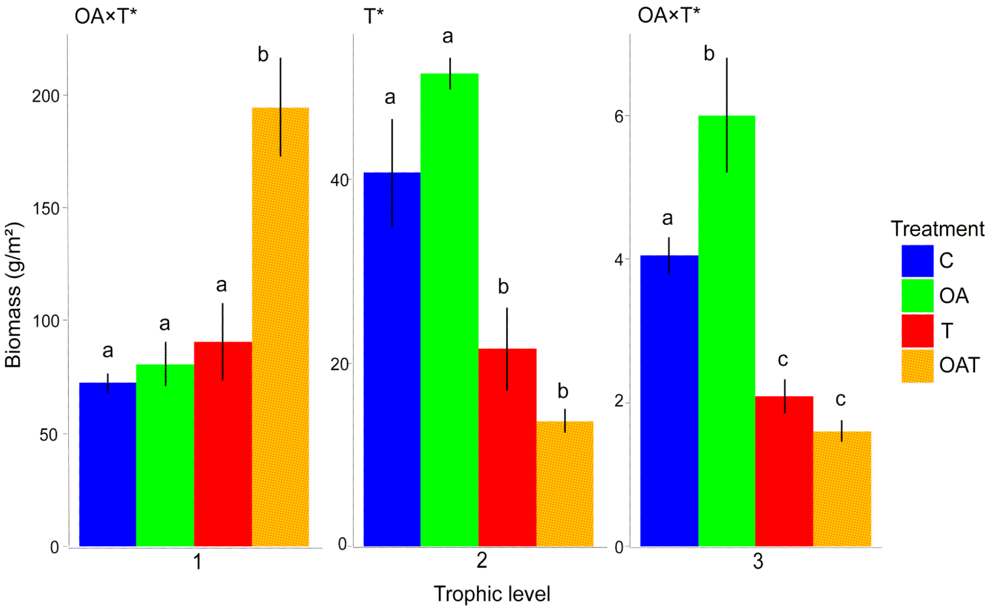

Fig 2. Living biomass of primary producers (trophic level 1), primary consumers (level 2), and secondary consumers (level 3) across functional groups within the mesocosms. The biomass of functional groups with intermediate trophic levels (e.g., trophic level of filter feeders = 2.4) was assigned to the levels 2 and 3 according to their relative contribution to trophic flow (e.g., 60% to level 2 and 40% to level 3). At the third trophic level, the decrease in biomass under T and OAT is primarily driven by filter feeders, while a negative effect was not apparent in most other functional groups such as the fishes (see S2 Fig). Living biomass includes 16 functional groups excluding detritus. Values are means ± SE across mesocosms ($n = 3$). Significant interactions or main effects ($p < 0.05$) within trophic levels are based on two-way ANOVAs (df = 1,8) and are indicated with asterisks. See S2 Table for statistical test outcomes. Means with different lowercase letters indicate significant difference among treatments based on posthoc tests corrected for false discovery rate and done separately for different trophic levels. C, control; OA, elevated CO_2, OAT, elevated CO_2 and temperature; T, elevated temperature.

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naturally complex food webs [4]. Moreover, few studies of ecological responses to climate change include predator–prey dynamics and competitive interactions or allow for the potential proliferation of opportunistic groups of species, all of which can greatly influence or reverse many of the predicted responses of species and communities to climate change [26]. In contrast, our experimental results account for complex multispecies interactions and biotic processes, providing an improved representation of natural systems and how these are likely to respond to global warming [42,43]. Our experimental data provide insights into how anthropogenic climate change can potentially affect food web dynamics for relatively short-lived taxa. This is because large scale mesocosm experiments such as ours bridge the gap between simplified experimental conditions and the real world [44], providing important opportunities to better understand the likely mechanisms by which primary productivity under certain future climate conditions propagates through the food web.

Increased standing biomass in our benthic mesocosm experiment was most evident for cyanobacteria under warming (irrespective of acidification). Warming is known to enhance the primary productivity of some taxa, particularly of weedy species such as turf algae [45]. Cyanobacteria form a major component of turf algae [46,47] and are predicted to proliferate and expand under eutrophication and climate change [48]. The potential for cyanobacterial

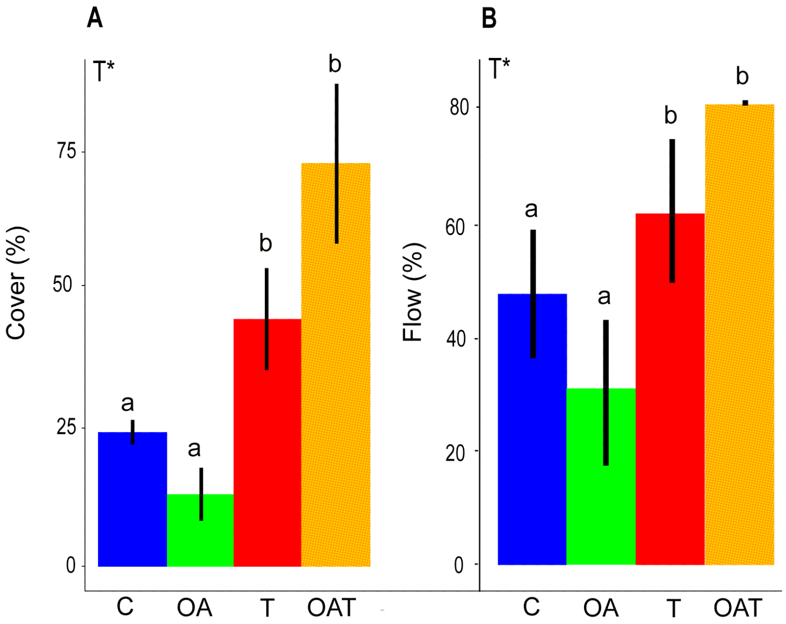

Fig 3. Relative proportion of cyanobacteria (as a percentage) to turf algae in mat-forming algae measured as benthic cover (A). Flows of production (%) to detritus pool relative to primary productivity (B). Mean ± SE values per mesocosm are given ($n = 3$). Significant main effects ($p < 0.05$) are based on two-way ANOVAs (df = 1,8) and are indicated with asterisks. Means with different lowercase letters indicate significant difference among treatments. See S3 Table for statistical test outcomes. C, control; OA, elevated CO_2, OAT, elevated CO_2 and temperature; T, elevated temperature.

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dominance in turf algal assemblages under future warming and acidification has been demonstrated previously using experimental approaches [49]. The effect of warming sea temperatures is expected to be greater in areas that are shallow and nutrient rich [50], providing ideal environmental conditions for cyanobacteria to invade other benthic primary producer groups [51,52]. Some cyanobacteria are known to be toxic and cause localized anoxia and mortality in marine organisms [48]. Cyanobacteria also produce potent allelochemicals that deter feeding and are difficult to control by grazers [53]. Herbivores like macroinvertebrates and small epifaunal invertebrates predominantly feed on mat-forming turf algae rather than cyanobacteria.

Metabolic theory suggests that consumers will show a greater response to temperature than producers [4,54,55]. Therefore, we hypothesised a priori that warming would drive an increase in metabolic and consumption rates for macroinvertebrates in our experiment. However, reduced food availability, brought about by palatable types of turf algae being replaced by unpalatable cyanobacteria, caused food limitation, preventing increased metabolic rates for macroinvertebrates at higher temperatures, suppressing the flow of energy to the second trophic level [16,56]. Furthermore, biomass of major prey groups such as copepods, small epifaunal invertebrates, and filter feeders, which largely form the diet of consumers at the third trophic level, collapsed under the warming treatments, resulting in significantly less energy available for the third trophic level. One of the reasons for this collapse is an excessive predation pressure on primary consumers by species at the third trophic level (i.e., predators) due to their higher energetic demand [28], which was not matched by any increase in productivity rates of primary consumers under warming. Alternatively, under warming, the consumer–producer relationship at the base of the food web could be nonsynchronous if consumption rates of herbivores peak earlier than the growth rates of producers, creating a mismatch between production and consumption [45]. This means that under certain conditions, even in the absence of herbivory-resistant primary producers, warming-induced metabolic stress of organisms can effectively decouple the consumer–producer relationship if consumer metabolism and consumption cannot keep pace with increasing production.

In our experiment, the collapse of biomass of major functional groups under warming played a major part in reducing the transfer efficiency of energy between trophic levels in a food web. A lower transfer efficiency of energy was evident between trophic levels 1 and 2. This is because transfer efficiency depends on both the availability of food, the biomass of all consumers, and their consumption rates. The lower standing biomass at trophic level 2 and reduced palatable food abundance at trophic level 1 collectively brought about lower overall transfer efficiency between these trophic levels under warming. Metabolic theory states that the structure and dynamics of ecological communities are based on the individual metabolism of organisms where the individual metabolic rate is primarily controlled by body size, body temperature, and resource availability [57]. Metabolic theory does not specifically consider the standing biomass of consumers, which is an important component of our model, allowing us to calculate transfer efficiency. Therefore, food web properties, such as transfer efficiency, are difficult to interpret from the perspective of metabolic theory, yet they can have important community-level effects [58].

The replacement of turf algae by cyanobacteria further resulted in a more detritus-based food web under warming. Detritus can be very important for sustaining food webs and ecosystem stability [59], but only when proper recycling occurs within the system [60]. Decreasing detritus recycling in ecosystems correlates with decreased system resilience to perturbations, with lower rates of recycling resulting in slower recovery [60,61]. We show (based on the Finn's cycling index) that warming significantly reduced the detritus recycling capacity of the system. The inability of herbivores to consume enhanced primary producer biomass and the simultaneous failure of detritivores to transfer excessive detritus production to the successive trophic levels resulted in an accumulation of detrital biomass at the base of the food chain. Therefore, warming-induced detritus accumulation, as observed in our study, might have far-reaching ecosystem consequences for future oceans, such as the spreading of 'dead zones' through increased microbial activity and consumption of dissolved oxygen in bottom waters [30].

Reduced secondary and tertiary production has been forecast under future acidification [2]. However, this pattern was not detected in our experiment in energy flows, a proxy for production at different trophic levels. We show that acidification can in fact exert positive bottom-up effects on energy flow towards secondary producers (trophic level 2). Ocean acidification could increase secondary productivity in situations where strong indirect positive effects dampen the direct negative effects of elevated CO_2, i.e., through increased habitat and food, as well as reduced predator abundances [62,63]. Only benthic carnivores and carnivorous fish at trophic level 3 experienced increased energy flows under acidification, which supports the finding of increased productivity of a carnivorous fish (*Favongobius lateralis*) in a previous study done in a similar ecological setting [28]. In contrast, omnivorous fish showed a decrease in flow and this group was the major contributor of energy flow to trophic level 3 under control conditions. Taken together, the positive effect of acidification on the energy flows of some functional groups and negative or lack of effects on other groups resulted in no overall significant increase in energy flow to trophic level 3 under acidification. Here we quantify secondary and tertiary production, using a more complex (and ecologically realistic) food web, which better captured real-world community structure and important species interactions, and how these are likely to change in response to future global warming and ocean acidification [8,39,64]. This broader food web model also allows us to quantify energy transfer efficiency across multiple trophic levels; an important ecosystem function which can regulate many ecological processes (i.e., trophic structure, food chain length) and mediate ecosystem services (i.e., fisheries production) [65–67]. Our results indicate that the response of future food webs to ocean acidification and temperature are likely to depend on the localized community composition and consumer–resource interactions of the specific ecosystem.

Although we used one of the most complex benthic mesocosm experiments to date, our approach is not devoid of caveats. For example, difficulties in separating the functional roles of turf and cyanobacteria meant that they were modelled as one functional group ‘mat-forming algae’. In our model, we did not consider regular bacteria (other than cyanobacteria) as a separate functional group, but rather considered them under detritus. Thus, detritivores are considered to mainly feed on detritus and its associated bacteria. We opted for not using an extra bacterial compartment because bacteria would largely overshadow any other trophic flows of the system [68]. Our study showed a relatively larger biomass flux between trophic levels 1 to 2 compared to between trophic levels 2 and 3 due to the presence of relatively large-bodied primary consumers (such as herbivorous macroinvertebrates: *Bulla quoyii*), which were too big to handle for the gape-limited predators in our system. The presence of a wider range of higher-order invertebrate predators, as is the case in natural ecosystems, would have reduced this disproportionally high flux between primary producers and primary consumers by stronger top-down control. However, since the focus of our study was to show relative difference among the climate treatments, the results still provide a valuable quantitative insight into the potential future of some benthic marine ecosystem under two co-occurring global climate stressors.

One of the weaknesses of earlier applications of the Ecopath model were assumptions of ‘steady-state’ or equilibrium conditions, meaning that the model outputs should only be considered for the period across which the model input parameters are deemed valid [69]. Ecopath modelling approaches now no longer assume steady-state conditions but instead the model parameterizations are based on a mass-balance assumption over a chosen arbitrary period. The mass-balance approach in Ecopath filters for mutually incompatible estimates of flow [69]. Moreover, under the Ecopath modelling approach, we assumed that mortality for a prey equals consumption of a predator and that all prey are equal in terms of energetic content. Additional care needs to be taken when inferences are drawn from ecosystem models built for highly dynamic systems due to likely nonlinearities in important food web properties of some functional groups, operating at fine temporal scales. Nevertheless, since we used multiple sampling points through time and averages based on multiple replicates for our model input, especially for taxonomic groups that have the potential to show large oscillations with environmental fluctuations, the model outputs are likely to be indicative of near-future ecological states. Lastly, model outputs were tested using the PREBAL diagnostic and pedigree index (see Supplementary Methods for details on model and data quality), and confirmed a stable model that is ecologically robust.

In summary, our results suggest that warming has the capacity to drive an energetic collapse at the base of marine food webs, and this effect can propagate to higher trophic levels—subsequently leading to a collapse in species biomass of the entire food web. The underlying mechanism for this collapse is the replacement of preferred turf algae by cyanobacterial biomass that drives the system towards food limitation for herbivores, with detrimental effects on their predators, combined with a switch towards a less efficient detritus-driven system. Several studies have reported an apparent increase in the occurrence of cyanobacteria in marine waters globally as a result of increasing temperatures [52], and regionally in temperate [70], tropical

[51,71], and subtropical [72,73] areas. Thus, these findings are particularly important in the context of climate change, as mismatches in trophic dynamics can decouple linkages between trophic levels driving ecosystems towards simplified, less productive systems, with cascading effects on ecosystem resilience and functioning.

Materials and methods

Ethics statement

This research was carried out under the approval of the University of Adelaide animal ethics committee (approval S-2012-193A). All the habitats and organisms collections were permitted by the Minister for Transport and Infrastructure and the Government Department of Primary Industry and Regions SA (exemptions: 9902676 and 9902752).

Experimental design

An indoor mesocosm experiment was maintained from February 2015 to July 2015. A total of 12 circular mesocosms, each holding 1,800 L of water were set up inside a large temperature-controlled room to simulate shallow temperate coastal ecosystems typical of the Gulf St. Vincent, South Australia (S4 Fig). All habitats and organisms used in the mesocosms were collected at a depth of 1–5 m within 60 km distance of the mesocosm facility. Each mesocosm comprised of a mosaic of the 3 primary local habitats (with 2 replicate patches per habitat per mesocosm): rocky reef, seagrass, and open sand [74].

Rocky reefs consisted of natural rocks collected in situ and included attached macrophytes dominated by an assemblage of fucoids (Order Fucales; mainly species belonging to the families Fucaceae and Sargassaceae) and benthic invertebrates. Rocks were selected to be as similar as possible in terms of presence and cover of major fucoid species. Seagrass habitat was mimicked by artificial green polypropylene ribbon harbouring epiphytes and planted into fine silica sand at a depth of 6 cm. The seagrass habitat resembled the most abundant local seagrass *Posidonia* spp. [74] and was incubated in situ for 2 weeks to allow for epiphytic colonization. The circular 'rocky reef' patches and 'artificial seagrass' patches were of equal size (0.42 m diameter). The space in between and around these patches was 'open sand' habitat, comprising fine silica sand with a depth range between 6–25 cm. The open sand and sand within the seagrass patches were additionally seeded with 0.025 m^3 natural sediment collected in situ between patches of live seagrass and included all infauna and flora.

Fish and invertebrates were introduced into the mesocosm and represented different feeding guilds (see S6 Table for a list of species associated with the mesocosms, their stocking density, and mean sizes). The fishes were selected based on their high local juvenile abundances in shallow coastal waters during summer, while the gastropods came from the rocks used to build the rocky reef patches and were redistributed evenly among all mesocosms. In the flow-through system, unfiltered seawater from 1.5 km off-shore and 8 m depth continuously supplied nutrients and planktonic propagules to each mesocosm at 2,300 L day^{-1}. A diffuser was used to form a light circular current in the mesocosms to simulate tidal water movement alternating direction in 6-hour intervals (S4 Fig). A lamp was mounted above each mesocosm with a spectrum close to sunlight, which is roughly equivalent to 72.83 ± 24.78 μmoles/m^2/second Photon flux corresponding to a local water depth of 6–7 m (14/10 light-dark cycle, 30-minute dawn and dusk dimming).

We applied a control temperature of 21.0˚C in our mesocosm experiment corresponding to the average summer temperature based on a 5-year dataset of 2 local temperature loggers (5 m depth, 2010–2015, SA Water). *OA* at each mesocosm was achieved through a header tank preconditioned to elevated $p\mathrm{CO}_2$ levels using pure CO_2 (control system ACQ110 Aquatronica, Italy). Additionally, each mesocosm was supported by a 60-L bin bubbled heavily with enriched air at 1,000 ppm $p\mathrm{CO}_2$ (PEGAS 4000 MF Gas Mixer, Columbus Instruments, Columbus, Ohio) or ambient air at 400 ppm $p\mathrm{CO}_2$, to maintain target levels. Submersible titanium heaters inside the 60-L bins were used for the future warming treatments. Temperature and pH were measured daily (Mettler Toledo SevenGo SG2, calibrated daily; S5 Fig), while salinity was measured fortnightly (SR6 refractometer; Vital Sine). The total alkalinity was also measured fortnightly by Gran titration from water samples (888 Titrando, Metrohm, Switzerland). The diurnal variability in pH (S6 Fig) confirms that our mesocosms were autonomous systems that mimicked natural day-night fluctuations. For a description of other seawater properties, see S7 Table.

Species sampling and processing

The fish community, herbivorous macroinvertebrates, small epifaunal invertebrates, filter feeders, and macro-crustaceans were all sampled and counted at the end of the experiment and their biomass measured as wet weight.

Biomass of tanaids, copepods, and meiobenthos was determined using benthic samplers (6.5 cm in diameter and 2 cm depth filled with 1.5 cm of mesocosm sand, with 2 replicate samplers per mesocosm), which were placed at the bottom of the tanks for about a month, allowing colonization of these species. Samples were collected twice from each mesocosm during the experimental period and pooled for each mesocosm prior to processing. Tanaids, meiobenthos, and copepods were extracted from the sand within the benthic samplers via floatation using a Ludox TM colloidal solution with a specific gravity of 1.18. The animals were then collected using a 120 μm sieve. Microzooplankton biomass was measured following volumetric method [75] by filtering 400 L of water from each mesocosm through a plankton sampler at the end of the experiment.

Phytobenthos biomass was measured using the same benthic samplers as above. Two samplers were placed in each mesocosm for biomass measurements. A micro-spatula was used to carefully scrape the thin phytobenthic layer from the upper surface (approximately 1 mm thick) of the sand. The remaining sand was filtered through a pre-combusted and pre-weighed Whatman GF/C glass fiber filters to determine the detritus biomass. In the laboratory, photosynthetic pigments were extracted from freeze-dried sand samples (0.3–0.6 g) with 10 ml 90% acetone. After 48 hours of darkness at −20˚C, the samples were stirred in a vortex, centrifuged at 3,500 rpm for 15 minutes, and extracts were analyzed in a 6,405 UV/Vis, Jenway spectrophotometer and their concentration calculated [76].

Phytoplankton biomass (measured as Chlorophyll *a*) was quantified based on photosynthetic pigment concentration. Four litres of water were filtered from each mesocosm with Whatman GF/C glass fiber filters of 4.7 cm diameter, and ground and extracted [76]. Samples for both phytobenthos and phytoplankton were collected twice during the experimental period, and the average of both was used as the model input.

To estimate the biomass of macrophytes and mat-forming algae, all habitats (rock, seagrass, and open sand) were sampled at the end of the study period. Their wet weight was determined to the nearest 0.1 mg. Mat-forming algae were defined as a mix of turf and cyanobacteria. The relative cover of cyanobacteria in mat-forming algae was estimated using the Coral Point Count with Excel Extensions (CPCe) Software [77]. In addition, community metabolism was measured as gross oxygen production ($\mathrm{mgO_2/m^3/min^1}$) once per mesocosm at the end of the study. Oxygen concentration was measured in 1 minute intervals over at least 30 minutes (HQ40d Portable Meter, sensor LDO101, HachTM). A linear regression model of O_2 production rate (where O_2 concentration was modelled as function of time) was fitted and confirmed a high level of precision in the measurement of O_2 concentrations across the 12 mesocosms (mean ± SD, $R^2 = 0.94 \pm 0.04$).

Food web model construction

We built mass-balanced food web models. Trophic links were weighted by material fluxes among functional groups using Ecopath [78]. We modelled energy or mass flow over a 4 month time step based on local summer conditions today and in the future. We then converted and expressed the model produced energy flow results from the experimental period to values/month to make it more comparable to other systems.

Our model used the following input parameters: biomass, represented by the value B; production per unit of biomass, represented by the value P/B; consumption per unit of biomass, represented by the value Q/B; diet matrix; and the model-estimated ecotrophic efficiency, represented by the value EE. The latter is a parameter that is derived from the model, describing the fraction of the productivity that is used in the system. Most of these model parameters were calculated using our empirical mesocosm data, including final biomass (end-of-experiment) and diet composition of consumers of various functional groups (see S8, S9 and S10 Tables). The Q/B ratio for most of the functional groups was calculated using stomach content analysis and in situ feeding trials that incorporated treatment effects. Therefore, it incorporates the direct effects of temperature on metabolism, accounting for estimates of trophic biomass fluxes and efficiencies. In cases where data were not available, data were derived from empirical equations and published information (see S1 Text).

Flow and transfer efficiency were based on the trophic aggregation routine [69] that aggregates the entire system into discrete trophic levels sensu [79]. The discrete trophic levels start with level I, corresponding to the primary producers and the nonliving, detrital compartments. Strict herbivores or detritivores consequently occupy a position of level II. This is followed by higher-order consumers that are allocated to several discrete trophic positions according to the type and amounts of food that reach them along feeding pathways.

Energy flows were calculated for different trophic levels following [80], where—for example—if a group obtains 40% of its food as an herbivore and 60% as a carnivore, the corresponding fractions of the flow through the group are attributed to the herbivore level and the carnivore level, respectively. The relative flows (these are proportions adding up to 1) were converted to absolute amounts and shown as the net amount of energy that flows to higher trophic levels through consumption (g/m^2/month). The 'transfer efficiency' is the percentage of trophic flows at trophic level n that is converted into flows at level $n + 1$. The transfer efficiency of a given trophic level (trophic level = n) not only depends on the available energy at a given trophic level (trophic level = n) but also the standing biomass at the next trophic level (trophic level = $n + 1$). The transfer efficiencies between successive discrete trophic levels were calculated as the sum of the flow that is transferred from any given level to the next higher level, plus exports from the original level relative to the throughput (or input) of the given (originating) trophic level [69,78]. The throughput is the sum of all flows (such as consumption, export, respiration, and flows to detritus) in a given trophic level and represents the 'size of the trophic level in terms of flow' [81].

Calculation of transfer efficiency from trophic level 1 to 2 is not possible without having information on gross primary production or respiration [82]. We measured net productivity and respiration in each mesocosm and used them to estimate the transfer efficiency between trophic level 1 and 2 for each mesocosm food web [69,78]. The initial output for both energy flow and transfer efficiency was obtained for discrete trophic levels I to V. However, for the simplicity of the model output and better visualization, we pooled the data for trophic levels III to Vand showed this as 1 integrated trophic level (i.e., trophic level 3).

We used the Ecopath pedigree routine to quantify the uncertainty associated with the model parameters by recording the origin and quality of the input data and assigning a value of uncertainty or a confidence interval to each input (e.g., biomass, P/B, Q/B, diets), which are then used to calculate the overall model pedigree index. The pedigree index varies between 0 (low precision information) and 1 (high quality, i.e., obtained from modelled system and highly precise), allowing a description of the quality of the model [78]. Our overall individual model pedigree index of 0.71, and a measure of fit of $t = 3.819$, indicates a very high quality and robust model compared to 393 previously constructed models from habitats from around the world, for which pedigree values ranged between 0.164 and 0.676 [83]. More details on the parameterization and model computation are given in the Supplementary Methods.

Statistical analysis

The effects of warming and ocean acidification on food web properties (response variables: absolute energy flow, transfer efficiency, and standing biomass) were analysed using two-way ANOVAs. Both climate factors were treated as fixed and orthogonal. Before analysis, normality was checked for all response variables using the Shapiro-Wilk test, and homogeneity of variances was assessed using a Levene's test as well as by evaluating plots of residuals against predicted values. Response variables were $\log_{10}$ transformed prior to analysis if they did not conform to a normal distribution. For significant interactions, posthoc multiple comparisons adjusted by false discovery rate were performed [84]. All data analyses were done with the software package R version 3.2.3 [85].

Supporting information

S1 Fig. Absolute flows ($gWWm^{-2}month^{-1}$) produced by the different functional group at trophic level 2. Mean ± SE values per mesocosm are given ($n = 3$). Significant interactions or main effects ($p < 0.05$) within functional groups are based on two-way ANOVAs (df = 1,8) and are indicated with asterisks. Means with different lowercase letters indicate significant difference among treatments based on posthoc tests corrected for false discovery rate and done separately for different functional group. No Sig = no significance. See S4 Table for statistical test outcomes.
(TIF)

S2 Fig. Absolute flows ($gWWm^{-2}month^{-1}$) produced by the different functional group at trophic level 3. Mean ± SE values per mesocosm are given ($n = 3$). Significant interactions or main effects ($p < 0.05$) within functional groups are based on two-way ANOVAs (df = 1,8) and are indicated with asterisks. Means with different lowercase letters indicate significant difference among treatments based on posthoc tests corrected for false discovery rate and done separately for different functional groups. No Sig = no significance. See S5 Table for statistical test outcomes.
(TIF)

S3 Fig. The Finn's cycling index expresses the amount of detritus that is recycled relative to the total throughput of the system. Mean ± SE values per mesocosm are given ($n = 3$). Significant effects ($p < 0.05$) are based on two-way ANOVAs with *OA* and *T* (df = 1,8) and are indicated with asterisks. Means with different lower case letters indicate significant difference among treatments. See S3 Table for statistical test outcomes. *OA*, elevated CO_2; *T*, elevated

temperature.
(TIF)

S4 Fig. The different structural components of the mesocosm used for this experiment. Each mesocosm comprises 4 'rocky reef' patches (A) and 4 'artificial seagrass' patches (B). The space in between and around these patches was considered 'open sand' habitat (C). The incoming seawater was led into 2 header tanks (800 L) at the beginning of the flow-through facilities, and from there gravity-fed into each mesocosm (D). The header tank was preconditioned to future $p\mathrm{CO}_2$ levels with pure CO_2 (control system ACQ110 Aquatronica, Italy) prior to supplying the water to the 6 acidified mesocosms. In addition, continuous water circulation (approximately 1,800 L per hour) was maintained between each mesocosm and a 60-L supporting bin positioned next to each mesocosm that was bubbled heavily with enriched air at 1,000 ppm $p\mathrm{CO}_2$ (PEGAS 4000 MF Gas Mixer, Columbus Instruments, Columbus, Ohio) or ambient air at 400 ppm $p\mathrm{CO}_2$, depending on the acidification treatment. These bins also contained the submersible titanium heaters for the *T* treatments. A diffuser pipe was used to generate a mild circular current inside the mesocosms using the water exchange between supporting bin and mesocosm and alternating direction every 6 hours (E). A filter column (approximately 20 μm) allowed water to flow back into the 60-L bin by gravity (F) and ensured that larger organisms were always retained within the mesocosms. In summary, this technically complex set-up ensured a mesocosm environment without unnatural disturbances such as pump noise, air bubbles, or electrical currents. A 250W metal halide lamp (Osram Powerstar HQI-T 250/D/PRO) mounted just above the mesocosm (G) ensured an irradiance that corresponded to approximately 6–7 m water depth in Gulf St. Vincent (Phillips et al. 1981). *T*, elevated temperature.
(TIF)

S5 Fig. Variability in pH and temperature over the 5-month study period. This includes 3 phases: 1) the first week of the acclimation period, 2) the progressive elevation to treatment levels, and 3) at maintained treatment levels. Mean ± SD are shown based on 3 mesocosms for each treatment. pH and temperature were both measured once daily in each mesocosm around midday.
(TIF)

S6 Fig. Diurnal variability in pH measured over a 5-day period in the middle of the study period. This analysis was only done for 1 mesocosm per treatment combination, serving as an example. For these 4 mesocosms in parallel, pH was recorded at 30-minute intervals with an automated pH logger (control system ACQ110 Aquatronica, Italy).
(TIF)

S7 Fig. Schematic diagram showing the different phases of model building and execution. A) data collection from the mesocosms and parameter estimation, B) mass-balance modelling in Ecopath, and C) model balancing and validation.
(TIF)

S8 Fig. PREBAL of the control and acidification models plotting (a) biomass estimates (gWWm^{-2}), (b) production/biomass ratio (per 4 months), and (c) consumption/biomass (per 4 months) on a log scale versus functional groups ranked by their trophic level, from lowest to highest trophic level. A constant of 1 was added to all response variables to avoid some negative values ($\mathrm{Log}_{10}\,[x + 1]$) prior to PREBAL plotting. For specific functional group name, refer to the legend. Herb. = herbivorous. PREBAL is shown only for base models that are built on the average of all the input parameters (B, P/B, Q/B) across mesocosms within

each climate treatment. B, biomass; P/B, production per unit of biomass; Q/B, consumption per unit of biomass.
(TIF)

S9 Fig. PREBAL of the temperature and temperature + acidification models plotting (a) biomass estimates ($gWWm^{-2}$), (b) production/biomass ratio (per 4 months), and (c) consumption/biomass (per 4 months) on a log scale versus functional groups ranked by their trophic level, from lowest to highest trophic level. A constant of 1 was added to all response variables to avoid some negative values ($\text{Log}_{10}\,[x + 1]$) prior to PREBAL plotting. For specific functional group name, refer to the legend. Herb. = herbivorous. PREBAL is shown only for base models that are built on the average of all the input parameters (B, P/B, Q/B) across mesocosms within each climate treatment. B, biomass; P/B, production per unit of biomass; Q/B, consumption per unit of biomass.
(TIF)

S1 Table. Analysis of variance of the effects of *OA* and *T* and their interaction on absolute flows and transfer efficiency between successive trophic levels of the food web. Significant differences are indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$. *OA*, elevated CO_2; *T*, elevated temperature.
(XLSX)

S2 Table. Analysis of variance of the effects of OA and *T* and their interaction on living biomass by trophic levels of the food web. Significant differences are indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$. *OA*, elevated CO_2; *T*, elevated temperature.
(XLSX)

S3 Table. Analysis of variance of the effects of *OA* and *T* and their interaction on cyanobacteria (% cover), flow (%) to detritus, and Finn's cycling index in the food web. Significant differences are indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$. *OA*, elevated CO_2; *T*, elevated temperature.
(XLSX)

S4 Table. Analysis of variance of the effects of *OA* and *T* and their interaction on the absolute flows of contributing functional groups from trophic level 1 to 2. Functional groups were ordered in terms of their contribution to total energy flows. Significant differences indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$. *OA*, elevated CO_2; *T*, elevated temperature.
(XLSX)

S5 Table. Analysis of variance of the effects of *OA* and *T* and their interaction on the absolute flows of contributing functional groups from trophic levels 2 to 3. Functional groups were ordered in terms of their contribution to total energy flows. Significant differences are indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$, and ***: $p < 0.001$. *OA*, elevated CO_2; *T*, elevated temperature.
(XLSX)

S6 Table. List of species/taxa and their respective functional group considered in the mesocosm food webs.
(XLSX)

S7 Table. Mean (± SD) seawater parameters in the experimental mesocosoms with 2 crossed factors of *T* and *OA*. Standard deviations represent the variability between individual

mesocosms. *OA*, elevated CO_2; *T*, elevated temperature.
(XLSX)

S8 Table. Input (nonitalic) and output (italic) parameters for the ecosystem components used in C models. TL: trophic level, B: biomass ($gWWm^{-2}$), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. CM1 represents control model 1, CM2 represents control model 2, and CM3 represents control model 3. The value in bold indicates that particular parameter varied among the models and mentioned below the table. C, control.
(XLSX)

S9 Table. Input (nonitalic) and output (italic) parameters for the ecosystem components used in the *OA* models. TL: trophic level, B: biomass ($gWWm^{-2}$), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. OAM1 represents acidification model 1, OAM2 represents acidification model 2, and OAM3 represents acidification model 3. The value in bold indicates that particular parameter varies among the models as mentioned below the table. *OA*, elevated CO_2.
(XLSX)

S10 Table. Input (nonitalic) and output (italic) parameters for the ecosystem components used in the *T* models. TL: trophic level, B: biomass ($gWWm^{-2}$), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. TM1 represents temperature model 1, TM2 represents temperature model 2, and TM3 represents temperature model 3. The values in bold indicate that particular parameters vary among the models as mentioned below the table. *T*, elevated temperature.
(XLSX)

S11 Table. Input (nonitalic) and output (italic) parameters for the ecosystem components used in the *OAT* models. TL: trophic level, B: biomass ($gWWm^{-2}$), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. OATM1 represents temperature and acidification model 1, OATM2 represents temperature and acidification model 2, and OATM3 represents temperature and acidification model 3. The value in bold indicates that particular parameter varies among the models as mentioned below the table. *OAT*, elevated CO_2 and temperature.
(XLSX)

S12 Table. Predator/prey matrix (column/row) for C models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to 1. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models. C, control.
(XLSX)

S13 Table. Predator/prey matrix (column/raw) for *OA* models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to 1. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models. *OA*, elevated CO_2.
(XLSX)

S14 Table. Predator/prey matrix (column/raw) for *T* models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to 1. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models. *T*, elevated temperature.
(XLSX)

S15 Table. Predator/prey matrix (column/raw) for *OAT* models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to 1. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models. *OAT*, elevated CO_2 and temperature.
(XLSX)

S16 Table. Source of additional information used (√) to parameterize base (control model) models for different functional groups, where similar values used across treatments were specified in the supplementary text.
(XLSX)

S1 Text. Supplementary methods.
(DOCX)

S1 Data. Data used to generate the manuscript figures.
(XLSX)

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Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation

SUPPLEMENTARY METHODS

A. Data collection and parameter estimation

Each of the twelve mesocosms had a surface area of 6.02 m^2 with a water depth of 0.74 m. For the model parameterization, the vertical wall of our mesocosm was considered as an extended horizontal habitat since the mesocosm walls acted as rich habitat for benthic producers and served as a feeding ground for many of the mesocosms prey and predator communities. The total surface area considered per mesocosm, therefore, covered a true benthic habitat surface of 2.14 m^2 (rocky reef = 0.60 m^2; seagrass = 0.60 m^2; sand = 0.92 m^2) and a wall habitat of 3.89 m^2.

Twelve food web models were built to represent the response of our mesocosms under different climate scenarios. Each climate treatment comprised three independent mesocosm food web models (see Table in S8,S9, S10 and S11 Tables for individual model descriptions). We used mesocosm-specific biomass data of each functional group for individual model inputs, whereas other input parameters (such as P/B, Q/B and diet data) were averaged across treatments. The food web models simulated a southern hemisphere summer period equivalent to 4 months (mid-March to mid-July 2015; maintained at treatment level. See S5 Fig for details). All parameters were standardized per unit surface area using wet weight (WW) for biomass (g $WW.m^{-2}$), while energy flows are expressed per month. There are indeed various ways of expressing units of energy, one of which is carbon. However, in studies of marine ecosystems, energy flows are most often represented as wet weights. Furthermore, in our study, a substantial part of our data to quantify energy transfer rates was directly measured as wet weight. Therefore it is logical to use wet weight as the measure of unit for this experiment because it avoids uncertainty associated with converting the data to other measures.

The output (energy flow and transfer efficiency) of these food web models are presented in Fig 1. A schematic diagram shows the different phases of model building and execution (S7 Fig).

The food web models consisted of 17 functional groups (ranging from primary producers to herbivores to carnivores across three trophic levels). Functional groups were categorized and grouped according to their similarities in ecological traits, such as feeding habits, size, habitat use, predator and life cycle [1].

We considered FishBase [2] and stomach content analysis (bio-volume) of the fishes in this study to allocate them to the different feeding guilds within the model. Two herbivorous fish species *Girella zebra* and *Acanthaluteres vittige* [2] partly consumed animal material which is not unusual for the juvenile life phase. However, they predominantly preyed on plant matter (~ 94%) in this experiment and therefore we considered them as herbivores. Each model included four functional groups of fish, two groups of invertebrates, one group of filter feeders, two groups of crustaceans, two groups of zooplankton, one group of benthic organisms, four groups of primary producers, and one detrital group.

We mostly used data from the mesocosms for estimating food web model parameters and creating the diet matrix for the different functional groups (Table in S12, S13, S14 and S15 Tables). In case of missing data for model parametrization, parameters were derived from empirical equations and the scientific literature (S16 Table).

Fish identification and grouping: At the beginning of the mesocosm experiment, fishes were placed onto a small tray with a ruler and then photographed with a camera (Canon EOS 60D). Every individual fish was measured for total length from the photographs using ImageJ software [3].

At the end of the experiment, individual fish length (total and standard length, cm) and wet weight were measured after carefully removing excess water by blotting with a paper towel. The weight of individual species for each mesocosm was summed, and biomass estimates were calculated as weight/area (g $\mathrm{WW.m^{-2}}$) for each mesocosm food web. Production/biomass (P/B) ratios are difficult to estimate directly. Therefore the P/B was considered to be equivalent to the instantaneous rate of total mortality (Z) [4], calculated as the negative natural logarithm of survival rate from the following equation,

$$Z = -\ln(S) \qquad (4)$$

where *S* (total survival rate) = the number (*N*) of animals alive at the end of the experiment at time *t+1* divided by the number alive at the start of the experiment at time *t* and expressed as,

$$S = (N_{t+1} / N_t) \tag{5}$$

Since our mesocosms are an unexploited (no fishing mortality) system, and there was no natural mortality for benthic carnivorous fish groups, initial P/B ratio was estimated as 0.001 (and not 0) for compatibility with Ecopath.

The food consumption per unit of biomass (Q/B) was estimated by dividing the average food consumption over the entire experimental period by average biomass gained by species/functional groups. Food consumption by fish species was calculated using feeding trials and based on 12 hours of feeding per day. The average biomass gained was calculated by deducting the average initial weight from the average final weight per species per mesocosm. The initial weight for each species was calculated using the length at the start of the experiment, based on an exponential growth model because it provided a better fit to the data compared to linear and non-linear growth models [5]. Therefore, the initial fish length was converted to wet weight using an exponential linear regression model derived from final length-weight data,

$$y = \alpha e^{\beta x} \tag{6}$$

where y = weight at length *"x"*, α = the constant with a value of *x+1,* β = rate of growth (when > 0) or decay (when < 0) and, *x* = length.

Herbivorous macroinvertebrates: Biomass of large herbivorous macroinvertebrates (e.g. *Bulla quoyii, Phasianella australis*, and *Thalotia conica*) was measured directly as wet weight (g WW.m^{-2}) for each mesocosm at the end of the experiment. These macroinvertebrate species were considered for this model group due to their relatively large size (>1g). P/B ratios were calculated following Equation 4. The Q/B ratio was calculated by dividing the total food consumption over the entire experimental period by total species biomass. We assumed that the consumption rate was similar throughout time. Feeding trials were conducted to determine the food consumption rate of herbivorous macroinvertebrates. Ten quadrats were randomly placed per mesocosm (20 × 20 cm) and allowed to grow turf for a week without herbivorous snails. Then snails were allowed to feed on five quadrats for 24 hours. Quadrats with and without grazing were then collected and scraped off algal turf. Freshly collected turf hold a lot of water and create large variability in biomass measurements. Therefore, turf samples were first dried in an oven for 48 h at 65 °C and subsequently converted to wet weight using a standardised factor of 10 [6]. We converted dry weight back to wet weight as the latter was the parameter used for all other groups too. Feeding rate was calculated from the average turf weight of both grazed and non-grazed quadrats and used to calculate Q/B ratio for herbivorous macroinvertebrates in each mesocosm. The Q/B ratio calculated from the feeding trials for "acidification and temperature" treatments was not reliable due to the very low standing biomass of herbivorous macroinvertebrates (due to high treatment-related mortality), so we used the average of acidification and temperature treatment as a model input for "acidification and temperature".

Small epifaunal invertebrates: Small epifaunal invertebrates comprise several groups of species such as small-sized herbivorous gastropods (average range 0.16-0.92 g; e.g., *Turbo undulates*, *Clanculus* sp.) occupying the open sandy habitat, and other small invertebrate herbivores (chitons, limpets, amphipods, juvenile abalone, juvenile sea urchins), detritivores (polychaetes, brittle stars), and predators (small sea stars and crabs) from the rocky reefs. Small-sized herbivores were counted, and their biomass was measured directly as wet weight to the nearest 0.1 g at the end of the experiment. Where individual animals were difficult to weigh due to their small size, individuals were pooled and weighed together as a group. The biomass of small epifaunal invertebrates was measured as wet weight (g $WW.m^{-2}$).

It was difficult to directly estimate P/B and Q/B ratios for the small epifaunal invertebrates in our mesocosms. We therefore used data from a similar ecosystem [7] to assign a P/B value of 3.67 and Q/B value of 18 for small epifaunal invertebrates group in control conditions. The estimates come from the Te Tapuwae o Rongokako (TTMR) ecosystem model [8], which has a similar ecological and biological setting to our system, comprising a temperate coastal intertidal and subtidal ecosystem with both rocky reef and soft sediments. The predation pressure on small epifaunal invertebrates varied among the treatments. Since predation can cause an increase in population turnover rate [9] we adjusted P/B ratios for each treatment according to the predation pressure on small epifaunal invertebrates by consumers (fish) relative to the control tank. Accordingly, P/B ratio of the control treatment tank was multiplied by a factor of 1.94, 1.85, and 1.44 to calculate P/B ratio for acidification, temperature and acidification and temperature treatments, respectively. Since approximately 89% of small epifaunal invertebrate biomass comprised herbivorous species, we opted to use the same relative factors derived from macroinvertebrate consumption data to adjust Q/B ratio for small epifaunal invertebrates.

Filter feeders: Filter feeders (e.g. sponges, ascidians, tunicates, bivalves) were collected from rocky reefs (see above) and biomass was estimated as wet weight (g WW.m^{-2}) for each mesocosm food web. We estimated the P/B and Q/B ratio using data from closely-related temperate marine systems [10-12]. We applied the same value across treatments because filter feeder biomass collapsed under the temperature and the combined temperature and acidification treatments.

Shrimps: Biomass of shrimps was estimated directly as final wet weight (g WW.m^{-2}) for each mesocosm. The production over biomass (P/B) ratio and consumption over biomass (Q/B) ratio were obtained from empirical relationships following [13] and published sources for non-fish groups [8,14].

Tanaids, copepods, and meiobenthos: We collected tanaids, copepods, and meiobenthos samples twice from each mesocosm during the experimental period, using three types of benthic samplers (small cages), specifically designed to estimate 1) biomass (entirely open and accessible to predators for measurement of standing biomass), 2) production (covered with ~ 5 mm mesh size to exclude herbivores for measurement of production), and 3) as procedural controls (covered with mesh, but open at the sides, allowing predators to enter). Two replicate samplers of each of the three types were placed in each mesocosm and replicated over two time periods. The six samplers within each mesocosm at any one time were placed randomly keeping an equal distance from each other to reduce the likelihood of confounding factors. After extraction with Ludox TM colloidal solution, all tanaids, copepods, and meiobenthos from each sampler were counted under a stereomicroscope. Large tanaids shrimps (~ 2-5 mm in length) were weighed on a microscale (± 0.1 mg). For smaller-sized copepods (~ 0.2-1 mm long) and meiobenthos (~ 0.6-5.3 mm), a subsample (7.5% for each sample by randomly selecting 30 out of the 400 cells on a counting tray) was photographed to determine average individual mass (biovolume) using ImageJ. In total, 368 individuals from 3 groups were measured using ImageJ (copepods n=159, polychaetes and oligochaetes n=65, and nematodes n=138) to determine their biovolume. Only for copepods, the treatment-specific average individual mass was used to calculate total biomass since biovolume of copepods differed between climate treatments (ANOVA: $F_{(1,155)}=4.13$, $p=0.0438$). Data were pooled for the two periods to get a representative biomass value for each of these functional groups.

The turnover rate (P/B) for tanaids and meiobenthos was calculated by dividing production over the experimental period by the standing biomass. We did not include data from one mesocosm (of the control treatment) to calculate biomass and production of meiobenthos due to a malfunction of the sampler. We used the same consumption rate per unit of biomass (Q/B) for tanaids and meiobenthos across treatments, based on [10]. The sampling method used to estimate copepod production did not work well due to the large mesh size used relative to copepod body sizes, and probably also due to the presence of carnivorous copepods inside the cage. Copepods are considered as one of the major prey items for shallow benthic carnivores as well as shallow water species [15]. We therefore used estimates of P/B and Q/B ratio for copepods from a closely related shallow, rocky reef dominated temperate marine ecosystem [8,16-18]. We assigned an average P/B value of 108.70 and Q/B value of 336.98 to parameterize the control model. We then adjusted the P/B ratio for other models based on the relative predation pressure on copepods by fishes compared to control treatments. Since production and consumption rate of functional groups is positively correlated, based on data provided in [18], Q/B ratio was further adjusted based on the corresponding P/B ratio through simple linear regression ($Y = 3.5739X - 51.536$; $R^2=0.98$). We used the same P/B and Q/B ratio across all treatments.

Microzooplankton biomass was measured by filtering 400 L of water from each mesocosm through a plankton sampler at the end of the experiment. Initially, all samples were checked under a stereomicroscope to visually confirm the presence of a significant proportion of microzooplankton in the samples. Samples were rinsed through a 38 µm mesh sieve and then poured into a 100 ml measuring cylinder and allowed to settle for 24 hours, after which settling volume (ml) was recorded. Settling volumes were converted into displacement volumes using a factor of 0.35 for samples without gelatinous zooplankton [19]. Displacement volumes were converted to biomass (mg wet-weight) using a factor of 800 [20]. The P/B and Q/B ratio for microzooplankton was based on [8,11,12,17,21].

Primary producer groups (phytoplankton, phytobenthos, mat-forming algae, macrophytes): Four litres of water was filtered from each mesocosm with Whatman GF/C glass fiber filters of 4.7 cm diameter to estimate phytoplankton biomass. Phytobenthos samples were collected using the benthic samplers described earlier. The biomass (measured via Chlorophyll *a*) of both phytoplankton and phytobenthos was measured following [22]. The phytoplankton biomass value was converted into square meter units by multiplying by the euphotic depth (0.74 m). Both the phytoplankton and phytobenthos values were then converted to wet weight using two successive conversion factors [23]. The first was to change Chlorophyll *a* to carbon using a

40:1 – carbon to Chlorophyll *a* ratio

The second conversion factor was used to convert carbon to wet weight using

Wet weight = Carbon × 10

Macrophytes and mat-forming algal biomass were sampled from all habitats (rock, seagrass, and open sand) at the end of the experiment. All samples were dried in an oven at 65 °C for 24-48 hrs. Then, a conversion factor of 10 was applied to convert dry weight (g $C.m^{-2}$) to wet weight (g $WW.m^{-2}$) [6].

P/B ratios for primary producer groups were estimated by measuring the community photosynthesis of each mesocosm. First, we used published P/B ratios for phytoplankton [8,18,24], phytobenthos [8,24], mat-forming algae [25,26] and macrophytes [8,27] from closely related shallow temperate marine ecosystems to calculate a standard average P/B ratio for primary producer groups. We then used these ratios to estimate a relative production rate for each functional group and their corresponding P/B ratios from *in situ* community photosynthesis using the following equation (separately for each mesocosm),

$$^{P}/_{Bi} = \left\{ \frac{\left(^{aP}/_{Bi} \times B_i \right) \times 100}{\sum {^{aP}/_{Bi}} \times B_i} \times \frac{\mathrm{CM}}{100} \right\} / Bi$$

where $^{P}/_{Bi}$ is turnover rate calculated for group *i* as model input*,* $^{aP}/_{Bi}$ is the standard average turnover rate assigned for group *i,* B_i is the biomass of group *i* sampled from each mesocosm*,* $\sum {^{aP}/_{Bi}} \times B_i$ is the total theoretical production for all functional groups, CM is the community photosynthesis measured *in situ* from the mesocosm, $\left\{ \frac{\left(^{aP}/_{Bi} \times B_i \right) \times 100}{\sum {^{aP}/_{Bi}} \times B_i} \times \frac{\mathrm{CM}}{100} \right\}$ is the calculated production of functional group *i* to total community production measured in each mesocosm.

The average P/B value across treatments was used as the final model input. The assumption made here is that the variability in P/B ratio is only biomass driven. Thus the sum of all relative production (for the four producer groups) equals total community production.

Community photosynthesis (primary production) was measured as gross oxygen production (mg $O_2.m^{-3}.min^{-1}$) based on production rates measured during daytime (net production) and consumption rate during night time (respiration):

Gross production = Net production + Respiration.

Each mesocosm had 14 hours of daytime and 10 hours of night time. The community photosynthesis was measured once per mesocosm at the end of the experiment. Mesocosms were sealed off from the atmosphere with a transparent plastic cover and seawater O_2 concentration was measured at 1-min intervals over a 30 min period (HQ40d Portable Meter, sensor LDO101, HachTM). Both net community production and respiration values were transformed using following equation,

$$(\text{mg } O_2.m^{-2}.day^{-1}) \times 0\ .375\times2\times10 = \text{mg WW}.m^{-2}.day^{-1}$$

where 0.375 is used to converts mass of oxygen to the mass of carbon and is a ratio of moles of carbon to moles of oxygen (12 mg C / 32 mg O_2 = 0.375); 2 is multiplied to convert carbon to dry weight and then multiplied by 10 again for dry weight to wet weight. Finally, the gross production was calculated as g $WW.m^{-2}$ per 4 months for initial model input.

Detritus: First, the benthic detritus layer was carefully separated from phytobenthos and zoobenthos (if any) from the top of the experimental samplers with a micro-spatula. Then the sediment samples were filtered through pre-combusted and pre-weighed Whatman GF/C glass fiber filters. Both the layer and extract were then oven-dried at 65 °C for 24-48 hrs. Finally, the dry weight was converted to wet weight (g $WW.m^{-2}$) using a factor of 5 [28]. Detritus was considered to be particulate organic matter (POM) only.

Diet composition of functional groups: A diet matrix was constructed based on feeding rates measured in the final month of the experiment. Prior to measurement, all fishes were starved for 20 hrs and then released into their respective mesocosm for 4 hrs of free feeding before they were caught again and frozen immediately using a liquid nitrogen Dewar (-196 ^{0}C) and placed in a cold freezer (-20 ^{0}C) afterwards. Fish stomach contents were then analyzed under a stereo microscope by counting individual taxa (such as tanaids shrimp, copepods, bivalve shell and annelids) and weighing the total fish stomach content. The weight of different prey (g) was then calculated by multiplying the average individual body mass of corresponding prey to the count of each sample.

Finally, the relative weight of different prey groups was calculated based on their relative contribution to the total prey weight and assigned for individual fish species. Diet composition of some functional groups was supplemented by local studies and relevant literature [8,10-12,17,27,29].

Seagrass: Previous lab studies found that maintaining seagrasses in indoor mesocosms is extremely difficult. We therefore had no other option than to use artificial seagrass to provide species with an important habitat for sheltering. This decision was made because habitat heterogeneity can have important implications for predator–prey interactions or heterospecific interactions [30,31] that are not captured by the model which is based on a homogenous environment. The predator–prey interactions are crucial to incorporate, to deliver a more realistic outcome at the food web level that can be strongly mediated by factors like habitat type and presence. We observed that these artificial seagrasses were frequently used by fish, shrimp and snails to obtain food and for sheltering purposes [32,33] and as such created a similar habitat to live seagrass beds that some of the species associate with in nature. The use of artificial seagrasses in itself is not expected to have major direct effects on the magnitude of energy flow or growth or turf algae and cyanobacteria.

B. Mass-balance modelling in Ecopath

Ecopath is a mass-balanced trophic model, which is grounded in general ecological theory [34-36]. Tests of Ecopath have proved the model capable of capturing real ecosystem dynamics in a variety of different ecosystem, ranging from temperate to tropical systems [37]. We used Ecopath to model the food webs in our mesocosms using linear equations for 17 functional groups. The parameterization of an Ecopath model is based on satisfying two 'master' equations: one for production (equation 1) and the other for the energy balance (equation 4)

The production of each group was calculated as (1):

Production = predation mortality + biomass accumulation + net migration + other mortality (1)

and, written as:

$$P_i = B_i \times M2_i + E_i + BA_i + P_i(1 - EE_i) \tag{2}$$

where P_i is the total production rate of group (*i*), Bi is the biomass of a group (*i*), $M2_i$ is the instantaneous predation rate for group (*i*), E_i is the net migration rate (emigration - immigration), BA_i is the biomass accumulation rate for (*i*), *EEi* is the ecotrophic efficiency of (*i*) describing the proportion of the production utilized in the system, and (1 − *EEi*) represents mortality other than predation.

This formula incorporates all the production (or mortality) except gonadal products which are assumed to be ending up being eaten by other groups, hence here considered under other mortality. Therefore Equation 2 can be expressed as:

$$B_i(P/B)_i \times EE_i - \sum_{j=1}^{n} B_j(Q/B)_j \times DC_{ji} - E_i - BA_i = 0 \qquad (3)$$

where P/B_i is the production/biomass ratio for (*i*), Q/B_j is the consumption/biomass ratio of the predator (*j)* and *DCji* is the fraction of prey (*i)* in the average diet of predator (*j)*. All other variables are the same as those described for Equation 2.

The energy input and output of all living groups is balanced using equation (4):

Consumption = production + respiration + unassimilated food (4)

and, written as:

$$Q_i = Pi + Ri + UAi \qquad (5)$$

where Qi is consumption by a group (*i)*, *Pi* is total production of group (*i)*, *Ri* is respiration of a group (*i)* and *UAi* is the unassimilated food of group (*i)*.

C. Model balancing and validation

Prior to model balancing, a set of pre-balancing (PREBAL) analyses was used to assess whether data abide by the general rules/principles of ecosystem ecology [38]: (i) biomass of functional groups should span 5–7 orders of magnitude when arranged against their trophic levels; (ii) the slope of biomass (on a logarithmic scale) by functional groups should decline by 5–10% across all the taxa when arranged against trophic levels; (iii) there is a general decline of vital rates (P/B; Q/B) across taxa/trophic levels with increasing trophic level [7,38]. Our tests showed that these general ecological rules were met by our model (S8 andS9 Figs).

We applied a manual mass-balanced procedure, using a ‘top-down’ approach (starting with the top predator groups and moving down the food web to balance inconsistencies) adjusting the input parameters of those groups ‘out of balance’ (EE > 1). The ecological models were considered balanced when the following thermodynamic and ecological rules were met [7,39].

1. Ecotrophic efficiency (EE) < 1. EE is a measure of the proportion of production that is utilized by the next trophic level through direct predation. The value for EE can never exceed 1.0 as it is not possible for more production to be passed on to the next trophic level than was originally produced.
2. Gross food conversion efficiency (GE) between 0.1 and 0.35.
3. Net efficiency > GE. Net efficiency is the value for food conversion after accounting for unassimilated food. GE can never exceed Net efficiency.
4. Respiration/assimilation biomass (RA/A) ratio < 1.0. The proportion of biomass lost through respiration cannot exceed the biomass of food assimilated.
5. Production/respiration (P/RA) ratio < 1.0. This ratio expresses the fate of assimilated food.

To achieve mass balance, we modified parameters with the highest levels of uncertainty, such as the diet matrix. Since biomass estimates were based on high-precision sampling, they were not modified. To obtain mass balance, we adjusted the diet matrix of non-fish groups such as filter feeders for the control and temperature models and small epifaunal cryptic invertebrates, filter feeders, tanaids and copepods for acidification and combined acidification and temperature models. We also had to manually adjust the diet data for omnivorous fishes in the temperature and combined acidification and temperature models. This is because diets of omnivorous fish are difficult to estimate by using gut content data alone [40]. We had to adjust P/B or Q/B ratio for tanaids to lower down the expected range for temperature and acidification and temperature models [1]. A model default value of 0.2 (dimensionless) was set for unassimilated consumption rate for all groups, except zooplankton where 0.3 was used [8]. Once balanced, EE values were < 1 for all functional groups confirming that the model fulfilled the first basic requirement of thermodynamic and ecological rules. The net efficiency was also lower than the gross food conversion efficiency. The gross food conversion efficiency (P/Q), production/respiration (P/RA) and the respiration over assimilation (RA/A) were within the expected ranges [1]. The resulting output parameters and the final diet matrix are shown for each model (S8, S9, S10, S11, S12, S13, S14 and S15 Tables).

Pedigree index and quality of the model: The robustness of our Ecopath models was assessed through a 'Pedigree index.' The pedigree of a model addresses the problem of propagating uncertainty, providing an index of model confidence. Pedigree values were assigned to each parameter for each group and then an overall model 'Pedigree index,' P, was calculated:

$$P = \sum_{i=1}^{n} \frac{I_{i,j}}{n}$$

where $I_{i,p}$ is the pedigree index value for group *i* and input parameter *j* for each of the *n* living groups in the ecosystem; *j* can represent either B, P/B, Q/B, Y or the diet composition [1].

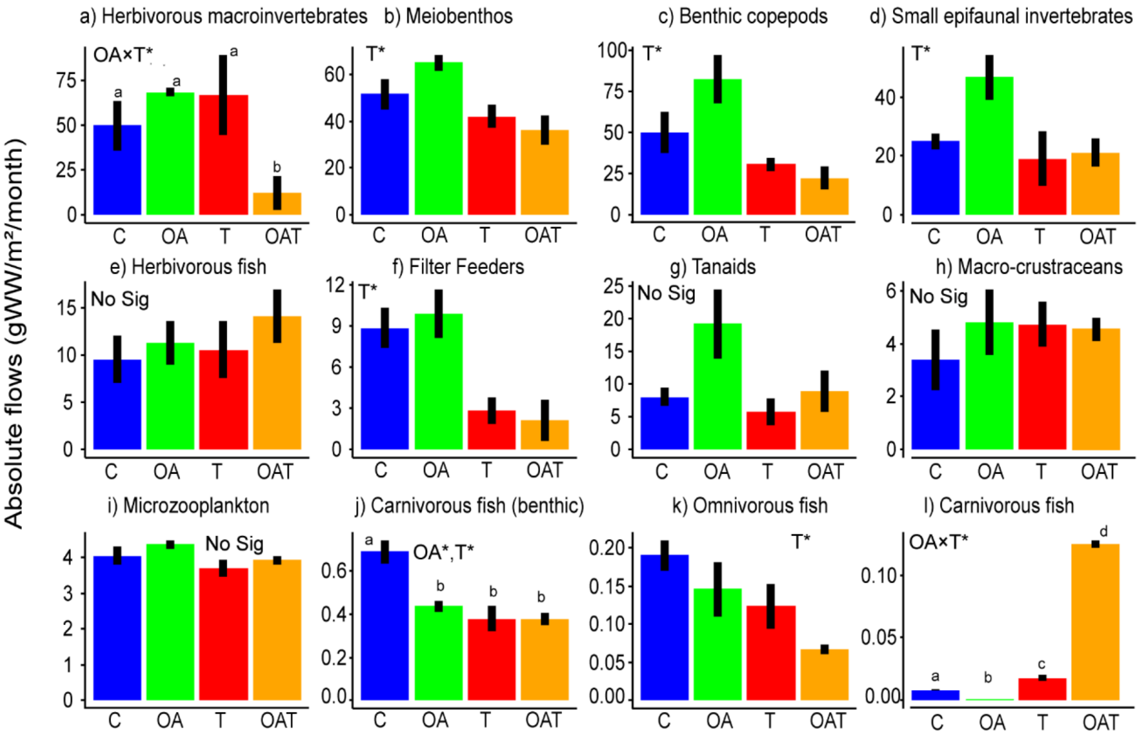
The P scales between 0 and 1 (inclusive). Models with a pedigree value ≥ 0.6 are considered robust [41]. The pedigree index P is, however, a function of the number of groups in the system. We therefore also calculated an overall measure of fit, t^*

$$t^* = P \times \frac{\sqrt{n-2}}{\sqrt{1-P^2}}$$

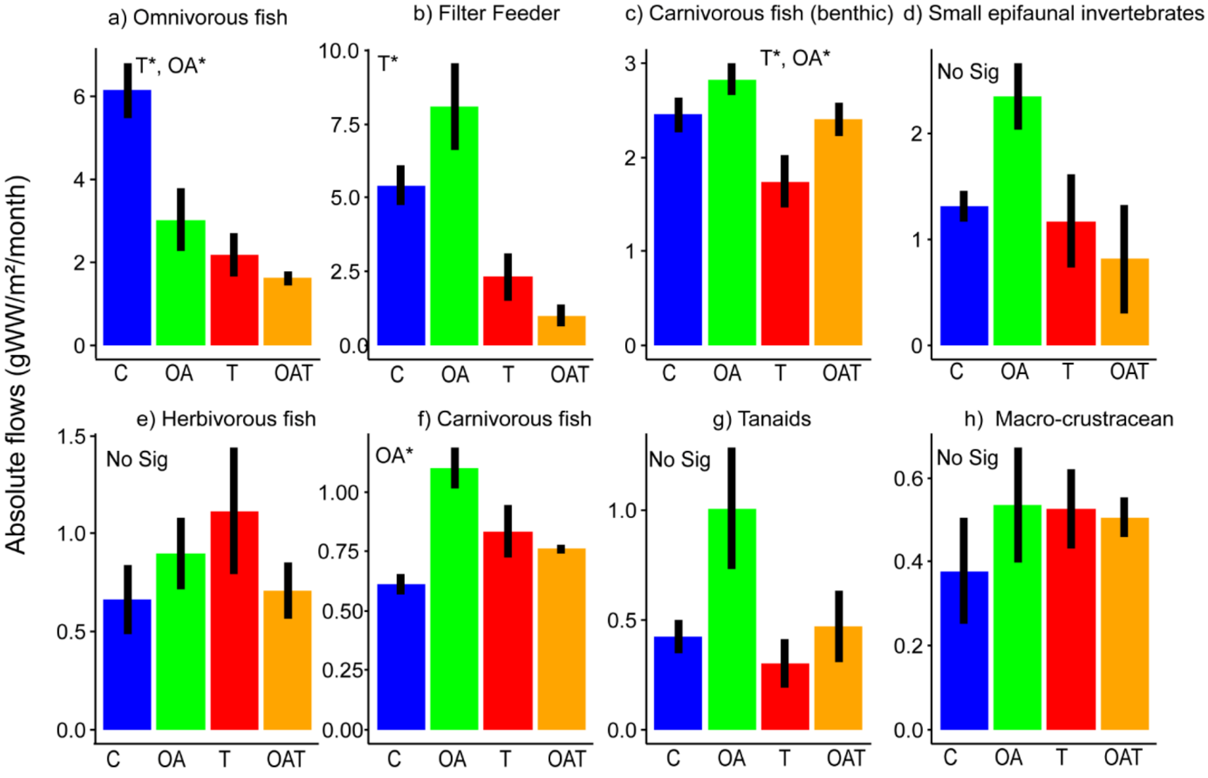
where *n* is the number of living groups in the given model.

The pedigree index for each of our mesocosm models was 0.71 (a measure of fit *t*=3.819), indicating that our models are robust [1,42].

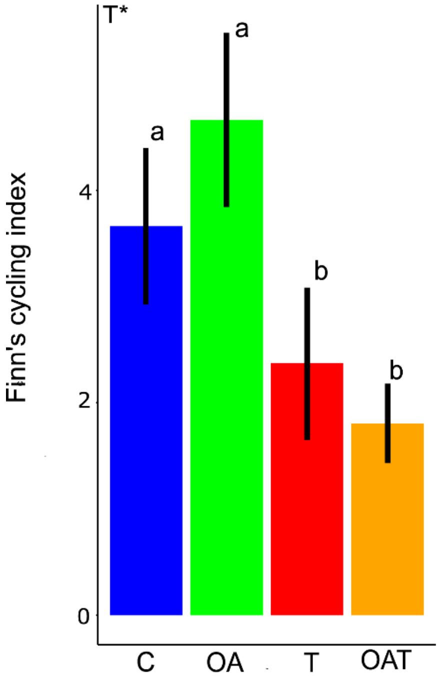
SUPPLEMENTARY FIGURES



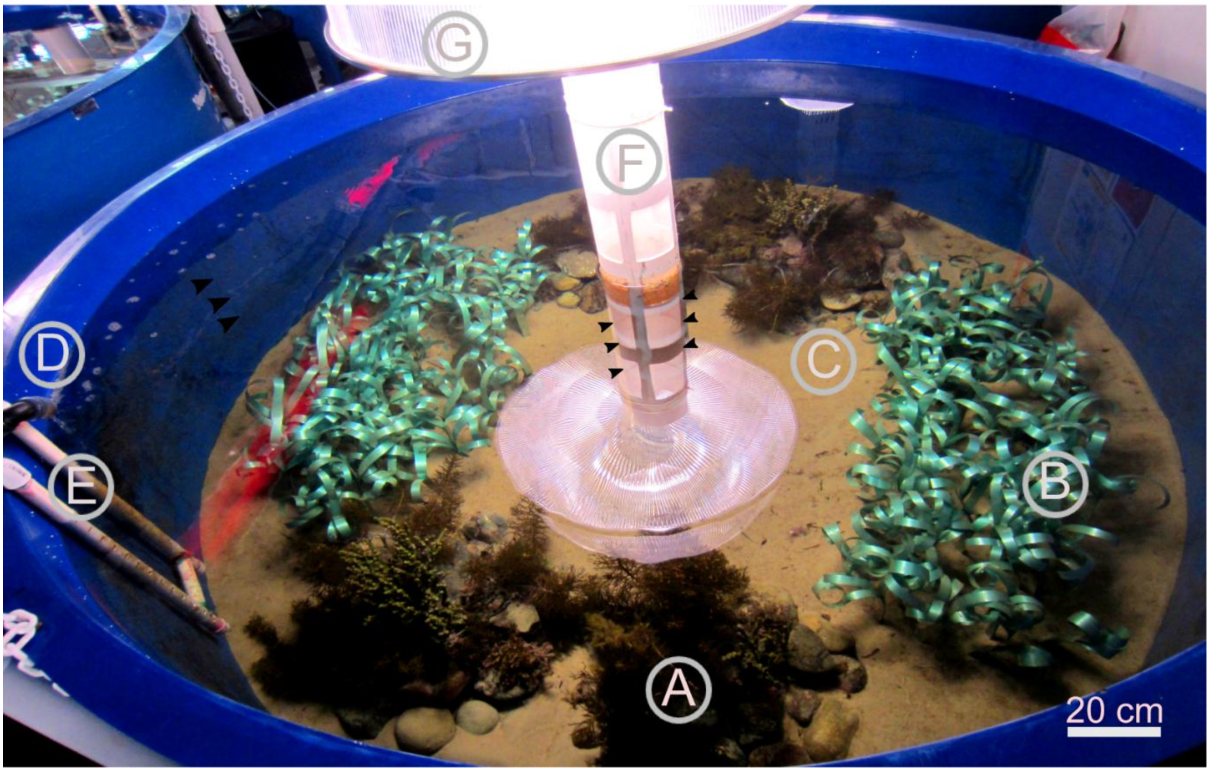
S1 Fig. Absolute flows (gWW/m^2/month) produced by the different functional group at trophic level 2. Mean ± SE values per mesocosm are given (n=3). Significant interactions or main effects (p<0.05) within functional groups are based on two-way ANOVAs (df=1, 8) and are indicated with asterisks. Means with different lower case letters indicate significant difference among treatments based on post-hoc tests corrected for false discovery rate and done separately for different functional group. No Sig = no significance. See S4 Table for statistical test outcomes.



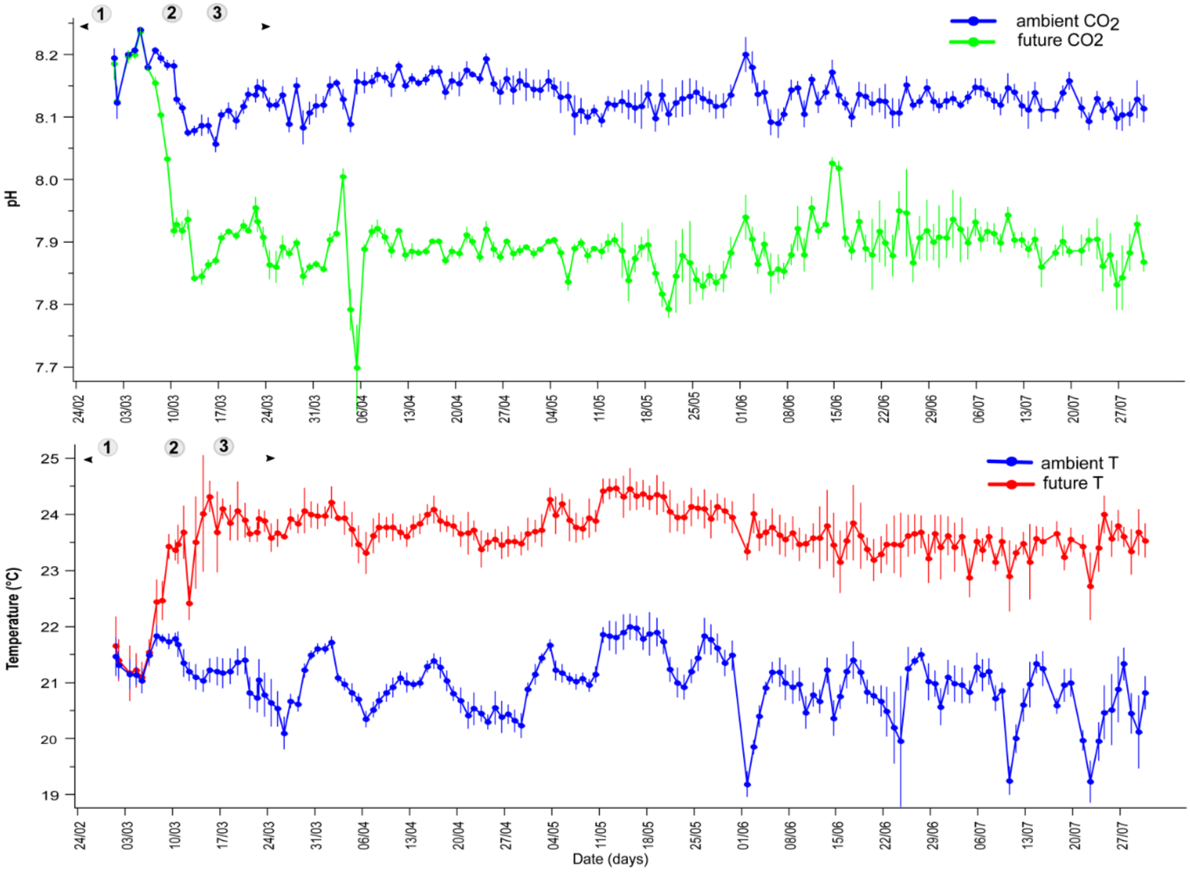
S2 Fig. Absolute flows (gWW/m^2/month) produced by the different functional group at trophic level 3. Mean ± SE values per mesocosm are given (n=3). Significant interactions or main effects ($p<0.05$) within functional groups are based on two-way ANOVAs (df=1,8) and are indicated with asterisks. Means with different lower case letters indicate significant difference among treatments based on post-hoc tests corrected for false discovery rate and done separately for different functional group. No Sig = no significance. See S5 Table for statistical test outcomes.



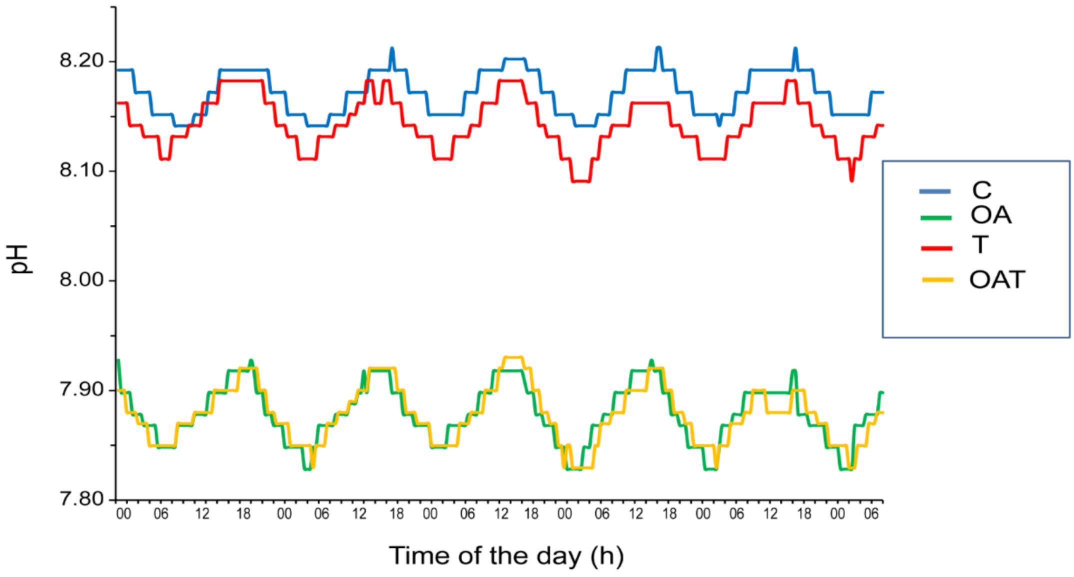
S3 Fig. The Finn’s cycling index, expresses the amount of detritus that is recycled relative to the total throughput of the system. Mean ± SE values per mesocosm are given (n=3). Significant effects ($p<0.05$) are based on two-way ANOVAs with ocean acidification (OA) and warming (T) (df=1, 8) and are indicated with asterisks. Means with different lower case letters indicate significant difference among treatments. See S3 Table for statistical test outcomes.



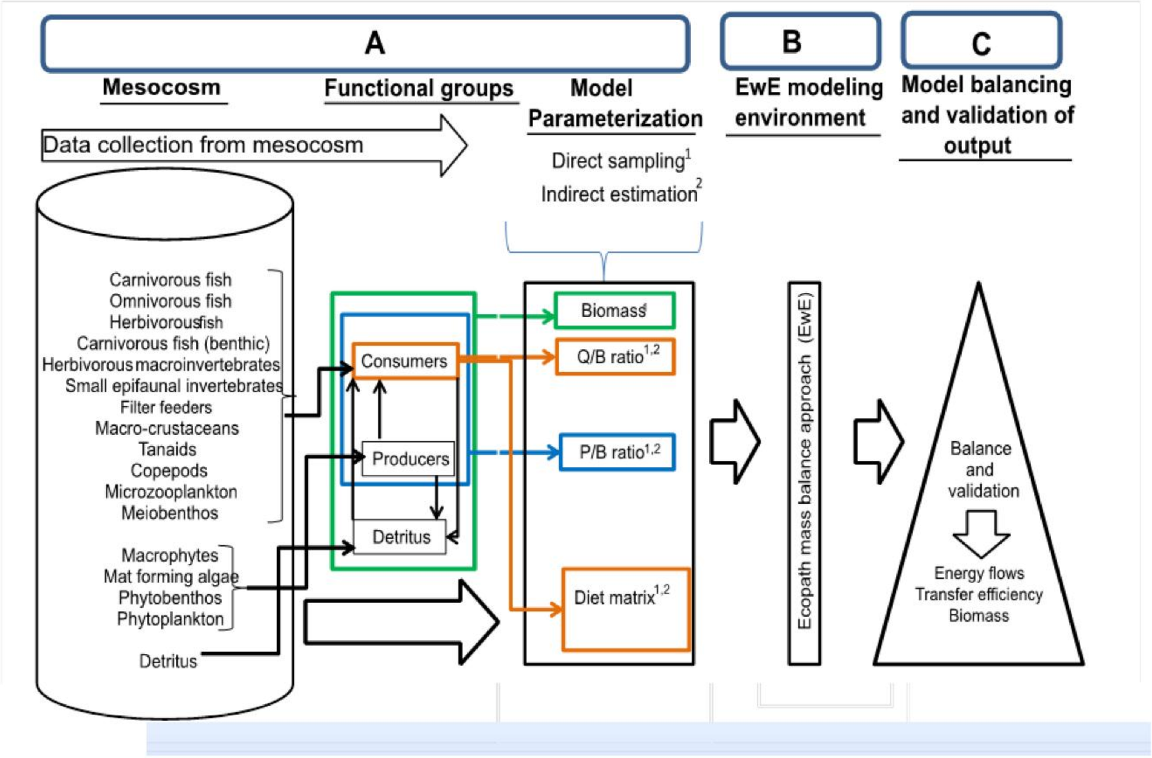
S4 Fig. The different structural components of the mesocosm used for this experiment. Each mesocosm comprises four 'rocky reef' patches (A) and four 'artificial seagrass' patches (B).The space in between and around these patches was considered 'open sand' habitat (C). The incoming seawater was led into two header tanks (800 L) at the beginning of the flow-through facilities, and from there gravity fed into each mesocosm (D). The header tank was pre-conditioned to future pCO_2 levels with pure CO_2 (control system ACQ110 Aquatronica, Italy) prior to supplying the water to the 6 acidified mesocosms. In addition, continuous water circulation (~ 1,800 L per h) was maintained between each mesocosm and a 60 L supporting bin positioned next to each mesocosm that was bubbled heavily with enriched air at 1,000 ppm pCO_2 (PEGAS 4000 MF Gas Mixer, Columbus Instruments, Columbus, Ohio) or ambient air at 400 ppm pCO_2, depending on the acidification treatment. These bins also contained the submersible titanium heaters for the elevated temperature treatments. A diffuser pipe was used to generate a mild circular current inside the mesocosms using the water exchange between supporting bin and mesocosm and alternating direction every 6 hrs (E). A filter column (~ 20 µm) allowed water to flow back into the 60 L bin by gravity (F), and ensured that larger organisms were always retained within the mesocosms. In summery, this technically complex set-up ensured a mesocosm environment without unnatural disturbances such as pump noise, air bubbles or electrical currents. A 250W metal halide lamp (Osram Powerstar HQI-T 250/D/PRO) mounted just above the mesocosm (G) ensured an irradiance that corresponded to approx. 6-7 m water depth in Gulf St. Vincent (Phillips et al. 1981).



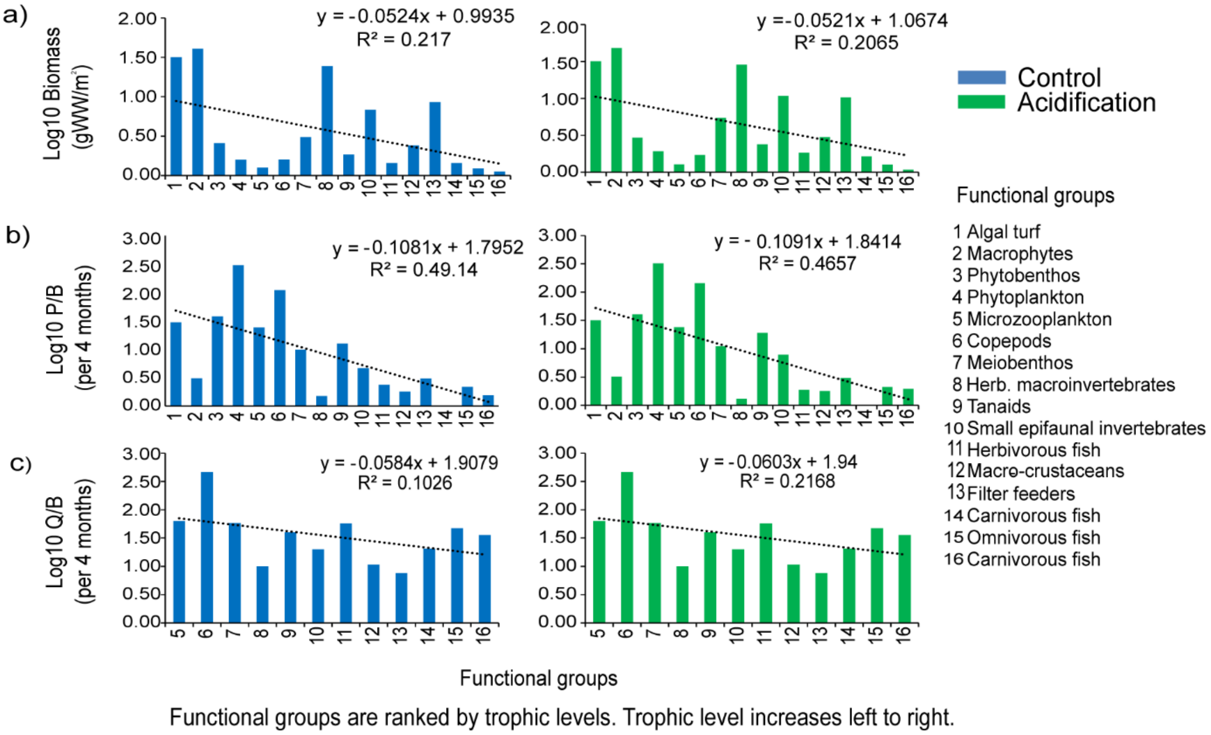
S5 Fig. Variability in pH and temperature over the 6-month study period. This includes three phases: 1) the first week of the acclimation period 2) the progressive elevation to treatment levels, and 3) at maintained treatment levels. Mean ± SD are shown based on three mesocosms for each treatment. pH and temperature were both measured once daily in each mesocosm around midday.



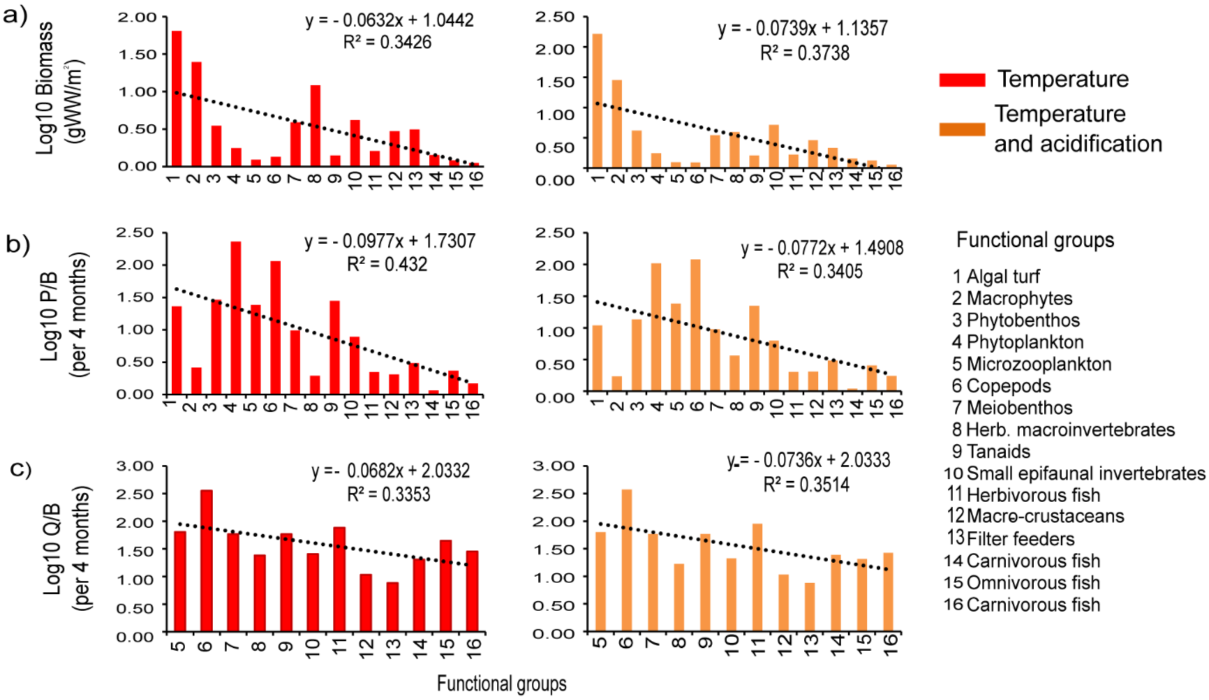
S6 Fig. Diurnal variability in pH measured over a 5-day period in the middle of the study period. This analysis was only done for 1 mesocosm per treatment combination, serving as an example. For these 4 mesocosms in parallel, pH was recorded at 30-min intervals with an automated pH logger (control system ACQ110 Aquatronica, Italy).



S7 Fig. Schematic diagram showing the different phases of model building and execution: A) Data collection from the mesocosms and parameter estimation, B) Mass-balance modelling in Ecopath, and C) Model balancing and validation.



S8 Fig. PREBAL of the control and acidification models plotting (a) biomass estimates (g WW/m^2), (b) production/biomass ratio (per 4 months), and (c) consumption/biomass (per 4 months) on a log scale vs functional groups ranked by their trophic level, from lowest to highest trophic level. A constant of 1 was added to all response variables to avoid some negative values (Log$_{10}$ (X+1) prior to PREBAL plotting. For specific functional group name refer to the legend. Herb. = herbivorous. PREBAL is shown only for base models that are built on the average of all the input parameters (B, P/B, Q/B) across mesocosms within each climate treatment.



Functional groups are ranked by trophic levels. Trophic level increases left to right.

S9 Fig. PREBAL of the temperature and temperature+ acidification models plotting (a) biomass estimates (gWW/m^2), (b) production/biomass ratio (per 4 months), and (c) consumption/biomass (per 4 months) on a log scale vs functional groups ranked by their trophic level, from lowest to highest trophic level. A constant of 1 was added to all response variables to avoid some negative values (Log$_{10}$ (X+1) prior to PREBAL plotting. For specific functional group name refer to the legend. Herb. = herbivorous. PREBAL is shown only for base models that are built on the average of all the input parameters (B, P/B, Q/B) across mesocosms within each climate treatment.

SUPPLEMENTARY TABLES

S1 Table. Analysis of variance of the effects of ocean acidification (OA) and warming (T) and their interaction on absolute flows and transfer efficiency between successive trophic levels of the food web. Significant differences are indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$.

Response variable [transformation]	Source of variation	df	MS	F	P
a) Absolute flow (Trophic level 1)	OA	1	20432	0.34	0.574
	T	1	244178	4.09	0.077
	OA × T	1	119	0.00	0.965
	Residuals	8	59686		
b) Absolute flow (log10) (Trophic level 1 to 2)	OA	1	<0.001	0.00	0.943
	T	1	0.81	25.81	0.001 **
	OA × T	1	0.46	14.74	0.005 **
	Residuals	8	0.03		
c) Absolute flow (Trophic level 2 to 3)	OA	1	0.21	0.03	0.857
	T	1	264.78	43.06	<0.001***
	OA × T	1	14.20	2.30	0.167
	Residuals	8	6.15		
d) Transfer efficiency (Trophic level 1 to 2)	OA	1	1.1	0.01	0.931
	T	1	1586.1	11.22	0.010**
	OA × T	1	416.1	2.94	0.124
	Residuals	8	141.4		
e) Transfer efficiency (Trophic level 2 to 3)	OA	1	0.6	0.31	0.594
	T	1	4.3	2.39	0.160
	OA × T	1	8.0	4.44	0.068
	Residuals	8	1.8		

Degrees of freedom (df), mean squares (MS), F-ratio (F), P-value (P).

S2 Table. Analysis of variance of the effects of ocean acidification (OA) and warming (T) and their interaction on living biomass by trophic levels of the food web. Significant differences are indicated with asterisks, with *: p < 0.05, **: p < 0.01 and ***: p < 0.001.

Response variable [transformation]	Source of variation	df	MS	F	P
a) Living biomass (log10) (Trophic level 1)	OA	1	0.117	10.62	0.012**
	T	1	0.161	15.33	0.004**
	OA × T	1	0.068	6.46	0.035*
	Residuals	8	0.011		
b) Living biomass (log10) (Trophic level 2)	OA	1	0.003	0.254	0.627
	T	1	0.569	44.91	0.000 ***
	OA × T	1	0.061	4.84	0.059
	Residuals	8	0.013		
c) Living biomass (log10) (Trophic level 3)	OA	1	0.002	0.36	0.564
	T	1	0.552	94.87	0.000***
	OA × T	1	0.058	10.01	0.013**
	Residuals	8	0.006		

Degrees of freedom (df), mean squares (MS), F-ratio (F).

S3 Table. Analysis of variance of the effects of ocean acidification (OA) and warming (T) and their interaction on cyanobacteria (% cover), flow (%) to detritus, and Finn's cycling index in the food web. Significant differences are indicated with asterisks, with *: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$.

Response variable	Source of variation	df	MS	F	P
a) Cyanobacteria (% cover)	OA	1	216.10	0.89	0.372
	T	1	4815.20	19.89	0.002**
	OA × T	1	1158.40	4.79	0.060
	Residuals	8	242.00		
b) Flow to detritus (%)	OA	1	4.50	0.01	0.912
	T	1	3164.90	9.12	0.017*
	OA × T	1	981.70	2.83	0.131
	Residuals	8	347.10		
c) Finn's cycling index	OA	1	0.14	0.10	0.758
	T	1	12.98	9.31	0.016*
	OA × T	1	1.83	1.31	0.285
	Residuals	8	1.39		

Degrees of freedom (df), mean squares (MS), F-ratio (F), P-value (P).

S4 Table. Analysis of variance of the effects of ocean acidification (OA) and warming (T) and their interaction on the absolute flows of contributing functional groups from trophic level 1 to 2. Functional groups were ordered in terms of their contribution to total energy flows. Significant differences indicated with asterisks, with *: p < 0.05, **: p < 0.01 and ***: p < 0.001.

Response variable (transformation)	Source of variation	df	MS	F	P
a) Herbivorous macroinvertebrates (log10)	OA	1	0.60	2.85	0.130
	T	1	0.85	4.00	0.081
	OA × T	1	1.14	5.39	0.049*
	Residuals	8	0.21		
b) Meiobenthos	OA	1	44.37	0.50	0.500
	T	1	1096.82	12.30	0.008**
	OA × T	1	279.13	3.13	0.115
	Residuals	8	89.20		
c) Copepods	OA	1	430.6	1.31	0.285
	T	1	4687.5	14.26	0.005**
	OA × T	1	1214.4	3.70	0.090
	Residuals	8	328.6		
d) Small epifaunal invertebrates	OA	1	426.94	3.29	0.107
	T	1	740.92	5.70	0.044*
	OA × T	1	287.70	2.21	0.175
	Residuals	8	129.97		
e) Herbivorous fishes	OA	1	20.619	0.95	0.358
	T	1	11.213	0.52	0.493
	OA × T	1	2.604	0.12	0.738
	Residuals	8	21.755		
f) Filter feeders	OA	1	0.10	0.02	0.903
	T	1	142.50	22.10	0.001**
	OA × T	1	2.21	0.34	0.574
	Residuals	8	6.44		
g) Tanaids (log10)	OA	1	1.20	4.41	0.069
	T	1	1.21	4.47	0.068
	OA × T	1	0.11	0.42	0.534
	Residuals	8	0.27		
h) Macro-crustaceans	OA	1	1.16	0.42	0.537
	T	1	0.86	0.31	0.594
	OA × T	1	1.88	0.67	0.435
	Residuals	8	2.79		
i) Microzooplankton	OA	1	0.21	1.88	0.207
	T	1	0.47	4.08	0.078
	OA × T	1	0.01	0.05	0.823
	Residuals	8	0.12		
j) Carnivorous fishes (benthic)	OA	1	0.05	8.47	0.020*
	T	1	0.10	17.58	0.003**
	OA × T	1	0.05	7.93	0.023*

	Residuals	8	0.01		
k) Omnivorous fishes	OA	1	0.01	3.84	0.085
	T	1	0.02	7.98	0.022*
	OA × T	1	<0.00	0.05	0.817
	Residuals	8	<0.00		
l) Carnivorous fishes (log10)	OA	1	0.01	618.02	<0.001***
	T	1	0.03	1306.41	<0.001***
	OA × T	1	0.02	902.34	<0.001***
	Residuals	8	0.00		

S5 Table. Analysis of variance of the effects of ocean acidification (OA) and warming (T) and their interaction on the absolute flows of contributing functional groups from trophic levels 2 to 3. Functional groups were ordered in terms of their contribution to total energy flows. Significant differences are indicated with asterisks, with *: p < 0.05, **: p < 0.01 and ***: p < 0.001.

Response variable (transformation)	Source of variation	DF	MS	F	P
a) Omnivorous fishes (log10)	OA	1	0.15	7.06	0.029*
	T	1	0.39	18.59	0.003**
	OA × T	1	0.04	1.72	0.226
	Residuals	8	0.02		
b) Filter feeders	OA	1	1.39	0.55	0.479
	T	1	78.21	30.97	0.001***
	OA × T	1	11.91	4.72	0.062
	Residuals	8	2.53		
c) Carnivorous fishes (benthic)	OA	1	0.81	6.29	0.037*
	T	1	0.95	7.45	0.026*
	OA × T	1	0.06	0.48	0.506
	Residuals	8	0.12		
d) Small epifaunal invertebrates	OA	1	0.35	0.81	0.393
	T	1	2.12	4.90	0.057
	OA × T	1	1.46	3.38	0.103
	Residuals	8	0.43		
e) Herbivorous fishes (log10)	OA	1	0.00	0.03	0.865
	T	1	0.01	0.37	0.561
	OA × T	1	0.08	2.51	0.152
	Residuals	8	0.03		
f) Carnivorous fishes	OA	1	0.13	8.13	0.021*
	T	1	0.01	0.65	0.443
	OA × T	1	0.23	14.86	0.005**
	Residuals	8	0.02		
g) Tanaids (log10)	OA	1	0.23	4.41	0.069
	T	1	0.23	4.47	0.067
	OA × T	1	0.02	0.42	0.534
	Residuals	8	0.05		
h) Macro-crustaceans	OA	1	0.01	0.42	0.536
	T	1	0.01	0.31	0.594
	OA × T	1	0.02	0.68	0.435
	Residuals	8	0.03		

S6 Table. List of species/taxa and their respective functional group considered in the mesocosm food webs.

Functional group	Common name	Species/taxon	Stocking density /mesocosm	Initial size	Status
Carnivorous fishes	Small-mouthed hardyhead	*Atherinosoma microstoma*	10	24 ± 5*	randomly distributed
Omnivorous fishes	Little weed whiting	*Neoodax balteatus*	7	30 ± 8*	randomly distributed
	Blue weedy whiting	*Haletta semifasciata*	7	31 ± 4*	randomly distributed
Carnivorous fishes (benthic)	Longfin goby	*Favonigobius lateralis*	7	22 ± 4*	randomly distributed
Herbivorous fishes	Zebrafish	*Girella zebra*	7	17 ± 2*	randomly distributed
	Toothbrush leatherjacket	*Acanthaluteres vittige*	7	30 ± 8*	randomly distributed
Herbivorous macro-invertebrates	Brown bubble snail	*Bulla quoyii*	10	400 ± 42**	randomly distributed
	Conical top shell	*Thalotia conica*	12	385 ± 218**	randomly distributed
	Australian pheasant	*Phasianella australis*	20	252 ± 770**	randomly distributed
	Small sea snails	*Cantharidus* spp.	10	150 ± 89**	randomly distributed
Macro-crustaceans	Rock-pool prawns	*Palaemon serenus*	10 (including both spp.)		randomly distributed
	Striped shrimp	*Palaemon intermedius*			randomly distributed
Small epifaunal invertebrates	Smaller snails, Abalone, Sea urchin, Polychaete, Leach worms, Slug worms, Amphipods, Brittle stars, Seastars, Crabs				introduced with habitat or seawater
Filter feeders	Sponges, Ascidians, Corals, Tunicates, Bivalves, Barnacles				introduced with habitat or seawater
Tanaids	Tanaids				introduced with habitat or seawater
Copepods	Copepods				introduced with habitat or seawater
Microzooplankton	Mostly heterotrophic nanoflagellates, ciliates and copepod nauplii				introduced with habitat or seawater
Meiobenthos	Meiobenthos				changed
Macrophytes	Macrophytes				introduced with habitat
Mat-forming algae	Turf and cyanobacteria				introduced with habitat or

			seawater
Phytobenthos	Phytobenthos		introduced with habitat or seawater
Phytoplankton	Phytoplankton		introduced with habitat or seawater
Detritus			System generated

The asterisks represents length in mm* and weight as mg** while ± represents standard deviation.

S7 Table. Mean (± SD) seawater parameters in the experimental mesocosoms with two crossed factors of warming (T) and acidification (OA). Standard deviations represent the variability between individual mesocosm.

Parameter	**C**	**OA**	**T**	**OAT**
Temperature (°C)	21.0 ± 0.14	20.9 ± 0.04	23.7 ± 0.19	23.7 ± 0.08
pH_{NBS}	8.14 ± 0.004	7.89 ± 0.009	8.12 ± 0.002	7.89 ±0.009
Salinity (ppt)	36.3 ± 0	36.3 ± 0	36.3 ± 0	36.3 ± 0
Total Alkalinity (μmol kg^{-1})	2482 ± 4	2485 ± 5	2486 ± 6	2493 ± 3
pCO_2 (ppm)	465 ± 5	905 ± 6	500 ± 8	915 ± 25
HCO_3 (μmol kg^{-1})	1995 ± 6	2186 ± 3	1985 ± 2	2166 ± 9
CO_3 (μmol kg^{-1})	200 ± 2	123 ± 1	206 ± 2	135 ± 3
Ω Calcite	4.74 ± 0.05	2.91 ± 0.02	4.90 ± 0.05	3.20 ± 0.07
Ω Aragonite	3.09 ± 0.04	1.90 ± 0.01	3.22 ± 0.03	2.10 ± 0.05

S8 Table. Input (non-italic) and output (italic) parameters for the ecosystem components used in control (C) models. TL: trophic level, B: biomass (g WWm^{-2}), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. CM1 represents control model 1, CM2 represents control model 2 and CM3 represent control model 3. The value in bold indicates that particular parameter varied among the models and mentioned below the table.

Functional groups	All models	CM1	CM2	CM3	All models		CM1	CM2	CM3	All models
	TL		B		P/B	Q/B		EE		P/Q
1 Carnivorous fishes	*3.02*	0.14	0.13	0.11	0.56	19.53	*0.00*	*0.00*	*0.00*	*0.03*
2 Omnivorous fishes	*2.99*	0.26	0.24	0.18	1.17	111.75	*0.00*	*0.00*	*0.00*	*0.01*
3 Herbivorous fishes	*2.07*	0.66	0.28	0.36	1.37	94.06	*0.00*	*0.00*	*0.00*	*0.01*
4 Carnivorous fishes (benthic)	*2.82*	0.50	0.40	0.40	0.00	28.99	*0.00*	*0.00*	*0.00*	*0.00*
5 Herbivorous macroinvertebrates	*2.00*	36.47	18.02	16.14	0.50	8.46	*0.00*	*0.00*	*0.00*	*0.06*
6 Small epifaunal invertebrates	*2.07*	5.27	5.10	7.12	3.67	18.00	*0.73*	*0.58*	*0.38*	*0.20*
7 Filter feeders	**2.4***	5.42	8.06	9.09	2.05	7.60	*0.43*	*0.28*	*0.34*	*0.27*
8 Macro-crustaceans	*2.10*	2.34	1.10	0.79	0.80	10.72	*0.00*	*0.00*	*0.00*	*0.07*
9 Tanaids	*2.05*	0.68	1.14	0.71	11.51	40.15	*0.97*	*0.59*	*0.81*	*0.29*
10 Copepods	*2*	0.57	0.86	0.35	108.71	336.98	*0.65*	*0.45*	*0.96*	*0.32*
11 Microzooplankton	*2*	0.25	0.23	0.29	23.11	63.49	*0.60*	*0.82*	*0.69*	*0.36*
12 Meiobenthos	*2*	3.43	4.37	2.80	8.88	58.40	*0.05*	*0.06*	*0.06*	*0.15*
13 Macrophytes	*1*	40.72	39.79	38.17	2.07		*0.51*	*0.36*	*0.50*	
14 Mat-forming algae	*1*	23.87	27.93	40.45	28.87		*0.74*	*0.46*	*0.26*	

15	Phytobenthos	*1*	1.25	1.89	1.57	36.69		*0.66*	*0.68*	*0.40*
16	Phytoplankton	*1*	0.55	0.59	0.63	299.29		*0.69*	*0.91*	*0.55*
17	Detritus	*1*	3.43	2.46	3.33			*0.40*	*0.36*	*0.16*

* Trophic level of filter feeders within control model 3 was 2.35

S9 Table. Input (non-italic) and output (italic) parameters for the ecosystem components used in the acidification (OA) models. TL: trophic level, B: biomass (g WWm^{-2}), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. OAM1 represents acidification model 1, OAM2 represents acidification model 2 and OAM3 represents acidification model 3. The value in bold indicates that particular parameter varies among the models as mentioned below the table.

Functional groups	All models	OAM1	OAM2	OAM3	All models		OAM1	OAM2	OAM3	All models
	TL	B			P/B	Q/B	EE			P/Q
1 Carnivorous fishes	*3.00*	0.12	0.11	0.14	0.97	35.66	*0.00*	*0.00*	*0.00*	*0.03*
2 Omnivorous fishes	*2.96*	0.39	0.26	0.16	1.10	47.15	*0.00*	*0.00*	*0.00*	*0.02*
3 Herbivorous fishes	*2.08*	1.16	0.81	0.56	0.88	57.49	*0.00*	*0.00*	*0.00*	*0.02*
4 Carnivorous fishes (benthic)	**_2.9*_**	0.69	0.56	0.65	0.00	20.60	*0.00*	*0.00*	*0.00*	*0.00*
5 Herbivorous macroinvertebrates	*2.00*	29.34	25.82	27.28	0.30	9.97	*0.00*	*0.00*	*0.00*	*0.03*
6 Small epifaunal invertebrates	*2.07*	9.61	12.74	7.24	6.84	19.87	*0.11*	*0.06*	*0.08*	*0.34*
7 Filter feeders	*2.45*	12.78	7.02	8.64	2.05	7.60	*0.36*	*0.80*	*0.41*	*0.27*
8 Macro-crustaceans	*2.10*	1.00	2.69	2.30	0.78	10.72	*0.00*	*0.00*	*0.00*	*0.07*
9 Tanaids	*2.05*	1.12	0.90	2.13	18.07	58.40	*0.37*	*0.36*	*0.16*	*0.31*
10 Copepods	*2*	0.89	0.78	0.46	143.81	462.43	*0.49*	*0.34*	*0.63*	*0.31*
11 Microzooplankton	*2*	0.29	0.26	0.28	23.11	63.49	*0.80*	*0.92*	*0.78*	*0.36*
12 Meiobenthos	*2*	4.83	4.03	4.51	10.06	58.40	*0.09*	*0.09*	*0.16*	*0.17*
13 Macrophytes	*1*	47.52	49.10	45.11	2.22	0.00	*0.53*	*0.86*	*0.38*	

14	Mat forming algae	*1*	49.41	18.32	24.34	30.85	0.00	*0.44*	*0.99*	*0.69*
15	Phytobenthos	*1*	2.75	1.61	1.46	39.21	0.00	*0.62*	*0.91*	*0.95*
16	Phytoplankton	*1*	1.01	0.88	0.86	319.85	0.00	*0.71*	*0.86*	*0.51*
17	Detritus	*1*	2.84	2.94	2.42			*0.23*	*0.53*	*0.42*

* Trophic level of carnivorous fishes (benthic) within the acidification model 2 was 2.80

S10 Table. Input (non-italic) and output (Italic) parameters for the ecosystem components used in the temperature (T) models. TL: trophic level, B: biomass (g WWm^{-2}), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. TM1 represents temperature model 1, TM2 represents temperature model 2 and TM3 represents temperature model 3. The values in bold indicate that particular parameters vary among the models as mentioned below the table.

Functional groups	All models	TM1	TM2	TM3	All models		TM1	TM2	TM3	All models
	TL		B		P/B	Q/B		EE		P/Q
1 Carnivorous fishes	*3.04*	0.12	0.09	0.15	0.48	28.32	*0.00*	*0.00*	*0.00*	*0.02*
2 Omnivorous fishes	*2.97*	0.30	0.13	0.20	1.34	44.28	*0.00*	*0.00*	*0.00*	*0.03*
3 Herbivorous fishes	**_2.11*_**	0.96	0.39	0.49	1.22	76.40	*0.00*	*0.00*	*0.00*	*0.02*
4 Carnivorous fishes (benthic)	*2.87*	0.30	0.44	0.53	0.15	20.20	*0.00*	*0.00*	*0.00*	*0.01*
5 Herbivorous macroinvertebrates	*2.00*	13.90	15.64	3.78	0.95	24.15	*0.00*	*0.00*	*0.00*	*0.04*
6 Small epifaunal invertebrates	**_2.13*_**	6.10	2.30	1.07	6.78	25.55	*0.45*	*0.58*	*0.84*	*0.27*
7 Filter feeders	*2.45*	2.97	1.75	1.76	2.05 *****	7.6 *****	*0.73*	*0.82*	*0.76*	*0.30*
8 Macro-crustaceans	*2.10*	1.42	2.62	1.84	1.04	10.72	*0.00*	*0.00*	*0.00*	*0.10*
9 Tanaids	*2.05*	0.22	0.31	0.71	19.50	58.40	*0.69*	*0.69*	*0.52*	*0.33*
10 Copepods	*2*	0.29	0.31	0.43	114.10	356.24	*0.85*	*0.41*	*0.33*	*0.32*
11 Microzooplankton	*2*	0.26	0.23	0.21	23.11	63.49	*0.59*	*0.38*	*0.59*	*0.36*
12 Meiobenthos	*2*	2.21	3.23	3.21	8.80	58.40	*0.03*	*0.03*	*0.07*	*0.15*

13	Macrophytes	*1*	29.80	21.14	20.60	1.59	0.00	*0.96*	*0.70*	*0.65*
14	Mat-forming algae	*1*	69.41	32.58	89.04	22.08	0.00	*0.35*	*0.69*	*0.11*
15	Phytobenthos	*1*	2.54	2.54	2.46	28.07	0.00	*0.22*	*0.26*	*0.46*
16	Phytoplankton	*1*	0.71	0.82	0.76	228.95	0.00	*0.51*	*0.35*	*0.46*
17	Detritus	*1*	2.81	2.79	4.75			*0.11*	*0.31*	*0.11*

Herbivorous fishes and small epifaunal invertebrates occupied a tropic level of 2.10 and 2.15, respectively, within TM3
P/B ratio of filter feeders was modified to 3.6 for TM2 and TM3 models
Q/B ratio of filter feeders was modified to 11.8 for TM2 and TM3 models

S11 Table. Input (non-italic) and output (italic) parameters for the ecosystem components used in the temperature and acidification (OAT) models. TL: trophic level, B: biomass (g WWm^{-2}), P/B: production/biomass ratio (per 4 months), Q/B: consumption/biomass ratio (per 4 months), EE: ecotrophic efficiency, P/Q: gross food conversion efficiency of each functional group. OATM1 represents temperature and acidification model 1, OATM2 represents temperature and acidification model 2 and OATM3 represents temperature and acidification model 3. The value in bold indicates that particular parameter varies among the models as mentioned below the table.

Functional groups	All models	OAT M1	OATM2	OATM3	All models		OATM1	OATM2	OATM3	All models
	TL		B		P/B	Q/B		EE		P/Q
1 Carnivorous fishes	*2.89*	0.13	0.13	0.14	0.74	26.56	*0.00*	*0.00*	*0.00*	*0.03*
2 Omnivorous fishes	*2.98*	0.31	0.39	0.28	1.54	20.52	*0.00*	*0.00*	*0.00*	*0.08*
3 Herbivorous fishes	*2.05*	0.52	0.93	0.54	1.02	89.21	*0.00*	*0.00*	*0.00*	*0.01*
4 Carnivorous fishes (benthic)	*2.90*	0.39	0.49	0.49	0.10	24.35	*0.00*	*0.00*	*0.00*	*0.00*
5 Herbivorous macroinvertebrates	*2.00*	1.35	7.30	0.16	2.63	16.74	*0.00*	*0.00*	*0.00*	*0.16*
6 Small epifaunal invertebrates	*2.08*	5.75	2.37	4.35	5.28	21.13	*0.18*	*0.62*	*0.32*	*0.25*
7 Filter feeders	*2.25*	2.33	0.72	0.42	**2.05***	**7.6***	*0.88*	*0.68*	*0.91*	*0.30*
8 Macro-crustaceans	*2.10*	1.63	2.23	1.81	1.05	10.72	*0.00*	*0.00*	*0.00*	*0.10*
9 Tanaids	*2.05*	0.59	0.20	1.06	**21.36***	**58.40***	*0.52*	*0.99*	*0.33*	*0.33*
10 Copepods	*2*	0.11	0.25	0.36	119.05	373.95	*0.95*	*0.51*	*0.27*	*0.32*
11 Microzooplankton	*2*	0.23	0.25	0.26	23.11	63.49	*0.80*	*0.32*	*0.32*	*0.36*
12 Meiobenthos	*2*	1.77	2.44	3.25	8.50	58.40	*0.11*	*0.04*	*0.11*	*0.15*

13	Macrophytes	*1*	28.48	34.89	18.87	0.71	0.00	*0.98*	*0.84*	*0.96*
14	Mat-forming algae	*1*	135.96	198.29	154.90	9.93	0.00	*0.13*	*0.14*	*0.13*
15	Phytobenthos	*1*	2.79	3.99	2.62	12.62	0.00	*0.86*	*0.32*	*0.97*
16	Phytoplankton	*1*	0.95	0.66	0.65	102.95	0.00	*0.52*	*0.82*	*0.98*
17	Detritus	*1*	3.99	3.86	4.25			*0.10*	*0.09*	*0.16*

P/B ratio and Q/B ratio of filter feeder was modified to 3.6 and 11.8, respectively, for OATM1 and OATM3 models
P/B ratio of tanaids was modified to 19.5 for OATM1 and OATM3 models and to 27.04 for OATM2 models
Q/B ratio of tanaids was modified to 85 for OATM2 models

S12 Table. Predator/prey matrix (column/row) for control (C) models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to one. Values with mean ± SD represent the adjustment of different prey groups in predators diet across models.

Functional groups	1	2	3	4	5	6	7	8	9	10	11	12
Carnivorous fishes												
Omnivorous fishes												
Herbivorous fishes												
Carnivorous fishes (benthic)												
Herbivorous macroinvertebrates												
Small epifaunal invertebrates	0.47	0.14	0.05	0.39								
Filter feeders						0.05						
Macro-crustaceans												
Tanaids	0.01	0.17	0.00	0.26								
Copepods		0.65	0.01	0.13			0.35	0.10				
Microzooplankton	0.51						0.05					
Meiobenthos		0.00	0.00	0.00					0.05			
Macrophytes		0.00	0.35	0.15		0.20						
Mat-forming algae	0.01	0.03	0.59		1.00	0.70		0.40	0.05	0.45		
Phytobenthos									0.40	0.10		
Phytoplankton							0.50			0.40	1.00	

Detritus				0.07		0.05	0.10	0.50	0.50	0.05		1.00
	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Tanaids		0.15±0.03										
Copepods		0.67±0.03					0.33±0.30					
Phytoplankton							0.52±0.03					

S13 Table. Predator/prey matrix (column/raw) for acidification (OA) models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to one. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models.

Functional groups	1	2	3	4	5	6	7	8	9	10	11	12
Carnivorous fishes												
Omnivorous fishes												
Herbivorous fishes												
Carnivorous fishes (benthic)												
Herbivorous macroinvertebrates												
Small epifaunal cryptic invertebrates		0.11	0.05	0.11								
Filter feeders						0.05						
Macro-crustaceans												
Tanaids	0.02	0.04	0.01	0.41								
Copepods		0.81	0.01	0.34			0.40	0.10				
Microzooplankton	0.75						0.05					
Meiobenthos	0.24			0.00					0.05			
Macrophytes		0.05	0.24	0.08		0.20						
Mat-forming algae			0.68		1.00	0.70		0.40	0.05	0.45		
Phytobenthos									0.40	0.10		
Phytoplankton							0.50			0.40	1.00	

Detritus				0.06		0.05		0.05	0.50	0.50	0.05		1.00
	1.00	1.00	1.00	1.00	1.00	1.00			1.00	1.00	1.00	1.00	1.00
Copepods								0.42±0.02					
Microzooplankton								0.03±0.02					
Macrophytes							0.25±0.09						
Mat-forming algae							0.68±0.03			0.08±0.04	0.40±0.09		
Phytobenthos										0.37±0.04	0.09±0.00		
Phytoplankton											0.46±0.08		

S14 Table. Predator/prey matrix (column/raw) for temperature (T) models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to one. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models.

Functional groups	1	2	3	4	5	6	7	8	9	10	11	12
Carnivorous fishes												
Omnivorous fishes												
Herbivorous fishes												
Carnivorous fishes (benthic)												
Herbivorous macroinvertebrates												
Small epifaunal cryptic invertebrates	0.44	0.17	0.08	0.17								
Filter feeders						0.10						
Macro-crustaceans												
Tanaids	0.02	0.00	0.00	0.46								
Copepods		0.78	0.01	0.18			0.40	0.10				
Microzooplankton	0.52						0.05					
Meiobenthos				0.00					0.05			
Macrophytes	0.02	0.05	0.38	0.15		0.18						
Mat-forming algae			0.52		1.00	0.70		0.40	0.05	0.45		
Phytobenthos									0.40	0.10		
Phytoplankton							0.50			0.40	1.00	

Detritus				0.03		0.02	0.05	0.50	0.50	0.05		1.00
	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Small epifaunal cryptic invertebrates		0.16±0.01	0.07±0.02	0.16±0.01		0.03±0.03						
Filter feeders						0.07±0.03						
Tanaids		0.02±0.02	0.01±0.02	0.47±0.01								
Macrophytes						0.15±0.04						
Mat-forming algae						0.71±0.02						
Phytoplankton						0.02±0.03						

S15 Table. Predator/prey matrix (column/raw) for temperature and acidification (OAT) models. The fraction of one compartment consumed by another is expressed as the fraction of the total diet, the sum of each column being equal to one. Values with mean ± SD represent the adjustment of different prey groups in predator diets across models.

Functional groups	1	2	3	4	5	6	7	8	9	10	11	12
Carnivorous fishes												
Omnivorous fishes												
Herbivorous fishes												
Carnivorous fishse (benthic)												
Herbivorous macroinvertebrates												
Small epifaunal cryptic invertebrates	0.41	0.18	0.03	0.16								
Filter feeders						0.07						
Macro-crustaceans												
Tanaids	0.00	0.05		0.54								
Copepods		0.73	0.02	0.16			0.40	0.10				
Microzooplankton	0.45						0.05					
Meiobenthos				0.00					0.05			
Macrophytes	0.14	0.04	0.08	0.08		0.25						
Mat-forming algae			0.87		1.00	0.62		0.40	0.05	0.45		
Phytobenthos									0.40	0.10		

Phytoplankton							0.50			0.40	1.00	
Detritus				0.06		0.06	0.05	0.50	0.50	0.05		1.00
	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Small epifaunal cryptic invertebrates				0.18±0.02								
Filter feeders						0.03±0.02						
Tanaids		0.07±0.04		0.50±0.08								
Copepods		0.70±0.04		0.19±0.05			0.35±.18					
Microzooplankton							0.06±0.03					
Macrophytes						0.15±0.09						
Mat-forming algae						0.72±0.10			0.08±0.05	0.47±0.03		
Phytobenthos									0.37±0.05			
Phytoplankton							0.53±0.15			0.38±0.03		

S16 Table. Source of additional information used (√) to parameterize base (control model) models for different functional groups. Where similar values used across treatments were specified in the supplementary text.

Group	Functional groups	P/B	Q/B	References
Consumers	Small epifaunal cryptic invertebrates	√	√	[93]
	Filter feeders	√	√	[95-97]
	Macro-crustaceans	√	√	[93,98,99]
	Tanaids		√	[95]
	Copepods		√	[93,101-103]
	Microzooplankton	√	√	[96,97,106,125]
	Meiobenthos		√	[95]
Producers	Macrophytes	√		[93,111]
	Mat-forming algae	√		[109,110]
	Phytobenthos	√		[93,108]
	Phytoplankton	√		[93,103,108]

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CHAPTER III

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Global warming likely to benefit fisheries in temperate marine ecosystems at a cost to biodiversity

Statement of Authorship

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Global warming likely to benefit fisheries in temperate marine ecosystems at a cost to biodiversity

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ABSTRACT

Global warming, in combination with the intensive exploitation of commercial marine species, has caused large-scale reorganizations of biological communities in many of the world's marine ecosystems. Accurate predictions of the potential effects of global warming (and fishing) at ecosystem-levels require a comprehensive understanding of how entire communities of species respond to global change (namely warming and acidification). We used a time-dynamic integrated ecosystem modelling approach (Ecosim) to investigate the independent and combined effects of global warming and ocean acidification in conjunction with local fishing on a coastal ecosystem. To quantify the effects of ocean acidification and increasing temperature at the community level, we incorporated physiological and behavioural responses of species to these stressors from our two large-scale mesocosm experiments, which included multiple trophic levels from primary producers to top predators such as sharks. Our ecosystem models accounted for complex species interactions such as predation and competition, and represent the likely future food web structure and fisheries productivity under climate change and different fishing regimes. We show that under continuation of the present-day fishing regime, warming and ocean acidification will benefit most of the higher trophic level community groups (e.g. mammals, birds, demersal finfish), except small pelagic fish which will be subject to increased top-down control under warming. Under increased fishing, however, the positive effects of warming and acidification are negated, decreasing the individual biomass of marine mammal, bird, chondrichthyans and demersal finfish taxa. Nevertheless, total future potential fisheries biomass will likely still remain high, particularly under acidification, compared to the present-day scenario because unharvested opportunistic species will likely benefit from decreased competition and an increase in biomass. However, ecological indicator such as the Shannon diversity index showed a significant decrease under all climate change scenarios, suggesting a trade-off between biomass gain and functional diversity. We conclude that sustainably-managed temperate marine ecosystems could benefit in terms of fisheries productivity from ocean

warming and ocean acidification due to boosting of generalist species, albeit to the detriment of functional species diversity.

3.1 INTRODUCTION

Marine ecosystems and fisheries stocks are facing significant challenges due to the cumulative effects of multiple global and local stressors such as overfishing, eutrophication, pollution, habitat destruction, climate change, and ocean acidification (Cheung, 2018, Cheung *et al.*, 2013, Gattuso *et al.*, 2015, Halpern *et al.*, 2015, Halpern *et al.*, 2012, Urban *et al.*, 2016). Yet, global demand for wild-caught fishes has only been increasing (Cheung, 2018, Delgado *et al.*, 2003). Hence, significant effort is needed to generate reliable predictions of future changes in marine food webs and fisheries productivity.

Past attempts to project future changes in populations of fisheries species under ongoing climate change, have incorporated the direct impact of temperature on species physiology using deterministic food web models (Brown *et al.*, 2010), end-to-end climate models (Fulton, 2011, Griffith *et al.*, 2012, Griffith *et al.*, 2011, Olsen *et al.*, 2018, Ortega-Cisneros *et al.*, 2018, Weijerman *et al.*, 2015), and species distribution models (Cheung *et al.*, 2011, Cheung *et al.*, 2009, Fernandes *et al.*, 2013, Peterson *et al.*, 2002). Most of these projections, however, are based on species' thermal niches, ignoring the potentially large role of indirect (e.g. shifting predator-prey relationships) and interactive stressor effects (e.g., with ocean acidification) on model outcomes. Although thermal niches play an important role in 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). Recent attempts to model the effects of acidification on a whole food web context based on pH sensitivity of functional groups also showed the importance of considering acidification on future ecosystem studies (Cornwall & Eddy, 2015, Marshall *et al.*, 2017). Although, crucial step has been made to improve our understanding of how multiple stressors such as warming, acidification and fishing interact and affect marine community (Griffith *et al.*, 2012, Koenigstein *et al.*, 2016); they lack incorporation of important biotic interaction in response to future climate change.

The role of indirect effects of climate change (e.g. shifting predator-prey relationships) on marine communities has received much less attention than direct effects, even though they can shape future marine communities (Lord *et al.*, 2017, Nagelkerken *et al.*, 2017). More reliable forecasts of the likely effects of future climate change on marine communities will be achieved if species interactions are accounted for in model projections (Brown *et al.*, 2010, Daufresne *et al.*, 2009, Zhang *et al.*, 2017). The importance of direct and indirect interactions in shaping community structure and species diversity is known (O'Connor *et al.*, 2013). However, uncertainty remains about the interactive effects of direct and indirect interaction, especially under climate change since they are the net result of multiple species responding to multiple changes in their environment (Tylianakis *et al.*, 2008). Empirical data on species interactions under near-future climate change scenarios is needed to address this key challenge. Large-scale mesocosm experiments can potentially provide suitable empirical data on the effect of global warming on the strength of biotic interactions, species turnover rate and their composition along with many other key ecological processes that drive population- and community-level responses to climate change (Fordham, 2015, Goldenberg *et al.*, 2018). Although scale, closed boundaries, simplified ecological communities, and replication can impose challenges for mesocosm research, they hold potential to quantify reliable data to parameterize computational ecological models (Sagarin *et al.*, 2016).

The large uncertainty related to current projections of future marine food webs and their subsequent effects on fisheries is primarily due to the variable response of ocean primary production to climate change and the dynamic nature of energy transfer through food webs (Brander, 2007, Stock *et al.*, 2017). To date, most simulation models reveal a general pattern of increased primary production in response to projections of future temperature or acidification (modelled in isolation), benefitting or affecting future fisheries (Brown *et al.*, 2010, Cheung *et al.*, 2010, Griffith *et al.*, 2011, Marshall *et al.*, 2017). Importantly, the cumulative effect of these two stressors in natural food webs integrating complex species interaction remains largely unexplored despite both of them occurring due to human greenhouse gas emissions. Furthermore, the parameterization of these models has predominantly been based on using data from single species experiments or the known range of population parameters under natural condition, which is problematic, since the ecological complexity of food webs can dampen the effect of climate change on individuals and communities (Goldenberg *et al.*, 2018). Also, parameterization of food web model should consider species response to perturbation from multilevel food web experiments since community response to global change could vary with food chain length (Hansson *et al.*, 2012).

Here, we build dynamic food web simulation models to test whether: (1) the combination of two global stressors (ocean acidification and warming) exerts synergistic, additive or antagonistic effect on the future food webs and fisheries stocks of a temperate coastal ecosystem, and (2) whether fishing effort as an additional local stressor amplifies or lessen the response of these two global stressors. To predict how ocean acidification and warming individually drive ecosystem change, we also modelled these stressors separately. We accomplished this by using climate-driven change in physiological and behavioral parameters (species interactions) of species as well as primary productivity obtained from two of our own large-scale mesocosm experiments that included food webs composed of primary producers to top predators such as sharks. Our results show some surprising ecological consequences of climate change on future food web and fish production capacity that is an increase in productivity of some fisheries species, albeit at the detriment of species diversity.

3.2 RESULTS

Biomass changes under future climate change

Our model simulations show that the total biomass of most of the higher-order community groups (mammals, cephalopods, chondrichthyes, and demersal finfish) is likely to benefit from ocean warming and acidification, when modelled separately as well as together, although the combined stressors have an antagonistic effect on biomass increase (Fig. 1). When considered at the levels of individual species or functional groups the positive effects on biomass are more disparate (Figs. S1, S2). Our models predict an average increase in marine mammal biomass of 71% under the combined effect of acidification and warming compared to no climate change and current level of fishing effort (‘no change’ scenario). Modelling acidification and warming separately resulted in even higher average increases in marine mammal biomass: 195% and 261%, respectively. Likewise, cephalopod biomass was predicted to increase by 75% under the combination of warming and acidification, while warming and acidification in isolation likely boost biomass by 302% and 118%, respectively. Demersal finfish and seabirds showed their largest biomass increase under ocean acidification (209% and 129 %, respectively), with a smaller increase under both warming scenarios. Pelagic finfish showed a negative response to the warming, irrespective of acidification (Fig. 1A): a decline under warming alone (23%), with groups such as small pelagics (mostly planktivores) showing severe depletions (>70%) under warming (Fig. S1).

Unlike higher trophic groups, ocean warming – either alone or in combination with ocean acidification – is predicted to exert a negative effect on two lower trophic-level faunal groups (Fig. 1A). These are (i) invertebrates (predominantly molluscs, and other invertebrates do not posses chitinous exoskeleton; Table S3), which are likely to experience biomass declines of 9-74%; and (ii) small pelagic crustaceans, which are likely to decline by 45-70% (Fig. 1). In contrast, benthic crustaceans (predominantly decapoda) are likely to experience a moderate increase in biomass (~30-49%) under elevated temperature scenarios, whilst all above three groups experience biomass increases under acidification alone (Fig. 1). Mixed-trophic impact analysis (Fig. S3) and keystone group analysis (Fig. S4) also suggested a likely increase in the biomass of benthic crustaceans and their relative influence as a major prey groups on the other community groups of the food web.

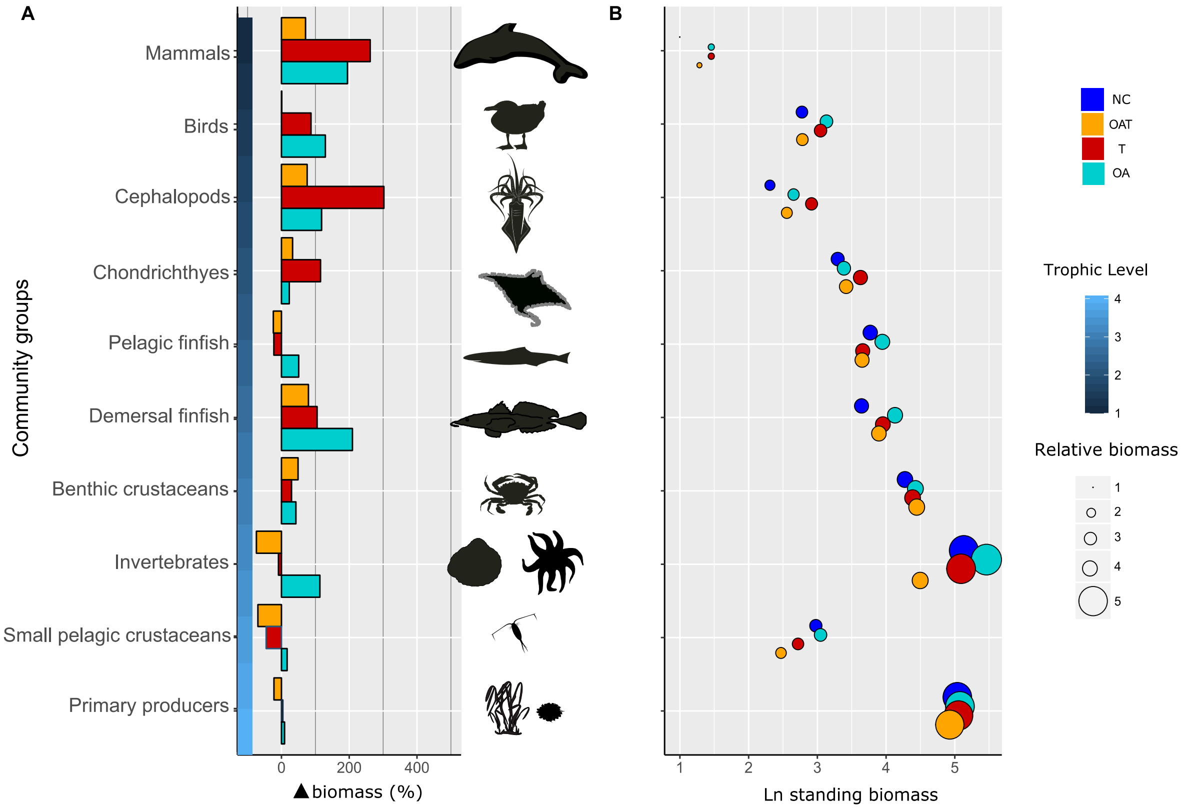

Figure 1: A) Change in biomass (Δ %) of different food web community groups under future climate change scenarios (RCP 8.5) relative to the biomass in 2100 under a scenario of no change in climate (NC), assuming the current level of fishing effort to continue at 2100. OA = ocean acidification, T= ocean 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 are based on the mean trophic level (shown in blue) obtained for each CG from corresponding Ecopath model functional groups. B) The future standing biomass (kg/km^2; ln transformed) estimates for each CG. The bubble size is proportional to its biomass. Biomass estimates were converted from t/km^2 to kg/km^2 to avoid negative (transformed) values.

The standing biomass of primary producers decreased by ~ 22%, due to an antagonistic effect of warming and acidification (Fig. 1A), largely driven by a reduction of phytoplankton, micro-phytobenthos and macro-algal biomass (Fig. S2). Turf algae, in contrast, will likely experience a large biomass expansion.

The combined effect of warming, acidification and fishing

Individual effects of fishing

In the absence of ocean warming and ocean acidification, fishing as an individual stressor is predicted to reduce the projected magnitude of biomass of most of the higher order community groups (mammals, birds, chondrichthyans, and cephalopods) by 9-21% in the year 2100 under a 1.5 and 2-fold increase in fishing effort (Fig. 2). Further increases in the effort (up to 5-fold) exacerbate this declining trend for the former three top predator groups (25-48%). For demersal finfish, however, this negative effect was not observed until a 5-fold increase in fishing effort was modelled, causing severe biomass declines of up to 81%. Under a 5-fold increase in fishing effort, the decline in biomass of top predators allowed an increase in biomass of opportunistic taxa such as cephalopods (52%) and pelagic finfish (18%) which were previously subjected to significant predation pressure.

Impact of multiple stressors

Under a 1.5–2-fold increase in fishing combined with ocean warming and acidification, the negative effects of fishing alone were overturned into positive effects for all higher trophic levels (except for pelagic finfish) (Fig. 2). Pelagic finfish were one of the major ecosystem prey groups that declined in biomass due to greater top down predation pressure which was intensified under warming. With a 5-fold increase in fishing combined with warming, biomass of mammals and birds collapsed except under acidification alone. This allowed generalist species like cephalopods to thrive and increase in biomass under warming (178%) and the combination of warming and acidification (144%). At functional group level, global stressors and increasing fishing effort however acted synergistically for some groups (e.g. cephalopods, rock flathead, spinney gurnard and silver trevally) and increased their biomass by releasing them from predation pressure and interspecific competition (Fig. S5).

Whilst both global stressors positively affected higher trophic level community groups, their largely negative effects on lower trophic levels (primary producers, small pelagic crustaceans and invertebrates) remained almost unchanged under increased fishing. For the latter two, the reduction in their predation pressure by removal of predator biomass through increased fishing could not compensate for their biomass losses due to global stressors alone (Fig. 2; Fig. S6).

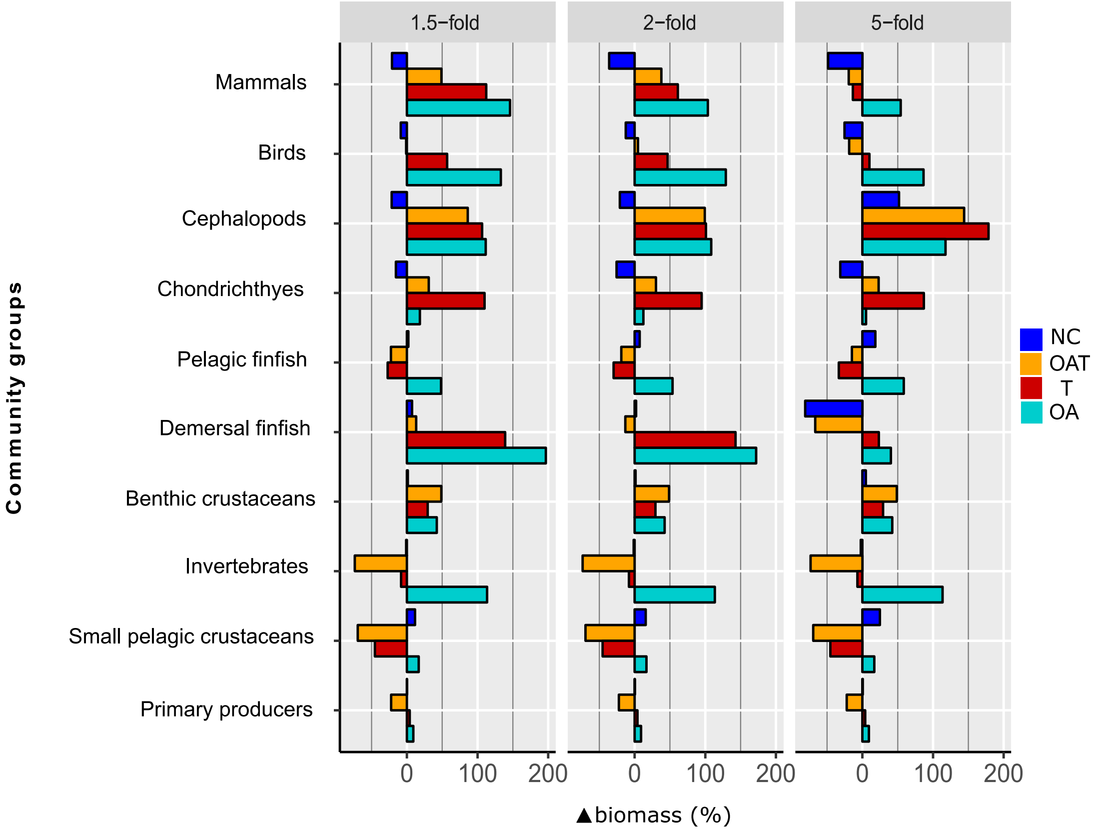

Figure 2: Change in biomass (Δ %) of different food web community groups under the combination of different climate and fishing effort scenarios relative to the biomass in 2100 under a scenario of no change in climate and fishing from present day levels (NC). OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. Functional groups 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 obtained for each CG from the corresponding Ecopath model functional group. Here the number with 'folds' refers to the magnitude of fishing increase that starts in year 2015 and is held constant up to 2100 compared to the NC scenario.

Ecological indicators

Under the no climate change scenario, the Shannon diversity index remained relatively stable in the future at a 1.5-2 fold increase in fishing, whilst it decreased by ~ 4% under a 5-fold increase in fishing (Fig. 3A). In contrast, diversity declined under all climate change scenarios with the greatest impact under the combination of warming and acidification, and this was only exacerbated at a 5-fold increase in fishing (Fig. 3A). Although acidification is predicted to show the largest positive effects on the biomass of most functional groups, it is predicted to show an immediate negative effect on diversity (especially for years 2020-2080).

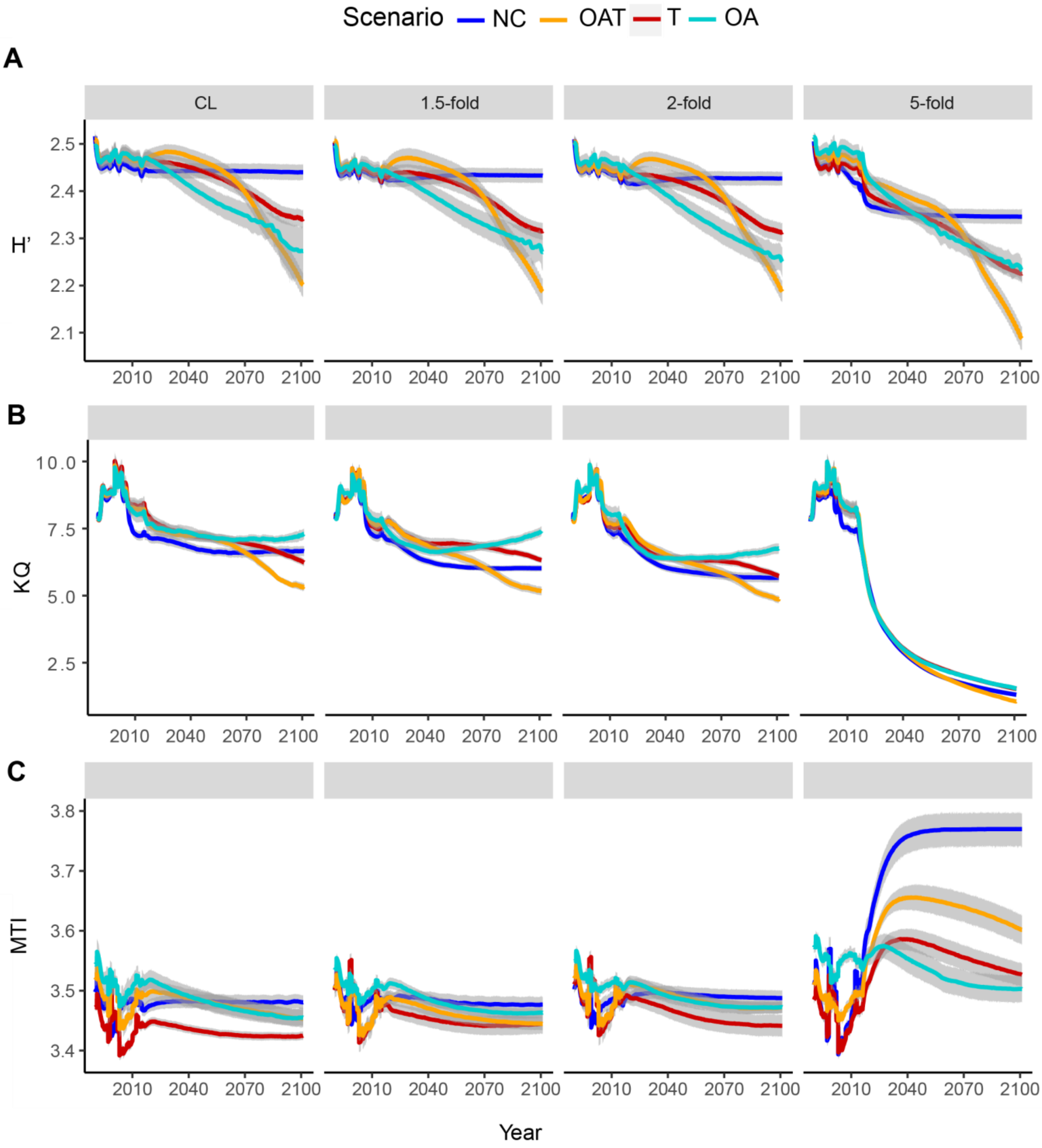

Figure 3: Ecological indicators of change in community composition of a temperate coastal ecosystem, including (A) Shannon diversity index (H'), (B) Kempton Q index (KQ), and (C) Marine trophic index (MTI), all estimated from the Ecosim models for the period 1990–2100. The grey shadows represent the 95% percentile and 5% percentile obtained through the Monte Carlo routine. NC denotes no change in climate from present-day levels (but fishing effort varies). OA = ocean acidification, T = ocean warming, and OAT = combined ocean acidification and warming. CL= current level of fishing effort. Here the number with 'folds' refers to the magnitude of fishing increase that starts in year 2015 and is held constant up to 2100 compared to the NC scenario.

The Kempton Q index, which is indicative of evenness in biomass of functional groups occupying trophic levels 3 or higher, showed a stronger decline (after 2070) under the combination of warming and acidification compared to the other scenarios (Fig. 3B). Under a fivefold increase in fishing alone or with other stressors, the Kempton Q index is likely to show an extreme decline suggesting an impact of extreme fishing on the top predators.

The Marine Trophic Index (i.e., the mean trophic level of the catch for all groups at trophic level 3.25 and higher) calculated based on the present day catch composition data was not influenced much by climate effects or by fishing effort at a ≤ 2-fold increase, but increased sharply at a 5-fold increase in fishing effort (Fig. 3C). The latter suggests that although future catches can comprise higher trophic level species in a no change scenario, warming and acidification together or in isolation with fishing could reduce the likelihood of such potential by reducing the biomass of major target fishery today.

Model validation

Historical projections of biomass from models parameterized using field data showed strong agreement with models parameterized using mesocosm data for carnivorous, herbivorous and omnivorous fish, and Port Jackson sharks (Fig. 4).

Predictions of carnivorous and omnivorous fish biomass were synchronous with independent biomass (survey) data, regardless of whether the models were parameterized using field (Correlation coefficient 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. In contrast, models parameterized with either field or mesocosm data did worse at predicting the trends in temporal variability of independent biomass data for Port Jackson shark (R = 0.12, RSME = 0.011, R = 0.29, RSME = 0.011, respectively) and herbivorous fish (R = 0.25, RSME = 0.007; R = 0.25, RSME = 0.008, respectively). Importantly, bias in model projections remained low for all functional groups either model-calibrated with field data (carnivorous fish: ≤ 0.0001 ± 0.0001; omnivorous fish: -0.0027 ± 0.0077; Port Jackson shark: -0.0003 ± 0.0123; herbivorous fish: 0.0014 ± 0.0014) or mesocosm data (carnivorous fish: ≤ 0.0001 ± 0.0001; omnivorous fish: -0.0001 ± 0.0079; Port Jackson shark: 0.0009 ± 0.0121; herbivorous fish: 0.0046 ± 0.0069).

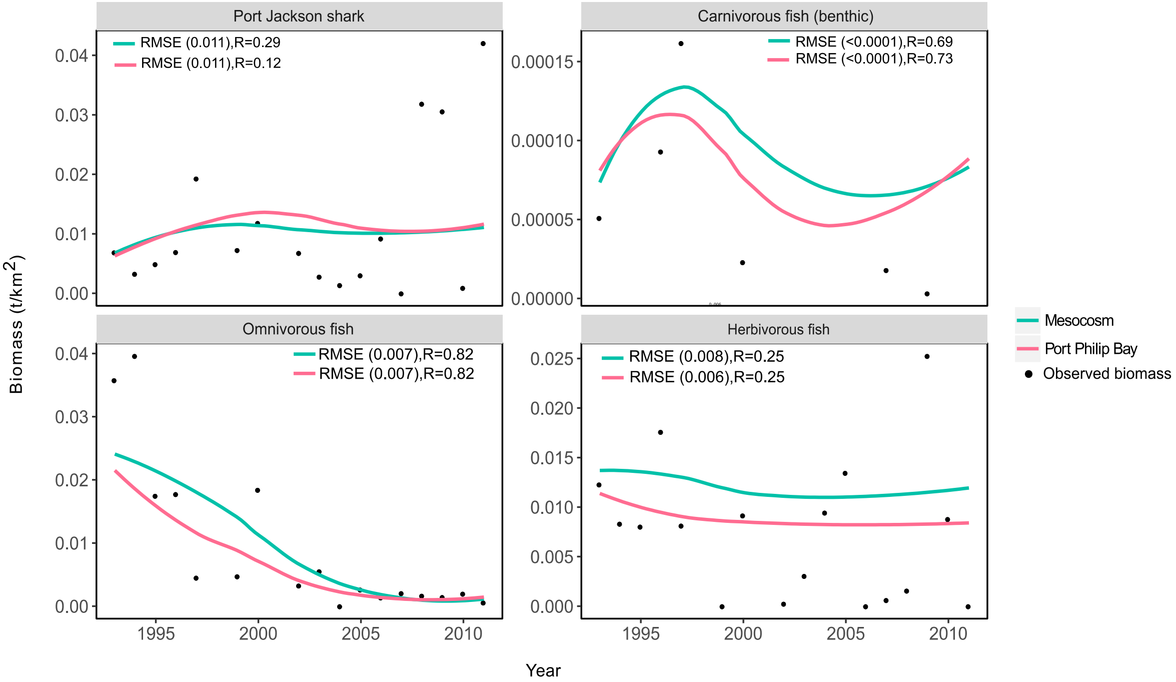

Figure 4: Retrospective tests of mesocosm transferability. Comparison of the Port Phillip Bay (PPB) model (pink), calibrated using data from our mesocosm experiments (green) and observed standing biomass (tonnes per km2) for four major functional groups between years 1993 and 2011. The PPB model was built with similar functional groups that comprise the mesocosm model. Black dots represent observed standing biomass in different years. Root-mean-square error (RMSE) indicates the differences (errors are measured in the same units as the response; here biomass (tonnes per km2) between observed and predicted values by a model; in this case both PPB and mesocosm models.

3.3 DISCUSSION

We combine empirical data on species physiological and behavioural performance from large-scale mesocosm experiments with that of two decades of fisheries catches to show that global warming and ocean acidification could benefit marine animals at higher trophic-levels including fisheries species in future temperate marine food webs, albeit at a potential cost to biodiversity. This increase in biomass results from a strengthened top-down control of consumers occupying higher trophic-levels in conjunction with a positive response of some of their prey groups to global warming. The structure of future temperate marine food webs under global warming will likely be controlled by top-down effects (reshuffling of predatory and prey species abundances leading to altered predator-prey dynamics) rather than a continuous fuelling of the food web from the bottom up.

Organisms at higher trophic levels are likely to increase their top down control on their prey, and therefore increase in biomass, in response to an enhanced metabolic rate due to warming (Brown *et al.*, 2010). Although an increase in top-down control by consumers has been predicted under elevated temperature in temperate regions for a three trophic level food chain (Marino *et al.*, 2018), we lack understanding of how higher trophic levels (i.e. higher-order consumers or apex predators) will respond to global warming and how this will affect all connected lower-order trophic levels when species interaction is considered in natural food webs. This is particularly important because the length of food chains can alter the response of ecological communities to global change (Hansson *et al.*, 2012). Our model predicted that under future scenarios of global warming, the biomass of all higher-order consumers and apex predators such as mammals, birds, cephalopods, chondrichthyes, and demersal finfish is likely increase compared to a no-warming scenario. Earlier studies focussing on maximum catch potential of exploited marine animals based on the preference of species environmental niche suggest that warming could benefit fisheries at the high latitudes regions (Barange *et al.*, 2014, Cheung *et al.*, 2010). Here using physiological response of species to warming and altered species interaction, we show that the increased biomass of top-consumers under elevated temperature is enabled by overconsumption of their prey (pelagic finfish, invertebrates and small crustaceans). This suggests that warming in general is likely to benefit higher trophic levels and negatively affect their prey at lower trophic levels in future temperate coastal food webs.

Ocean acidification can boost food webs from the bottom up due to the enrichment effect of elevated CO_2. Acidification alone is not expected to enhance top-down control by consumers as is the case for warming, because elevated CO_2 does not have positive effects on metabolism of consumes in most cases (Carter *et al.*, 2013, Kroeker *et al.*, 2013). Enhanced primary production can enlarge available prey resources, which can boost the growth of consumers under acidification. This has been confirmed by several recent food-web studies, both experimentally (Sswat *et al.*, 2018, Ullah *et al.*, 2018) and in the wild (Goldenberg *et al.*, 2018, Nagelkerken *et al.*, 2017). In our study, this was the case for all higher-order predators, although chondrichthyans showed the weakest increase. Elevated CO_2 is known to affect the foraging behaviour (e.g reduced prey search efficiency and impaired odor tracking) of chondrichthyans which might explain the reduced increase in biomass for this group (Dixson *et al.*, 2015, Pistevos *et al.*, 2015). Because of their different physiology, non-bony highly active fish predators such as marine mammals, birds, and cephalopods are appear to be tolerant of more acidic environmental condition (Melzner *et al.*, 2009) and hence such top-predators will only benefit from increased resource availability at the bottom of the food web that is transferred up the food web under future ocean acidification.

Although warming and acidification in isolation showed positive effects on biomass of predators, their combined effects acted antagonistically on the degree of biomass increase of many of the top consumers in the food web and had a negative effect on many of the lower-order consumers. Although not tested in a multi-trophic level food web, 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, Ullah *et al.*, 2018). Two of the major prey groups in our model (small pelagic crustaceans and invertebrates) collapsed in their biomass under the combined effect of warming and acidification, and thus reduced the availability of resources for higher level consumers, explaining why the latter showed a reduced biomass increase under this scenario. In contrast to other invertebrates, some groups such as benthic crustaceans sustained a biomass increase under all climate scenarios, and enabled a biomass increase of their consumers (e.g. demersal finish, and consecutively some higher-order predator). The highest KSI (keystonnes) index and mixed trophic impact analysis also suggested the positive role of benthic crustaceans as a prey in the food web both under no change and different climate change scenarios. Benthic crustaceans (e.g. lobsters, crabs, and shrimp) are generally considered to have a higher tolerance level to acidification than other invertebrates (Kroeker *et al.*, 2013, Whiteley, 2011) which may explain the reason behind their successful propagation under global warming. In short, the benefit of increased biomass in the top of the future food web may come through a trade-off between overall biomass gains and losses at higher and lower trophic levels respectively under global warming.

Fishing as a local human stressor negatively affected the biomass of all higher order community groups, except pelagic and demersal finfish. However, warming and acidification overruled these effects and boosted the biomass of top predators as long as fishing intensity did not increase up to five-fold. Global-scale studies, without considering the potential impacts of overfishing, suggest that some commercial fisheries (crustaceans to sharks) around high-latitude regions could experience an increase in the catch under future climate change (Cheung *et al.*, 2010). A recent model by (Merino *et al.*, 2012) predicts a 6 % increase in the yield of commercially valuable fish stocks by 2050 under future warming but only if fish resources are managed sustainably. The results of these models, however, provided in course resolution masking important regional differences, focused on exploited fisheries only and did not capture the potential decline in forage fish biomass or changes in the non-exploited consumers. We show here, however, that the magnitude of potential fisheries benefits under future warming as suggested by previous studies will be significantly dampened when ocean warming co-occurs with ocean acidification. Overall, it is clear that the greatest stressor effects on future food web arise due to the combined effect of warming and acidification, which is further exacerbated by fishing at the top of the food web.

Ocean warming and acidification have a much greater negative effect on functional diversity in food webs than overfishing. The Shannon diversity index showed that future global warming and acidification will significantly reduce diversity within food webs even under fishing effort at present-day levels. A significant decline in the biomass of community groups such as primary producers, small pelagic crustaceans, invertebrates, and pelagic fish species under global warming reflect such changes. The Kempton Q index which shows a loss of evenness for higher order groups in the food web reflects the strong decline of several fish and shark species under warming alone and in conjunction with acidification, respectively. This disproportionate distribution (decrease or increase) in functional group biomass allows ecological opportunistic species to flourish (Woodruff, 2001), such as “weedy” cephalopods at the top and turf algae at the bottom of our food web model. The loss in functional diversity and thus a relative reduction in functional redundancy under future climate change may also increase the vulnerability of some groups to a secondary extinction that is triggered by the primary extinction of a species in the ecosystem (Sanders *et al.*, 2018). This could then lead to a further simplification of community structure (Nagelkerken & Connell, 2015). Together, global warming and fishing will likely to reduce the biomass of many functional groups thus leading to a disproportional distribution of biomass within community and reduced diversity of the future food web.

Here, we attempted a unique approach by combining empirical data on species response to climate change from large mesocosms with historical population data (from scientific survey and fisheries landings) to predict future changes in food webs. This approach has been questioned earlier on the grounds that it is unlikely to build a realistic bridge between simplified experimental conditions and the real world (Carpenter, 1996). However, by independently validating our model predictions against historical biomass (survey) data, we not only show our model does a very good job at reconstructing historical trends in fish biomass (for selected functional groups), but that empirical parameters estimated in mesocosm experiments provide a close representation of ‘real world’ food web. In doing so, we show that mesocosm experiments with a realistic multifactorial experimental design that capture food web complexity can provide ecologically realistic outputs that can be used to parameterize end-to-end 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. The modelling approach in our analysis assumed a linear increase or decrease in all the forcing function parameters. Linear interpolation between two climate snapshots is a common practice in climate change ecology (Fordham *et al.*, 2012) and successfully used before in a food web context (Ainsworth & Mumby, 2015, Brown *et al.*, 2010, Griffith *et al.*, 2011, Marshall *et al.*, 2017). We acknowledge that the response of species and food web properties could vary in some instances if the relationship between forcing function and vulnerability was non-linear. This may weaken our ability to predict variability at the decadal scale. The scope of this study was, however, to forecast food web response at the end of the 21st century because a representative response data for different functional groups and trophic level to future climate change scenarios was only possible to collect and measure between the initial and end points of the experiments.

An important assumption in our model was to assign fish species into two major categories such as carnivorous and omnivorous based on their trophic function (feeding guilds) while calculating their vulnerability to predators. This is because we did not include any herbivorous fish as single functional group in our model due to the lack of important herbivory fish in terms of biomass and other biological parameters available for the PPB ecosystem. A relatively least fit observed for Port Jackson shark is not unexpected as we used relatively simple food web structure to validate PPB and mesocosm models that lacks apex predator. Abundance of meso-predator could also largely response to predator release in the food web (Baum & Worm, 2009). Hence, simple predator and prey dynamics may not be sufficient to explain the variability between predicted and observed pattern for some higher trophic level species (Weijerman *et al.*, 2017). A relatively poor fit in the herbivorous fish in our model calibration does not affect the outcome of our results as the model did not include herbivorous (fish) functional group.

Additionally, our modeling approach lacks scope to capture the spatial heterogeneity of species in response to global warming. Although we have included both juvenile stages and adult fish groups in our model, this only applied to four of the food web functional groups due to the lack of reliable data. Inclusion of more juvenile groups in the model could improve model performance. As we modeled a relatively shallow-water ecosystem, the role of top-predators could be underestimated or overestimated due to their high mobility.

We had to use commercial catch and effort time series data for pelagic functional to hindcast initial model since pelagic species lack biomass (survey) data. Pelagic species are important prey groups in the food web, more dynamic in their nature and characterized by large fluctuation overtime which is complex to model and may have important implication in the model outcome. For example, many of the higher trophic level predators (e.g. seabirds, marine mammals and piscivorous fish species) are strongly dependent on pelagic species (forage fish) due to their specialized diet and limited feeding areas (Engelhard *et al.*, 2014). Therefore, any large fluctuations in forage fish abundance can impact their predators, and if not well tracked, could mislead management decision for certain fishery. We also lack time series data for lower trophic level groups (<3 TL) which is important for model structure. Despite these limitations, our study included the best available historical data and parameterized functional groups to global warming up to a four trophic level food chain.

Here, we modelled the effects of global warming, ocean acidification, and fishing using empirical data on species interaction and physiology and historical fisheries data on their population dynamics. This allowed us to successfully quantify the potential magnitude and direction of the biomass changes of various functional groups in future marine food webs and fisheries under global change. Our findings suggest that the structure of future temperate marine food webs under global warming will be characterized by an altered predator-prey dynamics at the top of the food web rather than changes from the bottom up. We show that consumers at higher trophic level in future food webs might benefit from global warming but this will come at a potential cost to biodiversity.

3.4 MATERIALS AND METHODS

We integrated empirical data from two food web level mesocosm studies (and other sources) into a regional food web model to calculate community-level responses to future global and local stressors. We updated an existing food web model of the Port Philip bay (PPB) ecosystem (Koopman, 2005) with contemporary information, adding higher taxonomic resolution using the Ecopath mass-balance approach (Christensen *et al.*, 2008). Ecopath is a food-web modelling approach used to create a baseline snapshot of the ecosystem and quantify the flow of energy between food web functional nodes through feeding relationships in a given year. The model requires four key input variables: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), and diet composition. We calibrated the Ecopath model to a historical time series of biomass and fishing effort data through temporal hind-casting (1990–2015) analyses within Ecosim (Fig. S7 and Fig. S8).

Dynamic food web models such as Ecosim that incorporate realistic ecological interactions (e.g. as predation and competition) can be successfully used to estimate the ecological consequences of climate change on future food web and fish production capacity (Cury *et al.*, 2008). Differential equations are used in Ecosim to estimate biomass fluxes for each species and/or functional group within the food web using foraging arena theory (Ahrens *et al.*, 2012, Walters *et al.*, 1997). This theory defines each predator/prey interaction by vulnerability parameters that affect the predator consumption rate (Q_{ij}) (Equation 1). The quantification of consumption rates (Q_{ij}) is a nonlinear relationship between prey and predator which assumes that only a portion of their biomass can be vulnerable to a predator. This means that the biomass of prey *i* is divided between a vulnerable and a non-vulnerable state. The vulnerability concept incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen *et al.*, 2008, Christensen & Walters, 2004). The vulnerability rate can be presented both as top-down and bottom-up controls of the predator/prey interactions. For example, vulnerabilities greater than 2 describe top-down control of the predator-prey relationship, where the predator biomass drives the prey mortalities, whilst vulnerabilities below 2 define bottom-up control, where the biomass of the predator has little effect on the predation mortality of that prey. For details on modeling approach please see supplementary text.

For each predator-prey interaction, we calculated the consumption rates Q_{ij} at time *t* as,

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

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*. See (Christensen *et al.*, 2008) for more detail. The forcing function *f* (*t*) can be used to account for any external drivers changing over time that effect food web dynamics.

Exploring the effect of climate change on future food web requires projecting the effects of global warming on a “baseline scenario” of no climate change. We developed four 75-year simulations (2015-2100), these included a no climate change scenario (baseline) and three climate change scenarios: 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 (RCP8.5) (Bopp *et al.*, 2013). The no climate change scenario (NC) assumes that model parameters do not change in the future, with model drivers such as fishing effort set to that of the last year of the historical observed 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. Fishing effort was initially held constant at 2015 levels, because little is known about how fishing effort is likely to change by the end of the century. The effect of climate change was then assessed by comparing biomasses and ecological indicators of the NC scenario with that of climate change scenarios for the 21st century. Consecutively, to test the response of future food webs against combined global and local stressors, we ran some additional scenarios where we increased fishing effort by 1.5, 2 and 5-fold compared to present day fishing pressure.

We incorporated the effect of climate change in our modelling approach using forcing functions that affect the consumption and production of functional groups at a temporal scale (Ainsworth *et al.*, 2011, Alva-Basurto & Arias-González, 2014, Cornwall & Eddy, 2015, Guénette *et al.*, 2014). We used the calculated effects of warming, acidification and their combination on the vulnerability, search activity, mortality and productivity (primary producers) of trophic groups to alter their consumption (Q/B_i) and production (P/B_i) rate in the model. We used information from two large-scale mesocosm experiments (Pistevos *et al.*, 2015, Ullah *et al.*, 2018) to overcome the challenge of integrating species interactions in ecosystem models under future climate change scenarios and calculated relative effect size of different forcing function parameters (vulnerability, effective search rate, mortality, productivity). The relative effect size for different forcing functions (input) under future scenarios (OA, T, and OAT) and increased fishing effort was obtained by comparing the NC scenarios in 2100 with climate change scenarios (Table S6). 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. It is common practice in climate change ecology to interpolate temporally between climate snap shots (Fordham *et al.*, 2012). The forcing functions were applied to appropriate functional groups in the model (Table S6). We report details on the estimation of different forcing function parameters in the Supporting Information.

We quantified the relative impact of biomass change of any group either directly or indirectly through trophic cascades on the biomass of other groups in the food web using Mixed Trophic Impact (MTI) analysis (Ulanowicz & Puccia, 1990). We calculated a number of ecosystem-scale biodiversity indicators such as the Shannon index (Shannon & Weaver, 1963) and Kempton's Q index (Ainsworth & Pitcher, 2006) and trophic indices such as the Marine trophic index (MTI). The Shannon diversity index primarily reflects changes in evenness, whereas the Kempton's Q index tracks changes in both evenness and richness at the level of a functional group level. We calculated MTI as the average product of the weight of different functional group in the landings and their trophic level (TL ≥ 3.25) and demonstrate the effect of commercial fishing pressure on top predators and other large consumer fishes in the food web (see Supplementary text for details on the equation used for calculation).

We show simulation output for food web functional groups pooled into 10 community levels, including pelagic groups (mammals, birds, cephalopods, pelagic finfish), demersal groups (Chondrichthyans and demersal finfish) and their prey (benthic crustaceans, invertebrates, small pelagic crustaceans, primary producers) (Table S3). We used community-level groups because indicators at the community level of organization proved as most reliable in detecting effects of perturbations on marine ecosystems (Fulton *et al.*, 2005). Most of the future projections to date focused on exploited ecosystems. Here, we considered a temperate coastal marine system (Port Philip Bay, Victoria, Australia) which is designated as a sustainably managed ecosystem in terms of its fisheries exploitation (Flood *et al.*, 2014). Fishing pressure decreased by approximately fivefold between 1990 and 2016 in the Port Philip Bay (Fig. S9).

Scaling up mesocosm results to real-world conditions has long been a challenge (Fordham, 2015). We did a retrospective test to explore the ability to transfer model parameters from a mesocosm to the real world (mesocosm transferability) by building and comparing two simplified food web models with higher taxonomic resolution (Table S8; Also see Approach used for retrospective test and sensitivity analyses in the Supplementary text).

We further addressed the uncertainty in our model output by using the Monte Carlo (MC) simulation based on the coefficient of variation obtained from the model pedigree (Fig. S10) (Coll & Steenbeek, 2017, Heymans *et al.*, 2016). Prior to simulation, we also assessed the quality of input data and model validation following food web diagnostics approach (Link, 2010). Details of the data quality, model validation, sensitivity analysis and retrospective tests of mesocosm transferability are provided in the Supplementary text.

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Global warming likely to benefit fisheries in temperate marine ecosystems at a cost to biodiversity

3.6 SUPPLEMENTARY METHODS

3. 6.1 Modelling approach/Core concepts of EwE modelling

We used the Ecopath with Ecosim (EwE) approach to simulate the effect of future climate change and fishing effort on the biomass of different functional groups of the food web. This involves modelling the system in two steps.

First, we developed a static food web (Ecopath) model based on the trophic mass-balance principle where removals from the system (e.g. predation, fishing, emigration etc.) equal total production. Within this framework, we create a baseline snapshot of the ecosystem at the year 1990. The parameterization of an Ecopath model is based on satisfying two 'master' equations: one for production (equation 1) and the other for the energy balance (equation 2). The first equation ensures energy-balance among groups by distributing total production of a group into the catch, predators' diet, other mortality (death caused by other than predation and catch) (Eq. 1).

$$B_i \times (P/B)_i = Y_i + \sum_j B_j \times (Q/B)_j \times DC_{ji} + B_i \times (P/B)_i \times (1 - EE_i) + BA_i + E_i \qquad \text{(Eq. 1)}$$

where B_i is the biomass of a group (*i*), P/B_i is the production/biomass ratio for (*i*), *Y* for fishery catch of a group (*i*), Bj is the biomass of a group (*j*), Q/B_j is the consumption/biomass ratio of the predator (*j*) and DC_{ji} is the fraction of prey (*i*) in the average diet of predator (*j*), EE_i is the ecotrophic efficiency of (*i*) describing the proportion of the production utilized in the system, BA_i is the biomass accumulation rate for (*i*), E_i is the net migration rate (emigration-immigration) for (*i*) and $(1 - EE_i)$ represents mortality other than predation.

The second equation explains the energy balance within a functional group such as,

Consumption = Production + Respiration+ Unassimilated food and written as (Eq. 2)

$$Q_i = P_i + R_i + UA_i \qquad \text{(Eq. 2)}$$

Where Q_i is consumption by a group (*i*), P_i is the total production of the group (*i*), R_i is respiration of the group (*i*) and UA_i is the unassimilated food of the group (*i*).

In the second step, we use Ecosim module to simulate the dynamics of each functional group over time using Ecopath inputs as starting information and incorporating different forcing function or parameters that represent climate change effects on the future food web. Ecosim is the dynamic component of the EwE suite which keeps track of changes in the biomass of species (functional groups) as a function of temporal changes in their catch patterns, food-web complexity (predator-prey interaction), and environmental conditions. We modelled changes in biomass for each trophic group (*i*) over time through a series of differential equations (equation 3) which are derived from the first master equation of Ecopath:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \sum_j Q_{ji}\ (t) - \sum_j Q_{ij}\ (t) + I_i - B_i \times (M_i + F_i + e_i) \qquad \text{(Eq. 3)}$$

Where $\frac{dB_i}{dt}$ is the biomass growth rate of group *i* in the time dt, $\frac{P}{Q_i}$ is its production/consumption ratio, Q_{ji} is the consumption of group *j* (predator) on prey group(s) *i*, Q_{ij} is the consumption for predation by all predators *j* on group *i* (prey), I_i is the immigration rate, B_i is the starting biomass, M_i and F_i are the natural and fishing mortality rates of group *i*, respectively, and e_i is the density dependent emigration rate. In our case, e_i and I_i were set as zero.

The quantification of consumption rates is based on the "foraging arena" theory (Ahrens *et al.*, 2012, Walters *et al.*, 1997).

3.6.2 Food web model

Preliminary model

We used a previous Ecopath model in the region (Koopman, 2005) to update and develop a comprehensive food web model on the Port Philip Bay (PPB). The preliminary model of PPB by (Koopman, 2005) is primarily developed emphasizing the benthic-demersal system of the bay with a particular interest on sand flathead fishery. The preliminary PPB model composed of 30 different components or groups (that include single species, groups of species and developmental phases of one species) represents the PPB ecosystem at 1990 (**Table S1**). The input data of preliminary PPB model was obtained from a wide variety of sources (Table S2). This included both direct (from empirical studies carried out on PPB) and indirect estimates of parameters such as from the literature for either the same species from different systems, for similar species (preferably from the same genus) or, calculated empirically. Biomass for most species was estimated using swept area method from the four trawl surveys conducted in 1990 (Hobday *et al.*, 1999) to obtain a yearly average. Diet data (Table S3) were all obtained from the literature available on the bay, and when quantitative information was not available, proportions were estimated. A thorough technical description of the model, including all the data, basic input parameters, relevant assumptions, diagnostic features is available in (Koopman, 2005), located at http://dro.deakin.edu.au/view/DU:30026826.

Updated PPB model

We have updated the preliminary PPB model (Koopman, 2005) with recent and more reliable data that include single species, groups of species and developmental phases of species (spanning the main trophic components of the ecosystem) focusing on both pelagic and demersal component of the ecosystem. The updated PPB model comprises 23 additional species or functional groups to the preliminary PPB model including 3 multi-stanza functional groups (Table S1, S4). These includes species or groups in the top of the food web such as large sharks, large pelagic, bird, mammals, southern calamari, demersal finfish group such as silver trevally, yellow eye mullet, leatherjacket, rock flathead; pelagic finfish groups such as Australian sardine, southern anchovy, Australian salmon, pike (Longfin), southern garfish, invertebrate trophic groups such as filter feeding molluscs, other grazing molluscs, predatory molluscs, abalone, southern rock lobster, sea urchin, exotic sea star and one primary producer group algal turf. The inclusion of these functional groups in our new food web model was done to accommodate apex predators, species with a reasonable contribution in landings at recent times, the introduction of invasive species and to highlight the appearance of opportunistic producer group in the future. The model considered as the final model for PPB and represents PPB ecosystem at 1990. All these modification represent PPB model as a comprehensive food web model that includes a total of 53 functional groups, with 17 groups of demersal finfish, 7 groups of pelagic finfish, 7 groups of chondrichthyans, 11 groups of invertebrates, 2 groups of cephalopods, 5 groups of primary producer, one bird and mammal group, and a non-living group detritus (Table S4). The definition of the functional groups for the PPB model was based on the proxy of different biological and ecological characteristics of the species such as feeding habit, growth rates, size, consumption rates, diets, predators, and habitat distribution of the species.

Apex predators such as mammals are ecologically important because they can constrain the parameters of other consumers and influence ecosystem structure and function through strong predation-driven consumptive effects or fear-driven non-consumptive effects with relatively few individuals (Roemer *et al.*, 2009). We have therefore included marine mammals as a functional group in our PPB model. The inclusion of seabirds as a separate functional group in our model confirm that we account for the potential link between birds and vertebrate predators in the food web which also serves as a bioindicator of the health of marine ecosystems (Parsons *et al.*, 2008). Migratory patterns of seabirds were also taken into account by modelling a proportion of the diet composition of this group as imports to the system.

We have added rock flathead in the updated PPB model since rock flathead showed an increasing contribution in the landings of major species caught at PPB recent decades while other two major flatheads such as sand flathead species and yank flathead showed a decline. Cephalopod fishery in PPB consisted of southern calamari, octopus, and other squids; however, southern calamari is by far the most important target species both in the recreational and commercial fishery. We therefore modelled southern calamari as a separate functional group.

We have modelled complex trophic ontogeny and patterns in potential exploitation of juveniles for some key fish species (e.g. sand flathead) representing their life history stages (referred to as 'stanzas' here). We modelled juvenile sand flathead as a stanza group for sand flathead fishery which makes their dynamics more realistic and provides insights on stock-recruitment relationships. Juvenile sand flathead was a separate functional group in the preliminary model. In addition to sand flathead, we have added three more multi-stanza groups. This was done for the three species of highest commercial interest in recent times in the bay such as King George whiting, red mullet, and snapper. To represent multi-stanza groups, we used baseline estimates of total mortality rate (Z) and diet composition for each stanza and biomass and QB (consumption over biomass) for one "leading" stanza such as an adult. We also incorporated information on the estimates on age (in months) between stanzas (e.g. adult and juvenile) (Bani & Moltschaniwskyj, 2008, Froese R, 2018, Smallwood *et al.*, 2013), the von Bertalanffy *K* parameter (Froese R, 2018), and the estimate of weight at maturity as a fraction of weight at infinity (Wmat/Winf) (relative weight at maturity) (Froese R, 2018, Heymans *et al.*, 2016). Mortality rates and diet composition are assumed to be similar for individuals within each stanza.

We have added several trophic groups of small pelagic species such as Australian sardine, southern anchovy, southern garfish, Australian salmon, pike which were all pooled under small pelagic to the preliminary model. Small pelagic species are ecologically important forage fishes (Pikitch *et al.*, 2014) and could serve as target species in certain ecosystems such as PPB (e.g. sardine, anchovy). Additionally, including forage fishes with higher taxonomic resolution enables us to explore if any predators had high diet dependencies on individual forage fish species (Koehn *et al.*, 2016) and thus may become more vulnerable under disturbance. This was also done for small demersal fish given the importance of the benthic compartment of the shallow coastal ecosystem of PPB. However, there are several other small pelagic and demersal species which are modelled as an aggregated group due to their low individual biomass and importance in the model or due to their insufficient and unreliable taxonomic resolution. We have included an invasive species in our updated model. The exotic seastar (*Asterias amurensis*) is one of Australia's most serious invasive marine pests which was introduced into Port Phillip Bay in 1995 and by 2000 its biomass peaked at 56% of the resident fish biomass in the deeper region of the bay (Parry & Hirst, 2016). This species was found responsible for the decline of shovelnose stingaree, eagle ray, and globefish biomass and may potentially lead to the local extinction of its prey altering benthic community structure (Parry & Hirst, 2016). Functional groups such as abalone, rock lobster, and sea urchin were included in the model to fill the vacant link in the trophic flow in the ecosystem of the early 90s and also to track potential cascading effects in that may be overlooked in the absence of these groups.

Notably, we split molluscs into three functional groups given their importance for trophic flows (Covich *et al.*, 1999) and to ensure that competitive effects among ecological equivalents are considered. Among them, filter-feeding molluscs (bivalves) are one of the major prey groups in the PPB ecosystem. Algal turfs were incorporated as an additional functional group as they can dominate ecosystems prone to disturbances due to their fast-turnover rate (Hatcher & Larkum, 1983).

The basic model input parameters such as biomass (B); production per unit of biomass (P/B), consumption per unit of biomass (Q/B) and diet matrix were obtained for PPB taxa when available. We largely use diet, production, and consumption parameters in our model from two comprehensive reports on PPB based on extensive surveys and sampling (Officer & Parry, 1995, Parry *et al.*, 1995).We also obtained different parameters of several other species or model functional groups of the Bay from various sources (Table S2, S3). In case specific information was not available for PPB, we used the most appropriate estimates based on other ecosystems from the literature (Table S2)

Model balancing

Before balancing the model, underlying assumptions based on ecological and fisheries principles have to be checked. We used the pre-balancing (PREBAL) approach to ensure that model parameter is in line with energetic laws for ecosystem structure (Link, 2010). The PREBAL diagnostic criteria take account of few assumptions such as biomass estimates in an ecologically meaningful food web models should span 5–7 orders of magnitude. Additionally, the slope of the biomass (on a log scale) should decline by 5–10% across all taxa ordered by trophic level (Link, 2010). The initial diagnostics suggest that our model satisfies these underlying assumptions.

We then balance the model following the general ecological rules and the laws of thermodynamics (Jørgensen & Fath, 2004). We considered the model balanced when estimated ecotrophic efficiency (EE) values of all functional groups were lower than 1 and were high (≥ 0.95) for exploited species and more predated ones (such as small pelagic fish species) and low (< 0.5) for unexploited top predators (such as mammals and yank flathead). We assumed an EE value of 0.95 for some heavily predated species in the ecosystems such as those with forage fish (Christensen & Pauly, 1998, Christensen & Walters, 2004, Polovina, 1984). For groups with the little systematic study of catchability and gear selectivity and which are also exploited heavily (e.g. cephalopods and calamari), biomass was estimated by Ecopath, using an EE of 0.95 (Lassalle *et al.*, 2011). We also made sure that the values of production/consumption (P/Q) for functional groups of the model were between 0.1 and 0.35, with the exception of spinney gurnards (Christensen *et al.*, 2008). This was achieved through incremental changes of the diet matrix of functional groups of the model which are the most uncertain parameters in an ecological model. Updating the diet matrix with stomach content analysis based on local study is a powerful but often underused way of improving Ecopath models (Ainsworth & Mumby, 2015). Since we largely updated the preliminary model with additional functional groups in the model and with higher taxonomic resolution, it was essential to revisit the previous diet matrix and search for new and updated information, most of which came from the local ecosystem or similar species from a similar system. It was necessary to adjust the diet of a few functional groups such as birds and banjo ray from their original input data (< 5%). Adjusting predator diet data for some groups such as small pelagics and small demersal was also required as these groups were split into specific functional groups in the new model. These adjustments were crosschecked with FishBase (http://www.fishbase.org) to ensure confidence intervals of the estimation of trophic levels are reasonably close to the values published literature (Froese R, 2018). We recorded the origin of the data used to create the model and computed the quality of the model through the pedigree routine. Pedigree values for input data range from 0 (when it is not based on local data) up to 1 (fully rooted in local data). The pedigree routine describes the precision of the input data and sets confidence intervals which can be further used while undertaking Monte-Carlo simulations for uncertainty analysis (Christensen & Walters, 2004, Morissette, 2007). The pedigree index of our model was computed as 0.52 which suggests that results derived from it are reasonably robust.

Food web model calibration

The updated Ecopath model needed to be fitted with historical time series data to assess model performance and to perform simulations for climate change effects on food web. We applied the Ecosim approach to fit the model to observed time-series data using the sum of squares (SS) ratio between predicted and observed data for model evaluation (Christensen *et al.*, 2008). In this study, we used a total of 52 time series that included observed biomass, landed catch, fishing effort as well as environmental driving factors. The biomass time-series data were obtained from Marine Ecological Solutions Pty. Ltd (Gregory Parry, pers. com.) which mostly comprises the demersal and benthic groups. The surveys of demersal fish assemblages were carried out annually using demersal trawl nets at 20 stations stratified by depth in Port Phillip Bay from 1990 to 2011. These surveys cover about 78% (1506 km$^{2)}$ of the whole PPB area (317 km^2-shallow, 155 km^2-west, 403 km^2-intermediate and 631 km^2-deep). The shallowest trawl of the bay was at 7 m while the deepest was in 20 m. There was no trawling in 1998 and 2001. We used average biomass across depth as our biomass time series input for specific functional group. We also used this data to update the initial biomass in the preliminary PPB model for 1990. This was done as the biomass estimates in the preliminary PPB model was mostly based on using a prawn net (13 headline length) and towed for 5 min, but there were no sweeps (Hobday *et al.*, 1999). There may have been some biomass estimates based on the swept area of this net, but they would not be very representative of the bay as a whole as the sampling was concentrated at ~15 m depth. Furthermore, a number of sophisticated assumptions/corrections were made in the present data used for different depths and for different species, depending upon whether they were thought likely to be herded or not by the sweeps (Parry, 2011, Parry & Hirst, 2016). Such as trawl net efficiencies in front of net was assumed to be 90% (min 80%, max 100%) and between doors and net 40% (min 20%, max 60%). All of these changes greatly improved the accuracy of the biomass time series that we applied. The time series for the commercial fisheries landings and fishing effort were obtained from the Department of Primary Industries (VFA, 2016). The estimates of annual recreational catch in Port Phillip Bay for new functional groups were taken from (Fulton & Smith, 2004). Recreational bycatch fisheries were supplied by Conron (pers. com.). The chlorophyll data on the PPB was taken from (EPA, 2002), while the water temperature data was obtained from the Bureau of Meteorology of Australian Government (BOM, 2018).

The base Ecopath model was calibrated within time dynamic Ecosim approach using historic time-series data from 1990 to 2015 in order to reconstruct the historical trends. The hindcast approach was performed using the automated stepwise fitting procedure (Scott *et al.*, 2016). The fitting process identifies highly influenced and critical vulnerability interactions in the model and calibrates those to improve the statistical fit using the weighted sum of squared deviations (SS). The SS was calculated using the disparity between the log of observed and predicted catches (Christensen *et al.*, 2008). Then the Akaike Information Criterion (AIC) (Akaike, 1974) and the corrected AICc (Burnham & Anderson, 2004) were calculated as follows,

$$AIC = nlog\left(\frac{minSS}{n}\right) + 2k$$

$$AICc = AIC + 2k(k-1)/(n-k-1)$$

where n is the number of observations, minSS is the minimum sum of squares resulting from the comparison between predicted and observed time series, and k is the number of parameters. Thus, AIC can be used to test statistical hypotheses that aaccount changes in predator-prey dynamics (also called vulnerabilities: Vs); changes in primary production (PP anomaly, considering the number of PP spline points (sPP) for smoothing the time series); impact of fishing and possible combinations of all of the above-mentioned factors (Table S5). AIC penalizes for fitting too many parameters, and comes up with a "best" model (the one yielding the lowest AIC) considering a good fit and the least number of estimated parameters. For our model selection, we used the second-order Akaike Information Criterion (AICc) since it accounts for small sample sizes (n of observations) and calculated as follow:

Finally, the AICc values were used to compare the quality of the baseline model without any ecosystem drivers, environmental forcing function or trophic vulnerabilities and models with their combination. During the model fitting, we accounted for data quality of the available time series by weighing them using a factor of either 0.9 or 1. The value 0 denotes that the time series are not considered in the calculation of SS while 1 indicates that they are given full consideration (Christensen *et al.*, 2008). For the survey biomass time series, we used a weight of 1, while the time series constructed from catch and effort data were assigned a weight of 0.9. This was done to consider the relatively higher uncertainty of catch data and the inclusion of small pelagic/forage fish groups in the model which are highly variable in PPB.

The fitting process accounts for any changes in the associated parameter such as P/B or Q/B during vulnerability parameters estimation according to the corresponding value for the forcing function in the time series. Use of environmental forcing functions as a major driver in Ecosim fitting exercise is a common approach. We first fitted the model with chlorophyll as a sole environmental driver along with other parameters. This, however, did not show a good fit for some demersal groups in the model, particularly for chondrichthyans. We, therefore, added mean maximum annual temperature to account for its effect on the effective search rate on zooplankton by their predators. Temperature trends can affect the search rate and feeding area of a predator and at the same time change the vulnerability rate of a prey (Heymans *et al.*, 2016). Adding the effects of temperature as an additional environmental driver improved the performance of our model fitting (Table S5). During the model calibration, the stepwise fitting procedure tested a total of 752 different model interactions with a total of 501 observations (observed data points). The maximum number of parameters that could be estimated (k-1) during the model fitting was 51 (there were 52 time series of biomass, catch, environmental and effort data). The degrees of freedom accounted in the final model was 15 (the difference in number of parameters calibrated in the final model than baseline model) with 501 number of observations. We performed the fitting procedure choosing vulnerability parameters as to be "by predator" for all iterations assuming the same top-down or bottom-up control in the predator-prey relationship. The best model from the fitting exercise was obtained when trophic interactions and fishing were included together in the model run (Step 6 in Table S5). The fitted vulnerability values of all the model functional groups are shown in Supplementary Table S6.

3.6.3 Representing global warming and ocean acidification

Estimation of predator-prey interactions is challenging due to their dynamic nature and the complex trophic structure of an aquatic ecosystem, making a direct integration into ecosystem models difficult. The major challenge lies in parameterizing species interaction at higher trophic levels since they are neither straightforward to observe in nature nor easy to replicate in an experimental context.

We address this challenge by using output of species interaction obtained from mesocosm experiments which includes both direct (Ullah *et al.*, 2018) and indirect estimates of the vulnerability of a prey to its predator (Goldenberg *et al.*, 2018), effective search rate of a predator for its prey (Pistevos *et al.*, 2015) and mortality of some lower trophic prey groups accounted in the food web model (Ullah *et al.*, 2018). The strength of our modelling approach lies in the input data that were obtained from two community-level mesocosm experiments (Pistevos *et al.*, 2015, Ullah *et al.*, 2018). In both experiments, the mesocosm had the same crossed design of elevated CO_2 and temperature with 3 replicate mesocosms per treatment combination. Both mesocosm systems I) approximately simulate an RCP8.5 scenario, II) were multi-trophic (producer to predator) capturing the complexity of a food web, III) include a total habitat volume of ~2,000 L, IV) were supplied by a flow-through of seawater from the same source ensuring comparable nutrient levels. The similarity between the two 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).

The biomass of future ecosystems within the Ecosim approach is represented by the ‘‘foraging arena concept’’, where prey biomass is divided into vulnerable and non-vulnerable components. The transfer rate between these two components is the vulnerability rate, which determines whether the flow control is top-down (predator-driven), bottom-up (prey-driven) or both.

We used predation pressure which is the consumption rate (mg/4hr/individual) of species relative to control condition to estimate the vulnerability (direct estimate) of lower trophic level (trophic level ≤ 2) species/ functional groups to its predator. This is done using data from stomach content analysis and in situ feeding trials that incorporated different treatment effects (e.g. temperature, acidification or their combination) (Ullah *et al.*, 2018). The relative weight of different prey groups in the stomach was calculated based on their average individual body mass and relative contribution to the total prey weight. Thus, the predation pressure exerted by the predators (in our case fish) on their prey groups is directly accounted for as the vulnerability of the representative prey groups in our Ecosim model. The estimation of prey vulnerability through in situ feeding trials is a robust representation since successful feeding at the community level incorporate the complex interplay between morphology, physiology, behavior, population dynamics, and predator-prey interactions (Brodeur *et al.*, 2017). For details about the experimental design and stomach content analysis, see (Goldenberg *et al.* 2007) and (Ullah *et al.*, 2018), respectively.

We applied a combination of direct and indirect approaches to estimate the vulnerability of prey groups for higher order trophic groups (trophic level ≥ 2). The indirect approach of vulnerability estimation was based on a behavioral experiment on traits related to foraging and predation of consumers. A detailed description of the experimental setup is given in (Goldenberg *et al.*, 2018). Here we will only provide a brief summary of the behavioral experiment and information particularly relevant to our model. After 2.5 months of exposure to the climate treatments, a total of 3 behavioral trials lasting 7 min were conducted in each mesocosm in the presence of a predator. The scorpionfish *Gymnapistes marmoratus* was used as predator and presented to the prey in a cage for the duration of the trial to simulate an environment with high predation risk. Five prey species – little weed whiting (*Neoodax balteatus*), blue weedy whiting (*Haletta semifasciata*), longfin goby (*Favonigobius lateralis*), zebrafish (*Girella zebra*) and toothbrush leatherjacket (*Acanthaluteres vittiger*) – were included in our analysis. A small container placed in front of the predator cage emitted food cues to attract the prey species to the general area and encourage foraging related behaviours. Based on video recordings, the position of each prey individual throughout the trial was afterwards assessed through manual tracking using the software Solomon Coder. To be able to quantify foraging and risk-taking behaviours, the field of view of the camera was subdivided into an area distant to 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 further away.

Three response variables were derived and combined to estimate prey vulnerability. I) “Prey attraction” was calculated as the percentage of time spent in the area close of the 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 the food cue relative to the time spent in this area (Goldenberg *et al.*). III) ‘Boldness’ was measured as the percentage of time spent on the side directly in front of the predator within the area close to the food cue relative to the time spent in the entire area close to the food cue (this chapter). Prey fishes may approach a predator to inspect it – a characteristic behavior termed predator inspection (Pitcher *et al.*, 1986) – reducing their vulnerability to the predator. While searching for food, the prey individuals also displayed potentially risky competitive interactions (i.e. attacks, fights, and chases) amongst themselves. We excluded the data obtained during any predator inspection behavior for the calculation of the three response variables to obtain the vulnerable component of the prey isolated from its non-vulnerable components. Finally, we averaged across the three response variables, weighting each variable equally, to obtain a composite vulnerability index of prey to its predator.

Besides species vulnerability, each predator-prey interaction in Ecosim can be presented by the effective search rate of predators (on their prey), which also determines the flow of energy through the food web. We calculated effective search rates for chondrichthyans on their prey using data presented in (Pistevos *et al.*, 2015). In their mesocosm experiment, (Pistevos *et al.*, 2015) estimated the total time (s) taken by a Port Jackson shark to successfully locate (1st successful hit) prey hidden in the sand based on olfactory cues (see Methods in (Pistevos *et al.*, 2015) for details).

The direct mortality, vulnerability rate, and effective search rate were used as a forcing function to drive the Ecosim models. These functions are applied to appropriate species in the model (Table S7). We calculated the relative effect size of these rates under different climate scenarios compared to control conditions using the absolute values (Table S7). In all cases, the value for baseline model was considered 1. Finally, linear time series were constructed for all the forcing functions from 2015 to 2100 based on the relative effect size to drive the respective parameters in the model simulations.

3.6.4 Calculation of MTI and diversity indexes

The mixed trophic impact analysis (MTI) used to explore the relative impact of slight increase or decrease of the biomass of any group on the other groups of the food web is expressed as,

$$MTI_{ij} = DC_{ij} = FC_{ji}$$

where DC_{ij} is the diet composition term expressing how much j contributes to the diet of i, and FC_{ji} is the proportion of predation on j that is due to i as a predator, allows the quantification of the impacts that a theoretical change of a unit in the biomass of a group (including fishing effort) would have on other groups in the ecosystem (Christensen *et al.*, 2008).

We examined indices of diversity and evenness at broad taxonomic scales (functional group). The indices were estimated using the final mass-balance biomass estimates from Ecopath. We expressed diversity within general functional pools by using a form of the Shannon diversity index (Shannon & Weaver, 1963),

$$H' = \sum_{i=1}^{s} p_i \times \ln(p_i)$$

Where diversity (H') is a function of the proportion (p) of each functional group i that makes up the total biomass of the s pools that make up a general functional pool which in our case either individual species or a functional group such as zooplankton. As H' increases, species diversity increases.

The diversity index Kempton's Q (Kempton & Taylor, 1976) describes the slope of the cumulative species log abundance curve. This is adapted in our modeling approach in a way where taxonomic species are also grouped into aggregate biomass pools of functionally similar organisms, species are replaced by the species groups of the model, and the biomasses of these groups serves as a proxy for the number of individuals in that species or groups (Ainsworth & Pitcher, 2006). This modified Kempton's Q species diversity index was calculated considering organisms with trophic levels 3 or higher and defined as,

$$Q_i = \frac{0.8\,Fg}{\log(R_1/R_2)}$$

Where Fg is the total number of functional groups in the model; R_1 and R_2 are the representative biomass values of the 10th and 90th percentiles in the cumulative abundance distribution.

Within the Ecopath modeling approach, a functional group cannot be absolute extinct, but should rather be represented by a very low but non-zero biomass value. This means each simulation at its conclusion will contain the same number of functional groups as the base model. The Kempton's Q index is reasonably invariant to model structure since each functional group potentially can affect only one point on the log-abundance curve. Thus this may induce a change in the overall slope only marginally (Ainsworth & Pitcher, 2006). In contrast, the Shannon index is considered more sensitive to the aggregation style used by the mass balanced model. Aggregation style of functional groups in food web models can also influence the behavior of models (Fulton & Smith, 2004).

The calculation of the Marine trophic index (MTI) considered species caught and retained from a fishing operation with trophic level≥3.25. The retained fish may not necessarily target by a fishery and could be also retained as because they are of commercial interest (i.e. not discarded). MTI is calculated as follows (Shannon *et al.*, 2014):

$$MTI_{3.25} = \sum_{i=1}^{n} Y_i \times TL_i / Y_L$$

Where Y_L is total landings, Y_i is the landing of species *i* and TL_i is the trophic level of species *i* (note: Y_L, Y_i and TL_i vary in time).

3.6.5 Approach used for retrospective test and sensitivity analyses

Environmental models including those which are deterministic should consider accounting uncertainty of their outcomes to use in the decision support system. In our modelling approach, we have accounted for the uncertainty of our model output in two steps.

In the first step, we built two simplified Ecopath models, one for each of the mesocosm and Port Philip Bay, using species-specific (predominantly higher order) taxonomic data. The mesocosm model was based on (Ullah *et al.*, 2018) and further parameterized and updated (included Port Jackson as a model group) using data from (Pistevos *et al.*, 2015) while the PPB model was parameterized based on existing data of the Bay (Table S8). Both of the models comprise an equal number of functional nodes and similar food web functional groups which allowed us to conduct a retrospective test of mesocosm transferability. The mesocosm transferability test specifically address the applicability of mesocosm data used to parameterize the updated (full) Port Philip Bay model to different climate scenarios. To do this, we consider that the food web parameters of control condition (mesocosm) resemble the condition of Port Philip Bay between the model period 1990 and 2015. Models were fitted with time-series data using automated stepwise fitting procedure (Scott *et al.*, 2016) and the best model was chosen based on the corrected AICc to derive the vulnerability parameters. The output showed that the mesocosm model fitted the biomass trends for carnivorous fish (benthic) and omnivorous fish reasonably well (Fig. 4) but not for the Port Jackson shark and herbivorous fish, given the large fluctuation of biomass data for herbivorous species and the absence of true predators for Port Jackson shark in the simplified model. The two best fitted models for both the mesocosm (AICc 17.55; Total SS 59.85) and PPB model (AICc 7.33, Total model SS 47.95) produced AICc values closer to each other. Overall, we show that our modelling approach through the amalgamation of empirical results and contemporary secondary field data used within a computational model was successfully able to track ecologically realistic trends of a real-world ecosystem.

In a second step, we used the Monte Carlo (MC) routine to examine the uncertainty in the basic Ecopath input parameters (B, P/B, Q/B, EE) on the outputs of model simulation (biomass and ecological indicators). Within this approach, each MC simulation randomly selected a set of parameters within a 10% coefficient of variation (CV=0.1) for the B, P/B, Q/B, and *EE* based on their defined “Pedigree” (Coll & Steenbeek, 2017, Heymans *et al.*, 2016). We ran 100 MC simulations (each involving up to several thousand iterations to find a balanced model) and the results were used to plot the 5th and 95th percentile confidence intervals for the fitted biomass (Fig. S10). This approach was used for both the simplified Ecopath models (mesocosm and PPB) and updated PPB model.

3.7 SUPPLEMENTARY FIGURES

Figure S1: Change in biomass (Δ %) of different ecosystem functional groups (TL>3) groups under a future climate change scenario (RCP 8.5) with current level of fishing effort continuing at 2100, relative to the biomass in 2100 under a scenario of no change in climate or fishing effort from present day levels. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming.

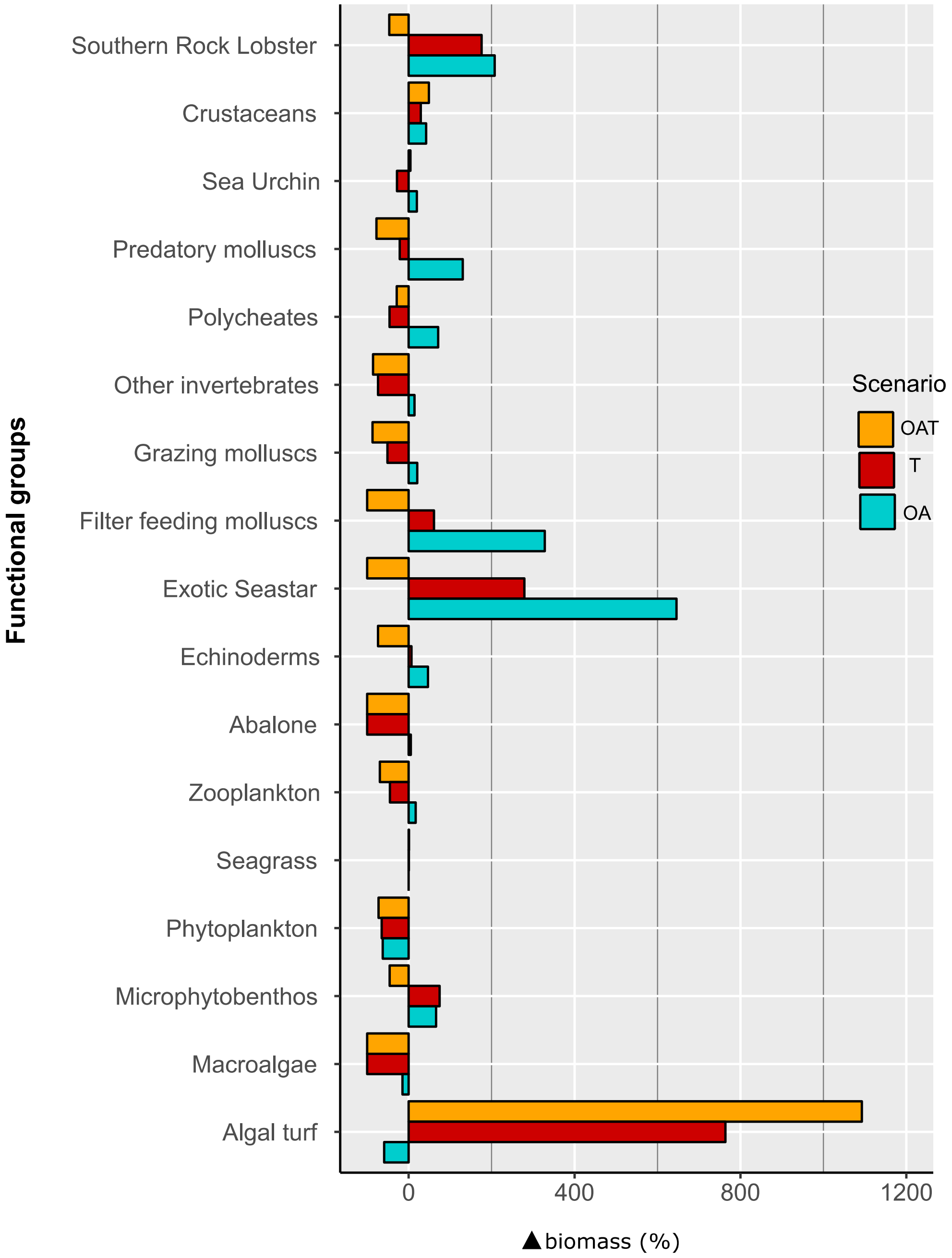

Figure S2: Change in biomass (Δ %) of different ecosystem functional groups (TL<3) groups under a future climate change scenario (RCP 8.5) with current level of fishing effort continuing at 2100, relative to the biomass in 2100 under a scenario of no change in climate or fishing effort from present day levels. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming.

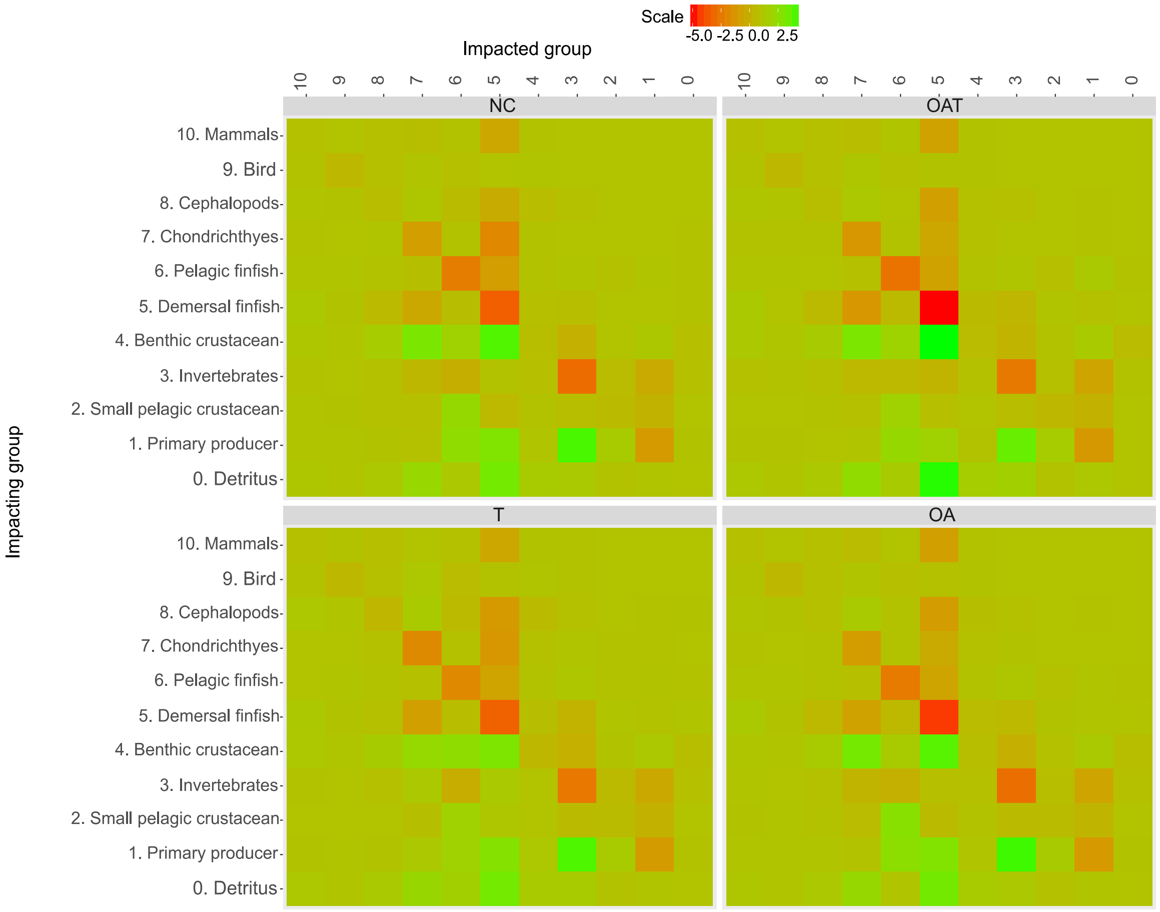

Figure S3: Mixed Trophic Impact (MTI) index for different community groups derived for NC, OAT, T and OA scenario. The MTI index, scaled from -1 to 1, was first calculated for every group of the model. The values of individual functional groups were then pooled under corresponding community groups and presented as a total net cumulative effect (positive plus negative) across all functional groups within a community. Therefore, the total effect could be >±1. The colours should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups. NC denotes no change in climate and fishing effort from present-day levels. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. The colour boxes show negative (red) or positive (green) impacts of a community group on others and the intensity is proportional to the degree of the impacts.

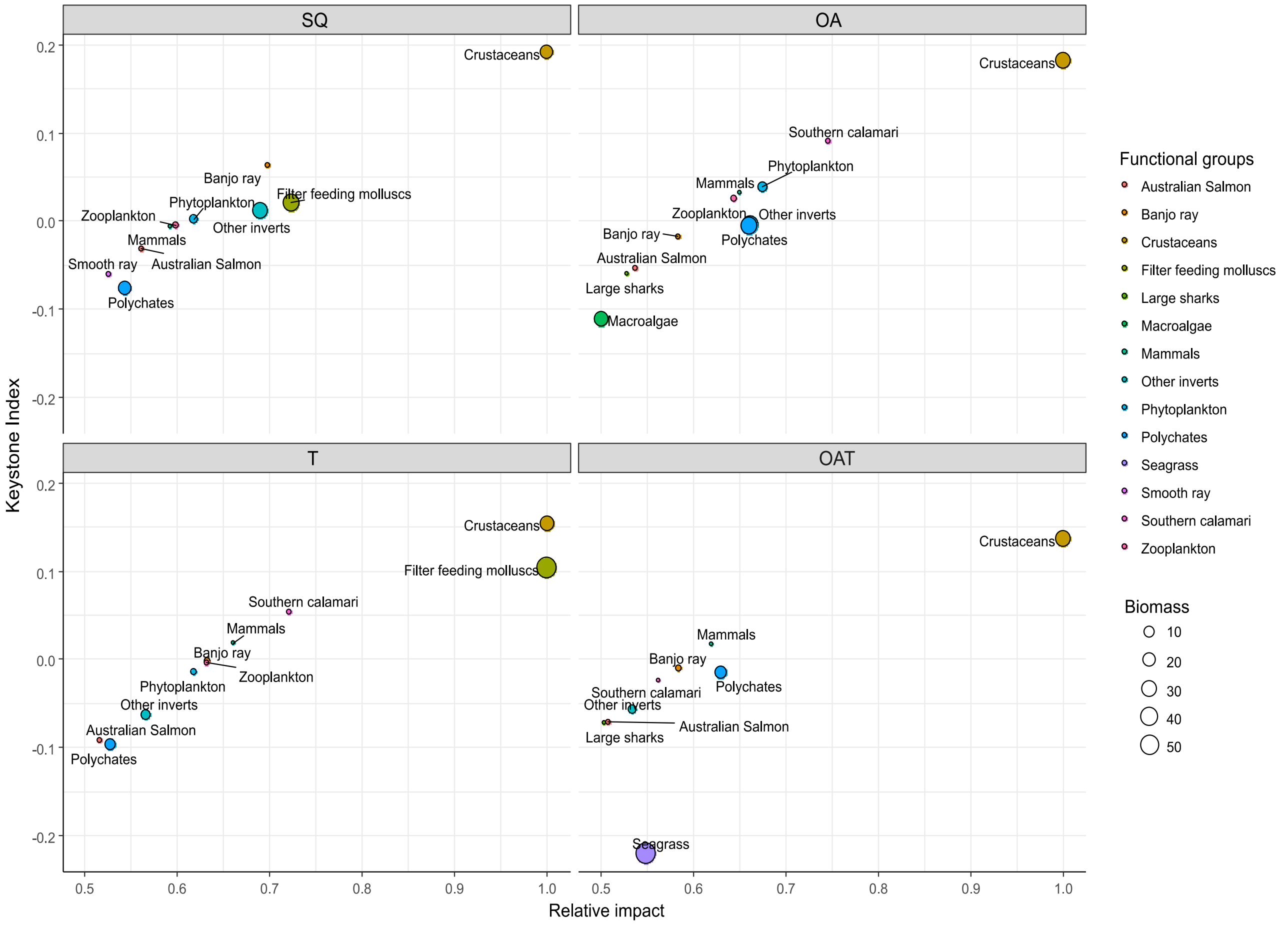

Figure S4: Keystoneness index for the different functional groups (only with a relative impact >0.50) of the food webs in four different climate scenarios. For each functional group, the keystoneness index (y axis) is reported against overall effect (x axis). Overall effects are relative to the maximum effect measured in each trophic web, thus for the x axis the scale is always between 0 and 1. Within each trophic web the species are ordered by decreasing keystoneness, therefore the keystone functional groups are those ranking between the first groups (values close or greater than zero). The circle sizes are relative to their standing stock biomass. NC refers to the biomass of PPB ecosystem, under no climate change and current level of fishing effort at 2100. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming.

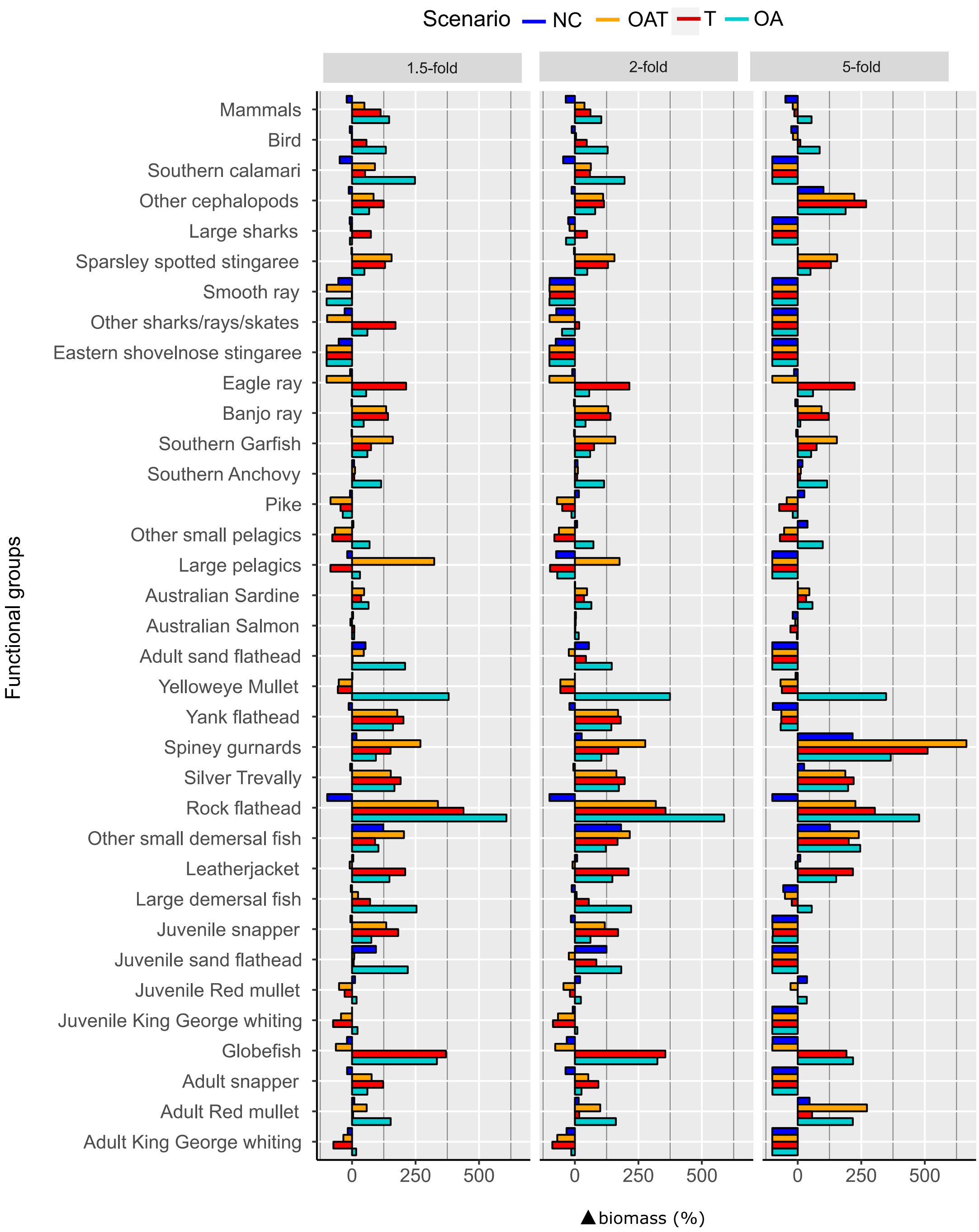

Figure S5: Change in biomass (Δ %) of different functional groups (TL>3) under the combination of different climate and fishing effort scenarios relative to the biomass in 2100 under a scenario of no change in climate from present day levels (NC). OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. Here the number with 'folds' refers to the magnitude of fishing increase that starts in year 2015 and is held constant up to 2100 compared to the NC scenario.

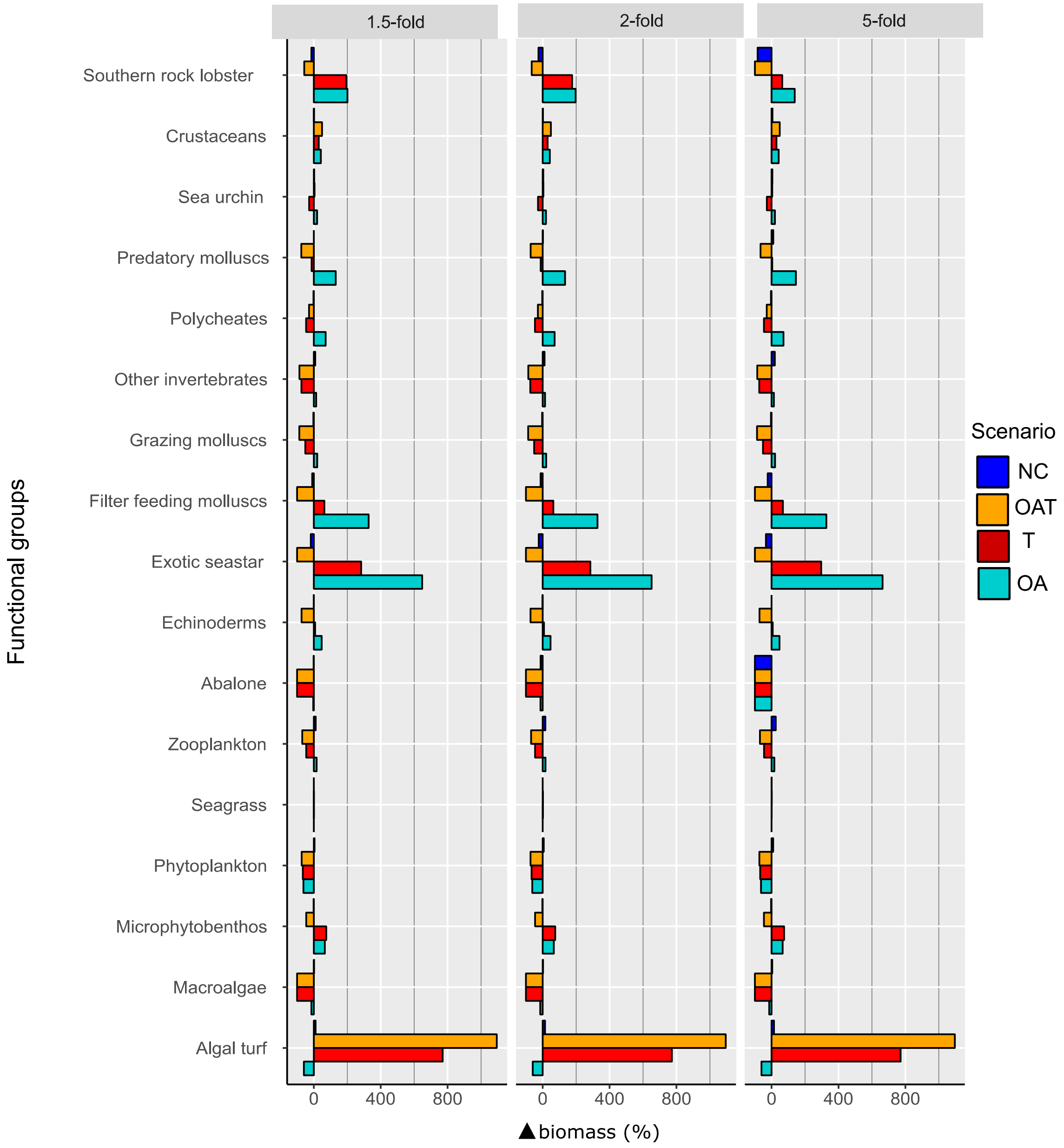

Figure S6: Change in biomass (Δ %) of different functional groups (TL<3) under the combination of different climate and fishing effort scenarios relative to the biomass in 2100 under a scenario of no change in climate from present day levels (NC). OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. Here the number with 'folds' refers to the magnitude of fishing increase that starts in year 2015 and is held constant up to 2100 compared to the NC scenario.

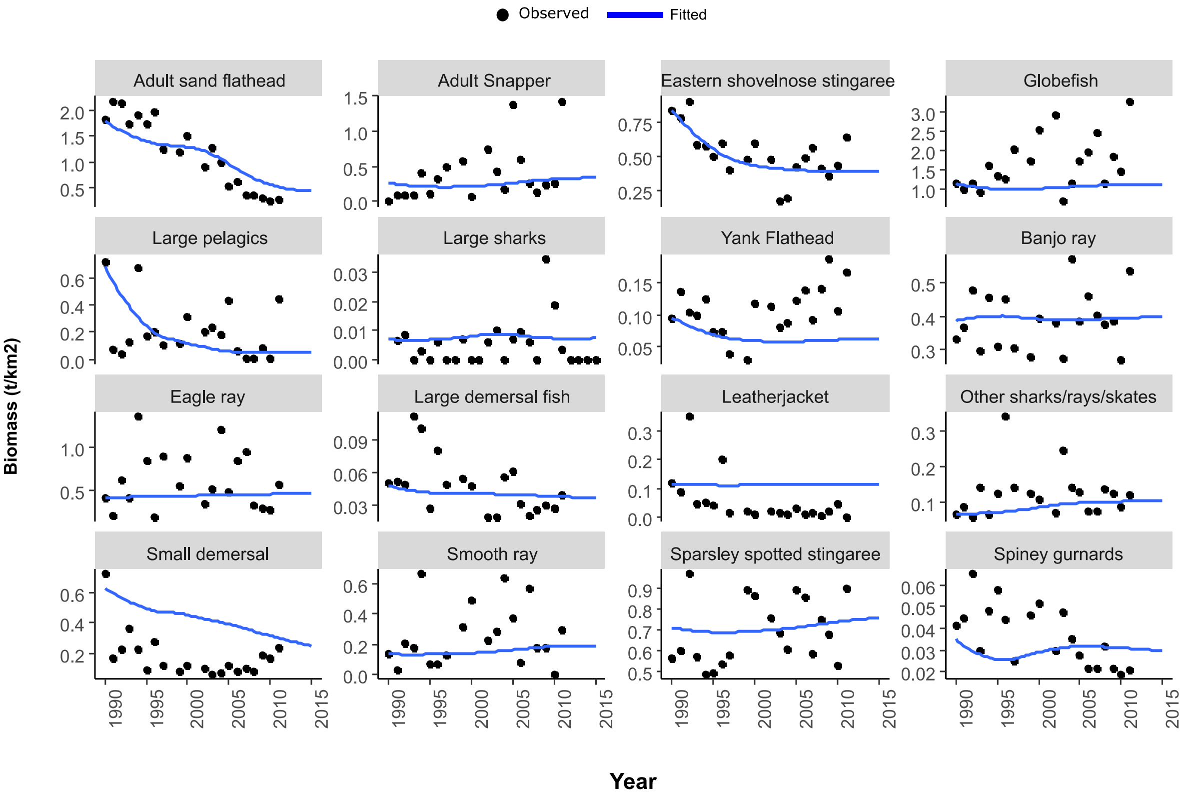

Figure S7: Predicted (solid lines) versus observed (dots) biomass (tonnes km^{-2}) for some of the groups with available data in the Port Philip Bay ecosystem model during the period 1990–2015.

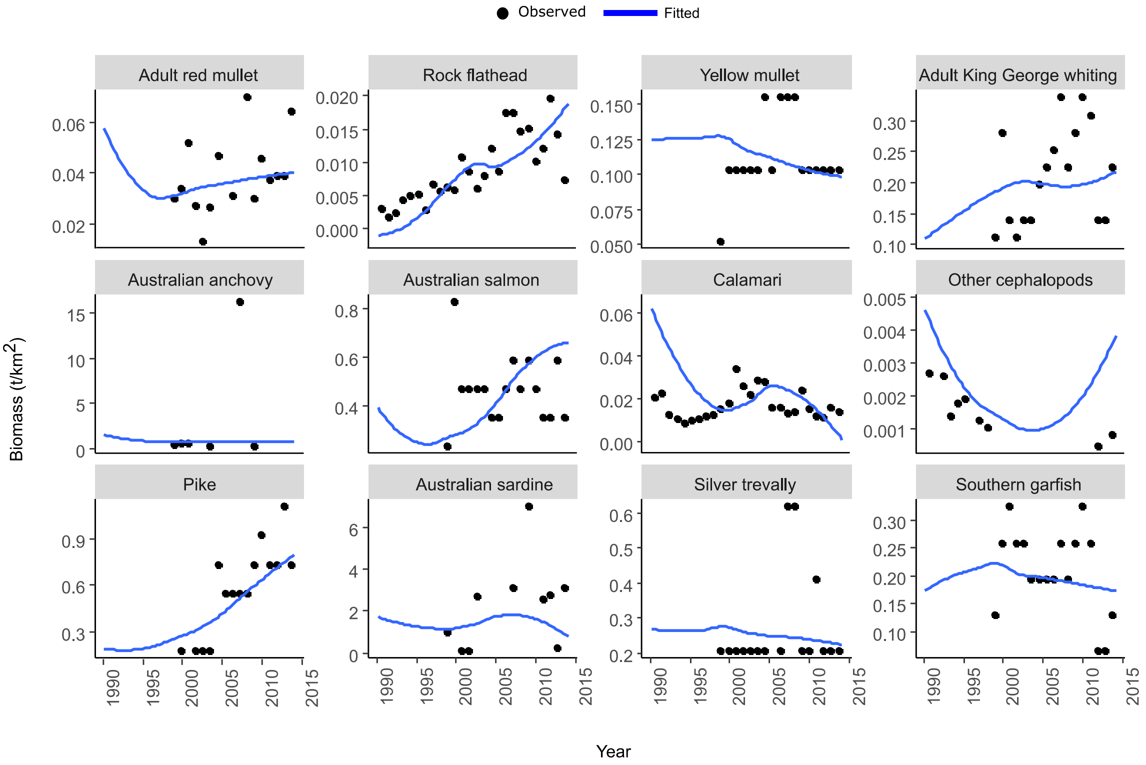

Figure S8: Predicted (solid lines) versus observed (dots) CPUE (tonnes km^{-2}) for some of the groups with available data in the Port Philip bay ecosystem model during the period 1990–2015. CPUE denotes catch per unit effort.

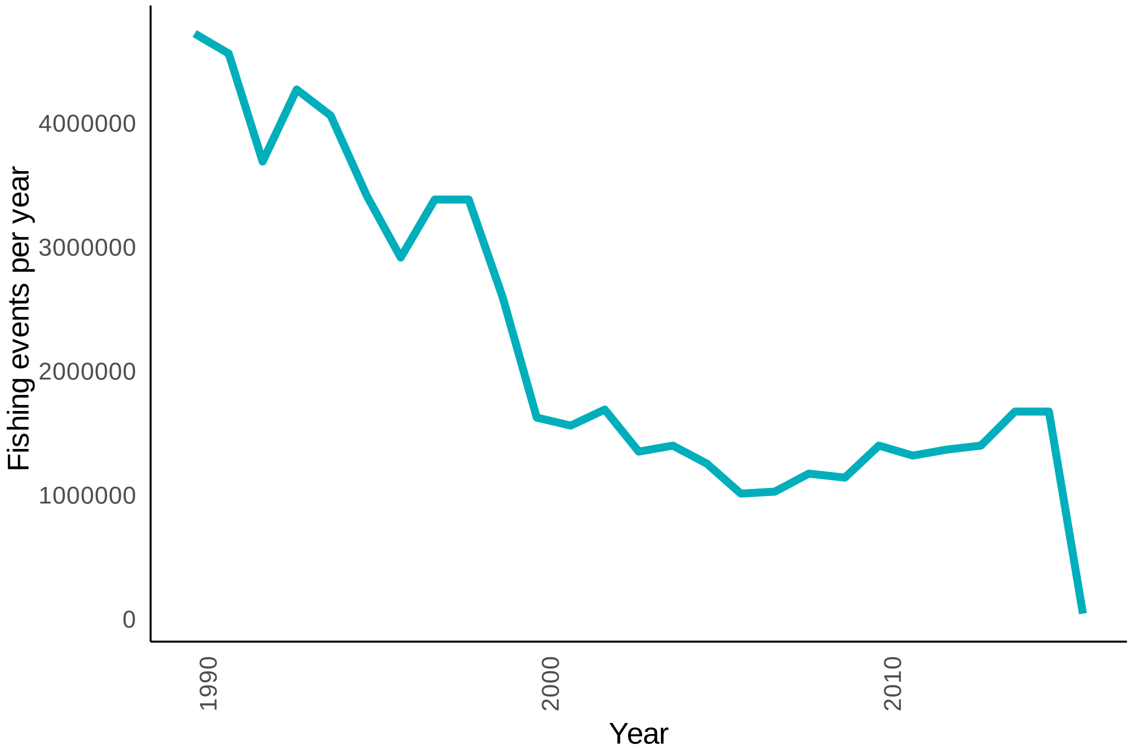

Figure S9: Historical trends of fishing efforts (Fishing events) obtained for commercial fishery in the Port Philip Bay ecosystem calculated by multiplying the number of fishing days and number of fishers.

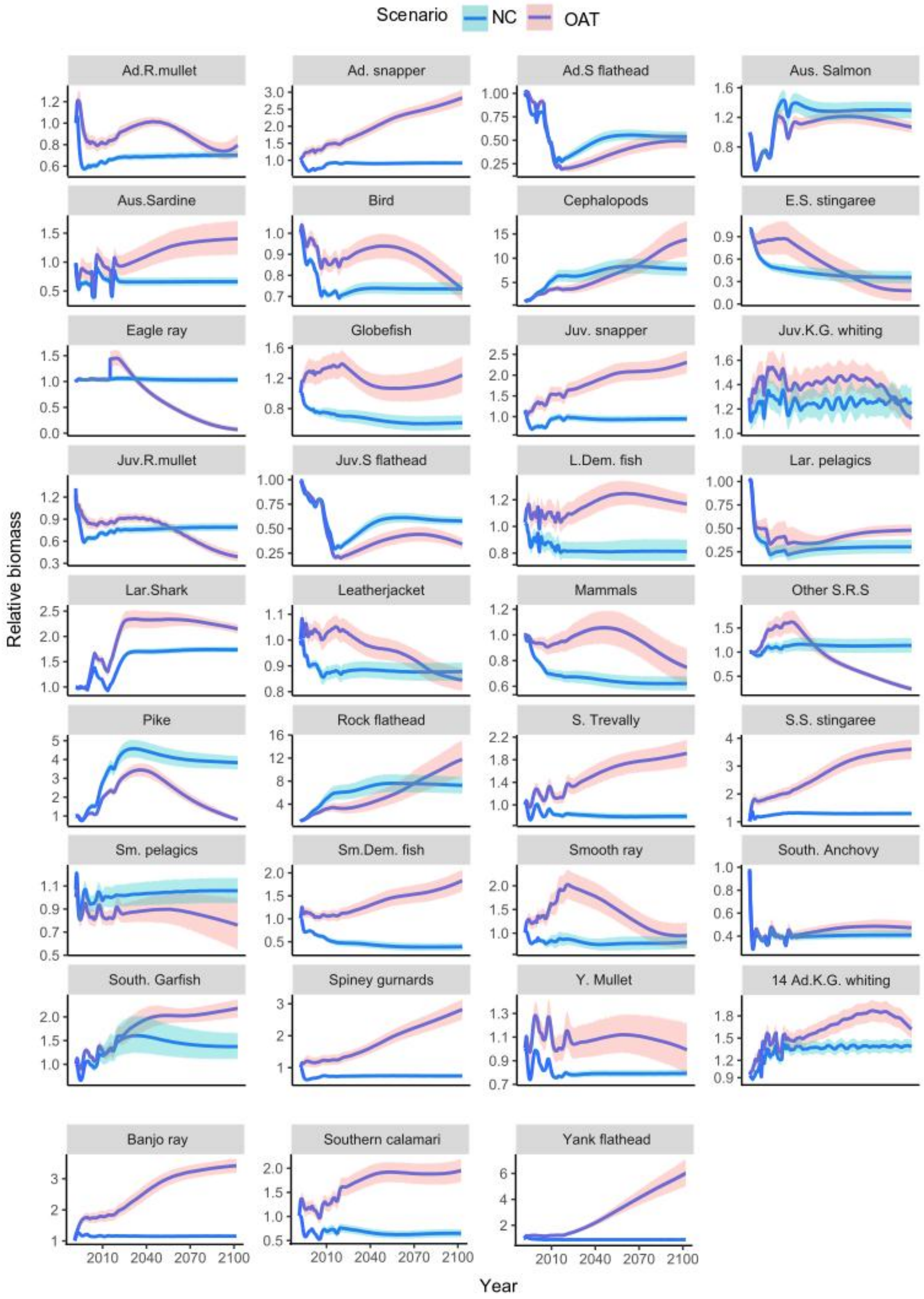

Figure S10: The results of Monte Carlo simulations (100 simulations run) of some higher trophic level food web functional groups of Port Philip Bay are plotted. Thick blue line represents the mean value of the fitted model. The 95% percentile and 5% percentile using 10% fixed variability of the model inputs (shaded areas) derived from model pedigree index are also shown. Results are only plotted for the most pervasive future scenario OAT (warming and acidification together) relative to no change scenario at 2100 under present day fishing effort.

3.8 SUPPLEMENTARY TABLES

Table S1. Biomass estimates (t km^{-2} total weight) and other functional group parameters of the updated Port Philip Bay (PPB) Ecopath model. Values of trophic level (TL), biomass, production/biomass (P/B) ratio, consumption/biomass (Q/B) ratio, ecotrophic efficiency (EE), and production/consumption (P/C) ratio were shown. Fg. denotes functional group and Fg. No. denotes functional group number.

Fg. No.	Group name	TL	Biomass (t/km²)	PB (/year)	QB (/year)	EE	P/C	Functional groups in PPB Model
1	Large sharks	4.33	0.01	0.18	1.75	0.60	0.10	Included
2	Large pelagics	4.02	0.72	0.40	3.92	0.62	0.10	Koopman, 2005
3	Bird	3.82	1.02	0.07	1.69	0.15	0.04	Included
4	Mammals	4.02	0.02	0.09	19.88	0.00	0.00	Included
5	Yank flathead	3.58	0.09	0.40	3.80	0.18	0.11	Koopman, 2005
6	Rock flathead	3.33	0.07	0.38	2.45	0.95	0.16	Included
7	Other cephalopods	3.48	0.18	1.70	6.00	0.95	0.28	Koopman, 2005
8	Southern calamari	3.47	0.25	1.83	8.00	0.95	0.23	Included
9	Smooth ray	3.33	0.14	0.32	2.72	0.47	0.12	Koopman, 2005
10	Adult sand flathead	3.46	1.84	0.40	2.31	0.43	0.17	Koopman, 2005
11	Juvenile sand flathead	2.40	0.42	0.40	4.20	0.95	0.10	Koopman, 2005
12	Banjo ray	3.45	0.33	0.23	2.37	0.22	0.10	Koopman, 2005
13	Eastern shovelnose stingaree	3.28	0.84	0.49	2.41	0.08	0.20	Koopman, 2005
14	Adult King George whiting	3.18	0.12	1.10	4.40	0.97	0.25	Koopman, 2005
15	Juvenile King George whiting	3.29	0.21	1.10	8.12	0.53	0.14	Included
16	Large demersal fish	3.40	0.05	0.92	4.33	0.79	0.21	Koopman, 2005
17	Adult Red mullet	3.13	0.05	0.92	5.19	0.92	0.18	Koopman, 2005
18	Juvenile Red mullet	2.02	0.01	1.84	13.04	0.69	0.14	Included
19	Eagle ray	3.14	0.41	0.20	3.37	0.02	0.06	Koopman, 2005
20	Other sharks/rays/skates	3.11	0.07	0.22	2.20	0.86	0.10	Koopman, 2005
21	Sparsley spotted stingaree	3.11	0.57	0.41	4.16	0.03	0.10	Koopman, 2005
22	Australian sardine	3.06	2.89	1.12	6.00	0.95	0.19	Included
23	Southern anchovy	3.04	2.54	0.70	5.04	0.95	0.14	Included
24	Australian salmon	3.96	0.41	0.44	4.20	0.95	0.10	Included

Table 5.1: Cont.

25	Pike	4.04	0.21	0.30	3.00	0.95	0.10	Included
26	Southern garfish	2.61	0.23	1.55	10.40	0.95	0.15	Included
27	Small pelagics	3.01	3.53	0.82	10.02	0.95	0.08	Koopman, 2005
28	Silver trevally	3.28	0.31	0.57	2.20	0.95	0.26	Included
29	Yelloweye mullet	3.02	0.15	1.32	10.60	0.95	0.12	Included
30	Leatherjacket	2.68	0.12	0.92	9.65	0.99	0.10	Included
31	Small demersal fish	3.10	0.72	1.42	12.31	0.95	0.12	Koopman, 2005
32	Globefish	3.11	1.17	0.68	3.04	0.14	0.22	Koopman, 2005
33	Spiny gurnards	3.05	0.04	0.87	2.40	0.95	0.36	Koopman, 2005
34	Adult snapper	3.31	0.26	0.49	2.20	0.98	0.22	Koopman, 2005
35	Juvenile snapper	3.05	0.20	0.55	3.71	0.77	0.15	Included
36	Other invertebrates	2.39	24.02	3.26	16.28	0.13	0.20	Koopman, 2005
37	Polychaetes	2.29	24.22	2.93	11.53	0.91	0.25	Koopman, 2005
38	Filter feeding molluscs	2.07	24.97	2.72	13.59	0.95	0.20	Included
39	Grazing molluscs	2.00	4.02	2.09	10.49	0.95	0.20	Included
40	Predatory molluscs	3.32	0.94	2.72	13.59	0.57	0.20	Included
41	Echinoderms	2.05	51.28	0.80	9.41	0.33	0.08	Koopman, 2005
42	Zooplankton	2.04	4.66	54.75	153.36	0.55	0.36	Koopman, 2005
43	Benthic crustaceans	2.05	25.97	4.50	22.48	0.95	0.20	Koopman, 2005
44	Abalone	2.00	0.26	0.73	12.41	0.70	0.06	Included
45	Southern rock lobster	3.23	0.03	0.73	12.41	0.53	0.06	Included
46	Sea urchin	2.00	4.72	0.88	11.68	0.71	0.08	Included
47	Exotic seastar	3.05	0.00	0.52	2.60	0.00	0.20	Included
48	Macroalgae	1	18.13	20.00	0.00	0.23		Koopman, 2005
49	Algal turf	1	0.71	30.85	0.00	0.97		Included
50	Phytoplankton	1	6.41	259.30	0.00	0.82		Koopman, 2005
51	Microphytobenthos	1	26.88	45.00	0.00	0.11		Koopman, 2005
52	Seagrass	1	58.21	11.13	0.00	0.07		Koopman, 2005
53	Detritus	1	12573.00			0.29		Koopman, 2005

Table S2: The source of basic input parameters for the Port Phillip Bay ECOPATH model. Juvenile fish groups represent those <3 years old. Production/biomass= P/B and consumption/biomass= Q/B, Natural mortality= M, total mortality=Z. Fg. No. denotes functional group number.

Fg. No.	Group name	Biomass (t/km²)	PB (/year)	QB (/year)	Ecotrophic efficiency (EE)
1	Large sharks	Model estimation	Average of M for bronze whalers and 7-gilled sharks (Froese and Pauly, 2017)	Calculated empirically (Palomares and Pauly,1998)	Assumed *EE* = 0.60
2	Large pelagics	Trawl survey	Annala et al. 1999 and Tilzey 1994 (Weighted by relative abundance of component species)	Calculated empirically (Palomares and Pauly,1998)	
3	Bird	Briggs et al. 1987; PICES, 1998	Briggs et al. 1987; PICES, 1998	Briggs et al. 1987; PICES, 1998	
4	Mammals	Fulton and Smith, 2004	Fulton and Smith, 2004	Fulton and Smith, 2004	
5	Yank flathead	Trawl survey	As for sand flathead	Calculated from Officer and Parry (1996)	
6	Rock flathead	Model estimation	Koopman, 2004	Averaged from sand and yank flathead	Assumed *EE* = 0.95 (Polovina,1984)
7	Other cephalopods	Model estimation	Manickchand-Heileman et al. 1998	O'Sullivan and Cullen 1983; Arreguin-Sanchez et al. 1993	Assumed *EE* = 0.95 (Polovina,1984)
8	Southern calamari	Model estimation	Fulton and Smith, 2004	Watson et al. 2013	Assumed *EE* = 0.95 (Polovina,1984)
9	Smooth ray	Trawl survey	Used *T*max from similar species (*Dasyatis C. chrysonota* (Cowley, 1997)) to estimate M	Calculated from data in Officer and Parry (1996)	
10	Adult sand flathead	Trawl survey	Z (Calculated from catch curve)	Calculated from data in Officer and Parry (1996)	
11	Juvenile sand flathead	Trawl survey	Z (Calculated from catch curve)	Model estimation	

12	Banjo ray	Trawl survey-2	M (Froese and Pauly, 2017)	Calculated from Officer and Parry (1996)	
13	Eastern S. stingaree	Trawl survey-2	M (Froese and Pauly, 2017)	Calculated from Officer and Parry (1996)	
14	Adult king george whiting	Trawl survey-2	M doubled to get Z (Fowler and McGarvey 2000)	Calculated empirically (Palomares and Pauly,1998)	
15	Juvenile King George whiting	Model estimation	M (Fowler and McGarvey 2000)	Model estimation	
16	Large demersal fish	Trawl survey-2	M (Froese and Pauly, 2017), then added F. F from catch rate/biomass =0.1552/0.357=0.4347	Q/B, average of related demersal fish (Froese and Pauly, 2017)	
17	Adult red mullet	Trawl survey-2	M, average of other species of goatfish (Froese and Pauly, 2017)	Q/B, average of other species of goatfish (Froese and Pauly, 2017)	
18	Juvenile red mullet	Model estimation	As for adult red mullet (Froese and Pauly, 2017)	Model derived	
19	Eagle ray	Trawl survey-2	Used *T*max from similar species (*Myliobatis californica*) (Martin and Cailliet 1988) to estimate M	Calculated from data in Officer and Parry (1996)	
20	Other sharks /rays/skates	Trawls survey	Froese and Pauly, 2017	Q/B, average of similar species (Froese and Pauly, 2017)	
21	Sparsely spotted stingaree	Trawl survey	Froese and Pauly, 2017	Calculated from data in Officer and Parry (1996)	
22	Australian sardine	Model estimation	Z value for similar species *Sardinella lemuru* (Gaughan and Mitchell, 2000)	Goldsworthy et al. 2013	
23	Southern anchovy	Model estimation	Goldsworthy et al. 2013	Goldsworthy et al. 2013	Assumed *EE* = 0.95 (Polovina,1984)
24	Australian salmon	Model estimation	Goldsworthy et al. 2013	Hughes et al. 2014	Assumed *EE* = 0.95 (Polovina,1984)
25	Pike	Model estimation	Froese and Pauly, 2017	Froese and Pauly, 2017	Assumed *EE*

					= 0.95 (Polovina,1984)
26	Southern garfish	Model estimation	Jones et al. 2002	Froese and Pauly, 2017	Assumed *EE* = 0.95 (Polovina,1984)
27	Small pelagics	Model estimation	M, average of all species of small pelagic (Froese and Pauly, 2017)	Calculated empirically (Palomares and Pauly,1998)	Assumed *EE* = 0.95 (Polovina,1984)
28	Silver trevally	Model estimation	Farmer et al. 2005	Calculated empirically (Palomares and Pauly,1998)	Assumed *EE* = 0.95 (Polovina,1984)
29	Yelloweye mullet	Model estimation	M doubled to get Z (Froese and Pauly, 2017)	Calculated empirically (Palomares and Pauly,1998)	Assumed *EE* = 0.95 (Polovina,1984)
30	Leatherjacket	Trawl survey-2	M, average of all species of the group (Froese and Pauly, 2017)	Calculated empirically (Palomares and Pauly,1998)	
31	Small demersal fish	Model estimation	Average for unvegetated sites in (Edgar and Shaw 1995a)	P/B divided by average P/Q for unvegetated sites in (Edgar and Shaw 1995b)	Assumed *EE* =0.95 (Polovina,1984)
32	Globefish	Trawl survey-2	Froese and Pauly, 2017	Calculated from data in Officer and Parry (1996)	
33	Spiny gurnards	Trawls survey	Used *M* from similar species within family (Booth 1997)	Calculated from data in Officer and Parry (1996)	
34	Adult snapper	Calculated empirically (Annala et al. 1999; Christensen et al. 2000.)	Fulton and Smith, 2004	Calculated empirically (Palomares and Pauly,1998)	
35	Juvenile snapper	Model estimation	Fulton and Smith, 2004	Model estimation	
36	Other invertebrates	Calculated from Wilson et al. 1993	Average of values for all species from literature presented in Edgar (1990) and Wilson et al. (1993)	Calculated assuming P/Q ratio of 0.2 (Arreguin-Sanchez et al. 1993)	
37	Polychaetes	Calculated from Wilson et al. 1993	Average values for Polychaetes from literature presented in Edgar (1990) and Wilson et al. (1993)	Poore, 1992; Wilson et al. 1993	
38	Filter feeding molluscs	Calculated from Wilson et al. 1993	Average values for molluscs from literature presented in (Edgar 1990)	Calculated assuming P/Q ratio of 0.2 (Arreguin-Sanchez et al. 1993)	

			and (Wilson et al. 1993)		
39	Grazing molluscs	Calculated from Wilson et al. 1993	Average values for molluscs from literature presented in Edgar (1990) and Wilson et al. (1993)	Calculated assuming P/Q ratio of 0.2 (Arreguin-Sanchez et al. 1993)	
40	Predatory molluscs	Calculated from Wilson et al. 1993	Average values for molluscs from literature presented in Edgar (1990) and Wilson et al. (1993)	Calculated assuming P/Q ratio of 0.2 (Arreguin-Sanchez et al. 1993)	
41	Echinoderms	Calculated from Wilson et al. 1993	Miller and Mann, 1973	Miller and Mann, 1973	
42	Zooplankton	Holloway and Jenkins, 1993	Holloway and Jenkins, 1993	Holloway and Jenkins, 1993	
43	Crustaceans	Model estimation	Average values for Crustaceans from literature presented in Edgar (1990) and Wilson et al. (1993)	Calculated assuming P/Q ratio of 0.2 (Arreguin-Sanchez et al. 1993)	Assumed *EE* =0.95(Polovina,1984)
44	Abalone	Fulton and Smith, 2004	Fulton and Smith, 2004	Fulton and Smith, 2004	
45	Southern rock lobster	Fulton and Smith, 2004	Fulton and Smith, 2004	Fulton and Smith, 2004	
46	Sea Urchin	Worthington and Blount, 2003	Fulton and Smith, 2004	Fulton and Smith, 2004	
47	Exotic seastar	Calculated from Parry et al. 2004	Harvey et al. 2012	Harvey et al. 2012	
48	Macroalgae	Murray and Parlsow, 1997	Murray and Parlsow, 1997		
49	Algal turf	Murray and Parlsow, 1997; Edmunds et al. 2004	Bozec et al. 2004		
50	Phytoplankton	Beardall et al. 1996	Beardall et al. 1996		
51	Micro-phytobenthos	Beardall and Light 1994	Beardall and Light 1994		
52	Seagrass	Bulthuis et al. 1992	Bulthuis and Woelkerling 1983		
53	Detritus	Calculated from Longmore et al. 1996 and Nicholson et al. 1996			

Table S3: The source of diet data for the Port Phillip Bay ECOPATH model. Juvenile fish groups represent those <3 years old.

Functional groups number	Group name	Diet
1	Large sharks	Ebert 1991, Last and Stevens 1994
2	Large pelagics	Officer and Parry 2000
3	Bird	Briggs et al. 1987; PICES, 1998
4	Mammals	Fulton and Smith, 2004
5	Yank flathead	Officer and Parry 2000
6	Rock flathead	Froese and Pauly, 2017
7	Other cephalopods	O'Sullivan and Cullen 1983; Arreguin-Sanchez et al. 1993
8	Southern calamari	Officer and Parry 1996, Parry et al. 1995, Gunthorpe et al. 1997
9	Smooth ray	Officer and Parry 2000
10	Adult sand flathead	Officer and Parry 2000
11	Juvenile sand flathead	Officer and Parry 2000
12	Banjo ray	Officer and Parry 2000
13	Eastern shovelnose stingaree	Officer and Parry 2000
14	Adult king george whiting	Officer and Parry 2000
15	Juvenile king george whiting	Officer and Parry 2000
16	Large demersal fish	Officer and Parry 2000
17	Adult red mullet	Officer and Parry 2000
18	Juvenile red mullet	Officer and Parry 2000
19	Eagle ray	Officer and Parry 2000
20	Other sharks/rays/skates	Officer and Parry 2000
21	Sparsely spotted stingaree	Officer and Parry 2000
22	Australian sardine	
23	Southern anchovy	Froese and Pauly, 2017

24	Australian Salmon	Hughes et al. 2014
25	Pike	Froese and Pauly, 2017
26	Southern garfish	Robertson and Klumpp, 1983
27	Small pelagics	Assumed to be 100% zooplankton
28	Silver trevally	French et al. 2012
29	Yelloweye mullet	Platell, 2006
30	Leatherjacket	Hallett, 2016
31	Small demersal fish	Officer and Parry 2000
32	Globefish	Officer and Parry 2000
33	Spiney gurnards	Officer and Parry 2000
34	Adult snapper	Officer and Parry 2000
35	Juvenile snapper	Officer and Parry 2000
36	Other invertebrates	See crustaceans
37	Polychaetes	See crustaceans
38	Filter feeding molluscs	See crustaceans
39	Grazing molluscs	See crustaceans
40	Predatory molluscs	See crustaceans
41	Echinoderms	See crustaceans
42	Zooplankton	Holloway and Jenkins, 1993
43	Crustaceans	Breakdown of feeding groups in (Wilson et al. 1993). Feeding groups allocated the following diet: Deposit feeder eat detritus; Predators eat inverts-distributed according to biomass; Scavengers eat detritus; Suspension feeders eat 7.5% zooplankton and 92.5% phytoplankton; Grazers eat micro-phytobenthos and seagrass
44	Abalone	Fulton and Smith 2004; Palomares and Pauly, 2018
45	Southern rock lobster	Fulton and Smith 2004; Palomares and Pauly, 2018
46	Sea Urchin	Fulton and Smith 2004; Palomares and Pauly, 2018
47	Exotic seastar	Ross et al.2003; Lockhart and Ritz, 2001

Table S4: Community groups considered for the representative model functional groups. Habitats and feeding guilds of the relevant groups were also presented. Feeding guild was only presented for finfish group because model input data on species interaction was based on omnivorous and carnivorous finfish group. Fg. No. denotes functional group number.

Fg. No.	**Functional group name**	**Community group**	**Major species/common name**	**Habitat (Water column)**	**Feeding guild**
1	Large sharks	Chondrichthyans	*Notorynchus cepedianus*	Pelagic	NA
2	Large pelagics	Pelagic finfish	*Thyrsites atun,Pomatomus saltatrix, Seriolella brama, Seriolella punctata,Trachurus declivis*	Pelagic	Carnivorous
3	Bird	Bird	Australasian Gannet *Morus serrator*	Bentho-pelagic	NA
4	Mammals	Mammals	Dolphins and seals	Bentho-pelagic	NA
5	Yank flathead	Demersal finfish	*Platycephalus speculator*	Demersal	Carnivorous
6	Rock flathead	Demersal finfish	*Platycephalus laevigatus*	Demersal	Carnivorous
7	Other cephalopods	Cephalopods	*Nototodarus gouldi*	Pelagic	NA
8	Southern calamari	Cephalopods	*Sepioteuthis australis*	Pelagic	NA
9	Smooth ray	Chondrichthyans	*Dasyatis brevicaudata*	Demersal	NA
10	Adult sand flathead	Demersal finfish	*Platycephalus bassensis*	Demersal	Carnivorous
11	Juvenile sand flathead	Demersal finfish	*Platycephalus bassensis*	Demersal	Carnivorous
12	Banjo ray	Chondrichthyans	*Trygonorrhina fasciata*	Demersal	NA
13	Eastern shovelnose stingaree	Chondrichthyans	*Trygonoptera imitata*	Demersal	NA
14	Adult king george whiting	Demersal finfish	*Sillaginodes punctata*	Demersal	Carnivorous
15	Juvenile king george whiting	Demersal finfish	*Sillaginodes punctata*	Demersal	Carnivorous
16	Large demersal fish	Demersal finfish	*Rhombosolea tapirina, Nemadactylus macropterus,Pentaceropsis recurvirostris,Eubalichthys mosaicus,Genypterus tigerinus,Gonorynchus greyi,Meuschenia freycineti,Platycephalus richardsoni*	Demersal	Omnivorous
17	Adult red mullet	Demersal finfish	*Upeneichthys vlamingii*	Demersal	Carnivorous

18	Juvenile red mullet	Demersal finfish	*Upeneichthys vlamingii*	Demersal	Carnivorous
19	Eagle ray	Chondrichthyes	*Myliobatis australis*	Demersal	NA
20	Other sharks/rays/skates	Chondrichthyans	*Squatina australis, Callorhynchus milii,Mustelus antarcticus,Dipturus whitleyi,Heterodontus portusjacksoni,Galeorhinus galeus,Urolophus gigas,Dentiraja lemprieri*	Demersal	NA
21	Sparsely spotted stingaree	Chondrichthyans	*Urolophus paucimaculatus*	Demersal	NA
22	Australian sardine	Pelagic finfish	*Sardinops sagax*	Pelagic	Carnivorous
23	Southern anchovy	Pelagic finfish	*Engraulis australis*	Pelagic	Carnivorous
24	Australian Salmon	Pelagic finfish	*Arripis trutta*	Pelagic	Carnivorous
25	Pike	Pelagic finfish	*Dinolestes lewini*	Pelagic	Carnivorous
26	Southern garfish	Pelagic finfish	*Hyporhamphus melanochir*	Pelagic	Omnivorous
27	Small pelagics	Pelagic finfish	*Hyperlophus vittatus, Cristiceps australis,Arripis georgianus*	Pelagic	Carnivorous
28	Silver trevally	Demersal finfish	*Pseudocaranx georgianus*	Demersal	Carnivorous
29	Yelloweye mullet	Demersal finfish	*Aldrichetta forsteri*	Demersal	Omnivorous
30	Leatherjacket	Demersal finfish	*Scobinichthys granulatus, Acanthaluteres vittiger,Acanthaluteres spilomelanurus,Thamnaconus degeni*	Demersal	Omnivorous
31	Small demersal fish	Demersal finfish	*Contusus brevicaudus,Ammotretis rostratus,Pseudophycis bachus,Neosebastes scorpaenoides,Neosebastes scorpaenoides,Neoodax balteatus,Contusus richei,Gymnapistes marmoratus, Kathetostoma laeve,Parequula melbournensis,Sillago flindersi, Vincentia conspersa, Lepidotrigla Vanessa, Tetractenos glaber, Chelidonichthys kumu, Aracana ornate, Scorpaena papillosa, Aracana aurita, Favonigobius lateralis*	Demersal	Omnivorous
32	Globefish	Demersal finfish	*Diodon nicthemerus*	Demersal	Carnivorous
33	Spiney gurnards	Demersal finfish	*Lepidotrigla papilio*	Demersal	Carnivorous
34	Adult snapper	Demersal finfish	*Pagrus auratus*	Demersal	Carnivorous
35	Juvenile snapper	Demersal finfish	*Pagrus auratus*	Demersal	Carnivorous
36	Other invertebrates	Invertebrates	Acidian, tunicate,sponge, coral	NA	NA
37	Polychaetes	Invertebrates	*Phyllochaetopterus socialis* and other annelida	NA	NA
38	Filter feeding molluscs	Invertebrates	Mostly bivalves such as *Notospisula trigonella, Chioneryx cardiodes,Fulvia tenuicostata, Mytilus edulis*	NA	NA

39	Grazing molluscs	Invertebrates	Gastropods such as *Actinoleuca calamus,Micrastraea aurea, Rhyssoplax tricostalis , Phasianella australis ,Bulla quoyii,* Tunicate	NA	NA
40	Predatory molluscs	Invertebrates	*Ectosinum zonale, Austroginella johnstoni, E. zonale, Sigaretotrema umbilicata*	NA	NA
41	Echinoderms	Invertebrates	mostly echinoids such as *Echinocardium cordatum* and other ophiuroids	NA	NA
42	Zooplankton	Small pelagic crustacean	Copepod, small copepods mostly *Paracalanus indicus* (Caldocera and larvaceans) and *Acartia tranteri,*	NA	NA
43	Benthic crustaceans	Benthic crustacean	Small decapoda such as *Neocallichirus limosa, Dimorphostylis cottoni*, amphipods, crab	NA	NA
44	Abalone	Invertebrates	Blacklip abalone and greenlip abalone	NA	NA
45	Southern rock lobster	Benthic crustacean	*Jasus edwardsii*	NA	NA
46	Sea Urchin	Invertebrates	Black urchin (*Centrostephanus rodgersii*) and white urchin (*Heliocidaris erythrogramma)*	NA	NA
47	Exotic seastar	Invertebrates	*Asterias amurensis*	NA	NA
48	Macroalgae	Primary producer		NA	NA
49	Algal turf	Primary producer		NA	NA
50	Phytoplankton	Primary producer		NA	NA
51	Microphytobenthos	Primary producer		NA	NA
52	Seagrass	Primary producer		NA	NA
53	Detritus	Detritus		NA	NA

Table S5. Results of the temporally dynamic fitting procedure of the Port Phillip Bay Ecopath model from 1990s to 2015. NVs are the number of vulnerabilities included in each iteration, sPP the number of primary production spline points (for smoothing of the time series), k is the number of parameters included in the each model run and T is temperature. SS is the weighted sum of squared deviations. NVs and sPP are shown only for those models with the lowest Akaike Information Criterion (AICc). The "best" model (shown in bold) is the one yielding the lowest AICc and used to fit the Port Philip bay model.

T	Sl	Steps	Description	K	NVs	sPP	SS	AIC	AICc
Yes	1	Baseline	Trophic interactions with default prey-predator Vulnerabilities (vij =2; mixed effect). No environmental or fishery data are used to drive the model.	0	0	0	462.99	-39.53	-39.53
	2	Baseline and trophic interaction	Trophic interactions with different vulnerabilities. No environmental or fishery changes are used to drive the model.	24	24	0	262.95	-272.45	-270.13
	3	Baseline and environment	The "PP anomaly" is used to drive the model. No fishery data are used to drive the model.	3	0	3	439.10	-59.60	-59.60
	4	Baseline, trophic interactions and environment	No fishery data are used.	27	25	2	270.00	-253.00	-250.00
	5	Fishery	Fishing effort is included as model driver. Trophic interactions are set as default and no environmental data are used.	0	0	0	456.51	-46.59	-46.59
	6	Trophic interaction and fishery	No environmental data are used.	**15**	**15**	**0**	**253.74**	**-309.83**	**-308.97**
	7	Fishing and PP anomaly	Trophic interactions are set as default	8	0	8	425.16	-65.94	-65.71
	8	Trophic interactions, environment and fishery	All the components are jointly included in the model as drivers.	21	18	3	246.58	-311.00	-309.00
No	1	Baseline, trophic interactions and environment	No fishery data are used.	21	14	7	328.3	-167.9	-166.2

Table S6: Model estimated vulnerability parameters for different functional groups of the Port Phillip Bay Ecopath model.

Sl.	Functional groups	Vulnerability	S.	Functional groups	Vulnerability
1	Large sharks	2	27	Small pelagics	2
2	Large pelagics	2	28	Silver Trevally	>1000
3	Bird	2	29	Yelloweye Mullet	2
4	Mammals	2	30	Leatherjacket	1
5	Yank flathead	1	31	Small demersal fish	2
6	Rock flathead	52	32	Globefish	>1000
7	Other cephalopods	2	33	Spiny gurnards	2
8	Southern calamari	2	34	Adult snapper	2
9	Smooth ray	>1000	35	Juvenile snapper	2
10	Adult sand flathead	2	36	Other invertebrates	28
11	Juvenile sand flathead	2	37	Polychaetes	2
12	Banjo ray	2	38	Filter feeding molluscs	>1000
13	Eastern shovelnose stingaree	2	39	Grazing molluscs	2
14	Adult King George whiting	2	40	Predatory molluscs	2
15	Juvenile King George whiting	2	41	Echinoderms	2
16	Large demersal fish	1	42	Zooplankton	1
17	Adult Red mullet	2	43	Crustaceans	2
18	Juvenile Red mullet	2	44	Abalone	2
19	Eagle ray	2	45	Southern Rock Lobster	2
20	Other sharks/rays/skates	2	46	Sea urchin	2
21	Sparsely spotted stingaree	2	47	Exotic seastar	2
22	Australian Sardine	2			
23	Southern Anchovy	2			
24	Australian Salmon	2			
25	Pike	5			
26	Southern Garfish	2			

Table S7. Index (forcing function) used to drive the vulnerability parameters of future food web simulations (OAT, T, and OA). The effect size between no change scenario (NC) and climate scenarios were presented. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. Source groups refer consumers whose consumption depends on the vulnerability (parameters) of their prey groups. Forcing function as direct mortality for some of the model functional groups was also applied. For model functional groups or species number please see Table S1.

Index used to drive vulnerability parameters	**Baseline value**	**Effect size**			**Applied on the following functional groups or species**	**Source group**
	NC	**OA**	**T**	**OAT**		
Vulnerability index of carnivorous fish	1	0.99	1.08	0.82	2 ,5, 6,10,11,14,15,17,18,22,23,24, 25,27,28,32,33,34,35	Relevant consumers/predators
Vulnerability index of omnivorous fish	1	1.07	1.16	0.85	16,26,29,30,31	Relevant consumer/predator
Vulnerability index of zooplankton	1	1.97	0.87	1.15	42	Carnivorous consumers
Vulnerability index of polychaetes	1	1.11	0.63	1.70	37	Carnivorous consumers
Vulnerability index of epifauna	1	0.99	1.24	1.79	36, 37	Carnivorous consumers
Vulnerability index of bivalves	1	0.78	1.43	2.15	38	Carnivorous consumers
Vulnerability index of gastropods	1	10.56	6.17	1.90	39	Carnivorous consumers
Vulnerability index of copepod	1	2.97	1.66	1.91	42	Omnivorous consumers
Vulnerability index of polychaetes	1	5.36	1.29	<0.00	37	Omnivorous consumers
Vulnerability index of epifauna	1	3.10	2.88	0.88	36, 37	Omnivorous consumers
Vulnerability index of bivalves	1	1.65	3.18	0.91	38	Omnivorous consumers
Vulnerability index of gastropods	1	14.60	1.81	0.60	39	Omnivorous consumers
Search efficiency of chondrichthyans	1	0.21	1.07	0.32	2,5-8,10,11,14,16,17,21,22,24,27, 28, 30, 33,34,36-41,43,	Chondrichthyans
Algal turf productivity	1	1.07	1.82	1.58	49	Relevant consumers
Macrophytes productivity	1	1.28	0.24	0.46	48	Relevant consumers
Phytobenthos productivity	1	1.32	0.69	1.23	51	Relevant consumers
Phytoplankton productivity	1	1.66	0.44	0.99	50	Relevant consumers

Forcing function	**NC**	**OA**	**T**	**OAT**		Type
Biomass grazing molluscs	1	1.17	0.47	0.12	39	Mortality (as a function of biomass)
Biomass of filter feeders	1	1.24	0.28	0.15	38	Mortality (as a function of biomass)
Biomass of crustaceans	1	1.38	1.25	1.44	43	Mortality (as a function of biomass)
Biomass of polychaetes	1	1.74	0.50	0.68	37	Mortality (as a function of biomass)
Biomass of zooplankton	1	1.16	0.57	0.68	42	Mortality (as a function of biomass)

Table S8. Basic input parameters for simplified Port Phillip Bay (PPB) and mesocosm models built for the retrospective test of mesocosm transferability. Values of trophic level (TL), biomass, production/biomass (P/B), consumption/biomass (Q/B), ecotrophic efficiency (EE), and production/consumption (P/C) ratios are shown. Fg. No. denotes functional group number.

Fg. No.	Group name	TL		Biomass (t/km^2)	PB (/year)		QB (/year)		EE		P/C	
		PPB	Meso		PPB	Meso	PPB	Meso	PPB	Meso	PPB	Meso
1	Port Jackson shark	3.04	3.09	0.01	0.20	0.40	2.60	2.60	0.00	0.00	0.08	0.15
2	Herbivore fish	2.07	2.17	0.01	0.72	1.37	14.10	94.06	0.08	0.04	0.05	0.01
3	Omnivorous fish	2.99	2.99	0.04	1.09	1.17	12.55	111.75	0.00	0.00	0.09	0.01
4	Carnivorous fish (benthic)	2.82	2.91	0.00	1.27	1.00	17.30	28.99	0.14	0.00	0.07	0.03
5	Echinoderms	2.06	2.06	51.28	0.80	0.80	9.41	9.41	0.00	0.00	0.08	0.08
6	Herbivorous macroinvertebrates	2.00	2.00	4.02	2.09	0.50	10.49	8.46	0.00	0.00	0.20	0.06
7	Small epifaunal invertebrates	2.07	2.07	0.32	2.72	3.67	13.59	18.00	0.54	0.54	0.20	0.20
8	Filter Feeder	2.40	2.40	24.02	2.80	2.05	11.80	7.60	0.11	0.15	0.24	0.27
9	Macro-crustaceans	2.41	2.26	25.97	4.50	0.80	22.48	10.72	0.07	0.37	0.20	0.07
10	Tanaids	2.05	2.05	2.61	11.51	11.51	40.15	40.15	0.81	0.95	0.29	0.29
11	Copepod	2.00	2.00	1.38	23.80	108.71	38.61	336.98	0.67	0.63	0.62	0.32
12	Microzooplankton	2.00	2.00	0.90	36.80	23.11	59.78	63.49	0.08	0.67	0.62	0.36
13	Meiobenthos	2.00	2.00	9.12	8.88	8.88	58.40	58.40	0.80	0.80	0.15	0.15
14	Macrophytes	1.00	1.00	25.91	20.00	2.07		0	0.02	0.17		
15	Algal turf	1.00	1.00	0.71	30.85	28.87		0	0.39	0.40		
16	Phytobenthos	1.00	1.00	26.88	45.00	36.69		0	0.24	0.20		
17	Phytoplankton	1.00	1.00	6.41	259.30	299.29		0	0.53	0.29		
18	Detritus	1.00	1.00	12573.00					0.39	0.41		

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CHAPTER IV

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Ocean warming negates positive CO_2 effects on the biomass and productivity of species by altering the magnitude of direct versus indirect trophic interaction strengths

Statement of Authorship

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Principal Author

Name of Principal Author (Candidate)	Hadayet Ullah		
Contribution to the Paper	Study design, data collection, data analysis, writing		
Overall percentage (%)	85		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

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Ocean warming negates positive CO_2 effects on the biomass and productivity of species by altering the magnitude of direct versus indirect trophic interaction strengths

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ABSTRACT

One of the biggest challenges in forecasting the effects of climate change on future food web dynamics relates to how climate change affects multi-trophic species interactions, particularly when multiple interacting stressors are considered. Using a dynamic food web model, we investigate the individual and combined effect of future climate change stressors (warming and acidification) on changes in trophic interaction strengths (both direct and indirect) and the consequent effects on biomass structure of the food web. We incorporated empirical data on climate-driven species interactions obtained from two large mesocosm experiments. Our results show that although climate change is likely to reshuffle community biomass structure by reducing or increasing the biomass of many resource and consumer groups within the food web, overall vertebrate biomass and productivity will likely increase due to an increase in trophic interaction strength. We show that temperature-driven changes in direct trophic interaction strengths (feeding and competition) will largely determine the magnitude of biomass change (either increase or decrease) of consumers. An increase in biomass at higher trophic levels under global warming, however, suppresses the biomass of lower trophic levels (herbivorous invertebrates and lower trophic level omnivores). Ocean acidification, in contrast, showed a much larger change in the number of indirect interactions (e.g. cascading effects of increased or decreased abundance of other groups) altered than warming, but induced a relatively small change in trophic interaction strength. Nevertheless, this small change in interaction strength enabled a much larger increase in biomass of consumers (vertebrates and invertebrates) under acidification than warming, due boosted primary productivity that increased invertebrate prey biomass and consequently also the biomass of carnivores. We argue that warming is a much stronger driver of positive as well as negative biomass changes than ocean acidification,

even though it affects a much smaller number of existing trophic interactions, with direct consumer-resource effects being more important than indirect effects. The way in which consumers will perform in future food webs and how this has negative cascading effects on the biomass of their resources is largely driven by alterations in direct trophic interaction strengths that act in synergy when ocean warming co-occurs with ocean acidification.

4.1 INTRODUCTION

The structure, functioning, and stability of ecological communities depend overwhelmingly on the strength of trophic interactions between consumers and their resources (Bascompte *et al.*, 2005, Schaum *et al.*, 2018). Ecological communities consist of many species that frequently interact with each other, although this usually results in many weak trophic interactions and only a few strong interactions (Paine, 1992, Wootton & Stouffer, 2016). These consumer-resource interactions are particularly important in food web dynamics since they determine the majority of energy fluxes between individuals, and through ecological communities and ecosystems (Dell *et al.*, 2014). Quantifying the strength of consumer-resource interactions is essential for understanding how ecological communities are organized and how they respond to any internal or external perturbations (Bascompte *et al.*, 2005).

Global climate change can induce changes in species distributions (Parmesan, 2006) and abundances (Van der Putten *et al.*, 2010), profoundly affecting species interactions (Tylianakis *et al.*, 2008). However, most models of species abundances and distributions ignore important biotic interactions when predicting climate change effects. This is not surprising, because understanding directly how climate change is likely to alter existing interactions, or create novel species interactions, is hindered by the difficulty of doing multi-trophic level experiments or appropriate field studies that incorporate this natural complexity (Nagelkerken & Connell, 2015). Consequently, forecast responses of species or communities to future climate conditions are predominantly based on correlative associations between present-day climate and species distributions (Pollock *et al.*, 2014).

Climate change could affect many trophic interactions (David A. Vasseur & Kevin S. McCann, 2005, Petchey *et al.*, 1999, Voigt *et al.*, 2003). Studies suggest that changes in biotic interactions such as alterations in foraging activity (Peacor & Werner, 1997), modifications of predator refuge and prey availability through habitat alterations (Lönnstedt *et al.*, 2014), altered behaviours (foraging-predation risk trade-offs) (Schmitz *et al.*, 2004) and changing abundances (Menge, 1995) could shape future distributions and realised assemblages of species. However, most studies so far have focused on either the direct effects of ocean warming on individual species, or if performed at the food-web scale only consider temperature to explore changes in biotic mechanism. Thus, earlier studies have failed to consider alterations of biotic interactions due to the combined effect of climate warming and ocean acidification. There is a need, therefore, to quantify and subsequently model the effect of ocean warming and ocean acidification on biotic interaction. Furthermore, the success of species in a community is determined not only by direct interaction (feeding and competition) between species but also by indirect interaction (e.g. cascading effects of increased or decreased abundance of other groups). Although, ecological communities are shown to shape by a complex array of both direct and indirect interactions (Miller, 1994, Walsh & Reznick, 2008), the effects of indirect species interaction could be more important than direct effects in structuring species communities (Ockendon *et al.*, 2014, Preisser *et al.*, 2005). This is further complicated by the fact that individual species may respond in opposite directions to climate change, with no net changes in the overall effect at the community level (Alsterberg *et al.*, 2013). This occurs when mean changes in direct and indirect effects cancel each other's influence among interacting species, since predator-prey relationship could be influenced by both positive and negative feedbacks (Suttle *et al.*, 2007, Tylianakis *et al.*, 2008).

The importance of indirect effects is further exemplified via its potential upward or downward cascading effect within food webs. For example, a prey which is directly linked to its predator through feeding interactions may also be involved in direct interference as a competitor if it shares a prey species with its predator. Species at different trophic levels vary in their sensitivity to warming due to differences in metabolic rates, thermal tolerance range as well as for thermal optima which can then induce mismatches between resource supply and demand (Allen *et al.*, 2005, López-Urrutia *et al.*, 2006, Nagelkerken & Connell, 2015). Such mismatches between two consecutive trophic levels can affect the next trophic level through cascading effects. Hence, studying multi-trophic level food webs such as those observed in nature is critical, since food chain length can alter community responses to global change (Hansson *et al.*, 2013, Preisser *et al.*, 2005).

Importantly, while there has been progress in understanding how direct effects of climate change could influence individual species (Gilman *et al.*, 2010), understanding how climate change is likely to indirectly as well as directly influence species interactions and its consequences in a food web context remains largely unexplored. Combining experimental studies with multi-species process-based models provides opportunities to study the effect of multiple stressors at the community level (Moe *et al.*, 2013). Whilst field-based experimental approaches have practical limitations (expensive, time-consuming and restricted in scope both spatially and temporally), mesocosm studies allow manipulating climatic condition to quantify species response to climate change (Goldenberg *et al.*, 2018, Ullah *et al.*, 2018). The experimental data from mesocosm studies provide strong empirical data that can be integrated into food web models (Fordham, 2015). Models that incorporate species interactions have the potential to generate improved predictions of future change (Heikkinen *et al.*, 2007, Memmott *et al.*, 2007).

Here we analyze a complete temperate coastal marine food web, developed and described in chapter 3, to quantify the changes in direct as well as indirect trophic interaction strengths under future ocean warming and ocean acidification, focussing on the direction of change (positive, negative, no change) as well as the magnitude of change (strength) in all species interactions. Trophic interaction strength was measured as the relative impact of biomass change of any group on the biomass of other groups (modifier). Using data on population parameters and species interactions from two large-scale mesocosm studies, we modeled the response of multiple food web functional groups to the individual and combined effects of future warming and acidification assuming a +2.8 ^{0}C increase in temperature and a 500 ppm $p\mathrm{CO}_2$ increase. We used a time-dynamic Ecosim model to study the consequence of global climate change on species and food web dynamics. We tested how the change in relative strength (change in magnitude) of direct and indirect trophic interactions altered (increased or reduced) the direction of biomass change for different food web groups under future global change.

4.2 RESULTS

Our model predicted an overall increase in vertebrate biomass and productivity under 21st century climate change compared to a no climate change scenario (‘no change’ scenario) (Fig. 1). Whilst acidification led to the greatest increase in vertebrate biomass and production (105% and 128%, respectively), warming caused a much lower increase (47% and 54%), and the increase was lowest under a combined warming and acidification scenario (21% and 17%). The lower increase in the biomass and production of vertebrates under both temperature scenarios (compared to acidification in isolation) was linked to a decline in the biomass (4-57%) and production of invertebrates (11-50%). In contrast, a boost in the biomass and production of invertebrates (103% and 64%, respectively) under acidification suggested the successful propagation of lower trophic level biomass towards higher trophic level vertebrate consumers.

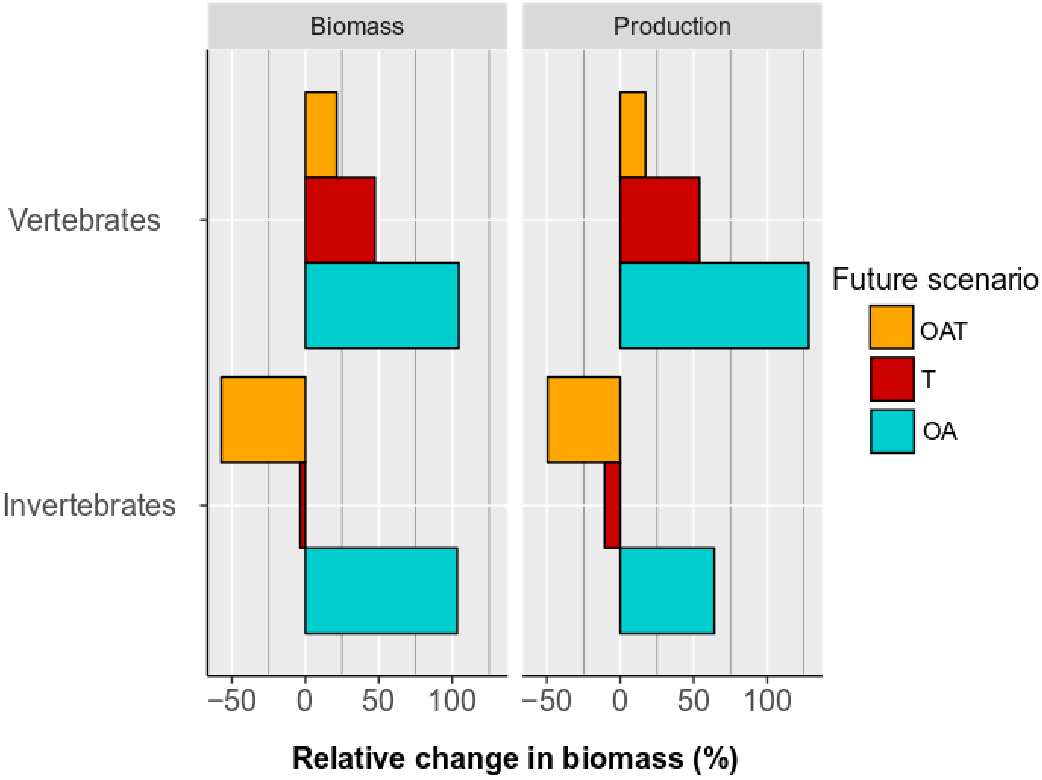

Figure 1: Percent change in total biomass and production of vertebrate and invertebrate under a future ocean warming (Δ 2.8°C) and acidification (Δ500 ppm *p*CO2) scenario, relative to the biomass in 2100 under a scenario of no change in climate from present-day levels. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. The 47 distinguished food web functional groups (animals) are aggregated here and presented across two animal groups.

The contrasting changes to the biomass and productivity of vertebrates versus invertebrates, particularly under both warming scenarios, were primarily driven by a change in trophic interaction strength. Warming, either in isolation or combined with acidification, is predicted to alter (either negatively or positively) ~ 53-54% of all trophic interactions (direct plus indirect), while acidification in isolation is likely to alter ~ 84% of all interactions (Fig. S1A). For all climate scenarios, the percent change in positive interactions was very similar to that of the negative interactions.

Out of the 2,809 pairwise species interactions in the entire food web matrix, 86% of the trophic interactions were indirect while 14% were direct (predator-prey) trophic interactions (Fig. S1B). The magnitude of change (interaction strength) was much larger for both warming scenarios than for acidification alone, and this was true for direct as well as indirect interactions (Fig. 2). Moreover, warming in combination with acidification acted synergistically and induced a greater magnitude of change in direct interaction strength than both stressors separately.

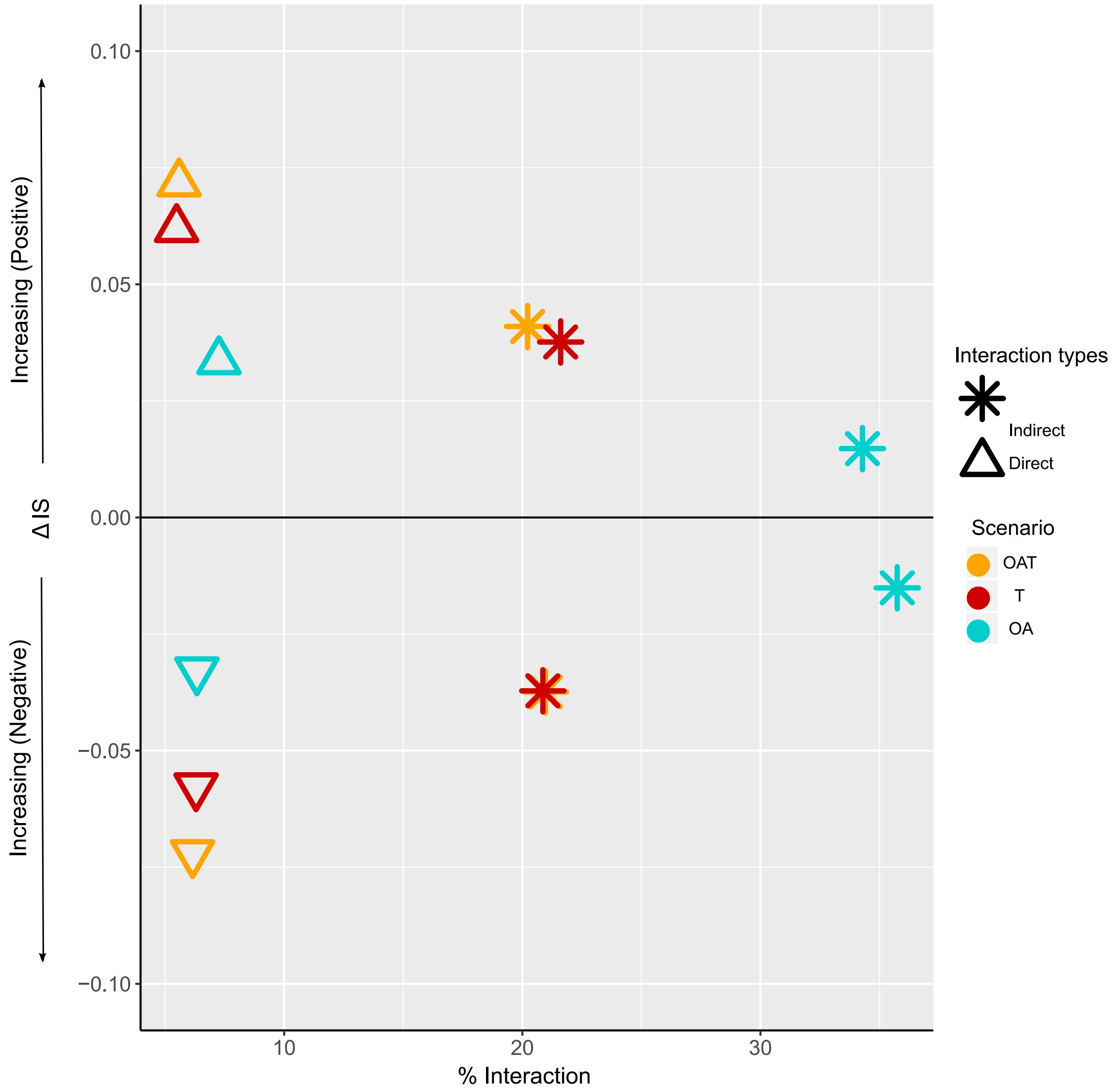

Figure 2: Change in the interaction strength (ΔIS; magnitude of change) across trophic interactions among all the functional groups of the food web under a future ocean warming (Δ 2.8°C) and acidification (Δ500 ppm *p*CO2) scenario, relative to the interaction strength in 2100 under a scenario of no change in climate from present-day levels. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. The X-axis represents the change in the number of direct and indirect interactions (% interactions modified) grouped by the direction of change (positive, no change and negative), which collectively sum to 100% for each scenario. Here only positive and negative changes in interactions are plotted for simplicity ('no-change' omitted). The Y-axis represents the strength of the interaction change (ΔIS = magnitude of change) under different combinations of interaction types and directions for each scenario.

The increase in strength of direct as well as indirect trophic interactions under global warming is predicted to result in disparate effects on biomass of the 53 different functional groups considered (Fig. 3, Figs. S3-S6). Warming combined with acidification increased the biomass of 42% of the carnivorous functional groups by ≥ 80% (Fig. 3, Fig. S4).

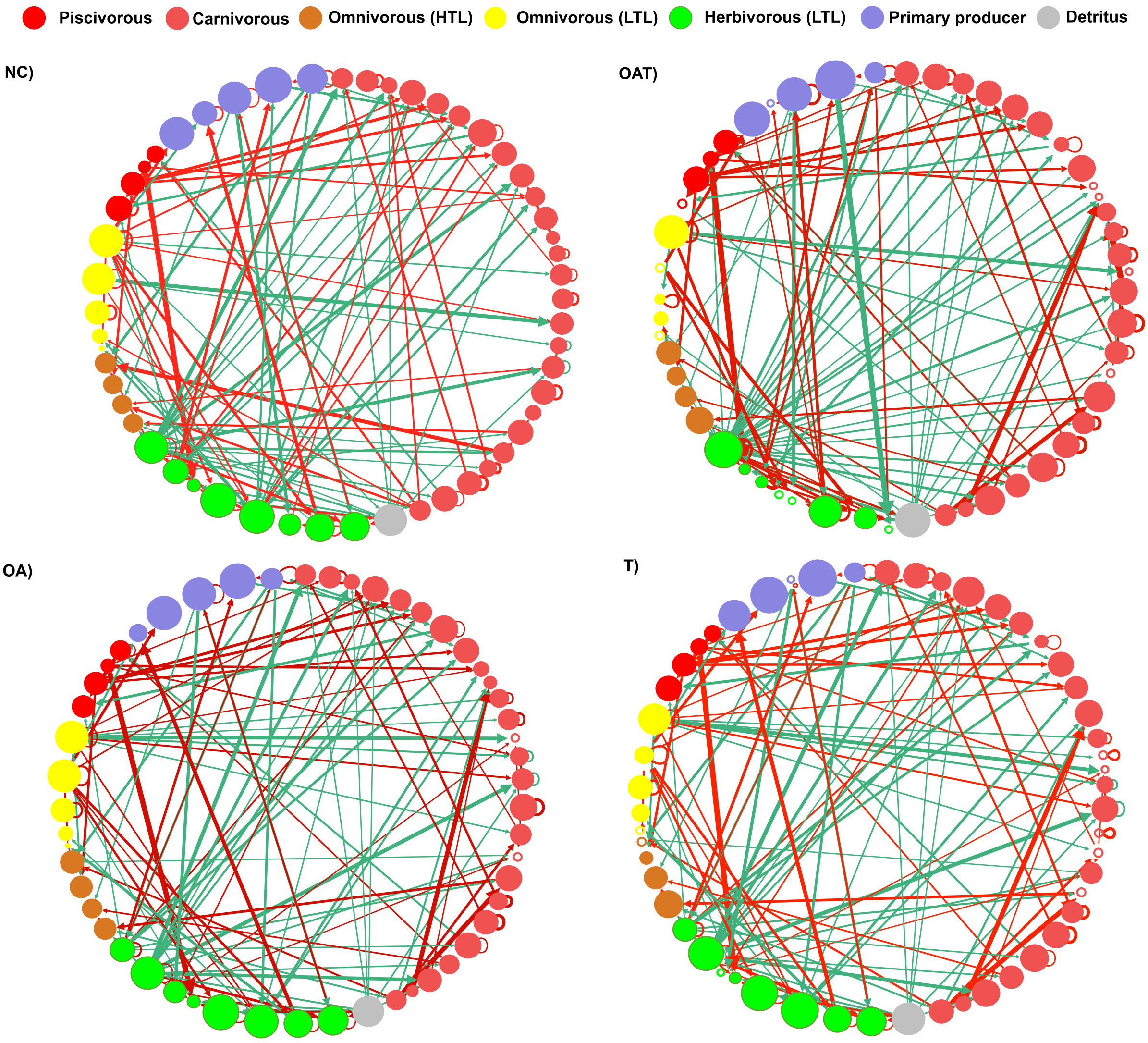

Figure 3: Distribution of biomass of different functional food web groups in 2100 under a future climate change scenario (Δ 2.8°C). NC= under a scenario of no change in climate from present-day levels, OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. The colour of nodes (pure red, soft red, strong orange, yellow, lime green, soft blue, and ash) represents different trophic groups (piscivores, carnivores, omnivores (higher trophic level), omnivores (lower trophic level), herbivores, primary producers and detritus). Red and green lines indicate negative and positive effects, respectively. Colour tone of the line scales with the magnitude of the effects. The functional node sizes are relative to the standing biomass (log transformed). Functional groups experiencing a decline in biomass of ≥ 80% compared to a NC scenario are represented as a small circle and empty inside. The colours of the lines in each food web should not be interpreted in an absolute sense: the impacts are relative. For details on species and their code numbers see Supplementary Figures S3-S6.

Lower trophic level omnivores (decline of 40% of the functional groups) and herbivores (decline of 38% of groups) showed the strongest negative responses to the combination of warming and acidification, while none of the groups of higher trophic level omnivores (fish) experienced a decrease (Fig. 3). Under temperature alone, omnivores (25% of functional groups declined but 50% increased) and carnivores (19% declined but 58% increased) showed the strongest responses among all groups (Fig. 3, Fig. S5). In contrast, under acidification alone, only carnivores (8%) are predicted to experience a decline in their biomass (of ≥ 80%) (Fig. 3, Fig. S6). Higher-trophic level omnivores (100%) showed the strongest positive response, following lower-trophic level omnivores (60%) and carnivores (53%) increasing in their biomass ≥80%.

Sensitivity analysis indicated that the model functional groups was relatively insensitive to changes in the different input parameters in response to future climate change scenarios (warming and acidification) except some lower trophic levels groups (e.g. Australian sardine, small pelagic, southern garfish and yellow eye mullet) and few of their predators (Birds and mammals). We only show results for the most pervasive future scenario OAT (warming and acidification together) relative to no change scenario at 2100 (Fig S7).

4.3 DISCUSSION

Our model simulations show how climate-driven changes in trophic interaction strengths alter the biomass and productivity of consumers and resources when direct and indirect species interactions are embedded in complex food-web networks. We find that direct and indirect trophic interaction strengths are strongly modified by global warming and this affects the biomass of consumers and resources within the food web. More specifically, we show that in a complex food web network, warming-driven changes in direct trophic interactions (feeding and competition), although fewer in number, would have large effects on the interaction strength between consumers and resources (increase or decrease), overruling the many weaker alterations to indirect effects under ocean acidification.

Weak versus strong interactions (magnitude of change) under warming

Our modelling results show that future food webs will likely experience alterations to most of their existing trophic interactions. This change will be driven by alterations to a low number of strong interactions distributed within a matrix of many weak interactions. This is observation is fundamental to ecological food web networks (Paine, 1992, Wootton & Stouffer, 2016), promoting community persistence and stability (May, 1973, McMeans *et al.*). We show that biomass change is largely driven by increases in the strength of direct (as opposed to indirect) trophic interactions, particularly under elevated temperature. Because warming is predicted to strengthen top-down control in temperate marine food webs (Marino *et al.*, 2018) and a greater negative impact on food web structure is expected under future warming compared to ocean acidification. Nevertheless, our model predicted increased vertebrate biomass under warming alone. This increase in consumer biomass at higher trophic levels appears to occur at the detriment of invertebrate prey, which are likely to suffer from overconsumption by their predators (Goldenberg *et al.,* Griffith *et al.*, 2012). We argue that future food webs under warming will still be structured by a few but strong direct trophic interactions, but that this effect is amplified under temperature increase and therefore can alter the biomass structure of future food webs, where positive effects on consumer biomass will occur to the detriment of their prey species.

Interactive effect of OAT

We show that warming and acidification will act synergistically to intensify the strength of direct trophic interactions but acted antagonistically in terms of biomass increase. Warming combined with acidification is likely to only enable a slight increase in biomass of vertebrate consumers at higher trophic levels compared to a much larger increase under temperature and acidification in isolation, while causing a strong decline in the biomass of invertebrate prey, particularly herbivorous invertebrates and lower trophic level omnivores. Although previous studies showed that temperature-driven increases in metabolic rates are likely to increase the strength of direct trophic interactions (Barton, 2011, Brose *et al.*, 2012, Kratina *et al.*, 2012, Sanford, 1999), these studies did not explore the interactive effects of warming and acidification. Consumer-resource interaction strength tends to be stronger when consumption exceeds resource production (Ruesink, 1998). Hence, we propose that higher interaction strength under warming and acidification in our study is related to a reduced (herbivore) prey availability combined with higher consumption rates of carnivores due to increased metabolic demands. Moreover, these combined stressors can also reduce the quality of algae (Poore *et al.*, 2013, Sampaio *et al.*, 2017) and/or increase the proportion of unpalatable algal species (Ullah *et al.*, 2018). A reduced quality of primary producers combined with increased direct trophic interaction strength of consumers under warming and acidification may jeopardize herbivore-plant interactions (Poore *et al.*, 2013), which can cascade up the food web due to reduced prey availability for carnivores (Goldenberg *et al.*). Thus, in contrast to individual stressors, synergistic effects of warming and acidification strengthen trophic interactions and weaken resource productivity, leading to more detrimental effects on the biomass and productivity of functional groups within future food web.

Role of acidification:

Ocean acidification mainly altered indirect trophic interactions and in such a way that it had positive overall effect on species biomass. Indirect interactions could play a more pervasive role than direct interactions in shaping marine communities under future acidification and warming (combination or in isolation) (Garrard *et al.*, 2014, Kamya *et al.*, 2017, Poore *et al.*, 2013). Even though acidification did alter the majority of indirect trophic links in our study, the magnitude of this effect was characterized by relatively lower trophic interaction strength. The weak trophic interaction strength, both direct and indirect, under acidification allowed available herbivorous prey resources to sustain themselves, in contrast to a collapse as seen under warming, and to support consumers at higher trophic levels. In contrast, a meta-analysis for terrestrial plants suggested that elevated CO_2 could significantly increase the biomass of plants but decrease herbivore abundance and growth in spite of their increased consumption rate (Stiling & Cornelissen, 2007). This discrepancy between the terrestrial and marine environment in biomass growth of herbivores could be explained by the poor quality of terrestrial plant grown under elevated CO_2 (Lincoln *et al.*, 1993) which is not seen in the coastal marine environment (Poore *et al.*, 2013). In fact, acidification is likely boost the nutritional quality of turf algae by increasing the relative nitrogen content (reduced C:N ratio) (Leung *et al.*, 2018) and likely to increase the feeding rate of herbivores enabling them to sustain or even boost in their biomass (Connell *et al.*, 2017, Goldenberg *et al.,* Vizzini *et al.*, 2017). A recent study suggested that direct negative effects of elevated CO_2 can be dampened and even reversed by indirect effects with increasing ecological complexity (Goldenberg *et al.*, 2018). Therefore, organisms living within a more natural setting with representative ecological complexity (such as our mesocosms) may overcome the direct negative effect of acidification, maintain their consumer-resource relationship, and could thus benefit from surplus resources even with lower trophic interaction strengths. Our results suggest that consumers under acidification are not food limited and have access to a wide range of prey resources, avoiding significant predation pressure on particular prey groups, which might otherwise drive their populations towards collapse. Thus, under trophic networks, increased primary production and herbivore biomass prevent biomass collapse of invertebrates and enables significant biomass increase of vertebrates under ocean acidification in isolation.

We have carried out a simple sensitivity analysis to evaluate how the model behaves to changes in the modified input parameters in response to climate change scenarios. Sensitivity analysis indicated that pelagic functional groups such as Australian sardine, small pelagic species groups and their predators such as birds and mammals are the most sensitive food web functional groups to changes in any model parameters under OAT. Small demersal such as southern garfish and yellow eye mullet are also found to be sensitive to the warming and acidification driven changes in the model parameters. Small pelagic are important prey groups in the food web, more dynamic in their nature and characterized by large fluctuation overtime which is complex to model. Many of the higher trophic level predators (e.g. seabirds, marine mammals) are strongly dependent on pelagic species (forage fish) due to their specialized diet and limited feeding areas (Cury *et al.*, 2011, Engelhard *et al.*, 2014). Thus, large fluctuations in forage fish abundance can impact their predators. Therefore, caution should be exercised for small pelagic and top predator groups before translating this output to any management decision. Other than this, the overall sensitivity analysis suggests that the food web functional groups is relatively insensitivity to changes in the parameters in response to the combined effect of ocean warming and acidification.

We conclude that ocean warming could negate positive effects of CO_2 enrichment on food webs through altering direct and indirect trophic interaction strengths. Particularly, warming-driven increase in direct trophic interaction strengths (feeding and competition) will largely determine the change in the magnitude of interaction strength (either increase or decrease) of consumers. This could result in a food web with excessively high biomass at the top, potentially driving a depletion of many resources (prey groups). Therefore, the degree to which consumers will benefit from future food webs affected by anthropogenic climate change depends on how direct versus indirect effects are altered in trophic interaction strength and the degree to which prey resources are sustained.

4.4 MATERIALS AND METHODS

We used a food web model developed for the Port Philip bay (PPB) ecosystem (Koopman, 2005) and updated with concurrent information by adding higher taxonomic resolution using the EwE (Ecopath mass-balance approach) (Christensen *et al.*, 2008). Ecopath with Ecosim (EwE) is based on a food-web approach which represents snapshot of the ecosystem and is used to quantify the flow of energy between functional groups within an ecosystem. Ecosim- a time dynamic version of Ecopath model representing PPB ecosystem during the 1995–2015 period was fitted to historical time series of biomass and fishing effort data (see Fig S7 and S8; Chapter- 3). The biomass of future ecosystem within the Ecosim approach is represented by the ‘‘foraging arena concept’’, where prey biomass is divided into vulnerable and non-vulnerable components. The transfer rate between these two components is the vulnerability rate, which determines whether the flow control is top-down (predator-driven), bottom-up (prey-driven) or both. A thorough technical description of the Ecosim model, including all input data to the model, assumptions, model validation and sensitivity analysis is presented in the Supplementary text of Chapter 3, so we will present only the information most relevant to this study (Chapter 4).

We developed four 75-year simulations (2015-2100) to explore the effect of climate change on future food web that included a no climate change scenario (baseline) and three climate change scenarios: warming (T) ocean acidification (OA) and their combination (OAT). We assumed a +2.8 ^{0}C of warming by 2100, representing a high representative concentration pathway scenario (RCP8.5) (Bopp *et al.*, 2013). The no climate change scenario (NC) assumes that model parameters do not change in the future. Fishing effort was held constant at 2015 levels as it is not evident that how future fishing effort likely be changed. We incorporated direct and indirect climate-driven changes in species interactions and mortality of trophic functional groups in the food web for all climate change scenarios (T, OA, and OAT).

We obtained data on species interaction from mesocosm experiments that includes both direct (Ullah *et al.*, 2018) and indirect estimates of vulnerability of prey to their predators (Goldenberg *et al.*, 2018). We included effective search rates of predators (e.g., sharks) on their prey (Pistevos *et al.*, 2015) and direct mortality of some lower trophic prey groups as well as productivity of primary producers (Ullah *et al.*, 2018). The strength of our modelling approach lies in the input data that were obtained from two community-level mesocosm experiments of the modelled food web (Pistevos *et al.*, 2015, Ullah *et al.*, 2018).

We used predation pressure to estimate the vulnerability (direct estimate) of lower trophic level (Trophic level ≤2) functional groups to its predator. This was done using stomach content analysis and in situ feeding trials that incorporated different treatment effects (e.g. temperature, acidification or their combination). Thus, the predation pressure exerted by the predators (in our case fish) on their prey groups is directly accounted for as the vulnerability of the representative prey groups in our Ecosim model.

We applied a combination of direct and indirect approaches to estimating the vulnerability of prey groups to higher order trophic groups (Trophic level ≥2). The indirect approach of vulnerability estimation was based on behavioral experiment on traits related to foraging and predation behaviour of consumers. Three response variables were derived and combined to estimate prey vulnerability. I) "Prey attraction" was calculated as the percentage of time spent in the area close of the 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 the food cue relative to the time spent in this area (Goldenberg *et al.*, 2017). III) 'Boldness' was measured as the percentage of time spent on the side directly in front of the predator within the area close to the food cue relative to the time spent in the entire area close to the food cue (this study). Prey fishes may approach a predator to inspect it – a characteristic behavior termed predator inspection (Pitcher *et al.*, 1986)– reducing their vulnerability to the predator. We excluded the data obtained during any predator inspection behavior for the calculation of the three response variables to obtain the vulnerable component of the prey isolated from its non-vulnerable components. Finally, we averaged across the three response variables, weighing each variable equally, to obtain a composite vulnerability index of prey to its predator. A detailed description of the experimental setup, diet analysis and behavioural trial can be found in the supplementary text. We have calculated effective search rates for Chondrichthyans on their prey based on the estimated total time (s) taken by Port Jackson shark to successfully locate (1st successful hit) prey hidden in the sand based on olfactory cues (see Methods in (Pistevos *et al.*, 2015) for details).

We incorporated the effect of climate change (changes in direct mortality, vulnerability rate, and effective search rate) in our modelling approach using forcing functions that affect the consumption and production of functional groups at a temporal scale (Ainsworth *et al.*, 2011, Alva-Basurto & Arias-González, 2014, Cornwall & Eddy, 2015, Guénette *et al.*, 2014). We calculated the relative effect size of these rates under different climate scenarios compared to control condition (using the absolute values (Table S2). The climate scenarios were assumed to focus on the year 2100 and the control conditions on 2015. We used bi-linear interpolation to generate separate annual time series for forcing functions for the period 2015 to 2100. It is common practice in climate change ecology to interpolate temporally between climate snap shots (Fordham *et al.*, 2012). The forcing functions were applied to appropriate functional groups in the model (Table S2). For details on the estimation of different forcing function parameters under future climate change scenarios please see Supplementary information in Chapter-3.

The effect of climate change was then assessed by comparing changes in trophic interaction strength and biomasses with that of climate change scenarios compare to NC scenario for the 21st century. We quantified the changes in the trophic interaction strength between pairwise species interaction based on the relative impact of biomass change of any group on the biomass of other groups either directly (direct trophic interaction) or indirectly through trophic cascade on the food web using Mixed Trophic Impact (MTI) analysis (Ulanowicz & Puccia, 1990) and expressed as,

$$MTI_{ij} = DC_{ij} = FC_{ji}$$

where DC_{ij} is the diet composition term expressing how much j contributes to the diet of i, and FC_{ji} is the proportion of predation on j that is due to i as a predator, allows the quantification of the impacts that a theoretical change of a unit in the biomass of a group (including fishing effort) would have on other groups in the ecosystem (Christensen *et al.*, 2008). We consider MTI values as direct trophic interaction where there is a direct feeding relationship exists between consumer and prey through predation and competition (two organisms compete for the same resource such as food and space by physically interfere and both individuals are negatively impacted by competition). Whilst indirect trophic interactions are mainly cascading effects of increased or decreased abundance of a group on other groups.

We show simulation output for animal groups at ecosystem scale (vertebrates and invertebrates) as well as into guild levels, including piscivorous, carnivorous, omnivorous-HTL (HTL; Higher trophic levels mostly fish), omnivorous-LTL (LTL; Lower trophic levels mostly small invertebrates), herbivorous, primary producer, and detritus (Table S1).

We assessed the quality of input data and tested the validity of the model using the diagnostics approach proposed by (Link, 2010). We also carried out an uncertainty analysis on estimating model parameters related to model output by using the Monte Carlo (MC) simulation. MC simulation is performed as sensitivity analysis which is based on the coefficient of variation obtained from the model pedigree index for production/biomass, consumption biomass and biomass where former two parameters directly linked and strongly influence the model vulnerability parameters (Heymans *et al.*, 2016).

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4.6 SUPPLEMENTARY FIGURES

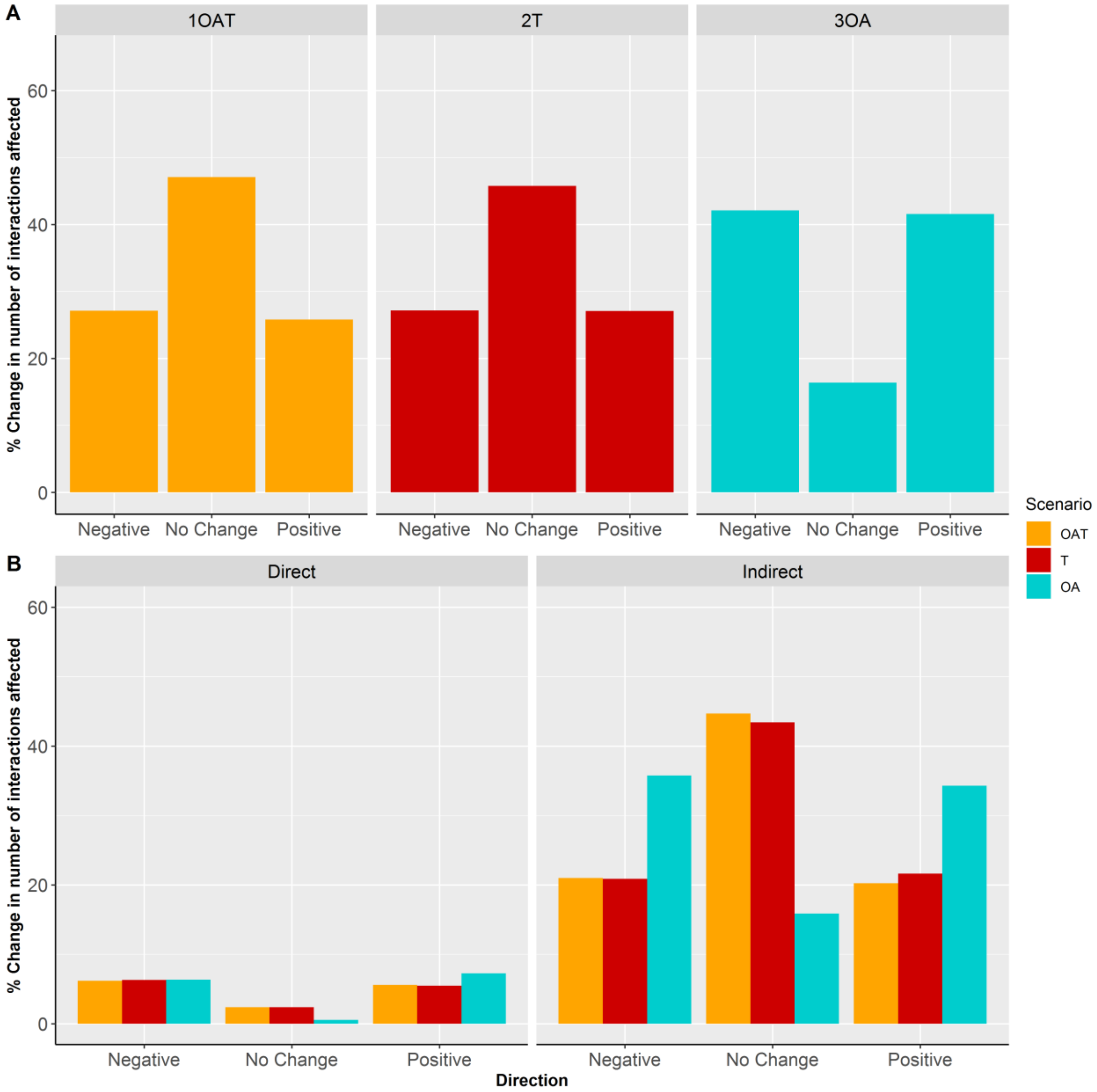


Figure S1. A. Directions of relative change in trophic interactions (n=2809) within food web under a future ocean warming (Δ 2.8°C) and acidification (Δ500 ppm *p*CO2) scenario relative to the interactions in 2100 under a no climate change scenario (NC). B. Same as S1A but split for direct vs indirect effects. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming.

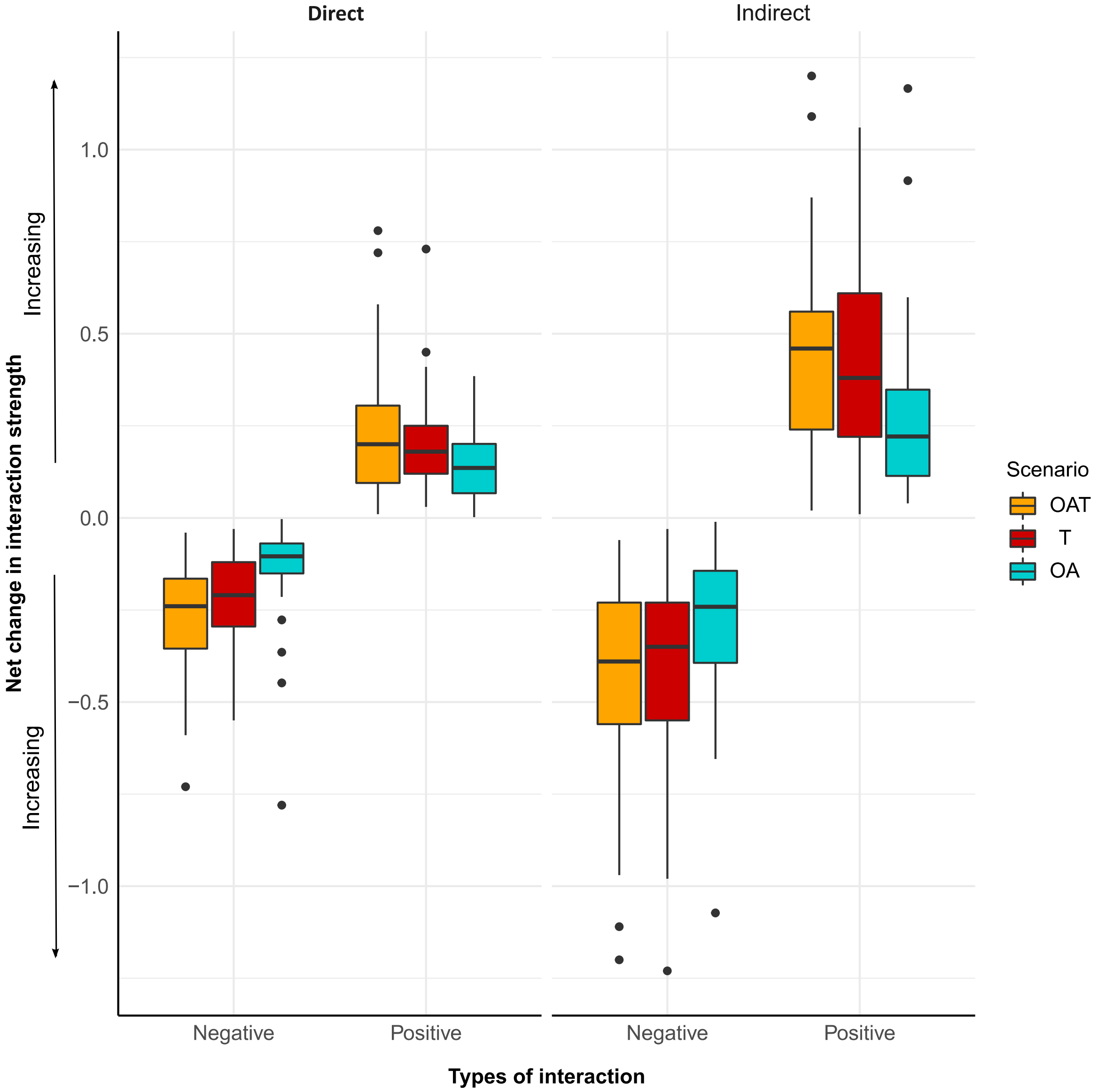
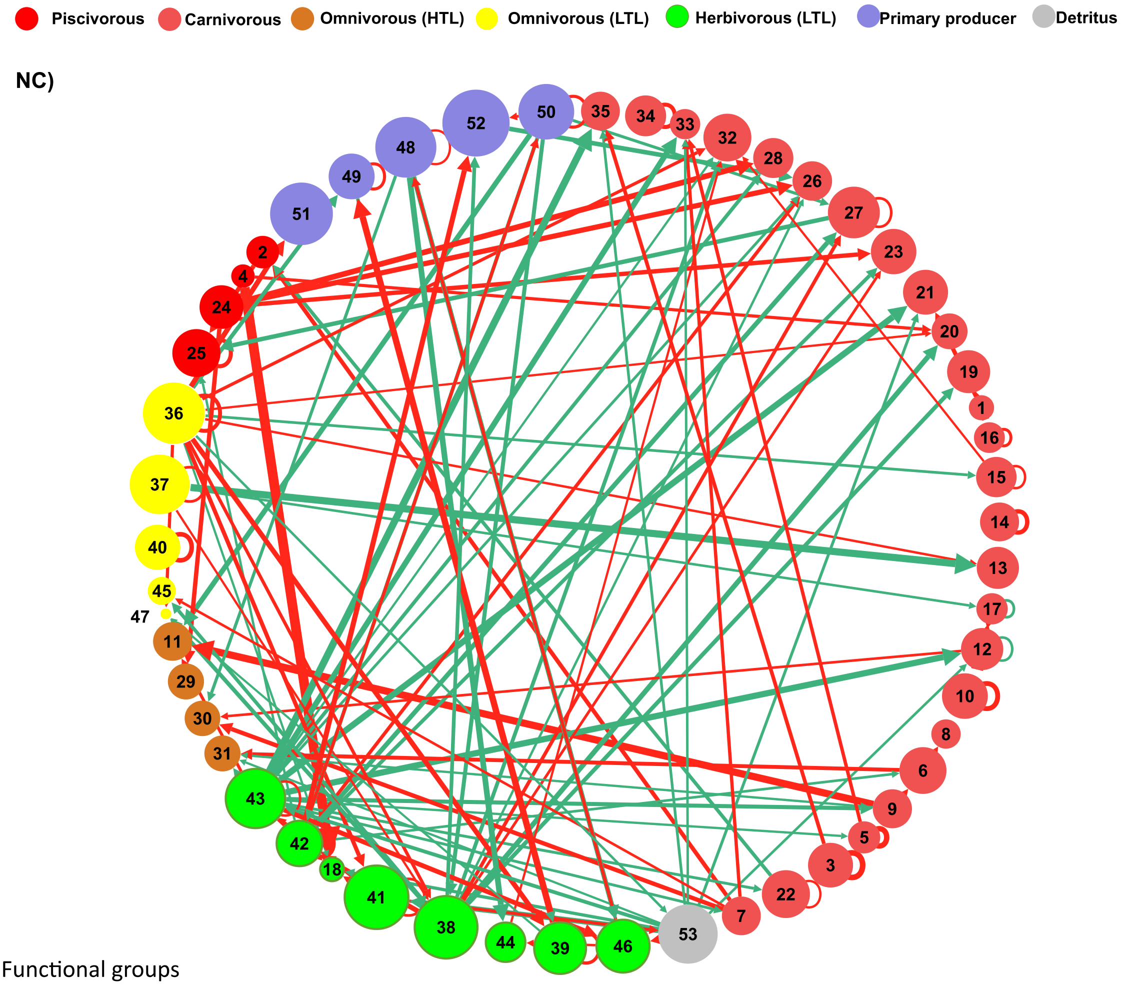


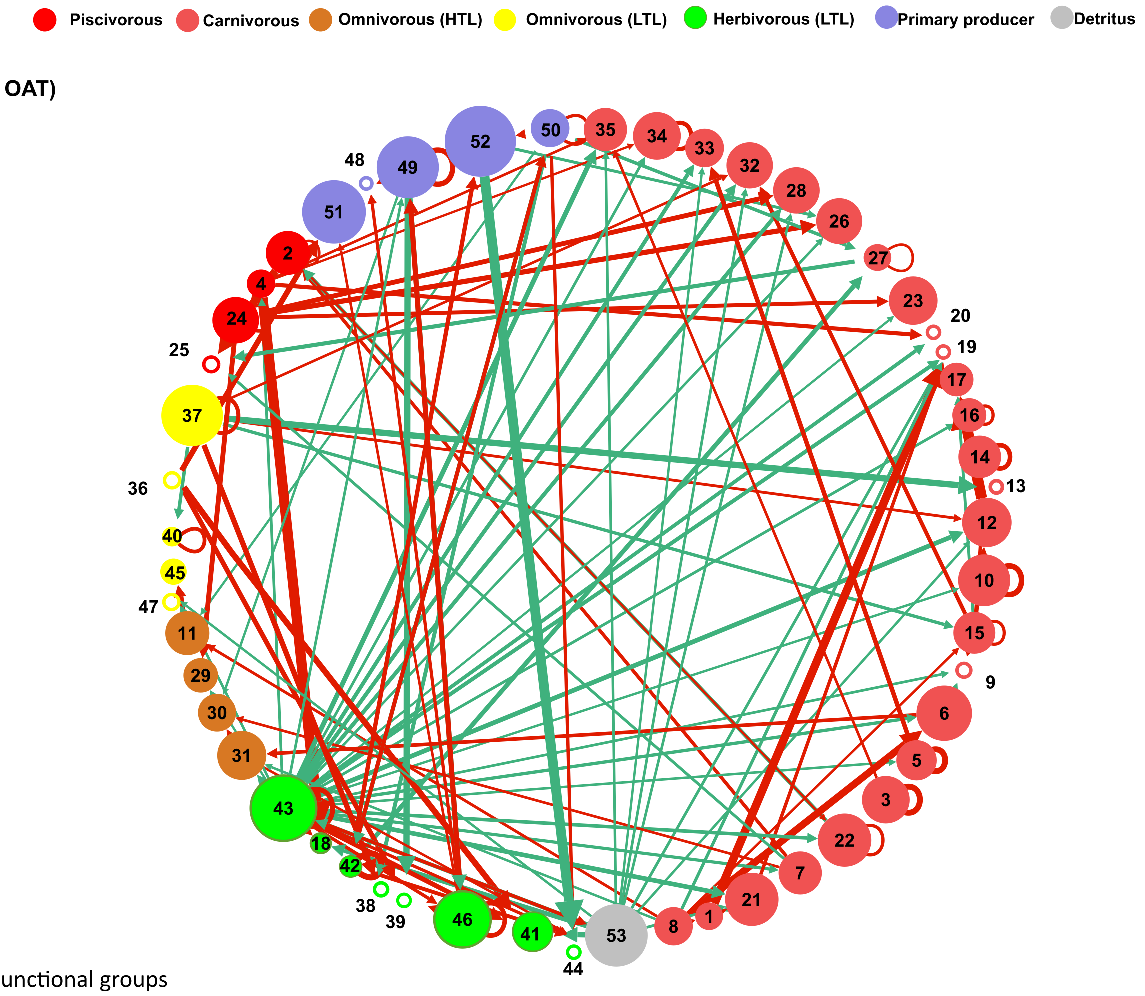
Figure S2. Change in the net interaction strength (ΔIS; magnitude of change) for direct (positive plus negative) and indirect (positive plus negative) interactions for each of the functional groups of the food web under a future ocean warming (Δ 2.8°C) and acidification (Δ500 ppm *p*CO2) scenario, relative to the 2100 under a scenario of no change in climate from present-day levels. Data are shown as Box-and-whisker plots (boxplots) with the horizontal black line inside the box representing the median value, the lower and upper limits of the box being the 25th and 75th percentile and the whiskers indicating the minimum and maximum value and outliers are also shown as individual data points. The default setting of 1.5 interquartile range (IQR) was used to identify outliers. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. The net change in the trophic interaction could be both positive and negative for each functional group and are plotted separately in the graph.



Functional groups

1. Large sharks	12. Banjo ray	23. Southern anchovy	34. Adult snapper	45. Southern rock lobster
2. Large pelagics	13. Eastern S. stingaree	24. Australian salmon	35. Juvenile snapper	46. Sea urchin
3. Bird	14. Ad. king george whiting	25. Pike	36. Other invertebrates	47. Exotic seastar
4. Mammals	15. Juv. king george whiting	26. Southern garfish	37. Polycheates	48. Macroalgae
5. Yank flathead	16. Large demersal fish	27. Other small pelagics	38. Filter feeding molluscs	49. Algal turf
6. Rock flathead	17. Adult red mullet	28. Silver trevally	39. Grazing molluscs	50. Phytoplankton
7. Other cephalopods	18. Juvenile red mullet	29. Yelloweye mullet	40. Predatory molluscs	51. Microphytobenthos
8. Southern calamari	19. Eagle ray	30. Leatherjacket	41. Echinoderms	52. Seagrass
9. Smooth ray	20. Other shark/skates/rays	31. Other small demersal fish	42. Zooplankton	53. Detritus
10. Ad. sand flathead	21.Sparsley S. stingaree	32. Globefish	43. Crustaceans	
11. Juv. sand flathead	22. Australian sardine	33. Spiny gurnard	44. Abalone	

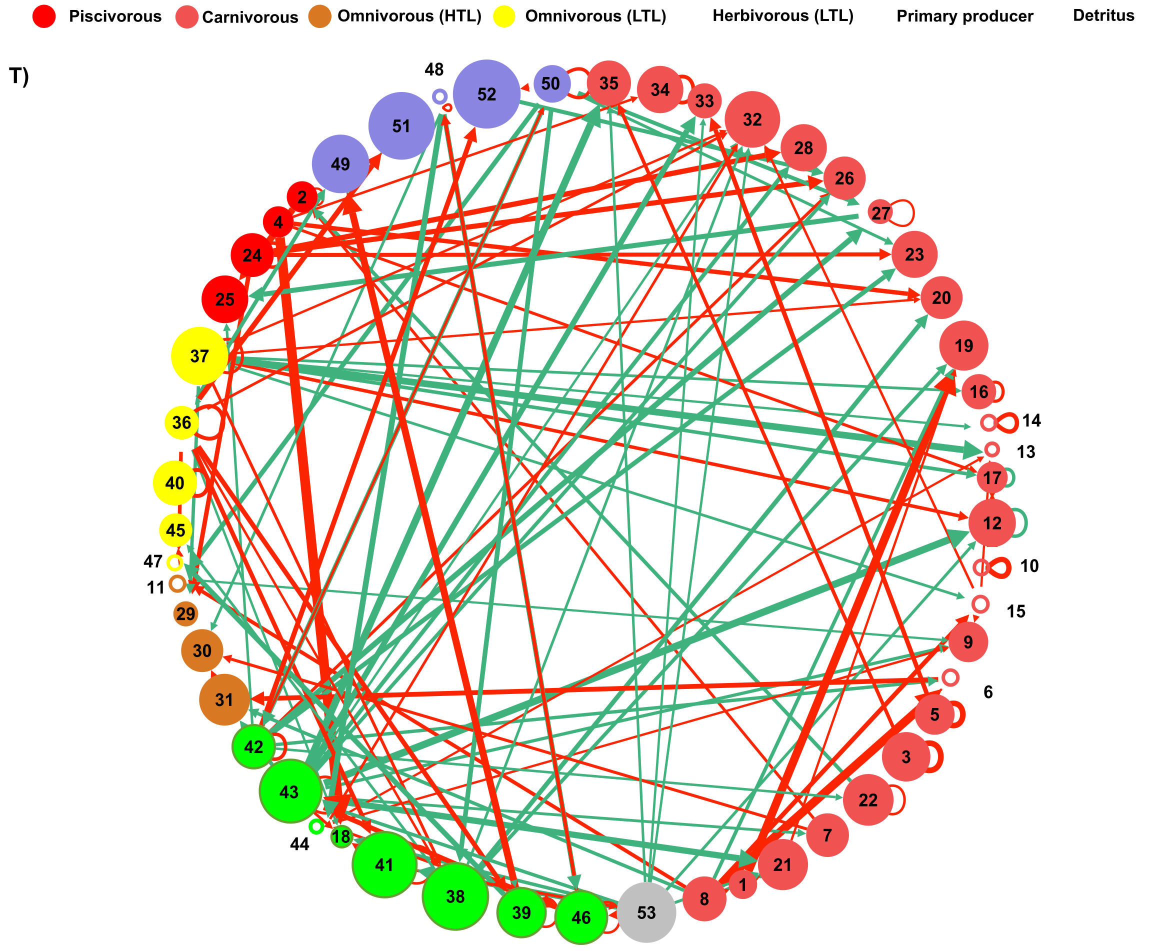
Figure S3: Distribution of biomass of different food web groups (numbered) in 2100 under a scenario of no change in climate from present-day levels NC-scenario. The colour of nodes (pure red, soft red, strong orange, yellow, lime green, soft blue, and ash) represents different trophic groups (piscivores, carnivores, omnivores (higher trophic level), omnivores (lower trophic level), herbivores, primary producers and detritus). Red and green lines indicate negative and positive effects, respectively. Colour tone of the line scales with the magnitude of the effects. The functional node sizes are relative to the standing biomass (log transformed). The colours of the lines in each food web should not be interpreted in an absolute sense: the impacts are relative. Different food web groups in the in the model are species or groups of species in the form of functional groups.



Functional groups

1. Large sharks	12. Banjo ray	23. Southern anchovy	34. Adult snapper	45. Southern rock lobster
2. Large pelagics	13. Eastern S. stingaree	24. Australian salmon	35. Juvenile snapper	46. Sea urchin
3. Bird	14. Ad. king george whiting	25. Pike	36. Other invertebrates	47. Exotic seastar
4. Mammals	15. Juv. king george whiting	26. Southern garfish	37. Polycheates	48. Macroalgae
5. Yank flathead	16. Large demersal fish	27. Other small pelagics	38. Filter feeding molluscs	49. Algal turf
6. Rock flathead	17. Adult red mullet	28. Silver trevally	39. Grazing molluscs	50. Phytoplankton
7. Other cephalopods	18. Juvenile red mullet	29. Yelloweye mullet	40. Predatory molluscs	51. Microphytobenthos
8. Southern calamari	19. Eagle ray	30. Leatherjacket	41. Echinoderms	52. Seagrass
9. Smooth ray	20. Other shark/skates/rays	31. Other small demersal fish	42. Zooplankton	53. Detritus
10. Ad. sand flathead	21.Sparsley S. stingaree	32. Globefish	43. Crustaceans	
11. Juv. sand flathead	22. Australian sardine	33. Spiny gurnard	44. Abalone	

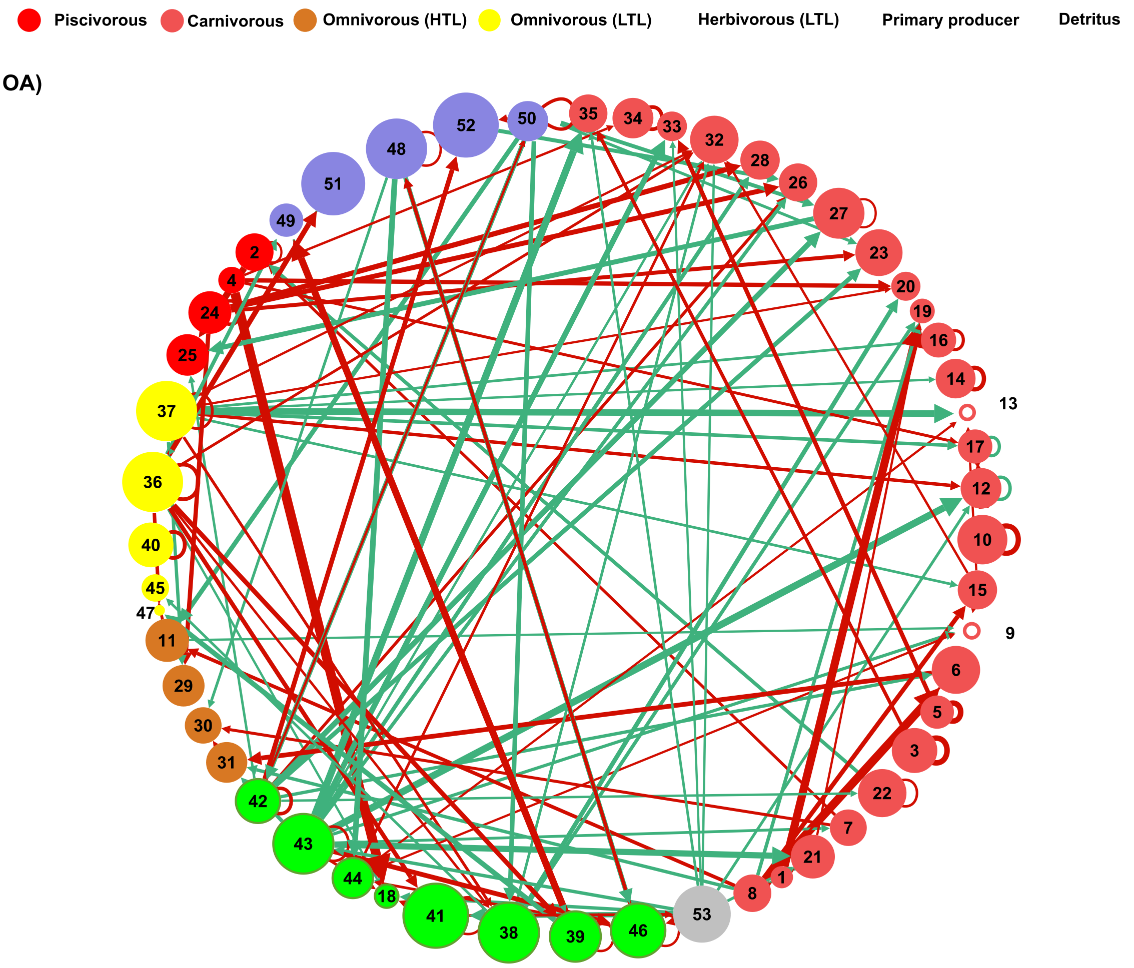
Figure S4: Distribution of biomass of different food web groups (numbered) in 2100 under OAT-scenario represents a combined ocean acidification (Δ pCO_2 500) and warming (Δ 2.8°C) scenario. The colour of nodes (pure red, soft red, strong orange, yellow, lime green, soft blue, and ash) represents different trophic groups (piscivores, carnivores, omnivores (higher trophic level), omnivores (lower trophic level), herbivores, primary producers and detritus). Red and green lines indicate negative and positive effects, respectively. Colour tone of the line scales with the magnitude of the effects. The functional node sizes are relative to the standing biomass (log transformed). Functional groups experiencing a decline in biomass ≥80% compared to a NC scenario are represented as a small circle and empty inside. The colours of the lines in each food web should not be interpreted in an absolute sense: the impacts are relative. Different food web groups in the in the model are species or groups of species in the form of functional groups.



Functional groups

1. Large sharks	12. Banjo ray	23. Southern anchovy	34. Adult snapper	45. Southern rock lobster
2. Large pelagics	13. Eastern S. stingaree	24. Australian salmon	35. Juvenile snapper	46. Sea urchin
3. Bird	14. Ad. king george whiting	25. Pike	36. Other invertebrates	47. Exotic seastar
4. Mammals	15. Juv. king george whiting	26. Southern garfish	37. Polycheates	48. Macroalgae
5. Yank flathead	16. Large demersal fish	27. Other small pelagics	38. Filter feeding molluscs	49. Algal turf
6. Rock flathead	17. Adult red mullet	28. Silver trevally	39. Grazing molluscs	50. Phytoplankton
7. Other cephalopods	18. Juvenile red mullet	29. Yelloweye mullet	40. Predatory molluscs	51. Microphytobenthos
8. Southern calamari	19. Eagle ray	30. Leatherjacket	41. Echinoderms	52. Seagrass
9. Smooth ray	20. Other shark/skates/rays	31. Other small demersal fish	42. Zooplankton	53. Detritus
10. Ad. sand flathead	21.Sparsley S. stingaree	32. Globefish	43. Crustaceans	
11. Juv. sand flathead	22. Australian sardine	33. Spiny gurnard	44. Abalone	

Figure S5: Distribution of biomass of different food web groups (numbered) in 2100 under T-scenario represents ocean warming (Δ 2.8°C) scenario. The colour of nodes (pure red, soft red, strong orange, yellow, lime green, soft blue, and ash) represents different trophic groups (piscivores, carnivores, omnivores (higher trophic level), omnivores (lower trophic level), herbivores, primary producers and detritus). Red and green lines indicate negative and positive effects, respectively. Colour tone of the line scales with the magnitude of the effects. The functional node sizes are relative to the standing biomass (log transformed). Functional groups experiencing a decline in biomass ≥80% compared to a NC scenario are represented as a small circle and empty inside. The colours of the lines in each food web should not be interpreted in an absolute sense: the impacts are relative. Different food web groups in the in the model are species or groups of species in the form of functional groups.



Functional groups

1. Large sharks
2. Large pelagics
3. Bird
4. Mammals
5. Yank flathead
6. Rock flathead
7. Other cephalopods
8. Southern calamari
9. Smooth ray
10. Ad. sand flathead
11. Juv. sand flathead
12. Banjo ray
13. Eastern S. stingaree
14. Ad. king george whiting
15. Juv. king george whiting
16. Large demersal fish
17. Adult red mullet
18. Juvenile red mullet
19. Eagle ray
20. Other shark/skates/rays
21.Sparsley S. stingaree
22. Australian sardine
23. Southern anchovy
24. Australian salmon
25. Pike
26. Southern garfish
27. Other small pelagics
28. Silver trevally
29. Yelloweye mullet
30. Leatherjacket
31. Other small demersal fish
32. Globefish
33. Spiny gurnard
34. Adult snapper
35. Juvenile snapper
36. Other invertebrates
37. Polycheates
38. Filter feeding molluscs
39. Grazing molluscs
40. Predatory molluscs
41. Echinoderms
42. Zooplankton
43. Crustaceans
44. Abalone
45. Southern rock lobster
46. Sea urchin
47. Exotic seastar
48. Macroalgae
49. Algal turf
50. Phytoplankton
51. Microphytobenthos
52. Seagrass
53. Detritus

Figure S6: Distribution of biomass of different food web groups (numbered) in 2100 under OA-scenario represents ocean acidification (Δ pCO_2 500) scenario. The colour of nodes (pure red, soft red, strong orange, yellow, lime green, soft blue, and ash) represents different trophic groups (piscivores, carnivores, omnivores (higher trophic level), omnivores (lower trophic level), herbivores, primary producers and detritus). Red and green lines indicate negative and positive effects, respectively. Colour tone of the line scales with the magnitude of the effects. The functional node sizes are relative to the standing biomass (log transformed). Functional groups experiencing a decline in biomass ≥80% compared to a NC scenario are represented as a small circle and empty inside. The colours of the lines in each food web should not be interpreted in an absolute sense: the impacts are relative. Different food web groups in the in the model are species or groups of species in the form of functional groups.

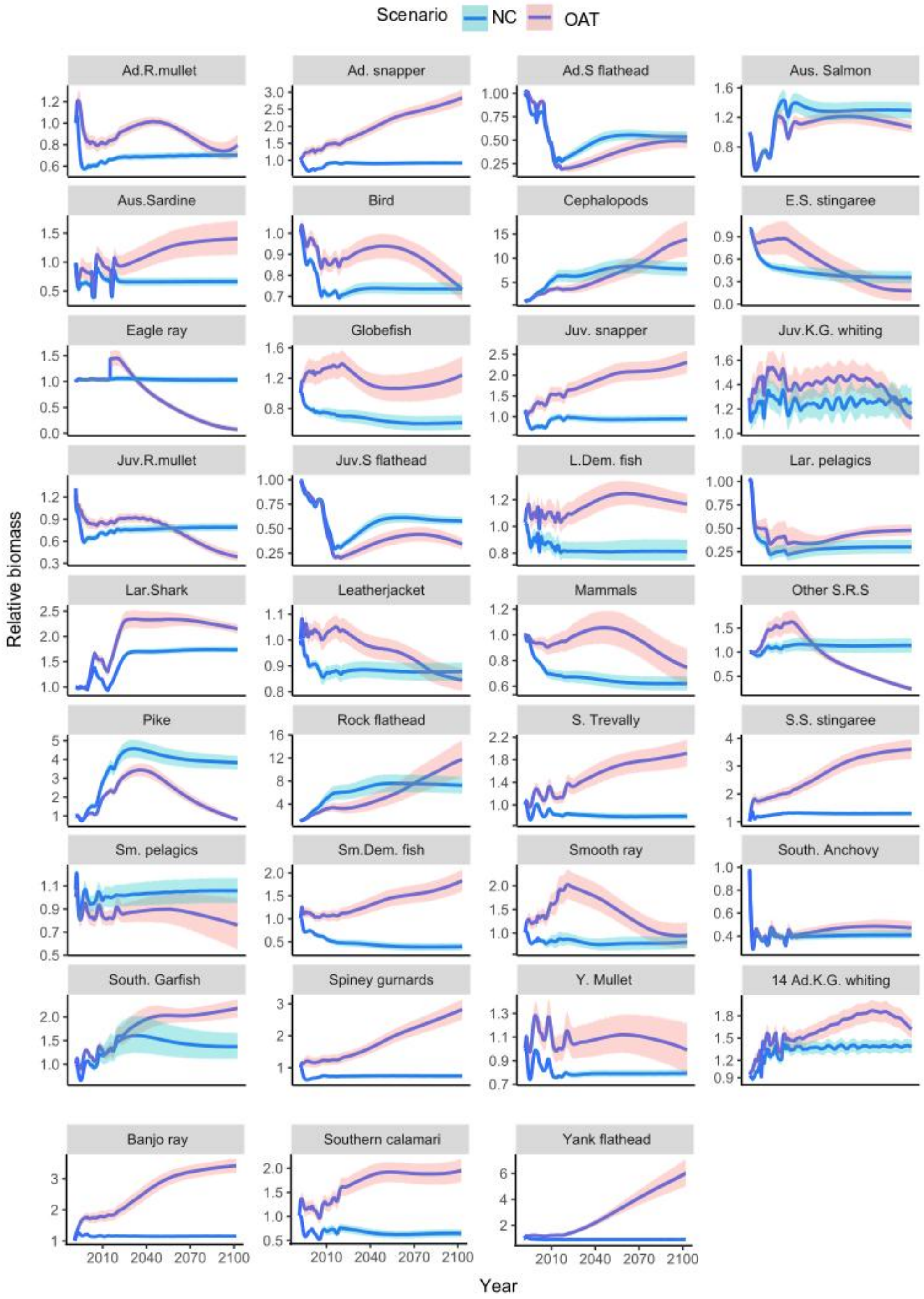


Figure S7: The results of Monte Carlo simulations (100 simulations run) of some higher trophic level food web functional groups of Port Philip Bay are plotted. Thick blue line represents the mean value of the fitted model. The 95% percentile and 5% percentile using 10% fixed variability of the model inputs (shaded areas) derived from model pedigree index are also shown. Results are only plotted for the most pervasive future scenario OAT (warming and acidification together) relative to no change scenario at 2100.

4.7 SUPPLEMENTARY TABLES

Table S1: Basic Ecopath input parameters for the baseline Ecopath model 1990. P/B= production/Biomass ratio; Q/B=consumption/biomass ratio, EE= ecotrophic efficiency and P/Q=consumption biomass ratio. FGs refer functional groups.

FGs number	Functional group name	Feeding guild	Trophic level	Biomass (t/km²)	Total mortality Year^{-1}	P / B (Year^{-1})	Q / B (year-1)	EE	P / Q
1	Large sharks	Carnivorous	2.61	0.23		1.55	10.4	0.95	0.15
2	Large pelagics	Piscivorous	4.04	0.21		0.3	3	0.95	0.1
3	Birds	Carnivorous	3.46	1.84	0.4		2.31	0.43	0.17
4	Mammals	Piscivorous	3.02	0.15		1.32	10.6	0.95	0.12
5	Yank flathead	Carnivorous	1	26.88		45	0	0.11	
6	Rock flathead	Carnivorous	3.32	0.94		2.72	13.59	0.57	0.2
7	Other cephalopods	Carnivorous	3.1	0.72		1.42	12.31	0.95	0.12
8	Southern calamari	Carnivorous	2	4.72		0.88	11.68	0.71	0.08
9	Smooth ray	Carnivorous	2	0.26		0.73	12.41	0.7	0.06
10	Adult sand flathead	Carnivorous	4.02	0.02		0.09	19.88	0	0
11	Juvenile sand flathead	Omnivorous	3.06	2.89		1.12	6	0.95	0.19
12	Banjo ray	Carnivorous	3.33	0.14		0.32	2.72	0.47	0.12
13	Eastern shovelnose stingaree	Carnivorous	3.18	0.12	1.1		4.4	0.97	0.25
14	Adult King George whiting	Carnivorous	4.02	0.72		0.4	3.92	0.62	0.1
15	Juvenile King George whiting	Carnivorous	3.11	0.07		0.22	2.2	0.86	0.1
16	Large demersal fish	Carnivorous	3.96	0.41		0.44	4.2	0.95	0.1
17	Adult red mullet	Carnivorous	3.82	1.02		0.07	1.69	0.15	0.04
18	Juvenile red mullet	Herbivorous	3.11	0.57		0.41	4.16	0.03	0.1
19	Eagle ray	Carnivorous	3.28	0.84		0.49	2.41	0.08	0.2
20	Other SRS	Carnivorous	3.05	0.04		0.87	2.4	0.95	0.36
21	Sparsley spotted stingaree	Carnivorous	1	0.71		30.85	0	0.97	
22	Australian sardine	Carnivorous	3.47	0.25		1.83	8	0.95	0.23
23	Southern anchovy	Carnivorous	3.23	0.03		0.73	12.41	0.53	0.06

24	Australian salmon	Piscivorous	3.48	0.18		1.7	6	0.95	0.28
25	Pike	Piscivorous	2.29	24.22		2.93	11.53	0.91	0.25
26	Southern garfish	Carnivorous	3.05	0		0.52	2.6	0	0.2
27	Other small pelagics	Carnivorous	3.05	0.2	0.55		3.71	0.77	0.15
28	Silver trevally	Carnivorous	2.05	25.97		4.5	22.48	0.95	0.2
29	Yelloweye mullet	Omnivorous	1	58.21		11.13	0	0.07	
30	Leatherjacket	Omnivorous	3.01	3.53		0.82	10.02	0.95	0.08
31	Other small demersal fish	Omnivorous	3.31	0.26	0.49		2.2	0.98	0.22
32	Globefish	Carnivorous	2.02	0.01	1.84		13.04	0.69	0.14
33	Spiny gurnards	Carnivorous	1	6.41		259.3	0	0.82	
34	Adult snapper	Carnivorous	3.58	0.09		0.4	3.8	0.18	0.11
35	Juvenile snapper	Carnivorous	3.04	2.54		0.7	5.04	0.95	0.14
36	Other invertebratess	Omnivorous (LTL)	3.11	1.17		0.68	3.04	0.14	0.22
37	Polycheates	Omnivorous (LTL)	2.07	24.97		2.72	13.59	0.95	0.2
38	Filter feeding molluscs	Herbivorous	3.13	0.05	0.92		5.19	0.92	0.18
39	Grazing molluscs	Herbivorous	3.14	0.41		0.2	3.37	0.02	0.06
40	Predatory molluscs	Omnivorous (LTL)	2	4.02		2.09	10.49	0.95	0.2
41	Echinoderms	Herbivorous	3.29	0.21	1.1		8.12	0.53	0.14
42	Zooplankton	Herbivorous	1	12573				0.29	
43	Crustaceans	Herbivorous	2.4	0.42	0.4		4.2	0.95	0.1
44	Abalone	Herbivorous	4.33	0.01		0.18	1.75	0.6	0.1
45	Southern rock lobster	Omnivorous (LTL)	1	18.13		20	0	0.23	
46	Sea urchin	Herbivorous	2.05	51.28		0.8	9.41	0.33	0.08
47	Exotic seastar	Omnivorous (LTL)	3.4	0.05		0.92	4.33	0.79	0.21
48	Macroalgae	Primary producer	3.28	0.31		0.57	2.2	0.95	0.26
49	Algal turf	Primary producer	3.33	0.07		0.38	2.45	0.95	0.16
50	Phytoplankton	Primary producer	2.39	24.02		3.26	16.28	0.13	0.2
51	Microphytobenthos	Primary producer	2.68	0.12		0.92	9.65	0.99	0.1
52	Seagrass	Primary producer	2.04	4.66		54.75	153.36	0.55	0.36
53	Detritus	Detritus	3.45	0.33		0.23	2.37	0.22	0.1

Table S2. Index (forcing function) used to drive the vulnerability parameters of future food web simulations (OAT, T, and OA). The effect size between no change scenario (NC) and climate scenarios were presented. OA = ocean acidification, T= ocean warming, and OAT = combined ocean acidification and warming. Source groups refer consumers whose consumption depends on the vulnerability (parameters) of their prey groups. Forcing function as direct mortality for some of the model functional groups was also applied. For model functional groups or species with different feeding guilds please see Table S1.

Index used to drive vulnerability parameters	**Baseline value**	**Effect size**			**Applied on the following functional groups or species**	**Source group**
	NC	**OA**	**T**	**OAT**		
Vulnerability index of carnivorous fish	1	0.99	1.08	0.82	2 ,5, 6,10,11,14,15,17,18,22,23,24, 25,27,28,32,33,34,35	Relevant consumers/predators
Vulnerability index of omnivorous fish	1	1.07	1.16	0.85	16,26,29,30,31	Relevant consumer/predator
Vulnerability index of zooplankton	1	1.97	0.87	1.15	42	Carnivorous consumers
Vulnerability index of polychaetes	1	1.11	0.63	1.70	37	Carnivorous consumers
Vulnerability index of epifauna	1	0.99	1.24	1.79	36, 37	Carnivorous consumers
Vulnerability index of bivalves	1	0.78	1.43	2.15	38	Carnivorous consumers
Vulnerability index of gastropods	1	10.56	6.17	1.90	39	Carnivorous consumers
Vulnerability index of copepod	1	2.97	1.66	1.91	42	Omnivorous consumers
Vulnerability index of polychaetes	1	5.36	1.29	<0.00	37	Omnivorous consumers
Vulnerability index of epifauna	1	3.10	2.88	0.88	36, 37	Omnivorous consumers
Vulnerability index of bivalves	1	1.65	3.18	0.91	38	Omnivorous consumers
Vulnerability index of gastropods	1	14.60	1.81	0.60	39	Omnivorous consumers
Search efficiency of chondrichthyans	1	0.21	1.07	0.32	2,5-8,10,11,14,16,17,21,22,24,27, 28, 30, 33,34,36-41,43,	Chondrichthyans
Algal turf productivity	1	1.07	1.82	1.58	49	Relevant consumers
Macrophytes productivity	1	1.28	0.24	0.46	48	Relevant consumers
Phytobenthos productivity	1	1.32	0.69	1.23	51	Relevant consumers
Phytoplankton productivity	1	1.66	0.44	0.99	50	Relevant consumers

Forcing function	**NC**	**OA**	**T**	**OAT**		Type
Biomass grazing molluscs	1	1.17	0.47	0.12	39	Mortality (as a function of biomass)
Biomass of filter feeders	1	1.24	0.28	0.15	38	Mortality (as a function of biomass)
Biomass of crustaceans	1	1.38	1.25	1.44	43	Mortality (as a function of biomass)
Biomass of polychaetes	1	1.74	0.50	0.68	37	Mortality (as a function of biomass)
Biomass of zooplankton	1	1.16	0.57	0.68	42	Mortality (as a function of biomass)

CHAPTER V

CHAPTER V

GENERAL DISCUSSION

5.1 SYNTHESIS OF THIS THESIS

If we evaluate the ecological response of marine ecosystems in the face of climate change, the most common patterns to emerge are as follows; I) ocean warming although produce divergent responses across marine organisms, many of the species is affected negatively, declining their abundances, biomass and productivity, and II) ocean acidification threatens numerous calcifiers in marine ecosystems (Kroeker *et al.*, 2013). What is important to note is that these patterns have tended to emerge from a synthesis of single-species studies, with stressors often modelled in isolation, over short time scales (typically days to weeks), or in microcosm studies, and are therefore unable to capture the complexity of whole food webs. Research studying the impacts of climate change on food web dynamics is usually based on either a component of the food web (i.e. one or two trophic levels) or the response of species solely against elevated temperature (Hoegh-Guldberg & Bruno, 2010). Recently, the importance of considering the combined effects of warming and acidification was illustrated by a quantitative meta-analysis that demonstrated these two global stressors together can disrupt ecosystem function (Nagelkerken & Connell, 2015). Attempts to model the food web level response of real-world ecosystem under future climate change have included species' physiological response to climate change, but only for lower trophic level species, such as primary producers or invertebrates, or using data from single species or single stressor studies. The key gap in this approach is that responses of species to global change are not individual-based; they are connected through a network of trophic relationships within and across trophic levels.

Food webs are chains of networks where energy flow and growth of species is determined and mediated by various biological interactions (e.g., predator-prey relationships, competition, facilitation, and mutualism) among species that are directly or indirectly linked to adjacent trophic levels (Nagelkerken & Munday, 2016, Woodward *et al.*, 2012, Woodward *et al.*, 2010). The sensitivity and response of individual species under climate change could be influenced by these biological interactions and could, directly and indirectly, impact species in the same trophic level or next trophic level. Thus, the response of individual organisms or functional groups could differ significantly when considered at a food web level. Furthermore, increasing food chain length can alter the response of community levels which is not evident in food webs with a lower number of trophic levels (Hansson *et al.*, 2013). Including the entire food web, from producers to top predators and species interactions, in global change studies can considerably advance our understanding of future climate change and its associated losses and gains.

Although conducting experiments with multilevel food webs comprised of diverse communities and increasing ecological complexity is challenging, but important to include in ecological models to ensure more ecologically realistic forecast of future food webs. This will also allow us to produce robust evidence that could suggest how this translates to the higher trophic level in a real-world food web. This thesis attempted to fill the above-mentioned gaps by combining multi-level experimental food web with an integrated food web modelling approach.

Synthesis of the key findings

To address the knowledge gap described above, we need to develop a holistic understanding of food web responses to global climate change, where the important first step is setting up an experiment that comprises all elementary biological components of a food web. In chapter 2, I describe and show the importance of building such mesocosm experiments and explain how it improves our understanding of ecosystem response against global change. In particular, how energy fluxes are likely to change in marine food webs in response to future climate remains unclear, hampering forecasts of ecosystem functioning. This study provides strong empirical evidence that global warming has the capacity to drive a collapse in some marine food webs by altering energy flows between successive trophic levels.

I show that in an ecologically complex mesocosm food web, the combination of warming and acidification can decouple increased basal productivity from herbivore production, while warming in isolation can reduce predator production. However, the metabolic theory of ecology (Brown *et al.*, 2004) suggest that temperature driven increased primary production is likely to propagate through food webs via strong top-down control (Carr & Bruno, 2013, O'Connor, 2009), resulting in greater levels of heterotrophic biomass, relative to autotrophic biomass (O'Connor *et al.*, 2009). The decoupling of energy between basal productivity and herbivore showed in this study is related to the proliferation of cyanobacteria, less preferred or unpalatable food, that completely dominates assemblages of mat-forming algae under warming. Herbivores like macroinvertebrates and small epifaunal invertebrates predominantly feed on mat-forming turf algae rather than cyanobacteria. Some cyanobacteria are known to be toxic produce potent allelochemicals that deter feeding by grazers (Nagle & Paul, 1998) and could also cause localized anoxia and mortality in marine organisms (O'Neil *et al.*, 2012).

In this study, it was not possible to identify the specific species of cyanobacteria. However feeding trial and later stable isotope analysis that was done for another project confirm that herbivorous macroinvertebrates did not feed on cyanobacteria grown under warming. Several studies have reported an apparent increase in the occurrence of cyanobacteria in marine waters globally (Paerl & Paul, 2012), and regionally in temperate (Wiedner *et al.*, 2007), tropical (Bif & Yunes, 2017, HW *et al.*, 2008), and subtropical (Albert *et al.*, 2005, Glibert *et al.*, 2004) areas. Thus, I conclude that reduced food availability, brought about by palatable types of turf algae being replaced by unpalatable cyanobacteria, caused food limitation, preventing increased metabolic rates for macroinvertebrates at higher temperatures, suppressing the flow of energy to the second trophic level (Dillon *et al.*, 2010, Johansen *et al.*, 2015). This was further exacerbated by a collapse of their biomass of other primary consumers such as copepods, small epifaunal invertebrates, and filter feeders mostly due to increased predation pressure by species at the third trophic level (i.e., predators) due to their higher energetic demand (Goldenberg *et al.*, 2017). These, in turn, make most of the primary production unavailable further up the food chain, reduce the transfer efficiency between primary producer and herbivores and thus converted surplus primary production to detritus to the base of the food web. Thus, the results from this study (Chapter 2) suggest that energy from enhanced primary producer biomass under future climate conditions may not always transfer through to successive trophic levels. This decoupling between food demand and supply in successive trophic levels may alter dietary preferences of consumers, modifying consumer-prey relationships and induce trophic mismatch within food webs.

On the other hand, this chapter shows that ocean acidification could affect the food web positively by bottom-up effects on energy flow towards secondary producers and by increasing the biomass of carnivores. This is not surprising because the direct negative effects of elevated CO_2 could be dampened by the strong indirect positive effects i.e., through increased habitat and food, as well as reduced predator abundance (Connell *et al.*, 2017, Nagelkerken *et al.*, 2016).

I conclude that ocean warming can potentially weaken some marine food webs through reduced energy flow to higher trophic levels and a shift towards a more detritus-based system, leading to food web simplification and altered producer-consumer dynamics both of which have important implications for the structuring of benthic communities. I then use the findings of this chapter

(Chapter 2) to parameterize and build models for different climate change scenarios for a representative temperate natural food web system.

Here, I tried to address one of the most difficult challenges that ecosystem modelers have faced in the recent years: determining how entire food webs (natural food web) respond to external perturbations (Chapter-3). To date, our ability to directly investigate food web response to major global threats such as warming and acidification is limited to simultaneous experimental manipulation of three trophic levels only. However, computer simulations can improve our understanding of future global threats on entire food webs. The accurate prediction of these models, however, largely depends on the input parameters, which relate to system-wide information of the food-web structure and biological details of species-interactions and cascading effects. Exclusion of information on particular groups or trophic levels can have potential large consequences for understanding the functioning of entire food webs. While significant effort has been made in recent years to explore the impact of climate change on food webs, our ability to produce reliable forecasts of the likely effects of future climate change on marine communities is hindered due to a failure of incorporating climate-driven change in species interactions (experimental output or in situ measurements) in model projections (Brown *et al.*, 2010, Daufresne *et al.*, 2009, Zhang *et al.*, 2017). Additionally, simulating fishing effort within laboratory experiments is very challenging. Furthermore, natural food webs in general comprise four trophic levels. However, in some cases natural food webs comprise five trophic levels, when they contain carnivorous apex predators such as killer whales and sharks (Pauly *et al.*, 1998).

Thus, we need novel approaches that allow us to model food webs with up to 5 trophic levels (primary producers to apex predators). Modeling an entire food web is exceedingly important as food-chain length can alter community responses to global change (Alsterberg *et al.*, 2013, Hansson *et al.*, 2013). In this chapter, using a time-dynamic integrated ecosystem modeling approach I show how the independent and combined stressors such as global warming and ocean acidification in conjunction with local fishing affects a temperate coastal ecosystem. To quantify the effects of ocean acidification and increasing temperature at the species community level, this chapter included physiological and behavioral responses of species to these stressors from two of our own large-scale mesocosm experiments, which included multiple trophic levels from primary producers to top predators such as sharks.

The results of this chapter elucidate that under a continuation of the present-day fishing regime, warming and ocean acidification will benefit most of the higher trophic level community groups (e.g.

mammals, birds, demersal finfish), except small pelagic fish. Small pelagic fish are one of the major forage fish groups in the food web which is subject to increased predation pressure under warming and likely decline in their biomass. The increase in biomass of consumers is predominantly driven by strong top-down control combined with a few prey groups responding positively to global warming. In line with metabolic theory, such increase in top-down control by consumers has been predicted in colder regions in response to increased temperature (Marino *et al.*, 2018) and could benefit fisheries in some temperate or high latitude marine ecosystems (Barange *et al.*, 2014, Brown *et al.*, 2010, Cheung, 2018, Cheung *et al.*, 2010).

In contrast, acidification is likely to boost food-webs from the bottom up enhancing the availability of prey resources due to the enrichment effect of elevated CO_2. Enhanced primary production can boost the growth of consumers under acidification as confirmed by several recent food-web studies, both experimentally (Sswat *et al.*, 2018, Ullah *et al.*, 2018) and in the wild (Goldenberg *et al.*, 2018, Nagelkerken *et al.*, 2017).

While warming and acidification in isolation positively affect the biomass of predators, a smaller increase is predicted under their combination. This is because warming and acidification acted antagonistically. Such antagonistic effect between warming and acidification have been shown to affect prey search time of predators (Pistevos *et al.*, 2017) or reduce prey resources to herbivores (Clements & Darrow, 2018, Poore *et al.*, 2013, Sampaio *et al.*, 2017) and thus lead to a failure in the capacity of consumers to allocate resources towards maximal somatic growth (Nagelkerken & Connell, 2015).

As global per capita consumption of seafood is expected to increase, many coastal ecosystems around the world are likely to face increasing fishing pressure. Therefore, I explored the likely consequences of increasing fishing effort together with warming and acidification on a marine food web and show that fishing and global warming would likely act antagonistically. Under increased fishing, the positive effects of warming and acidification are negated, decreasing the individual biomass of marine mammals, birds, chondrichthyans and demersal finfish taxa. Nevertheless, total future potential fisheries biomass will likely still remain high, particularly under acidification, compared to the present-day scenario because unharvested opportunistic species will likely benefit from decreased competition and increase in biomass.

While many consumers benefited from the global warming, primary consumers such as invertebrates (e.g., grazing mollusc, filter-feeding mollusc, predatory mollusc and other invertebrates) and small pelagic crustaceans drastically collapsed in their biomass. Invertebrates and small pelagic crustaceans could not sustain themselves under increasing top-down control by their predators. The collapse of these prey groups is evident through ecological indicators such as the Shannon diversity index which showed a significant decrease under all climate change scenarios, suggesting a trade-off between biomass gain and functional diversity in the future food web. In short, it is clear that the greatest stressor effect on future food webs will arise under the combined effect of global and local stressors where warming is mostly predicted to negatively affect the bottom while fishing the top of the food web.

Here I uniquely modeled the effects of global warming, ocean acidification, and fishing using empirical data on species interaction and physiology and historical fisheries data on their population dynamics. This study thus showed a novel approach to quantify the potential magnitude and direction of the biomass changes of various functional groups in future marine food webs and fisheries under global change. Ecosystem models considered in this study accounted for complex species interactions such as predation and competition, and represent the likely future food web structure and fisheries productivity under ocean warming, acidification and different fishing regimes. While I describe the potential end state of future temperate food web and fisheries is that a reshuffling of predatory and prey species biomass in this chapter (Chapter 3), the mechanism behind such changes is not illustrated in details. Understanding the mechanism behind such alteration in the predator-prey dynamics is important, and therefore, I aim to explore that in the following chapter.

In chapter 4, I studied the alterations to trophic interaction strengths that drive many of the changes in food webs (e.g. as observed in the previous chapters) under present day and future climate conditions. The structure, functioning, and stability of ecological communities depend overwhelmingly on the strength of trophic interactions between consumer and resources (Bascompte *et al.*, 2005, Schaum *et al.*, 2018). These consumer-resource interactions are of particular importance in food web dynamics since they determine the majority of energy fluxes between individuals and throughout ecological communities and ecosystems (Dell *et al.*, 2014). Quantifying the strength of consumer-resource interactions is essential for understanding how ecological communities are organized and how they respond to any internal or external perturbations such as future global climate change (Bascompte *et al.*, 2005).

I investigated the individual and cumulative effect of future climate change stressors (temperature and acidification) on the modification of trophic interaction strength and its likely effects on the biomass and productivity of consumers and their resources in a temperate marine food web. This was done by incorporating empirical data on climate-driven change in species interactions from large experimental manipulations (mesocosms).

I show that although climate change is likely to reshuffle community biomass structure by reducing or increasing the biomass of resources and consumers within the food web, overall vertebrate biomass and productivity in the future food web will likely increase due to an increase in trophic interaction strength. This change in trophic interaction strength is driven by elevated temperature where an increase in both direct and indirect trophic interaction strength is likely to be observed in future food webs. Although both direct and indirect trophic interactions increase in their strength, direct trophic interactions (feeding and competition) will largely determine the direction of biomass change (increase or decrease) of consumers due to higher mean interaction strengths (magnitude of change). Thus increased biomass at the higher trophic levels under global warming, due to increased trophic interaction strengths, will result in a decrease in the biomass at the lower trophic levels that comprised many functional groups of invertebrates.

In contrast, although acidification induced a relatively small increase in trophic interaction strength it showed a much larger change in percent interactions altered by indirect interactions and is still likely to propagate boosted primary consumer biomass to higher trophic levels.

I conclude that warming in combination with acidification can amplify trophic interaction strengths (both direct and indirectly) and the degree to which the consumers will benefit in the future food web will largely depend on the direct trophic interaction strengths and availability of prey resources.

Strength, weakness of the modelling approach and mesocosm transferability

Large mesocosms are a close experimental representation of nature since they can maintain a natural community in a relatively self-sustaining condition and can incorporate mechanisms such as indirect effects, biological compensation and recovery, and ecosystem resilience (Stewart *et al.*, 2013). The outputs of such an experimental approach, however, can strongly depend on community structure, the level of ecological complexity included in the mesocosm and the number of trophic levels considered. In chapter 2, with a 3-trophic level food web, I showed how warming, irrespective of acidification, reduces the flow of energy to carnivores whilst in chapter 4 an increase in the biomass at the top of the trophic level (top carnivorous or apex predator) is predicted for natural food web.

Studies suggest 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 increase in the biomass of carnivores and apex predators in a four trophic level natural food web (chapter 4) is mostly driven by strong top down control and partly the ability of some of the food web prey groups to respond positively to climate stressors. For example, whilst benthic crustaceans at the bottom of the food web responded positively under all climate scenarios, small pelagic fish occupying the mid-trophic level of the food web (forage fish) significantly declined in their biomass but other functionally similar pelagic groups such as sardines and anchovies maintained their positive biomass and continued their role as prey species. It is observed that while some of the functional groups declined under different climate scenarios, many others increased in biomass, occupying vacant ecological niches and benefitting from less competition.

In this study, the two models (mesocosm and Port Philip Bay) is nothing but an illustration of a similar shallow marine rocky reef ecosystem built with simple (small number of functional groups) and more comprehensive food web models (most of the major functional groups). The results suggests that the modelled natural food web, comprised of 53 functional groups and multiple species with similar ecological roles at the same trophic level (Chapter 3), likely to have higher functional redundancy compared to the mesocosm food web (comprised of only twelve functional groups) that was modelled in Chapter 2. More complex food web communities with higher functional redundancy and diversified trophic links are likely to be less vulnerable and more stable than simple food webs (Sanders *et al.*, 2018), showing greater adaptive capacity to sustain desirable states in the face of disturbances (Elmqvist *et al.*, 2003) such as climate change (Hoppe *et al.*, 2017). Therefore, even though I observed a similar level of proliferation of cyanobacteria (algal turf) in the natural food web (Chapter 3) as in the mesocosm food web (Chapter 2) the overall impact on species biomass in the natural food web was lower than in the mesocosms. This is mostly because of the strong role played by the alternative prey groups for carnivores in the natural food web, such as benthic crustaceans which had minimal contribution in the trophic flow up the food web in the mesocosm food web due the absence of appropriate predator. However, I acknowledge that this mechanism could be better explained if the mesocosm experiments could be conducted on a range of food webs with increasing complexity/number of species. Benthic crustaceans (with the highest trophic impact value) were a major prey resource (trophic link) for higher order consumers in the natural food web. The natural food web model (Chapter 3) was further able to capture the significant loss of herbivorous biomass as also observed in mesocosm model (Chapter 2).

In summary, increasing top-down control due to higher trophic interaction strength and inclusion of predator-prey dynamics through species interactions at higher trophic levels combined with greater diversity in prey resources and less influence of less desirable basal resources in the diet of consumers of the natural food web than mesocosm food web explain the outcome (disparity and comparability) of a 3-trophic level mesocosm food web and a 4- trophic level natural food web.

It is important to note that all research suffers from some general limitations. The experimental manipulation and modelling approach used in this study are not devoid of such pitfalls either. I used Port Philip Bay as a model ecosystem to project the changes in the future food web and fisheries in response to increases in temperature and decreasing pH level both of which are based on global averages. I assume that ecological setting of mesocosm experiment reasonably mimics the shallow coastal ecosystem of Port Philip Bay. However, I acknowledge that there is substantial variation in the dynamics of climate change processes among regions. For example, the South East coast of Australia is warming considerably faster than the global average. Therefore, the output of the model (Chapter 3) may not necessarily reflect the potential future changes of Port Philip Bay ecosystem at 2100. Therefore, to elucidate when exactly we may observe the likely consequences of such changes in the ocean warming and acidification in Port Philip Bay and their consequences on the food web further work is necessary such as using the regional climate models to forecast trends in future temperature and acidification of Port Philip Bay.

Also, the simulation of the future food web is solely based on two scenarios–present-day conditions and projected global averages for temperature and acidification at 2100 following RCP 8.5. I also assume a linear increase or decrease in all the forcing function parameters since realistic model parameters were only possible to collect at the beginning and end of the mesocosm experiments. In reality, many studies show that the performance of individual species in relation to climate change is not linear. I acknowledge that the response of species and food web properties could vary in some instances if the relationship between forcing function and vulnerability was non-linear. This may weaken our ability to predict variability at the decadal scale. However, linear interpolation between two climate snapshots is a common practice in climate change ecology (Fordham *et al.*, 2012) and successfully used before in a food web context (Ainsworth & Mumby, 2015, Brown *et al.*, 2010, Griffith *et al.*, 2011, Marshall *et al.*, 2017).

I used artificial, as opposed to natural, seagrass in the mesocosm experiment, and hence the ecosystem models. Seagrass could be an important source of primary production for shallow coastal ecosystems, such as PPB and thus can have important implications in the model outcome. For example, seagrass can store more carbon than forests and work as an important source of carbon dioxide sinks (Fourqurean *et al.*, 2012). However, previous lab studies found that maintaining seagrasses in indoor mesocosm for long-term is extremely difficult. I, therefore, had no other option than to use artificial seagrass by which this study at least able to capture the importance of seagrass as sheltering habitat for species. This decision was made because habitat heterogeneity can have important implications for predator-prey interactions or heterospecific interactions (Ljungberg *et al.*, 2013, Oksanen, 1990) that are not captured by the model which is based on a homogenous environment. I observed that these artificial seagrasses were frequently used by fish, shrimp, and snails to obtain food and for sheltering purposes (Adams *et al.*, 2004, Bell *et al.*, 1985) and as such created a similar habitat to live seagrass beds that some of the species associated with in nature. However, I admit that we need to find a way to include natural seagrass to the model future ecosystem which will certainly improve our model forecast.

Ecopath with Ecosim which is a data-driven modelling approach has some of its own shortcomings too. The performance of the model largely relies on the quality and availability of good representative data. One of the weaknesses of earlier applications of the Ecopath model were assumptions of ‘steady-state’ or equilibrium conditions, meaning that the model outputs should only be considered for the period across which the model input parameters are deemed valid (Christensen & Pauly, 1992). Ecopath modelling approaches now no longer assume steady-state conditions but instead, the model parameterizations are based on a mass-balance assumption over a chosen arbitrary period. An important assumption in the foraging arena formulation in Ecosim simulation is that predators are usually hungry and seek food is open to debate and therefore it is important to explore the likely consequences of alternative feeding interactions. The Ecopath modelling approach also assumes that mortality for a prey equals consumption of a predator and that all prey are equal in terms of energetic content. Thus the absence of a distinct energetic content parameter could be problematic in scenarios where there are substantial differences in the energy density of prey (Plagányi & Butterworth, 2004). This could mislead the true food requirements of a predator when prey abundances change. Further development and implementation of statistical procedures for estimating model parameters and sensitivity analysis which is computationally efficient are recommended to be useful in the fisheries resource management context for highly dynamic ecosystems that lacks in the present approach (Plagányi & Butterworth, 2004).

An important limitation of Ecopath and Ecosim approach is that it does not consider changes in the species size structure. Earlier studies reported that warming can shift the body-size distributions of species (Brose *et al.*, 2012, Jochum *et al.*, 2012), leading to a dominance of more small over large-bodied species such as cyanobacteria in this study. This change in size structure can influence the top-down and bottom-up process and may ultimately lead trophic cascades and yield novel communities (Brose *et al.*, 2012, Jochum *et al.*, 2012).

Another important aspect which is needed to be taken into account is that I simulated the future state of a shallow temperate marine ecosystem. The applicability of the model output from this study should be exercised with caution for deep sea ecosystem or for ecosystems at tropics. More experiments in different geographical locations with this kind of highly sophisticated food web experimental approach are necessary to better forecast the future ecosystem state. Additionally, I have to acknowledge that although this study includes one of the most complex mesocosm experiments to date, someone may argue about the mismatch between the scale of mesocosm and naturals systems.

However, by independently validating the model predictions (Chapter 3) against historical biomass and catch data, I not only show that the model does a very good job at reconstructing historical trends in fish biomass (for selected functional groups), but also show that the empirical parameters estimated in mesocosm experiments (Chapter 2) provide a close representations of natural food webs (Chapter 3). In doing so, I show that mesocosm experiments with a realistic multifactorial experimental design that capture food web complexity and can provide ecologically realistic outputs can be used to parameterize end-to-end ecosystem models and help bridge the gap between simplified experimental conditions and the real world .

Future research directions

I used one of the most near-natural coastal marine food web experiments to date to predict the response of ecological communities to global change at the end of the 21st century (Chapter 2). However, there is room for further improvement and extension of such experimental approaches. This thesis considered an extended summer season to mimic future climate conditions. However, we have little knowledge of how future communities with novel species compositions due to range extensions will respond to winter temperatures. Future studies should consider this as well as other seasons to model future response of ecological communities. A particular emphasis could be given to collect samples from multiple time points (experimental approach) for diverse community group including higher trophic levels with appropriate approaches which will allow us to predict decadal patterns in community response more accurately. In addition, future models and mesocosm experiments should also consider how species range shifts (both expansions and retractions) will impact food webs into the future.

Integrating data from other emerging and relevant fields such as genomics will allow developing more comprehensive understanding of the adaptive capacity of marine communities to future climate change (Bernatchez *et al.*, 2017). When integrating mesocosm data with ecosystem modelling tools, one of areas of improvement could be to build food web models with more species functional groups. For example, homogeneity in taxonomic resolutions (representing functional groups at the species level equally at higher and lower trophic levels) could be improved of ecological groups in higher and lower trophic levels of the food web. In addition, time series data (biomass of fisheries and other ecological groups) collected through well designed long term survey programs would improve model performance.

With increasing human populations, many coastal ecosystems will face the problem of increasing anthropogenic nutrient inputs into the sea resulting in toxic algal blooms and thus deoxygenating the water column (Davidson *et al.*, 2014). An increase in the hypoxic zone in the global ocean is reported and is a ubiquitous characteristic of many of the coastal ecosystems around the world (Diaz & Rosenberg, 2008). The metabolically mediated co-occurrence of acidification and hypoxia has also been well established especially in the in coastal environments over a range of spatial and temporal scales (Baumann *et al.*, 2015, Wallace *et al.*, 2014). Future studies should consider these multiple stressors in a modelling framework to improve our understanding on how communities respond to several external perturbations. Finally, the next big challenge is to incorporate the response (e.g. physiological and species interactions) of future communities using a spatially-explicit food web modelling approach. Effort has been made to explore this within the framework of Atlantis food web models (Marshall *et al.*, 2017, Olsen *et al.*, 2018, Ortega-Cisneros *et al.*, 2018); but these lack incorporating realistic biotic interactions such as those can be obtained from large scale mesocosm or in situ experiments that captures novel species interaction in response to ocean warming and acidification. This will allow us to include other important attributes such as habitat use of species and life-history trait such as dispersal rate both of which can greatly influence population dynamics of species.

5.2 CONCLUSIONS

This thesis has provided evidence that the effect of future global warming and ocean acidification on food web communities will vary depending on the complexity and structure of the food web. In general, warming is likely to increase the top down control of consumers on their prey resources and will likely determine the community biomass structure of the food web. The greatest negative effect is likely to be on lower trophic level groups such as invertebrates (collapse). In contrast, we may see an emergence of opportunistic species such as algal turf which potentially can weaken the trophic link between producer and herbivorous consumers. However, this mechanism might not be seen in a more complex natural food web characterized by higher functional redundancy (alternative available prey species) compared to more simple food webs (e.g. a mesocosm food web). In a more diversified and functionally rich natural food web, most of the consumers at the higher trophic level could be benefited, albeit to a cost of biodiversity. More specifically, the increase in the biomass of higher trophic level consumers could put lower trophic level species under tremendous pressure through increased predation owing to the higher metabolic demand from increased temperatures. On the other hand, fishing will more likely negatively affect higher order consumers in the food web. While warming irrespective of acidification is likely to jeopardize some of the functional groups of the food web, acidification in isolation is likely to benefit most of the functional groups that include producers to top predators. In summary, the findings of my thesis suggest that the degree to which warming and acidification will be beneficial or detrimental to a particular functional group in future food webs will largely be depend on how interaction strengths affects individual consumers or resource groups and could be mediated by the availability of prey resources and the complexity of food web considered (e.g. three or four trophic level and more diverse ecological communities).

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From: Katie Prud'homme

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To: Md. Hadayet Ullah

Subject: Re: [info@the-scientist.com] mesocosm infographic

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Have a wonderful day!
Best,
~Katie

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On Tue, Sep 18, 2018 at 6:00 AM, Md. Hadayet Ullah <mdhadayet.ullah@adelaide.edu.au> wrote:
Hi Rob,
This is Hadayet. I am doing my PhD at the University of Adelaide. Today, I have come across the beautiful mesocosm infographic (below link).
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Thank you so much.
Regards
Hadayet Ullah