THE ROLE OF HERBIVORES IN A NEAR FUTURE OCEAN: POSITIVE AND NEGATIVE EFFECTS OF CLIMATE CHANGE ON HERBIVORE ECOLOGICAL FUNCTION

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CONTENTS

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"All's well that ends well"
William Shakespeare

ABSTRACT

Earth's climate is characterised by abrupt change through its history, yet human induced climate change is warming and acidifying our oceans at unprecedented rates. Such alterations in the seawater's chemical and physical properties are anticipated to disrupt a multitude of ecological processes leading to potential reductions in productivity and biodiversity of marine systems. Functional groups such as marine herbivores are renowned for meditating competition between benthic organisms, affecting the physical structure and primary production in marine systems, countervailing the deleterious effects of global and local disturbances. Within this context, it is important to not only understand how herbivorous species respond to climate change, but also how their overall functional role are affected and how this might have cascading effects on other species. In this thesis, I reveal that whilst populations of many species are forecast to collapse due to the effects of future climate, some herbivorous species may capitalize on environmental change and boost their densities by increasing the carrying capacity of the environment by actively modifying the habitat under an otherwise stressful condition. I also show that the modifications performed by herbivorous species trough the strengthening of positive interaction under ocean acidification can assist other species to densify, stimulating species coexistence and ecosystem function, and perhaps mitigate the deleterious effect of CO_2 enrichment expected at population and community level. Therefore, under ocean warming the functional role of herbivores is eroded releasing opportunistic algae from trophic control which can potentially lead marine systems to undergo structural modification. I show that loss of this functional role, reduces the capacity of the system to control the expansion of opportunistic algae. The identification of the circumstances as to whether herbivores functional role in marine systems will strengthen or decrease provides insights into the impacts of ocean warming and acidification at local scale and their potential management.

CHAPTER I

GENERAL INTRODUCTION

EARTH’S CLIMATE AND THE MARINE STABILITY

The Earth’s climate has been ever changing during its 4.5 billion years of existence. The majority of climatic records suggests that our planet is characterised by repeatedly abrupt climatic changes[1,2] over the course of its history. Whilst the trigger of such events is normally linked to a variety of geological and astronomical events (tectonic movement, volcanic activity and, comets and asteroids impacts)[3,4] their main culprit and the overall ecological effects of climate change are generally similar. It is not hard to find evidence in climatic records showing a strong correlation between the rising of CO_2 concentration in the atmosphere with geological and astrological events, which has been recognised as the main driver of climate change and global warming in the last 300 million yrs[5–7]. The historical ecological records suggest that the outcome of these abrupt climate change driven by higher CO_2 concentrations disrupted a multitude of ecological processes, instigating environmental change and biotic turnover leading to extinction events[2,8–11].

Past climatic events have shown us the catastrophic outcomes of climate change. Yet, Earth’s climate is currently changing at a velocity never documented before[12,13]. However, the trigger of such abrupt climatic change is different from those of the past (geological and astronomical), and now it is a human-induced rise of atmospheric CO_2 concentration[13]. In the past 60 years or so the Earth’s already warmed by 0.6°C[14] and atmospheric CO_2 concentration has jumped from 300 ppm to >400 ppm due to anthropogenic activity and forecasts suggest even stronger increases for the next 100 years[15]. The Representative Concentration Pathway (RCP) 8.5 for the year 2100, which represents a business-as-usual CO_2 emission scenario[15] forecasts future CO_2 concentration to reach ~900 ppm and a future temperature increase of + 2.8°C of the ocean surface. Such predictions have led scientists to believe that Earth is entering a new geological cycle (i.e. Anthropocene) driven by human activities and that it already started to trigger a new extinction event[16,17].

A few studies have uncovered the causes of such extinction events during past climate change, such as the end-Permian extinction event, which was one of the most severe mass extinction ever registered[18]. It is believed that such events were driven by a collapse of primary productivity[19], and a sharp decrease in water pH which drove heavy losses in calcified marine biota[20]. Therefore, the identification of the mechanisms that lead to such disproportional alteration of marine productivity and by consequence diversity is hard to be disentangled using palaeontological data. Nowadays, scientists have revealed that animals in order to maintain their homeostasis during warming periods are required to intensify their foraging activity, to cope with the increased metabolic demands and modification of food quality[21–23], increasing by consequence the interaction strength between consumers and producers[24–26]. In that case, the collapse of primary production would heavily impact the entire trophic structure.

Primary production collapse might be the result of the expansion of faster growing and opportunistic algae under warming and acidification[27,28]. In that case, it is crucial to understand the relationship between algae and their consumers. Herbivores are a renowned functional group responsible to mediate competition between benthic organisms affecting the physical structure and primary production in marine systems[29,30]. Additionally, they can countervail the positive effects of global and local disturbances on the expansion of opportunistic weedy species [31] avoiding dominance alternation in benthic communities of in natural systems.

Hence, a fundamental aspect of the role played by this functional group is that the magnitude of their counter-feedback response should be proportional to the effect of environmental change allowing natural systems to resist under disturbances[32] despite near continuous environmental change[33–35]. Understanding how such stabilizing process is affected by climate change has become a key ecological quest. This happens because they involve a multitude of mechanisms that can vary in response intensity and duration. For example an increase in primary production can be compensated by consumption either by increased the feeding rates[31] or increased consumers abundance[36] which stabilize the system. However, climatic stressors may also lead to overconsumption or runaway primary production[25,37,38] which can trigger species domination shifts in marine systems.

Such different responses without understanding the underlying mechanisms responsible for such variation in the feedback interaction under climatic stress renders great difficulty in predicting the state of marine environments under persistent climatic stress. This is exacerbated by the lack of knowledge of whether and how the loss of sensitive species and their replacement by less sensitive species (functional compensation)[39] could affect the stability of marine systems. Additionally, a few herbivorous species are known for their capacity of actively engineering their environment[40], such as marine herbivorous farming damselfishes. Likewise, these herbivorous farming species are able to maintain, modify or create habitats, and control – either directly or indirectly – the resources available to them via a wide range of behavioural strategies[41–44]. Due to their unique ability to modify their habitat such farmers may have the capacity to adapt and persist under intensifying climatic stressors.

Hence, herbivorous farmers can also act as facilitators to promote niche creation and population expansion for themselves and co-occurring species, and bolster species coexistence and ecosystem functioning[45,46]. Such positive relationships have been long-neglected[47] but the necessity to understand how such interactions affect community structure is growing fast[48,49]. Positive interactions become more evident in environments under local and climatic disturbances[50-51,52]. The major problem with the incorporation of positive interactions in species community models lies in the lack of understanding the role of positive interactions in trophic processes, which is one of the most important ecological feedbacks in ecosystems. Trophic processes centre largely on negative interactions, such as producers and consumers regulating each other's populations through bottom-up (production) and top-down (consumption) interactions. Therefore, understanding the effects of positive interactions in food webs, particularly with regards to producer-consumer dynamics, might be the key to recognising whether future communities might resist ecological collapse. This is important because, the intensification of climate disturbances will surely disrupt changes in food web dynamics[28].

Here, I evaluate how ecosystem engineering species and the herbivore functional group could counter-balance and stabilize marine ecosystems against the negative effects of climatic stressors. This was done using empirical data (field observations and experiments) collected at natural volcanic CO_2 vents, which can act as natural analogues of end-of-century environments under a business-as-usual CO_2 emission scenario (RCP 8.5), and from a large and complex mesocosm experiment which housed hundreds of species (1,800 l tanks with >100 species) over six months simulating the effects of future ocean warming and acidification in isolation and combination. The data collected for this thesis is presented in four data chapters.

In the first chapter, I assess how farming and CO_2 enrichment drive changes in crop production and population sizes of a wild animal that farms its food, using field experiments at volcanic CO_2 vents. I studied a common, territorial benthic fish species (*Parma alboscapularis*) that is a specialized farmer and feeds on algal turfs. The densities and behaviour of a farming damselfish (*Parma alboscapularis*) were assessed through in situ observations. Changes in crop productivity within the territories of farms were estimated by measuring biomass and O2 production of algal turfs from habitat cores in control and vents areas. Exclusion experiments separated the effect of farming and CO_2 on algal productivity and biomass.

In the second chapter, I studied the trophic interactions within a three-level benthic marine food web to show how positive interactions under ocean acidification – mediated by animal behaviour – can drive community reshuffling by simultaneously altering bottom-up and top-down process. I used in situ experiments at volcanic CO_2 vents. I studied the trophic interactions between a common territorial herbivorous fish species that is a specialised algal farmer (the ‘keystone’ damselfish *Parma alboscapularis*, which can moderate interspecific interactions), primary production of algal crops within farms, a common algal herbivore (snail), and a common site-attached fish predator (the common triplefin *Forsterygion lapillum*).

In the third chapter, I tested the strength of compensatory dynamics in a marine system of weak to moderate herbivory (i.e. a coast free of urchin barrens). Using a large complex of species harboured in a mesocosms (1,800 l tanks with >100 species) over a long-term (six months) I simulated the effects of future ocean warming and acidification. I assessed whether the various mechanisms of stability (i.e. trophic compensation, density compensation, and functional redundancy) could counter-balance an anticipated boost to primary production by ocean warming and acidification. These tests would indicate the vulnerability or robustness of coasts of lower herbivory to expansion of turfs under future ocean climate.

In the fourth chapter, I used a six months mesocosm experiment to reveal the herbivore community ability to change trophic niche under climatic stress. I also tested if the variations on the herbivores trophic niche would boost, buffer or diminish herbivore community and groups (specialists and generalists) abundance under simulated climate stresses. By revealing the presence/absence of this density compensation mechanism might lead to an understanding of how organisms could better exploit the continuous novelty of opportunity created by climate change on their adaptive advantage.

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CHAPTER II

CO_2 EMISSIONS BOOST THE BENEFITS OF CROP PRODUCTION BY FARMING DAMSELFISH

Statement of Authorship

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Name of Principal Author (Candidate)	Camilo Moitinho Ferreira		
Contribution to the Paper	Designed, built, maintained and performed the experiment; Analysed the data; Wrote the manuscript.		
Overall percentage (%)	80%		
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	22/10/2018

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.

Name of Co-Author	Ivan Nagelkerken		
Contribution to the Paper	Supervised and helped to write the manuscript.		
Signature		Date	10/11/18

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Contribution to the Paper	Supervised and helped to write the paper		
Signature		Date	10/11/18

Please cut and paste additional co-author panels here as required.

Name of Co-Author	Silvan U. Goldenberg		
Contribution to the Paper	Helped to maintain the experiment; Revised and helped to write the manuscript.		
Signature		Date	24.10.2018

ABSTRACT

Farming is a technique employed by both humans and animals to enhance crop yields, allowing their populations to increase beyond the natural carrying capacity of the environment. Whilst populations of many species are forecast to collapse due to the effects of future climate, some species may capitalize on environmental change by actively farming their environment. Here, using manipulative experiments at volcanic CO_2 vents, a natural analogue of future ocean acidification, we investigate how a species of herbivorous fish (the black scalyfin *Parma alboscapularis*) may use increasing anthropogenic CO_2 emissions to enhance its crop yields. We found that these farming fish can take advantage of this resource enrichment, to grow crops within smaller territories and increase the capacity of the environment to support more densely packed fish populations. By taking advantage of resource enrichment, crops could be grown within smaller territories, allowing for more densely packed farmer populations. We reveal that farming can capitalize on CO_2-enriched production of crops to increase the carrying capacity of farms so that populations can densify under an otherwise stressful environment due to climate change.

INTRODUCTION, RESULTS AND DISCUSSION

Population expansion is intrinsically linked to resource availability. Various species are able to maintain, modify or create habitats, and control – either directly or indirectly – the resources available to them (1). Just like humans, such 'ecosystem engineers' can act as facilitators to promote niche creation and population expansion for themselves and co-occurring species, and bolster species coexistence and ecosystem functioning (2).

Climate change is largely considered as a disruptor of ecological processes, triggering regime shifts (3) and accelerated rates of species loss (4). Whilst populations of many species may indeed collapse (5), some species may thrive under environmental changes by actively engineering their environment. As carbon emissions are set to intensify, it is useful to understand whether some species will be able to maintain homeostasis in such novel environments (6). Marine farming by damselfishes enables increased food production within their territories by employing a wide range of behavioural strategies (i.e. weeding, territorial defence, and fertilization; 7-10). Such farmers may have the capacity to adapt to intensifying climatic stressors, allowing for their persistence in a rapidly changing world.

Here, we assess how farming and CO_2 enrichment drive changes in crop production and population sizes of a wild animal that farms its food, using field experiments at volcanic CO_2 vents. We studied a common, territorial benthic fish species (*Parma alboscapularis*) that is a specialized farmer and feeds on algal turfs. Visual surveys showed that the density of farmers at CO_2 vents was double that of controls (Fig. 1a; $F_{1,6} = 19.04$; $p = 0.0047$, Supplementary Table 1), as reflected in both juvenile and adult densities (Supplementary Figure 1; Supplementary Table 2). Farmers were the only herbivorous fish observed during the visual surveys. Whilst farmers contributed only 2.6% and 2.5% to the total benthic fish density at controls and vents, respectively, they were the single species that contributed most to the total biomass at both control (77.9%) and vents (89.5%) (Supplementary Table 3). Territory size of farmers shrunk by almost 67% at vents compared to controls (Fig. 1b; $F_{1,38} = 56.36$; p <

0.0001). Yet, territorial intra- and interspecific agonistic interactions and feeding rates did not differ between controls and vents (Figs. 1c, d). In contrast, algal farming behaviour was more intense at CO_2 vents, with farmers spending twice as much time weeding their considerably smaller territories (Fig. 1e; $F_{1,36} = 6.46$; $p = 0.0152$).

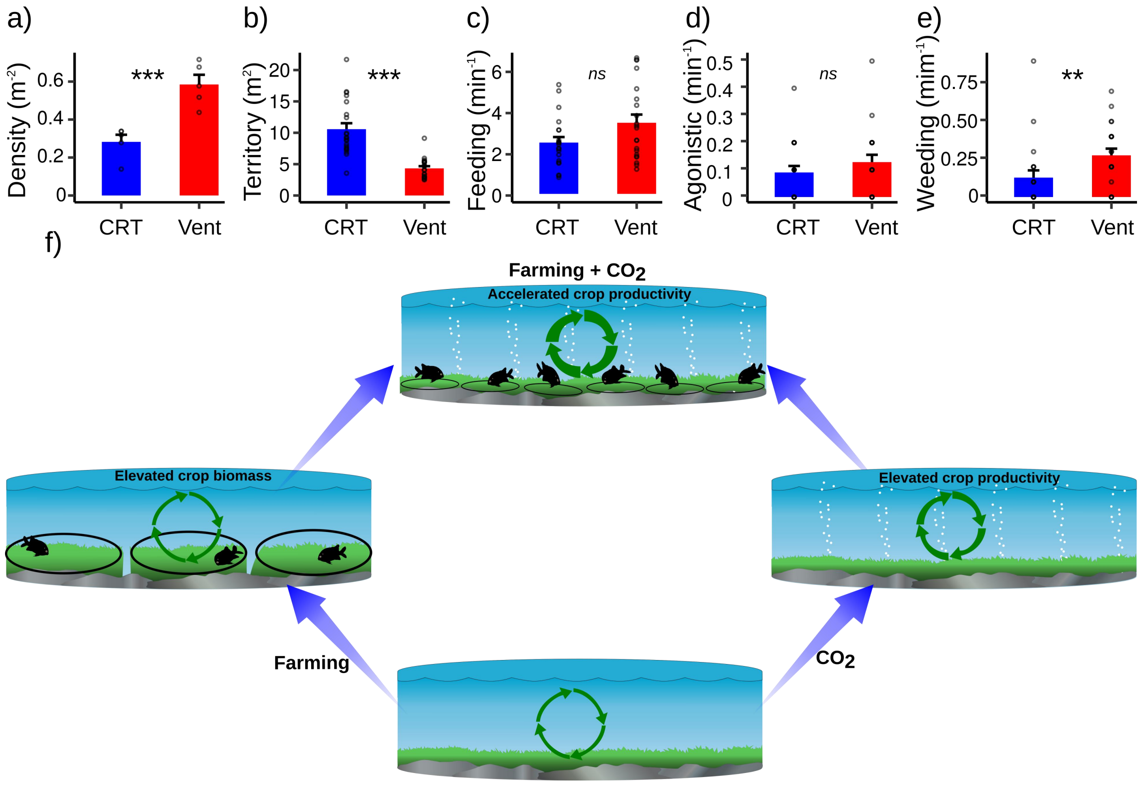

Figure 1. Effect of elevated CO_2 on (a) density (*n* = 5 at each CO_2 treatment), (b) territory size (*n* = 20 at each CO_2 treatment), and principal behaviours (*n* = 20 at each CO_2 treatment) such as (c) feeding rates, (d) agonistic encounters, and (e) weed removal rates. CRT = control, vent = elevated CO_2. Data are represented as mean ± SEM and ANOVA results are shown as: non-significant = ns; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Individual data points for each bar are represented by the small circles. (f) Conceptual diagram showing the individual and combined effects of farming vs. CO_2 enrichment on: i) crop standing biomass (different vertical elevations of green algae), ii) crop productivity rates (width of circular arrows), and iii) territory sizes (width of ellipses).

Exclusion experiments separated the effects of farming from CO_2 enrichment on algal productivity and biomass (see Supplementary Figure 2). Under contemporary CO_2 conditions, farming increased the biomass of turf algae by a factor of 1.5 (Fig. 2, Supplementary Table 4). Under enriched CO_2 conditions, however, farming enhanced productivity rather than standing biomass. Whilst CO_2 enrichment boosted algal productivity fivefold, farming behaviour alone created a twofold increase in productivity. Together, CO_2 enrichment and farming drove a 10-fold enhancement of productivity. No cage effect was observed for algal biomass (procedural control: $F_{1,20} = 0.09$; $p = 0.7660$) or productivity ($F_{1,20} = 0.52$; $p = 0.4773$) (Supplementary Figure 2; Supplementary Table 5), meaning that the observed patterns inside the cages were due to the absence of farmers rather than presence of a metal cage. Whilst algal community composition was similar within farmer territories at vent and control sites at the start of the caging experiment ($F_{1,32} = 0.54$; $p = 0.7202$; Supplementary Table 6) they differed ($F_{1,32} = 7.63$; $p = 0.0002$) at the end of the experiment solely due to the farming effect (Supplementary Figure 3; Supplementary Table 7), and mainly driven by differences in cover of articulated coralline algae ($F_{1,32} = 27.65$; $p = 0.0078$; Supplementary Table 8) and filamentous algae ($F_{1,32} = 43.091$; $p < 0.0001$). Whilst articulated coralline algae cover almost doubled in the absence of farmers, filamentous algae decreased in cover by approximately 40%.

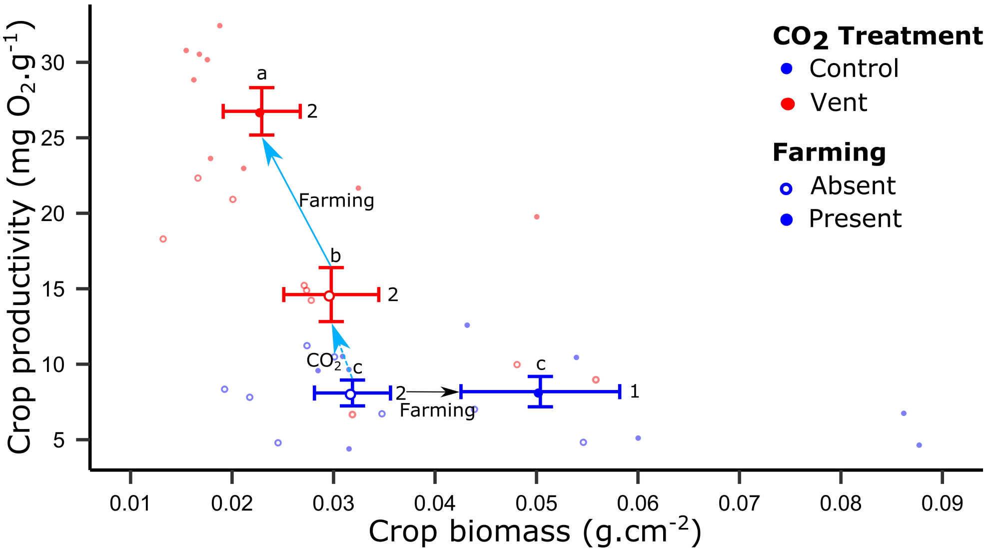

Figure 2. The influence of farming vs CO_2 enrichment on crop biomass and productivity. Farming was allowed (open circles, *n* = 9 at each CO_2 treatment) or excluded (filled circles, *n* = 9 at each CO_2 treatment) at control (dark blue) vs. vent (red) sites. Light blue dotted arrow represents the CO_2 enrichment effect in isolation. Data are represented as means, and error bars represent standard error of the mean. Individual data points for each mean are represented by the small circles. Different letters (for crop productivity) and numbers (for crop biomass) indicate significant differences ($p < 0.05$) based on *a posteriori* comparison of the means (shared letters and numbers indicate no difference).

We show here that the combination of direct (CO_2 nutrient enrichment) and indirect effects (fish behaviour) on algal turf communities can alter the underlying mechanisms of crop productivity; i.e. by swapping enhanced standing biomass with enhanced turnover rates (Figure 1f). In our study, CO_2 enrichment boosted the productivity of algal turfs, reinforcing the notion that CO_2 functions as a natural fertilizer in some marine plants by acting as a resource (*11*), and may drive changes in algal communities. Enhanced resources boost the carrying capacity of the system to support larger population sizes at higher trophic levels (*12,13*), including herbivores that directly benefit from elevated primary productivity (*14*, and this study).

Where CO_2 enrichment enhanced crop productivity, farming acted in synergy to further boost crops. Farming by fish encompasses a range of techniques that enhance standing crop biomass under present-day conditions (*7*). These include: protection of crops against weed proliferation by weeding plants of poor productivity (*8*), defending territories from intruders and competitors (*9*), and fertilization of territories through defecation (*10*). Under CO_2 enrichment, however, farmers altered their farming strategy. They switched from gardening for enhanced biomass to gardening for higher turnover of crops. This increase in productivity allowed farmers to reduce their farm territories, freeing up space that could accommodate more individuals.

Population densification did not increase intra- and interspecific competition – as would be expected – due to the improved efficiency of production of the farms (i.e. via resource enrichment). Aggressiveness and territorial defence form part of animal foraging strategies and are a direct competitive response to limited food availability (*13*). Despite the long-held idea that aggression is usually density-dependent, species can alter their behaviour to ensure an optimal foraging territory and diet in order to maintain energetic homeostasis (*14*). This synergy between CO_2 enrichment and farming increased resource availability (extended carrying capacity) in the system to enable co-existence among individuals and densification around boosted resources without the necessity to intensify agonistic interactions.

Damselfish farmers are one of the most conspicuous herbivorous species across many tropical (*15*) and temperate (*16*) shallow marine environments, with their farms covering a substantial part (25–70% benthic cover) of the substratum in some areas (*17,18*). As such, they can exert a strong influence on benthic community structure and their ecological processes (*19*). For example, farmers damage or weed live corals from their territories and inhibit coral recruitment (*20*). On some reefs, farmers are important sources of coral mortality and through their weeding behaviour they can jeopardize the recovery of coral reefs after disturbances (*21*). In some kelp forest systems, their intense gardening can prevent kelp re-establishment, maintaining temperate reefs in a canopy-free, turf-dominated state (*22*). Yet, farmers can also have positive effects on benthic ecosystems, by boosting primary productivity in areas with low nutrient levels, similar to ants whose farming enhances nutrient and energy fluxes in habitats with poor fertilization (e.g. leaf-cutter ants, *23*).

In conclusion, we show that marine farmers are not demographically impaired by elevated CO_2, but can increase their crop yields to densify their populations under future climate. Human populations have increased dramatically by replacing naturally diverse vegetation with productive monocultures of food; a benefit that is shared with farming fishes who appear set to increase benefits as CO_2 emissions increase.

METHODS

STUDY SITE

Observational and manipulative research was conducted during the summer (February–March 2016) on a rocky reef with CO_2 seeps (i.e. vents) at the volcanic island of White Island, Bay of Plenty, New Zealand. We used two vent and control sites situated on the north-eastern coast where vents emit a CO_2 plume (~ 580 m^2). The difference in pH levels at vent vs. control sites (pH = –0.28 ± 0.06 units; mean ± SD) are similar to those forecast for the year 2100 (~ –0.33 ± 0.003 units) according to an RCP 8.5 emission scenario (business-as-usual). The pH levels at the vent sites are relatively stable over time (Supplementary Table 9). The control sites were selected in an area ~ 25 m away from the vent plume borders. Seawater at the control sites has pH levels similar to contemporary ambient oceanic conditions (Supplementary Table 9). The benthic community at these vents is characterised by the dominance of turf algae < 10 cm in height, whereas that of the control sites constitutes a mosaic of kelp forests (*Ecklonia radiata*), turf algae, and exposed hard-substratum (barren) formed by sea urchin grazing (*24*). Despite the presence of habitat mosaics, territories of damselfish are only associated with turf algae. No differences in turf algal community composition was observed within farmer territories prior to the start of the exclusion experiment (Supplementary Table 6).

CO_2 vents can act as analogues of ocean acidification but also have some limitations. They are restricted in size and known to fluctuate in their CO_2 release, which can potentially alter biological responses (*25*). Spikes in CO_2 release due to vent activity are responsible for occasional drops in pH levels, but these spikes occur on a very short time scale (no longer than a few hours) and do not have a meaningful effect on species behaviour or physiology, which operate at a much broader time-scale. Additionally, the range and diurnal fluctuations of pH at the vents were comparable in magnitude to fluctuations found in other marine environments, including kelp forests, estuaries and upwelling zones (*26*). To overcome the limitation of animals moving in and out of CO_2 plumes, we only used territories that were well inside the plume (i.e. at least 4 m inside the CO_2 plume boundary) or outside (i.e. at least 25 m away from the CO_2 boundary).

SEAWATER CHEMISTRY

Water chemical and physical parameters were sampled *in situ* and used to calculate the CO_2 concentration at both vents and control sites (i.e. temperature, salinity, pHNBS, and total alkalinity (TA)). All water samples (n = 130) were randomly taken at ~ 20 cm from the sea floor where the survey and experiments were performed. The temporal fluctuations of temperature and pHNBS were recorded using a multi-parameter probe and data logger (Sonde 6600V2, YSI; calibrated daily) and the salinity was measured with a SR6 refractometer (Vital Sine). Total alkalinity was measured after water samples had been fixed with mercuric chloride in Duran glass bottles (Schott) in accordance with standard procedures for ocean CO_2

measurements (*27*). Alkalinity was measured using a potentiometric titrator (888 Titrando, Metrohm, USA). Values for standards were maintained within 1% accuracy from certified reference material from Dr A. Dickson (Scripps Institution of Oceanography). To calculate the pCO_2 concentrations the CO_2SYS software (mac version 1.0) with constants K1 and K2 from Mehrbach *et al.* (*28*) and refit by Dickson and Millero (*29*) (Supplementary Table 9) was used. CO_2 and carbonate ion concentrations are not the only water chemistry parameters that can differ from background seawater at vent sites. However, control and vent sites at our study location did not show differences in other seawater parameters or had concentrations (mean ± SD concentrations in ppm) below detection limits (*26*): arsenic (<0.008 vs < 0.008), cadmium (< 0.003 vs < 0.003), iron (< 0.15 vs < 0.15), manganese (< 0.05 vs < 0.05), mercury (< 0.006 vs < 0.006), rubidium (0.12 ± 0 vs 0.11 ± 0), sulfur (475 ± 6.1 vs 472 ± 8.2) and zinc (< 0.006 vs < 0.006) (Supplementary Table 10). During 2016, the total alkalinity was not measured and we used values from previous years (2013, 2015) to calculate pCO_2. Since alkalinity is relatively stable across years (*30*) (Supplementary Table 9) we can ascertain that potential differences in alkalinity between 2016 and previous years would only slightly affect the absolute values of pCO_2 in 2016, but it would not affect the relative differences between controls and vent sites.

FARMER ABUNDANCE

Using stationary visual counts, we estimated the abundances of the territorial farmer, the damselfish *Parma alboscapularis*. Visual estimates were done on SCUBA by a single observer who had a high level of experience visually estimating fish sizes underwater at a fixed period of the day (10 am - 4 pm), since this species have diurnal behaviour with peak activity towards the mid-day and afternoon. For this approach, a 4-m tape marked at 2 m intervals was laid on the substratum to delimit the census area. The 2 m and 4 m marks on the tape represented the radius of two circles in which the total number of fish was counted. Fish counting started approximately 1 min after the tape had been laid down. In order to avoid recounting the same individuals, their abundance was counted during a single 360° body rotation of the observer within the transect (approx. 1–2 min). Inside the smaller circle (2 m radius), total fish lengths (TL) were visually estimated and assigned to one of the following size classes: <2, 2–5, 5–10, 10–20, 20–30, 30–40, and >40 cm, respectively. For the larger circle (2–4 m radius), only animals > 10 cm were counted and assigned to one of the following size classes: 10–20, 20–30, 30–40, and >40 cm, respectively. Consecutively, each individual farmer was assigned to one of two life stages based on their body size: annual recruits and juveniles (TL < 10 cm), and adults (TL > 10 cm). The total number of replicate censuses of farmer algal territories was five at controls and five at vents (3 at vent site A and 2 at site B, and 3 at control site C and 2 at site D), with a total area of ~ 250 m^2 surveyed at each treatment.

To understand the effects of the damselfish populations on the broader community of benthic fish we also estimated the density and biomass of site-attached fishes (e.g. *Chironemus marmoratus, Forsterygion lapillum, Forsterygion varium, Parablennius laticlavius, Notoclinops yaldwyni* and *Notoclinops segmentatus*). The abundance of all benthic site-attached fishes was evaluated in randomly placed quadrats (1 × 1 m) at both control and vent sites (20 replicates per treatment; ~ 5 min per quadrat, with 10 quadrats at each vent site and 10 at each control site). Densities of all benthic fishes were then converted to biomass using length–weight ratios. When species-specific length–weight relationships were not available, those of congeneric or confamiliar coefficients for species from the same biogeographic region were used instead.

FARMER BEHAVIOUR

We estimated the body size, feeding and weed removal rates, agonistic interactions, and territory size of individual damselfish within 10-min observation periods between 10am and 4pm to match species activity period. Feeding rates were quantified by counting the number of bites a farmer took from the substratum. Weed removal was assessed based on the number of times that an individual removed algae from the substratum and disposed of it in the water column. For each agonistic interaction observed, we recorded the fish species involved on the interaction, its body size, the interaction type (e.g. chasing, bites and dorsal exposure), and which species won or lost the competitive interaction. Territory size of the farmers was assessed by dropping lead-weight markers at 1-min intervals at the respective positions that the fish occupied during the preceding time interval so as to not affect the behaviour of the fish. At the end of the behavioural observations, the longest and smallest diameters between all dropped lead weights were measured and then the surface area of an ellipse ($A = \pi * a * b$, with a = shortest radius and b = longest radius) was calculated, representing the territory size of each individual.

Underwater observations were performed during the same time of day (12:00–16:00 h) for all individuals, with samples distributed as evenly as possible between different hours of the day for each control and vent site. A total of 420 min of observations was performed at vent and control sites (n = 42 individuals in total, with 11 at vent site A and 10 at site B and 12 at control site C and 9 at site D, respectively). Animals with territories at the border of the vents were excluded to avoid the possibility of short-term exposure to elevated CO_2 concentration due to constant movement in and out of the CO_2 plume.

CROP PRODUCTIVITY

To separate the effect of farming from CO_2 enrichment on productivity, we compared crop productivity as a function of farming (exclusion experiment) and CO_2 treatment (vent vs controls). To test farming and CO_2 enrichment effects on crop production and standing biomass, we observed algal production among 36 plots (18 at vents and 18 at controls, with 7 at vent site A and 2 at site B and 6 at control site C and 3 at site D, respectively). Eighteen of the 36 plots (9 at vents, 9 at controls) were covered by a cage to exclude damselfish feeding and farming, whilst 18 (9 at vents, 9 at controls) were open plots in which the damselfish was allowed to feed and weed. Cages and open plots each covered an area of substratum of 225

cm^2 (Supplementary Figure 4). The exclusion cages were constructed from reinforced construction metal grid and were covered by wire mesh (12 × 12 mm mesh size), with a total dimension of 15 × 15 × 15 cm. This mesh size was selected because previous studies have shown that this mesh size (if regularly cleaned off fouling algae) does not affect the total light intensity needed for saturation of the photosynthetic rate of a broad variety of algae (*18*). All cages were placed in the centre of the damselfish territories and fixed to the substratum with 2-mm heavy duty multi-filament rope. The cages were scrubbed every 12 days.

Algal crop standing biomass and productivity were measured one month after the deployment of the plots and cages. One core (diameter 4.25 cm) of turf algal habitat was sampled from inside each open plot and cage inside the territories. Core samples from territory boundaries (with no farming effects; n = 5 at vent and control sites, respectively) were collected and acted as procedural controls (i.e. were compared to the cages that excluded farming) to assess cage effects (e.g. alteration in water flow or presence of iron as a nutrient) on algal biomass and productivity (see Supplementary Figure 2). Algal crop productivity was estimated based on oxygen production rates per unit of algal weight ($mg\ O_2.g^{-1}$) measured on board. Algal turfs were placed in air-tight incubation chambers (73 ml) under water and then taken to the boat. To avoid CO_2 desaturation due to photosynthetic activity the chambers were refilled with water of similar pCO_2 concentrations as that of the controls and vents, respectively, prior the start of the productivity measurements. To maintain the chambers' water temperature to ambient seawater temperature (~ 21ºC) we used water baths of which the water was exchanged every 10 min, as well as the chambers rotated position every 10 min (to avoid the effects of shading on algal productivity). Chambers were slightly agitated every 10 min by turning then upside down four times. Strong agitation as suggested by Littler (*31*) was not used to avoid detachment of filamentous algae from turf samples, which could lead to a biased estimation of the biomass of the algal core sample. Baseline respiration was first determined following 30 min dark exposure, followed by net photosynthesis with one hour light exposure (O_2 produced = final $[O_2]$ – initial $[O_2]$), using an oxygen sensor (Fibox 4, PreSens, Germany). For crop standing biomass estimation, the algae from the same cores used for the productivity measurements were oven-dried at 60 °C.

Benthic algal turf community composition was assessed by high-resolution photographs taken at the beginning and end of the exclusion experiment on: open, exclusion and procedural control plots. The photographs were taken from above at a fixed distance of 30 cm from the bottom. The benthic organisms were identified to the lowest taxonomic level possible and subsequently categorised into: (1) filamentous algae; (2) cyanobacteria; (3) *Dictyota* spp.; (4) *Liagora* spp.; (5) *Ulva* spp.; (6) *Stypopodium* spp.; (7) *Turbinaria* spp.; (8) calcareous coralline algae; (9) articulated coralline algae; (10) sponges; (11) ascidians; (12) unidentified macroalgae; and (13) other living animals (e.g. fishes, snails and polychaetes). The relative cover of these 13 groups was estimated using the Coral Point Count with Excel Extensions (CPCe) Software, through the identification of 22 randomly distributed points per image.

DATA ANALYSIS

Differences between CO_2 treatments (control vs. vents) on farmer density, territory size, feeding and weeding activity, as well as agonistic interactions were each tested separately using a two-way ANOVA with site nested in the fixed factor CO_2 treatment. Normality and homoscedasticity were improved by logarithmic or square root transformation. Three-way ANOVAs with CO_2 treatment and farming (cage exclusion) as a fixed factor and site as a nested factor were used to test the effects on (1) crop biomass and (2) crop productivity. Where significant interactions were detected, Student-Newman-Keuls (SNK) multiple comparisons of the means were performed. To test the procedural effects of using cages on (1) crop biomass and (2) crop productivity among the CO_2 treatments we used a three-way ANOVA, with CO_2 treatment and cage presence (i.e., comparing enclosure cages vs procedural controls at the border of farmer territories) as fixed factors and site as a nested factor. To test for differences in benthic cover of algal turf communities between controls and vents, we used a three-way MANOVA with 'CO_2 treatment' and 'farmer presence' as fixed factors and site as a nested factor. This analysis was performed using 4999 permutations and the Bray-Curtis dissimilarity distance. The same analysis was used to show that algal community composition in exclusion and open plots did not differ before the start of the experiment (see Supplementary Table 6). To visualise the similarity of algal turf communities between CO_2 treatments in the presence or absence of farmers at the end of the exclusion experiment, we used a nonmetric multidimensional scaling plot based on a Bray-Curtis distance matrix (see Supplementary Figure 3).

AUTHOR CONTRIBUTIONS

C.M.F, I.N., S.G. and S.D.C. designed the experiment. C.M.F built, maintained and performed the experiment and analysed the data. C.M.F., I.N. and S.D.C. wrote the paper and S.G. contributed to the writing of the manuscript.

DATA AVAILABILITY

The data that support the findings of this study are available from the lead contact Ivan Nagelkerken (ivan.nagelkerken@adelaide.edu.au).

ACKNOWLEDGEMENTS

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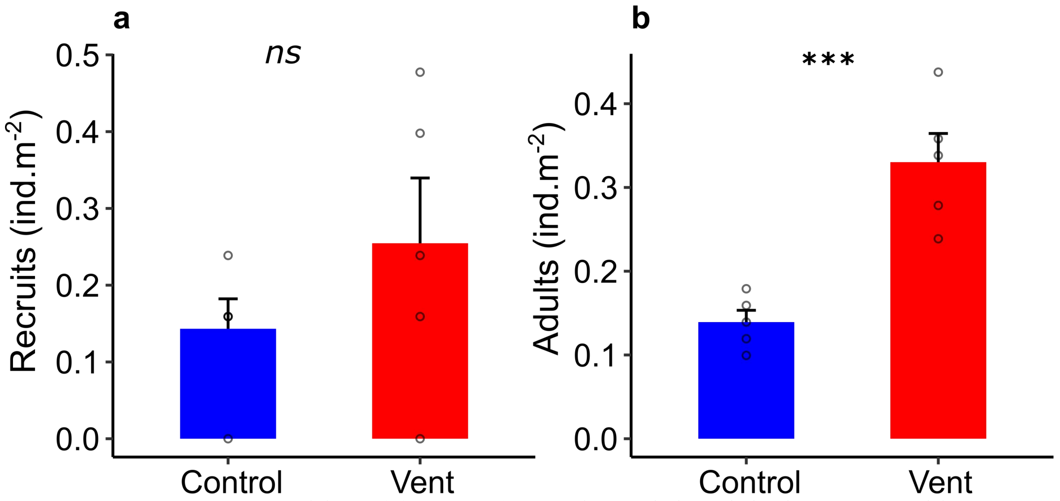
SUPPLEMENTARY INFORMATION

SUPPLEMENTAL DATA ITEMS

Supplementary Table 1. Two-way ANOVA testing for differences in farmer density, territory size, feeding rates, weed removal rates, and agonistic interactions per unit area between ambient CO_2 (control) vs. CO_2 enrichment (vent) treatments, and sites. Significant results are indicated in **bold**.

		df	*MS*	F-value	p
Farmer density	CO_2 treatment	1	0.0211	19.0450	**0.0047**
	Site	2	0.0004	0.3480	0.7193
	Residuals[Site(CO_2 treatment)]	6	0.0012		
Territory size	CO_2 treatment	1	1.1108	56.3640	**<0.0001**
	Site	2	0.0523	1.3260	0.2780
	Residuals[Site(CO_2 treatment)]	38	0.0197		
Feeding rates	CO_2 treatment	1	0.0979	3.5950	0.0656
	Site	2	0.0173	0.6340	0.5358
	Residuals[Site(CO_2 treatment)]	38	0.0272		
Weeding rates	CO_2 treatment	1	0.0311	6.4640	**0.0152**
	Site	2	0.0068	1.4150	0.2555
	Residuals	38	0.0048		
Agonistic rates	CO_2 treatment	1	0.0022	1.1820	0.2840
	Site	2	0.0018	0.9450	0.3970
	Residuals[Site(CO_2 treatment)]	38	0.0019		



Supplementary Figure 1. Densities of farmer (a) recruits and (b) adults between ambient CO_2 (Control) vs. CO_2 enrichment (Vent) treatments. Data are represented as mean ± SEM (Standard Error of the Mean) and codes above bars indicate significant differences between means (*** = $p < 0.0001$; ns = non-significant; see Supplementary Table 2 for output of statistical tests). Individual data points are indicated by the overlaying small circles ($n = 5$ at control and $n = 5$ at vent).

Supplementary Table 2. Two-way ANOVA evaluating the differences in juvenile and adult farmer density between ambient CO_2 (control) and CO_2 enrichment (vent) treatments and site. Significant results are indicated in **bold**.

		df	MS	F-value	p
Recruits	CO_2 treatment	1	0.0035	1.0900	0.3370
	Site	2	0.0018	0.5610	0.5800
	Residuals[Site(CO_2 treatment)]	6	0.0032		
Adults	CO_2 treatment	1	0.0112	27.1730	**0.0019**
	Site	2	0.0003	0.7120	0.5279
	Residuals[Site(CO_2 treatment)]	6	0.0004		

Supplementary Table 3. Densities (individuals per m^2) and biomass (grams per m^2) of the benthic fish community quantified by visual surveys at control and vent sites. The relative contribution (%) of each species to the total benthic fish community is provided based on density as well as biomass. N represents the sampling effort of the visual surveys. Density and biomass of the farmer species are indicated in **bold**.

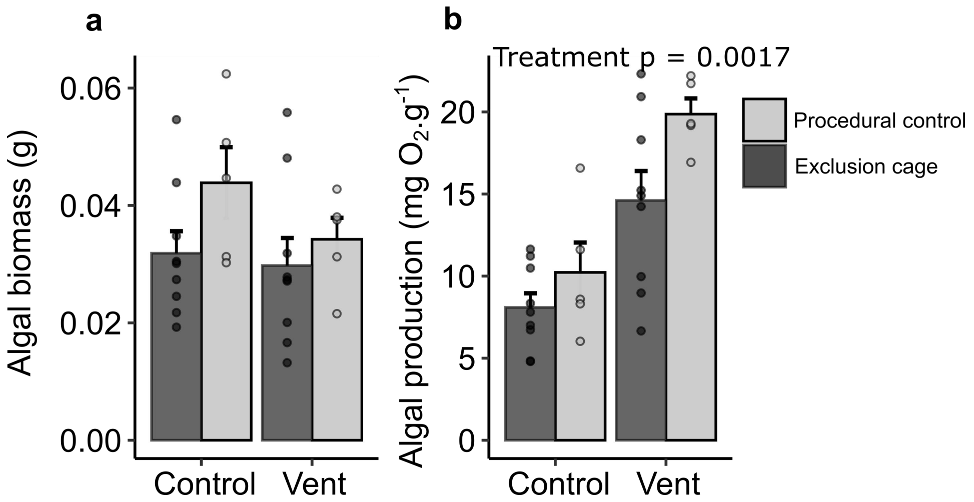
		Control				Vents			
		Density		Biomass		Density		Biomass	
Fish Species	N	Mean ± se	Contribution (%)	Mean ± se	Contribution (%)	Mean ± se	Contribution (%)	Mean ± se	Contribution (%)
Chironemus marmoratus	20	0.05±0.05	0.5	4.65±4.65	8.1	0±0	0	0±0	0
Forsterygion lapillum	20	6.45±0.63	58.7	3.84±0.38	6.7	19.8±2.84	83.9	10.99±1.57	8.9
Forsterygion varium	20	0.95±0.34	8.6	3.18±1.13	5.6	0.25±0.12	1.1	0.84±0.41	0.7
Notoclinops segmentatus	20	0.65±0.20	5.2	0.12±0.04	0.2	0.2 ±0.12	0.9	0.02±0.01	0.02
Notoclinops yaldwyni	20	2.25±0.35	20.5	0.71±0.11	1.2	1.6 ±0.17	6.6	0.53±0.06	0.4
Parablennius laticlavius	20	0.35±0.15	3.2	0.18±0.08	0.3	1.2 ±0.49	5.1	0.62±0.25	0.5
Parma alboscapularis	**5**	**0.28±0.04**	**2.6**	**44.7±4.9**	**77.9**	**0.59 ±0.05**	**2.5**	**111.0±9.62**	**89.5**

Supplementary Table 4. Three-way ANOVA testing for differences in crop biomass (dry weight per cm^2) and crop O$_2$ productivity (maximum algal photosynthetic potential, AP$_{max}$, measured as mg O$_2$ per gram algal weight) between ambient CO$_2$ (control) and CO$_2$ enrichment (vent) treatments and sites, in the presence and absence (fixed factor: farming) of farmers. Significant results are indicated in **bold**.

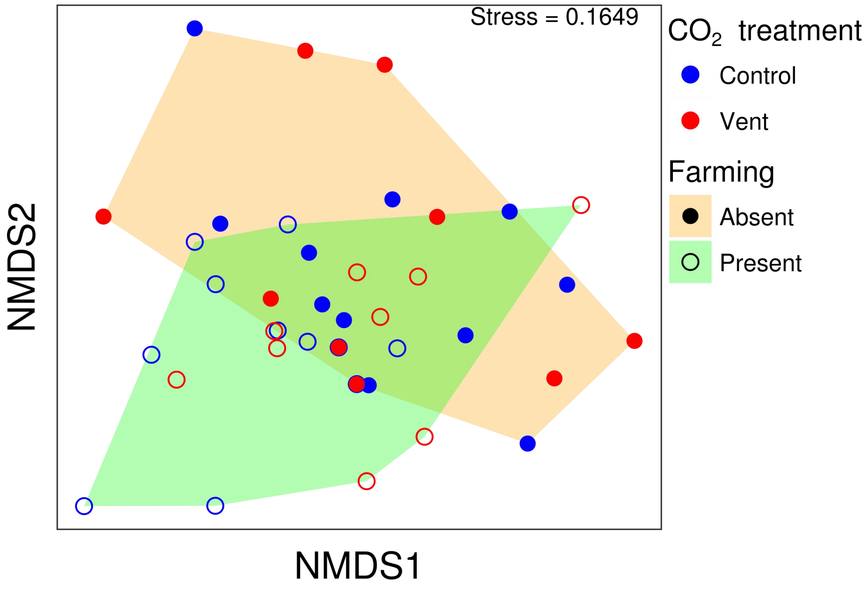
		df	MS	F-value	*p*
Crop biomass (g.cm^{-2})	CO$_2$ treatment	1	0.0003	8.0440	**0.0084**
	Site	2	0.00001	0.2380	0.7910
	Farming	1	0.00005	1.1930	0.2840
	Farming × Site	2	0.00008	1.9100	0.1669
	CO$_2$ treatment × Farming	1	0.0002	5.9499	**0.0220**
	Residuals[Site(CO$_2$ treatment) × Farming]	28	0.00004		
Crop productivity (mg O$_2$.g^{-1})	CO$_2$ treatment	1	1.1745	58.3900	**<0.0001**
	Site	2	0.0013	0.06500	0.9375
	Farming	1	0.1603	7.9680	**0.0087**
	Farming × Site	2	0.0042	0.2070	0.8144
	CO$_2$ treatment × Farming	1	0.1664	8.2740	**0.0076**
	Residuals[Site(CO$_2$ treatment) × Farming]	28	0.0201		

Supplementary Table 5. Three-way ANOVA testing for differences in crop biomass (dry weight per cm^2) and crop O$_2$ productivity (mg O$_2$.g^{-1}) between ambient CO$_2$ (control) and CO$_2$ enrichment (vent) treatments, sites and cage effect (exclusion cage vs. procedural control) as fixed factors. Significant results are indicated in **bold**.

		df	MS	F-value	*p*
Crop biomass (g.cm^{-2})	CO$_2$ treatment	1	0.0013	1.1930	0.2880
	Site	2	0.0013	1.2010	0.3220
	Cage effect	1	0.0027	2.5801	0.1240
	Farming × Site	2	0.0018	1.6730	0.2130
	CO$_2$ treatment × Cage effect	1	0.0001	0.0910	0.7660
	Residuals[Site(CO$_2$ treatment) × Farming]	20	0.0010		
Crop productivity (mg O$_2$.g^{-1})	CO$_2$ treatment	1	8.0850	21.4300	**0.0002**
	Site	2	0.0360	0.0960	0.9084
	Cage effect	1	1.7270	4.5790	**0.0449**
	Farming × Site	2	0.0080	0.0210	0.9791
	CO$_2$ treatment × Cage effect	1	0.1980	0.5250	0.4773
	Residuals[Site(CO$_2$ treatment) × Farming]	20	0.3770		



Supplementary Figure 2. Cage effect for crop (a) biomass and (b) productivity, between ambient CO_2 (Control) vs. CO_2 enrichment (Vent) treatments (n = 5 procedural controls and n = 9 exclusion cages per treatment). Data are represented as mean ± SEM. Error bars represent (Standard Error of the Mean). The small circles indicate individual data points.



Supplementary Figure 3. Multidimensional scaling showing the dissimilarity in the benthic cover composition in ambient CO_2 (Control) and CO_2 enrichment (Vent) treatments in the presence (n = 9 in Control and n = 9 at Vent) and absence (n = 9 in Control and n = 9 at Vent) of farming at the end of the exclusion experiment. Group formation based on the similarity of the benthic composition is highlighted by the polygons in the presence (green) and absence (orange) of farming.

Supplementary Table 6. Three-way MANOVA testing for differences in benthic composition between ambient CO_2 (control) and CO_2 enrichment (vent) treatments, in the presence and absence of farmers (farming) as fixed factors before initiating the farmer exclusion experiment.

	df	SS	F-value	p
CO2 treatment	1	0.0831	1.8967	0.1094
Site	2	0.1679	1.9148	0.0668
Farming	1	0.0237	0.5403	0.7202
Farming × Site	2	0.0363	0.4136	0.9040
CO2 treatment × Farming	1	0.0246	0.5614	0.7020
Residuals[Site(CO_2 treatment) × Farming]	32	1.4025		

Supplementary Table 7. Three-way MANOVA testing for differences in benthic composition between ambient CO_2 (control) and CO_2 enrichment (vent) treatments, in the presence and absence of farmers (fixed factors) at the end of the exclusion experiment. Significant results are indicated in **bold**.

	df	SS	F-value	*p*
CO_2 treatment	1	0.1134	2.0942	0.0824
Site	2	0.0733	0.6774	0.6992
Farming	1	0.4132	7.6326	**0.0002**
Farming × Site	2	0.0431	0.3983	0.8950
CO_2 treatment × Farming	1	0.0263	0.4861	0.7426
Residuals[Site(CO_2 treatment) × Farming]	32	1.723		

Supplementary Table 8. Three-way ANOVA testing for differences in benthic cover of ascidian (AS); articulated coralline algae (ACA); calcareous coralline algae (CCA); cyanobacteria (CY); *Dictyota* spp. (DIC); filamentous algae (FI); *Liagora* spp. (LI); other living animals (e.g. fish, snail and polychaetes) (OT); *Stypopodium* spp. (ST); *Turbinaria* spp. (TU); *Ulva* spp. (UV); unidentified macroalgae (UN); and sponges (SP) between ambient CO_2 (control) and CO_2 enrichment (vent) treatments, in the presence and absence of farmers (fixed factors) at the end of the exclusion experiment. Significant results and are indicated in **bold**, * identifies benthic groups that had significant differences in their cover after Bonferroni p-adjustment.

		df	MS	Pseudo F	p
ACA*	CO_2 treatment	1	1.457	0.392	0.5355
	Site	2	1.734	0.467	0.6311
	Farming	1	31.037	8.357	**0.0069**
	CO_2 treatment × Farming	1	8.0865	2.3216	0.1363
	Site × Farming	2	1.540	0.415	0.6641
	Residuals[Site(CO_2 treatment) × Farming]	32	3.714		
AS*	CO_2 treatment	1	8.9580	5.8030	0.02190
	Site	2	0.5190	0.3360	0.7169
	Farming	1	0.9900	0.0640	0.8020
	CO_2 treatment × Farming	1	0.9250	0.5990	0.4446
	Site × Farming	2	1.2400	0.8030	0.4568
	Residuals[Site(CO_2 treatment) × Farming]	32	1.5440		
CCA	CO_2 treatment	1	0.7800	0.1670	0.6850
	Site	2	4.0350	0.8660	0.4300
	Farming	1	11.5360	2.4750	0.1260
	CO_2 treatment × Farming	1	0.9050	0.1940	0.6620
	Site × Farming	2	0.6640	0.1420	0.8680
	Residuals[Site(CO_2 treatment) × Farming]	32	4.6610		
CYA	CO_2 treatment	1	0.4167	1.1410	0.2930
	Site	2	0.1082	0.2960	0.7460
	Farming	1	0.3409	0.9330	0.3410
	CO_2 treatment × Farming	1	0.4167	1.1410	0.2930
	Site × Farming	2	0.1082	0.2960	0.7460
	Residuals[Site(CO_2 treatment) × Farming]	32	0.3653		

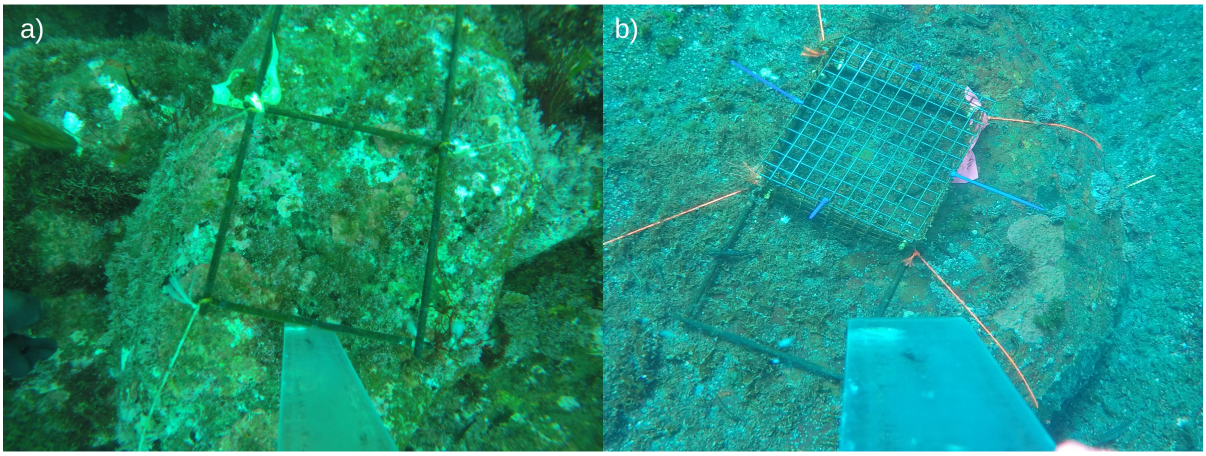
		df	MS	Pseudo F	p
DIC	CO_2 treatment	1	0.0462	0.1240	0.7270
	Site	2	0.1127	0.3020	0.7420
	Farming	1	0.0173	0.0460	0.8310
	CO_2 treatment × Farming	1	0.7042	1.8840	0.1790
	Site × Farming	2	0.1127	0.3020	0.7420
	Residuals[Site(CO_2 treatment) × Farming]	32	0.3737		
FI*	CO_2 treatment	1	0.1900	0.2220	0.6400
	Site	2	1.1400	1.3180	0.2820
	Farming	1	44.9500	52.050	**<0.0001**
	CO_2 treatment × Farming	1	1.1400	1.3200	0.2590
	Site × Farming	2	0.1800	0.2140	0.8090
	Residuals[Site(CO_2 treatment) × Farming]	32	0.8600		
LI*	CO_2 treatment	1	12.9800	7.3750	**0.0106**
	Site	2	0.7640	0.4340	0.6516
	Farming	1	0.1080	0.0610	0.8062
	CO_2 treatment × Farming	1	0.0140	0.0080	0.9301
	Site × Farming	2	2.6110	1.4830	0.2421
	Residuals[Site(CO_2 treatment) × Farming]	32	1.7600		
OT	CO_2 treatment	1	0.0094	0.0110	0.9162
	Site	2	1.1950	1.4290	0.2544
	Farming	1	2.9896	3.5760	0.0677
	CO_2 treatment × Farming	1	1.3250	1.5850	0.2172
	Site × Farming	2	07820	0.9350	0.4029
	Residuals[Site(CO_2 treatment) × Farming]	32	0.8361		
ST*	CO_2 treatment	1	0.7060	1.8420	0.1842
	Site	2	2.0918	5.4570	**0.0091**
	Farming	1	0.0570	0.1490	0.7022
	CO_2 treatment × Farming	1	0.0467	0.1220	0.7294
	Site × Farming	2	0.1383	0.3610	0.6999
	Residuals[Site(CO_2 treatment) × Farming]	32	0.3833		
TU	CO_2 treatment	1	0.1023	0.7480	0.3940
	Site	2	0.0461	0.3120	0.7340
	Farming	1	0.1250	0.9140	0.3460
	CO_2 treatment × Farming	1	0.1023	0.7480	0.3940
	Site × Farming	2	0.0426	0.3120	0.7340
	Residuals[Site(CO_2 treatment) × Farming]	32	0.1367		

		df	MS	Pseudo F	p
UL	CO_2 treatment	1	0.1136	0.7480	0.3940
	Site	2	0.0474	0.3120	0.7340
	Farming	1	0.1389	0.9140	0.3460
	CO_2 treatment × Farming	1	0.1136	0.7480	0.3940
	Site × Farming	2	0.0474	0.3120	0.7340
	Residuals[Site(CO_2 treatment) × Farming]	32	0.1519		
UN	CO_2 treatment	1	0.9099	1.1960	0.2822
	Site	2	0.4802	0.6310	0.5384
	Farming	1	2.3729	3.1190	0.0869
	CO_2 treatment × Farming	1	0.9099	1.1960	0.2822
	Site × Farming	2	0.4802	0.6310	0.5384
	Residuals[Site(CO_2 treatment) × Farming]	32	0.7607		
SP	CO_2 treatment	1	1.0367	2.1290	0.1540
	Site	2	0.2693	0.5530	0.5810
	Farming	1	0.0609	0.1250	0.7260
	CO_2 treatment × Farming	1	0.0744	0.1530	0.6980
	Site × Farming	2	0.0193	0.0400	0.9610
	Residuals[Site(CO_2 treatment) × Farming]	32	0.4870		

SUPPLEMENTAL METHODS ITEMS

Supplementary Table 9. Average (± SE) temperature (T), pH_{NBS}, and total alkalinity (TA; µmol/kg seawater) across years (2013, 2015, 2016) at White Island (extracted from Nagelkerken et al. 2017). Samples were taken over multiple days, during daytime, close to the bottom, and in the same areas as where visual surveys were performed. The first column of N represents that of T, pH, and pCO_2, while the second row of N represents that of TA. * highlights that in 2016 the TA was not measured and the mean TA values from previous years (2013, 2015) were used instead (adapted from Nagelkerken et al. 2017). # = average based of multiple measurements using a YSI 6600v2 sonde.

	2013		2015		2016*	
	Control	Vent	Control	Vent	Control	Vent
T (°C)	19.5 ± 0.5	19.0	21.3 ± 0.1	21.4 ± 0.0	21.0 ± 0.1	21.3 ± 0.1
pH_{NBS}	8.05 ± 0.01#	7.72 ± 0.01#	8.14 ± 0.01	7.84 ± 0.01	8.11 ± 0.01	7.82 ± 0.02
pCO_2	399.0 ± 8.7	988.6	418.8 ± 12.5	948.1 ± 29.0	474.7 ± 14.9	1038.9 ± 113.3
N	2	1	30	30	27	27
TA	2333.0 ± 2.0	2329.0	2244.8 ± 1.2	2242.3 ± 2.5	mean of 2013 and 2015	
N	2	1	4	6	0	0



Supplementary Figure 4. Photos showing (a) an open plot and (b) an exclusion cage.

Supplementary Table 10. Average (± SE) of heavy metals and chemicals at open ocean (OO), control (CTR) and vent (VENT) sites at White Island (extracted from Brinkman & Smith 2015). Samples were taken during the winter at the same areas where visual surveys were performed. Magnesium (Mg), Sulfur (S), Potassium (K), Calcium (Ca), Iron (Fe), Manganese (Mn), Rubidium (Rb), Mercury (Hg), Zinc (Zn), Arsenic (As) and Cadmium (Cd). Significant results are indicated in bold with their respective a posteriori comparisons of the mean (SNK) (adapted from Brinkman & Smith 2015). Some measurements were below detection limits, values are an overestimation and standard deviations could not be calculated. Significant results and are indicated in **bold.**

	OO	CRT	VENT	*df*	SS	*F*-value	*p*	*SNK*
Mg	1440.6 ± 5.6	1482.3 ± 27.6	1477.3 ± 15.3	2	3356	5.463	**0.028**	OO< VENT = CRT
S	455.6 ± 8.1	475 ± 6.1	471.5 ± 8.2	2	13023	72.63	**0.0001**	OO< VENT = CRT
K	455.6 ± 8.1	475 ± 6.1	471.5 ± 8.2	2	674.7	5.58	**0.0265**	OO< VENT = CRT
Ca	513.6 ± 5.1	537.3 ± 12.1	533.1 ± 6.8	2	1016.5	7.912	**0.0104**	OO< VENT = CRT
Fe	< 0.15	< 0.15	< 0.15	N/A	N/A	N/A	N/A	N/A
Mn	< 0.05	< 0.05	< 0.05	N/A	N/A	N/A	N/A	N/A
Rb	0.11± 0.005	0.12 ± 0	0.11 ± 0	2	0.00016	5.344	**0.0295**	OO< VENT = CRT
Hg	< 0.006	< 0.006	< 0.006	N/A	N/A	N/A	N/A	N/A
Zn	< 0.06	< 0.06	< 0.06	N/A	N/A	N/A	N/A	N/A
As	< 0.008	< 0.008	< 0.008	N/A	N/A	N/A	N/A	N/A
Cd	< 0.003	< 0.003	< 0.003	N/A	N/A	N/A	N/A	N/A

CHAPTER III

POSITIVE SPECIES INTERACTIONS STRENGTHEN IN A HIGH-CO_2 OCEAN

Statement of Authorship

Title of Paper	Positive species interactions strengthen in a high-CO_2 ocean.
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Principal Author

Name of Principal Author (Candidate)	Camilo Moitinho Ferreira
Contribution to the Paper	Designed, built, maintained and performed the experiment; Analysed the data; Wrote the paper
Overall percentage (%)	80%
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 22/10/2018

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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ABSTRACT

Negative interactions among species are a major force shaping natural communities, yet positive interactions are predicted to play increasingly important roles as climate change intensifies. We used *in situ* experiments at natural volcanic CO_2 vents to show that under future ocean acidification, positive interactions can drive community reshuffling by altering bottom-up and top-down processes simultaneously through various indirect and direct pathways. A single keystone species (the algal-farming fish, *Parma alboscapularis*) enhanced primary productivity under CO_2 enrichment through its weeding behaviour. The accelerated primary productivity translated into boosted densities of secondary consumers (invertebrate prey, snails), which indirectly supported increased mesopredator densities (benthic fish) (strengthening of bottom-up fuelling). However, this keystone species also directly altered mesopredator densities through behavioural interference, releasing prey from predation pressure and enabling a further boost in prey abundances (weakening of top-down control). We uncover a novel mechanism where a single herbivorous species can mediate bottom-up and top-down processes simultaneously through its behaviour and boost populations of a co-existing herbivore, resulting in altered food-web interactions and predator populations under future ocean acidification

INTRODUCTION

Ecological theory has largely evolved through the lens of negative interactions (e.g. competition and predation). These interactions are considered to propel population dynamics, community structures and species adaptation, shaping a multitude of ecological processes and ecosystem functions in natural environments (Bouche 1985). Whilst the study of negative interactions has driven major advances in ecological theory, it has led to ecologists putting less emphasis on the role of positive interactions (e.g. mutualism and commensalism) that may have effects of the same magnitude (Stachowicz, 2001). However, recent efforts have addressed the long-neglected importance of positive interactions and argued for their incorporation in species population and community models (see Bruno *et al.*, 2003). This effort has propagated new attempts to identify mechanisms that underpin positive interactions and their potential effects at community (Filotas *et al.*, 2010a) and ecosystem (Wright *et al.*, 2017) levels. The incorporation of positive interactions in community structure models allows scientists to better understand the spatial distribution and population dynamics of species, environmental diversity (Filotas *et al.*, 2010a, 2010b), and the susceptibility of natural systems to ecological invasions (Bulleri *et al.*, 2008). The implications and effects of positive interactions are believed to become more evident in environments under disturbance (Malanson & Resler, 2015) and it is set to strengthening under future climate (Kordas *et al.*, 2011; Alexander *et al.*, 2016).

Trophic interactions create some of the most important ecological feedbacks in ecosystems, yet the role of positive interactions in food webs is less studied. Many trophic processes are based on negative interactions where producers and consumers regulate each other's populations through bottom-up (production) and top-down (consumption) interactions, with ensuing consequences for productivity and species diversity of natural systems (Worm *et al.*, 2002). As climatic stress is set to intensify in the near future, changes in food web dynamics are also anticipated (Ullah et al. 2018). Whilst warming often increases the interaction strength between consumers and producers (Bazzaz, 1990, O'connor 2009) – leading to an intensification of top-down control of prey populations (Nagelkerken & Connell, 2015) – producers might capitalise on CO_2 enrichment which acts as a resource to fuel food webs (Connell et al., 2017; Nagelkerken et al. 2017). Therefore, understanding the effects of positive interactions in food webs, particularly with regards to producer-consumer dynamics, might be the key to recognising whether future communities might resist ecological collapse.

Here, we study trophic interactions within a three-level benthic marine food web to show how positive interactions under ocean acidification – mediated by animal behaviour – can drive community reshuffling by simultaneously altering bottom-up and top-down processes. We used *in situ* experiments at volcanic CO_2 vents, which can act as natural analogues of an end-of-century acidified ocean under a business-as-usual CO_2 emission scenario (RCP 8.5). We studied the trophic interactions between a common territorial herbivorous fish species that is a specialised algal farmer (the 'keystone' damselfish *Parma alboscapularis*, which can moderate interspecific interactions), primary production of algal crops within farms, a common algal herbivore (snail), and a common site-attached fish predator (the common triplefin *Forsterygion lapillum*).

METHODS

STUDY SITE

Our observations and experiments were conducted during summer (February–March, 2016 and 2017) on a rocky reef of White Island, Bay of Plenty, New Zealand. This island has a unique natural formation of CO_2 vents. We used two vent and control sites at depths ranging between 6-8 m, situated at the north-eastern coast of the island. The vent sites together have a CO_2 plume dimension of ~580 m^2. The difference in pH levels at vent vs. control sites (Δ pH = –0.28 ± 0.06 units; mean ± SD) are similar to those forecast for the year 2100 (~ –0.33 ± 0.003 units) according to an RCP 8.5 emission scenario (business-as-usual) (Bopp et al. 2013).

The pH levels at the vent sites are relatively stable over time (Table S3). The control sites were located in an area ~ 25 m away from the edge of the vent plume. Seawater at the control sites has pH levels similar to contemporary ambient oceanic conditions (Table S3). The benthic community at these vents is characterised by the dominance of turf algae < 10 cm in height, whereas that of the control sites constitutes a mosaic of kelp forests (*Ecklonia radiata*), turf algae, and exposed hard-substratum (barrens) formed by sea urchin grazing.

Spikes in CO_2 release due to vent activity are responsible for occasional drops in pH levels, but these spikes occur on a very short time scale (not longer than a few hours) and do not have a meaningful effect on species behaviour or physiology which operates at a much broader time-scale. To overcome the limitation of animals moving in and out of CO_2 plumes, we used site-attached species.

SEAWATER CHEMISTRY

Water chemistry and physical parameters (i.e. temperature, salinity, pHNBS, and total alkalinity (TA)) were sampled in situ and used to calculate the $p\mathrm{CO}_2$ concentrations at both vent and control sites. All water samples (n=130) were randomly taken at ~ 20 cm from the sea floor where the survey and experiments were performed. The temporal fluctuations of temperature and $\mathrm{pH}_{\mathrm{NBS}}$ were recorded using a multi-parameter probe and data logger (Sonde 6600V2, YSI; calibrated daily) and the salinity was measured with a SR6 refractometer (Vital Sine). Total alkalinity was measured after water samples had been fixed with mercuric chloride in Duran glass bottles (Schott) in accordance with standard procedures for ocean CO_2 measurements (Dickson et al. 2007). Alkalinity was measured using a potentiometric titrator (888 Titrando, Metrohm, USA). Values for standards were maintained within 1% accuracy from certified reference material from Dr A. Dickson (Scripps Institution of Oceanography). To calculate the $p\mathrm{CO}_2$ concentrations, the $\mathrm{CO_2SYS}$ software (mac version 1.0) with constants K1 and K2 from Mehrbach et al. (Mehrbach et al. 1973) and refit by Dickson and Millero (Dickson & Millero 1987) (Table S5) were used. CO_2 and carbonate ion concentrations are not the only water chemistry parameters that can differ from background seawater at vent sites. However, control and vents sites at our study location did not show differences in other seawater parameters, such as heavy metals and sulphates (Brinkman et al. 2015). During 2016, the total alkalinity was not measured and we used values from previous years (2013, 2015) to calculate pCO_2. Since alkalinity is relatively stable across years (Pearson & Palmer 2000) (Table S3) we can ascertain that potential differences in alkalinity between 2016 and previous years would only slightly affect the absolute values of pCO_2 in 2016, but it would not affect the relative differences between controls and vent sites.

MESOPREDATOR ABUNDANCE

The abundance of the common triplefin (*Forsterygion lapillum*), an important mesopredator of benthic gastropods, was assessed inside and at the border of the farmers' territories during two years (2016 and 2017). The abundances were assessed by taking photos inside and at border of the farming damselfish territories, with each photo covering an area of approximately 0.5 m^2. A total of 40 photos were taken during each year at the vents vs control (20 inside and 20 at the territory border).

PREY ABUNDANCE AND PRIMARY PRODUCTIVITY

To separate the effect of farming, predation and CO_2 enrichment on both invertebrate prey (i.e. herbivorous gastropods) densities and benthic primary productivity we performed an exclusion experiments and we also collected data inside and outside the territories. First, we separated the effect of farming vs. CO_2 enrichment on prey densities and primary productivity. We compared the response of prey densities and turf algal productivity to farming (exclusion experiment) and CO_2 enrichment (vents vs controls). We used 36 plots (18 at vents and 18 at controls) to test farming and CO_2 enrichment effects on prey densities and algal production (calculated as mg of O_2 produced per algal biomass, O_2 $mg.g^{-1}$). Eighteen of the 36 plots (9 at vents, 9 at controls) were covered by a cage to exclude damselfish feeding and farming, whilst 18 (9 at vents, 9 at controls) were open plots in which the damselfish was allowed to feed and weed. Cages and open plots covered a substratum area of 225 cm^2. The exclusion cages were constructed from reinforced construction metal grid and were covered by wire mesh (12 × 12 mm mesh size), with a dimension of 15 × 15 × 15 cm. This mesh size was selected because previous studies have shown that this mesh size (if regularly cleaned off fouling algae) does not affect the total light intensity needed for saturation of the photosynthetic rate of a broad variety of algae. All cages were placed in the centre of the damselfish territories and fixed to the substratum with 2-mm heavy duty multi-filament rope. The cages were scrubbed every 12 days.

Turf algal standing biomass, productivity and gastropods were only assessed during the first exclusion experiment and were measured one month after the deployment of the plots and cages. One core (diameter 4.25 cm) of turf algal habitat was sampled from inside each plot and cage. Core samples from territory boundaries (with no farming effects; n = 10 at vent and control sites, respectively) were collected and acted as procedural controls (i.e. were compared to the cages that excluded farming) to assess cage effects (e.g. alteration in water flow or presence of iron) on algal biomass and productivity. These data were used to assess the effects of farmer presence on mesopredator densities. Algal crop productivity was estimated based on oxygen production rates per unit of algal weight (mg $O_2.g^{-1}$) measured on a boat. Algal mats were placed in air-tight incubation chambers (73 ml) under water and then taken to the boat. To avoid CO_2 desaturation due to photosynthetic activity the chambers were refiled with water of similar pCO_2 concentrations as that of the controls and vents, respectively, prior the start of the productivity measurements. Baseline respiration was first determined following 30 min dark exposure, followed by net photosynthesis with one hour light exposure (O_2 produced = final $[O_2]$ – initial $[O_2]$), using an oxygen sensor (Fibox 4, PreSens, Germany). For algal standing biomass estimation, the algae from the same cores used for the productivity measurements were oven-dried at 60 °C. This same core was also used to sample the abundance of gastropod prey among the plots at vents and controls. All gastropods were collected and quantified from each independent plot.

DATA ANALYSIS

Differences between CO_2 treatments (control vs. vents) and farmer presence (*Parma alboscapularis*) on primary productivity, and prey and mesopredator densities were each tested using a two-away ANOVA. Normality and homoscedasticity were improved by square root transformation. Where significant interactions were detected, Student-Newman-Keuls (SNK) multiple comparisons of the means were performed. To evaluate the causal relationships in our hypothesized interaction model between CO_2 treatments and farmer presence on primary productivity, and on prey and mesopredator densities, we fitted a piecewise structural equation model (SEM). Piecewise SEMs have the capacity to estimate indirect and direct effects as well as causal links within complex networks. Different from traditional SEMs, piecewise SEMs are capable of including nested models, random effects, non-normal distributions, and are less dependent on large sample sizes. Our model was constructed taking the known relationships between all measured variables into account (Table S4). Thus, we specifically predicted an influence of both CO_2 treatments and farmers on primary production. This relationship was then hypothesised as a cascading effect on secondary consumers (invertebrate prey; snails) and tertiary consumers (mesopredator fish). Due to the nature of our samples (26.3% missing data for primary productivity), data imputation was required to perform the piecewise SEM. We replaced the missing data using missForest (NRMSE = 0.055; Table S5), a robust method widely used in medical and human sciences were the presence of missing data is a norm. To ensure and validate the imputation of the data, we randomly generated 10 data tables where 25% of the true data points were randomly excluded from a data matrix with no missing data (missing data were previously excluded) and then compared the data tables containing the imputation with the data set with no missing data using a mixed-effect size analysis using imputation samples and farming presence as fixed factors (Table S6). No difference was found between the 10 data sets where 25% of missing data were imputed and the data set with no missing value (Figure S1; Table S6), allowing us to conclude that the imputation method used was robust and would not have any effect on the findings presented here.

RESULTS

The effect of the keystone farming fish through its behaviours resulted in a strong positive effect on bottom-up processes under both contemporary and future CO_2 conditions. In the presence of the farmers, densities of benthic invertebrate herbivores increased two-fold under contemporary conditions, but with no effects on primary production (Fig. 1a). In contrast, CO_2 boosted primary productivity by almost two-fold, whilst the synergistic effect of elevated CO_2 and farmer's presence resulted in an almost three-fold increase in primary productivity (Fig. 1a, Table S1). This synergism translated to a four-fold increase in density of the invertebrate herbivore (prey) compared to contemporary concentrations of CO_2 in the absence of farmers. This boosted prey density, as a result of elevated CO_2 alone, was associated with a doubling of mesopredator densities (Fig. 1b, Table S1). However, in the presence of the keystone fish under elevated CO_2, mesopredator densities were halved and associated with weaker top-down control. Likewise, keystone fish presence reduced mesopredator densities under ambient CO_2 conditions. Competitive exclusion of mesopredators by the farmers was the underlying mechanism that altered mesopredator densities, reducing prey from predation pressure and enabling a further boost in prey abundances on top of that resulting from boosted bottom-up forcing (increased food).

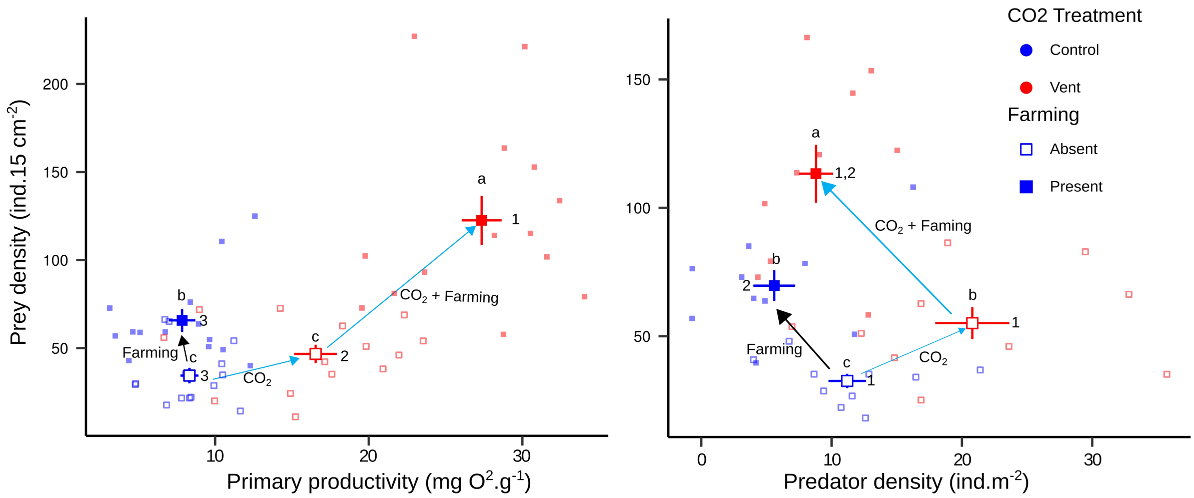

Figure 1. The influence of a keystone (fish) on: (a) bottom-up (primary production) and (b) top-down (competitive exclusion) processes under ambient and future enrichment of CO_2, with cascading effects on mesopredator (benthic fish) and prey abundances (invertebrate herbivores). Error bars represent standard error of the mean. Different letters (for prey abundance) and numbers (for (a) primary productivity and (b) predator densities) indicate significant differences ($p < 0.05$) based on an a posteriori comparison of the means (shared letters and numbers indicate no difference).

We further quantified the interaction strength of CO_2 versus farmer's effects on various bottom-up and top-down processes (Fig. 2). A piecewise structural equation model did not identify missing pathways or any probability that the pathways occurred by chance, supporting an acceptable goodness-of-fit for both the ambient and CO_2 treatment (control: $C_{10} = 2.72$, $p = 0.257$; and CO_2 vent: $C_{10} = 4.87$, $p = 0.087$). Our results show that the keystone fish species had a noticeable positive effect on primary productivity ($R^2 = 0.50$; $p < 0.001$; Table S2) under elevated CO_2. The positive effects of the keystone species on primary productivity consequently had a positive effect ($R^2 = 0.62$; $p < 0.0001$) on invertebrate prey densities. The same keystone species also had a strong negative effect on mesopredator densities in both CO_2 treatments (control: $R^2 = 0.11$; $p < 0.0001$; CO_2 vent: $R^2 = 0.16$; $p < 0.001$). However, this negative effect was 30% stronger under elevated CO_2 than control sites. Whilst mesopredators also had a strong negative influence on prey densities under ambient CO_2 conditions, this effect was negated by the keystone species which indirectly reduced the negative effect of mesopredators on their invertebrate prey by 28% under elevated CO_2.

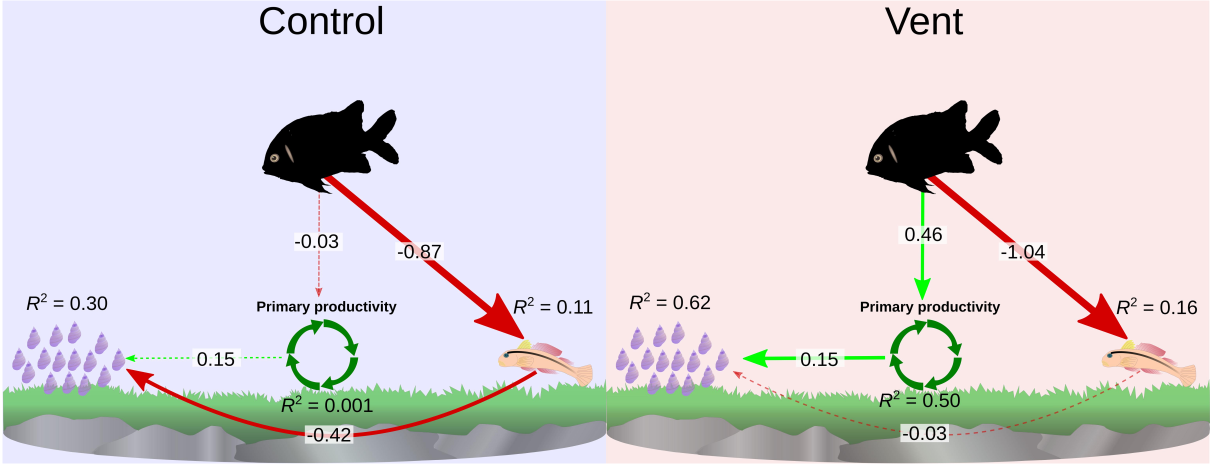

Figure 2. Piecewise structural equation model exploring the individual and combined effects of a keystone species (an algal-farming damselfish) and CO_2 enrichment on: i) primary productivity (circular arrows), ii) prey abundances (invertebrate herbivores: snails), and iii) mesopredators (benthic fish feeding on snails). Arrows represent unidirectional relationships and the strength of each interaction (R^2), with green arrows showing positive relationships and red arrows showing negative ones. Arrows for non-significant paths ($p > 0.1$) were excluded and arrows with near-significant p-values ($0.05 < p < 0.10$) are and dashed. Numbers overlaying the arrows represent the standardized regression coefficients.

DISCUSSION

We here show how a single keystone species, through its behavioural interactions, can modify food web linkages and population sizes of carnivores and herbivores in a high-CO_2 ocean by simultaneously altering bottom-up and top-down processes. The mediating role played by the farming damselfish is not only driven by negative interactions (behavioural displacement of mesopredators), as is normally emphasized in the literature (Paine, 1966). Instead, the alteration in their behaviour (algal weeding) allowed them to capitalize on CO_2 enrichment and enhance primary productivity (Ferreira *et al.*, 2018). The boost in primary productivity fuelled bottom-up process, increasing the carrying capacity of the environment, enabling secondary consumers to increase their densities. This reveals strengthening of a commensal interaction (Hunter & Aarssen, 1988) under elevated CO_2, where one herbivore drives the density increase of another herbivore without gaining any benefits.

CO_2 enrichment can act as a resource to boost primary production (increasing bottom-up forces in natural environments) (Bender *et al.*, 2014) that triggers regime shifts in benthic communities (Connell *et al.*, 2018). However, recent studies in the ocean acidification field have shown that generally the bottom-up effects triggered by CO_2 enrichment are propagated upwards through the food web (Goldenberg *et al.*, 2017; Ullah *et al.*, 2018), and can benefit secondary consumers, even when the metabolic cost of living in such harsh environments are high (Connell *et al.*, 2017). Thus, an increase in bottom-up processes can boost the interaction strength between herbivores and plants maintaining environmental stability and avoiding runaway expansion of primary production (Ghedini et al. 2015). Bottom-up process will play a primary role on how consumer communities will be shaped in future oceans principally under the interaction effect of ocean warming and acidification which could potentially bring natural systems closer to collapse (Ullah *et al.*, 2018). Hence, the mediating effects of keystone species such as damselfishes could help maintain environmental stability by boosting the densities of important functional groups (herbivores).

The farmers excluded mesopredators through its behaviour (negative interaction resulting in a weakening the top-down control) indirectly leading to an increase in prey abundances (positive effect). This mesopredator exclusion forms a critical counterbalance against mesopredator expansion under elevated CO_2 due to reduced abundances of higher-order predators that would keep mesopredators in balance under contemporary conditions (Nagelkerken et al., 2016, 2017). A release of mesopredators from top-down control via reduced population sizes of top predators (trophic cascade; Peterson et al. 2017) in natural systems might have catastrophic outcomes, sparkling a quick depletion of prey densities and in some cases driving them to extinction (Crooks & Soulé, 1999). This negative effect could be more evident in future scenarios due to a mismatch in prey production and predator consumption rates, especially in a warmer ocean (Nagelkerken & Connell, 2015). Yet our study shows that species such as farming damselfish can counter such effects by reducing mesopredator densities when higher-order predators are depleted due to ocean acidification (Nagelkerken et al. 2016). Such complex species interactions can only be revealed by experiments under more natural conditions, but can significantly enhance our understanding of the inherent capacity of nature to buffer ecological change under a changing climate.

In conclusion, we uncover a novel mechanism where a single species can modify – through its behavioural interactions – bottom-up and top-down processes simultaneously. Such mediation effects on food chains can drive alterations to food-web interaction strengths, triggering changes in species communities under ocean acidification. The revelation of this mechanism provides insights into the inherent capacity of complex interactions to buffer environmental stress.

AUTHOR CONTRIBUTIONS

C.M.F, I.N., S.G. and S.D.C. designed the experiment. C.M.F built, maintained and performed the experiment and analysed the data. C.M.F., I.N. and S.D.C. wrote the paper and S.G. contributed to the writing of the manuscript.

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SUPPLEMENTARY INFORMATION

Table S1. ANOVA testing for differences in primary O_2 productivity (maximum algal photosynthetic potential, AP_{max}, measured as mg.O_2 per gram algal weight), prey density (secondary consumers) and mesopredators between ambient CO_2 (control) and CO_2 enrichment (vent) treatments in the presence and absence (fixed factor: farming) of algal farmers. Significant results are indicated in **bold**. * identifies a different data set where mesopredator densities were assessed.

		df	MS	*F*	*p*
Primary productivity (mg O2.g^{-1})	CO_2	1	45.910	149.900	**<0.0001**
	Faming	1	4.060	13.240	**0.0006**
	CO_2:Farming	1	6.080	19.850	**<0.0001**
	Residuals	52	0.310		
Prey (indiv.cm^{-2})	CO_2	1	0.707	42.881	**<0.0001**
	Faming	1	1.504	91.283	**<0.0001**
	CO_2:Farming	1	0.154	9.347	**0.0032**
	Residuals	52	0.017		
*Mesopredator (indiv.m^{-2})	CO_2	1	10.387	11.424	**0.0018**
	Faming	1	19.960	21.952	**<0.0001**
	CO_2:Farming	1	0.258	0.284	0.5974
	Residuals	36	0.909		
*Prey (indiv.cm^{-2})	CO_2	1	37.84	22.371	**<0.0001**
	Faming	1	84.8	50.138	**<0.0001**
	CO_2:Farming	1	0.86	0.57	0.4810
	Residuals	36	1.69		

Table S2. Piecewise SEM coefficients from each pathway and correlated error structures based on a theoretical trophic interaction model for present CO_2 ocean conditions (Control) and future CO_2 concentration (Vent). Significant p-values are indicated in **bold**.

Treatment			Response	Predictor	Estimate	SE	*p*
Control	Fisher.C	11.36					**0.003**
	AICc	39.52	Primary	Farmer	-0.01695288	0.069559009	0.8088
	n	38	Secondary	Farmer	1.03108027	0.209091937	>**0.0001**
	df	2	Secondary	Tertiary	-0.02871711	0.009904783	**0.0065**
			Secondary	Primary	0.16522305	0.077402547	**0.0401**
			Tertiary	Farmer	-0.44527434	0.039922509	>**0.0001**
Vent	Fisher.C	144.55					>**0.0001**
	AICc	173.01	Primary	Farmer	0.23440476	0.04200778	>**0.0001**
	n	37	Secondary	Farmer	1.98788103	0.43846112	**0.0001**
	df	2	Secondary	Tertiary	-0.03817239	0.01622992	**0.0248**
			Secondary	Primary	-0.04663064	0.0640397	0.4717
			Tertiary	Farmer	-0.53083095	0.0365045	>**0.0001**

Table S3. Average (± SE) temperature (T), pH_{NBS}, and total alkalinity (TA; μmol/kg seawater) across years (2013, 2015, 2016) at White Island (extracted from Nagelkerken et al. 2017). Samples were taken over multiple days, during daytime, close to the bottom, and in the same areas as where visual surveys were performed. The first column of N represents that of T, pH, and $p\text{CO}_2$, while the second row of N represents that of TA. * highlights that in 2016 the TA was not measured and the mean TA values from previous years (2013, 2015) were used instead (adapted from Nagelkerken et al. 2017). # = average based of multiple measurements using a YSI 6600v2 sonde.

Year	2013		2015		2016*	
	Control	Vent	Control	Vent	Control	Vent
T (°C)	19.5 ± 0.5	19.0	21.3 ± 0.1	21.4 ± 0.0	21.0 ± 0.1	21.3 ± 0.1
pH_{NBS}	8.05 ± 0.01#	7.72 ± 0.01#	8.14 ± 0.01	7.84 ± 0.01	8.11 ± 0.01	7.82 ± 0.02
$p\text{CO}_2$	399.0 ± 8.7	988.6	418.8 ± 12.5	948.1 ± 29.0	474.7 ± 14.9	1038.9 ± 113.3
N	2	1	30	30	27	27
TA	2333.0 ± 2.0	2329.0	2244.8 ± 1.2	2242.3 ± 2.5	mean of 2013 and 2015	
N	2	1	4	6	0	0

Table S4. Piecewise SEM model specifications focusing on the farmer effect on each trophic group, including transformations (Trans) or distributions (Distrib) used in the model. All models were performed using generalised linear models (GLM).

Treatment	Trophic level	Model	Trans/Distrib	Model variables
Control	Primary	GLM	Square-root	Farmer
	Secondary	GLM	Square-root	Farmer + Primary + Predator
	Tertiary	GLM	Poisson	Farmer
Vent	Primary	GLM	Square-root	Farmer
	Secondary	GLM	Square-root	Farmer + Primary + Predator
	Tertiary	GLM	Poisson	Farmer

Table S5. Variation on the Normalized Root Mean Square Error (NRMSE) of the Random Forest prediction and missing values imputation on 25% of missing values randomly generated from the primary productivity data matrix, this procedure was performed 10 times and is listed as Sample. Final* represents the imputation of primary production missing values that were used to perform the Structural Equation Model.

Sample	Missing Value (%)	NRMSE
1	25	0.0535
2	25	0.0600
3	25	0.0606
4	25	0.0615
5	25	0.0588
6	25	0.0496
7	25	0.0487
8	25	0.0495
9	25	0.0607
10	25	0.0580
Final*	26.3	0.0548

Table S6. Weighted mixed-effects size testing the variation between the 10 samples containing 25% of the data imputed and a control sample were no imputation was used (factor Sample) in the presence and absence of farming (factor Farming). Significant results are indicated in **bold**.

Factor	Heterogeneity		Moderator			Post-hoc tests	
	Q_E	*P-value*	df	F-ratio	P-value	Samples	Farming
Imputation	4.2683	<0.0001	2	140.1629	<0.0001	0.8943	<0.0001

Q_E = Q-statistic for residual heterogeneity; df = nominator and denominator degrees of freedom

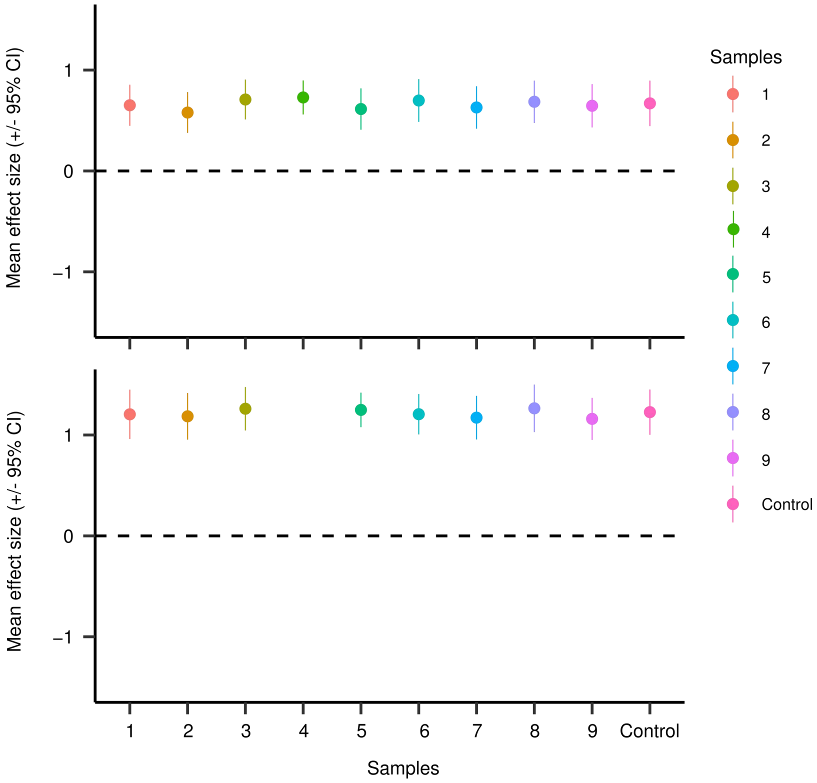

Figure S1. Overall mean effect sizes of the different missing data samples illustrating the variability and range of data imputation on primary productivity.

CHAPTER IV

GENERALISTS ARE BETTER PREPARED FOR OCEAN CHANGE THAN SPECIALISTS

Statement of Authorship

Title of Paper	Generalists are better prepared for ocean change than specialists
Publication Status	☐ Published ☐ Submitted for Publication ☐ Accepted for Publication ☑ Unpublished and Unsubmitted w ork w ritten in manuscript style
Publication Details	

Principal Author

Name of Principal Author (Candidate)	Camilo Moitinho Ferreira		
Contribution to the Paper	Designed, built, maintained and performed the experiment; Analysed the data; Wrote the paper		
Overall percentage (%)	80%		
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	22/10/2018

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.

Name of Co-Author	Ivan Nagelkerken		
Contribution to the Paper	Helped designing the experiment; Supervised and helped to write the manuscript.		
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Contribution to the Paper	Helped designing the experiment; Supervised and helped to write the manuscript		
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Please cut and paste additional co-author panels here as required.

Name of Co-Author	Silvan U. Goldenberg		
Contribution to the Paper	Designed, built, and maintained the experiment; Helped revising the manuscript.		
Signature		Date	24.10.2018

ABSTRACT

To persist environmental change, is it better to be a generalist or specialist? To answer this question, we compare how specialist and generalist marine herbivores adjust their trophic niches to cope with the simulated effects of a future ocean under global change (based on a 6-month mesocosm experiment of ocean warming and acidification). We show, by using isotopes signatures as a proxy to evaluate trophic niche, that whilst both types of herbivores were able to adjust (expand or shrink) their trophic niches in response to ocean change, the biomass of generalists were able to persist as opposed to specialists that collapsed. This collapse occurred even though specialists experienced reduced competition for resources (niche overlap with generalist) and greater resources (abundance of food). If climate change represents a continuous transformation of the environment, which reduces or liberates resources, then these shifting opportunities might best be exploited by species that can adjust to exploit them to their adaptive advantage.

INTRODUCTION, RESULTS AND DISCUSSION

The idea that generalist species are better able to persist in changing environments, whilst specialists are better suited to persist in stable systems has attracted considerable attention[1–5]. This idea is derived from the premise that the flexible nature of generalists allows them to be quickly responsive to change, but the phenotypic rigidity of specialists restricts their response to rapid change[6,7]. Whilst this issue has intrigued those seeking to anticipate the ecological future of changing climate[8,9], there have been few specific tests of this fundamental idea. However, specialist species generally contribute significantly to the total diversity of natural systems and they are also the most abundant in many natural ecosystems[10,11]. Yet, their distribution is confined to narrow pockets of preferential environmental conditions where they can maximise their individual performance[12]. Because their great specificity (narrow niches) and inflexible niche use (low ability to adjust their niche), specialists are highly susceptible to disturbances[2]. Where environmental change is rapid, or intensifies without respite, the probability that specialists will become more vulnerable to population losses or need to evolve to survive (i.e. escape an evolutionary trap[13]) increases. Either way, a broadening niche appears necessarily to survive persistent change.

Separating the niches of generalist vs specialist species has been challenging due to the high-dimensionality and complexity of niches. A niche is defined as a multidimensional environment of abiotic and biotic conditions that a species needs to maintain a self-sustaining population[2]. Because it is difficult to study or quantify an entire species' niche, the most common approach is to simplify a species niche by focusing on one or a few environmental conditions. The trophic niche of species is one of the most frequent niche dimensions studied[14]. This niche is particularly important because it dictates the trophic structure of entire ecosystems and determines the energetic and biomass flows throughout a system[15,16]. Under future climate conditions, species niche are forecast to collapse leading to the persistence of one or a few community members[8,17]. These changes can propagate through food webs[18] and could drive widespread alterations in diversity and abundance of key species[19].

To visualise the influence of climate change on trophic niches and species persistence, we present a conceptual model based on three main premises (figure 1A,B) which can be adapted and used in other studies on niche dimensions and species communities undergoing abrupt environmental disturbances. First, despite species having an inherent capacity of niche flexibility, for many species this might only entail, slight modifications under stressful conditions[7,12,20]; either contributing to population maintenance[21,22] or collapse[8,9]. Second, based on the metabolic theory of ecology[23], environmental change (physical and/or chemical) may lead to an increase in interaction strength between resources and their consumers[24–26], through an intensification of foraging activity due to enhanced metabolic demands and food quality modifications which would secure animal homeostasis[27], and consequently population stability. Third, although specialists generally constitute disproportionately to the overall abundance of natural communities[15,16], this might not apply to all ecosystems.

Using our empirical results we construct a conceptual model that provides an account of the contribution of specialists and generalist to the overall community biomass. We assumed that both specialist and generalist equally contributed to the total abundance of the community in terms of collapses or persistence. We propose that the ability to maintain overall community biomass (figure 1Aii,iii) will rely on: (1) the capacity of either specialists to increase their niche and maintain stable biomass (figure 1B4); (2) generalist to shrink or enlarge their niche and maintain stable biomass (figure 1Bb,f); or (3) collapse of specialists independent of any niche changes (figure 1B2, B5) to be buffered by increases in generalist species independent of any niche changes (figure 1Bc-e). However, increases in the overall community biomass (figure Avi-viii) would be only achieved if both guilds boost their biomass independent of niche flexibility, or one guild would increases their biomass with the same strength as the magnitude of collapse of the other guild.

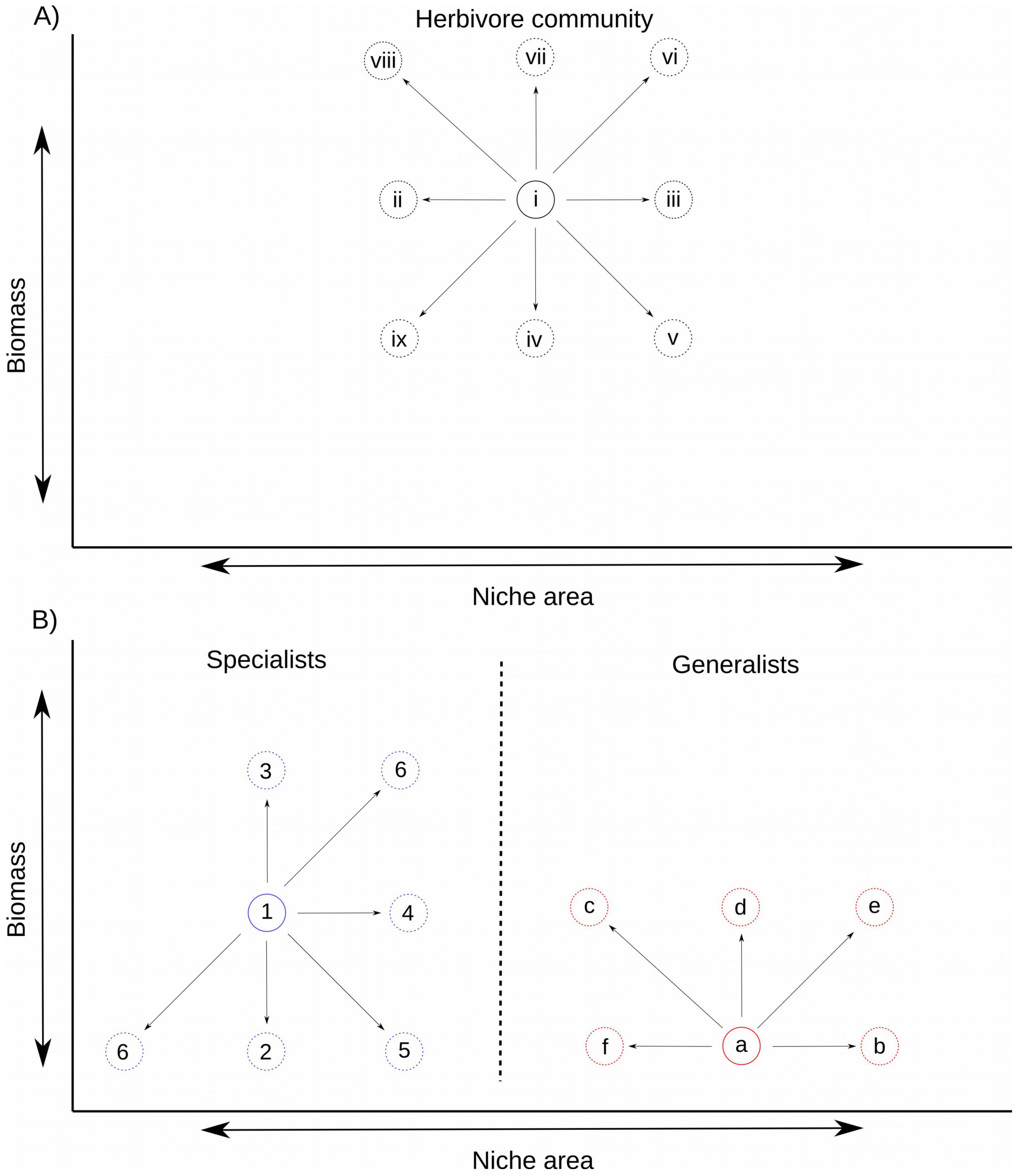

Figure 1. Conceptual model based on the theories of niche conservatism and shift ability[7-9,12,20-22], metabolic ecology of species[23-27] and abundance patterns of the specialist and generalist guilds[10,11] illustrating the effects of niche alteration on biomass under disturbance on (A) a natural community, and (B) the compartments of this community here comprised of specialist and generalist guilds. Components of the community are expected to either maintain their niche (1 and a) or change it to stabilise biomass (4, b and f) resulting in maintenance of overall community biomass (Ai-iii). Yet, when specialist niche modifications fail to prevent biomass loss in this guild (2,5) collapse in overall community biomass is expected (iv, v). If generalist niche changes result in biomass enhancement (c-e), the latter effect could be buffered and community biomass may remain stable (Ai-iii). Overall community biomass will only be able to increase (vi-viii) if one of the guilds (specialists or generalists) can maintain their biomass (1 and 4; a, b and f) while the other thrives independent of niche modifications (3,6; c-e).

To parameterise this conceptual model, we tested whether species of a herbivore community from a natural temperate rocky reef habitat would be able to adjust their trophic niche under the simulated effects of future ocean warming and acidification and how this affected the overall herbivore community biomass. The herbivore community comprised four specialist and five generalist species. Their ability to adjust their trophic, thermal and pH niche and maintain biomass was tested using a 6 months mesocosm with 12 tanks (1,800 l tanks) simulating future ocean warming (elevated temperature: +2.8 °C) and ocean acidification (pH = 7.89; 910 pCO$_2$) based on the end-of-century projections (RCP 8.5[28]). Niche breadth was measured using stable δ^{15}N and δ^{13}C isotope signatures and used to estimate trophic niche area of generalists and specialists within the food web [14,29]. Using a random forest model, we coupled the trophic niche with others niche dimensions (pH and thermal niches) and variables that are recognised to have major impact on population dynamics, such as competition (niche overlap) and resource availability (food). The model was used to evaluate how the biomass of specialist and generalist herbivores might respond to future climate, and the implications for overall grazer community biomass. This experimental approach demonstrated that despite trophic niche plasticity by specialist herbivores this was insufficient to maintain their biomass, and under this collapse generalists were unable to maintain overall community biomass.

Experimental results revealed that the total biomass of the herbivore community declined at elevated temperature treatments (reduction of 41%), especially under the combined effect of ocean acidification and warming (reduction of 71%) when compared to ambient conditions (figure 2A; supplementary table 1). Similarly, specialist total biomass sharply decreases under elevated temperature (by 63%) and this was exacerbated when combined with elevated CO$_2$ (by 75%) (figure 2C). Only one of four taxonomic group of specialists (tanaids) was able to maintain their biomass under all three climate treatments (supplementary figure 1D; supplementary table 2). Generalists, however, appeared to maintain their total biomass under all climate treatments (figure 2E), and one of the five individual taxonomic groups (amphipods) was positively affected by ocean acidification (supplementary figure 1E). Trophic niche area of specialists increased significantly (8%) under ocean warming in isolation, but decreased (21%) under ocean warming combined with acidification (figure 2D). Generalists, in contrast, increased their trophic niche area by 33–28% under both ocean acidification treatments (figure 2F). All taxonomic groups from specialist and generalist guilds showed either significant enlargement or shrinkage of their trophic niche area under the climatic stressors (supplementary figure 2; supplementary table 3). For example, under ocean acidification in isolation had no effect on the trophic niche of two specialists (copepods, and one group of gastropods, gastropods1) and two generalists (fish and shrimps). In contrast, under warming conditions while two specialist taxonomic groups showed increase in their trophic niche, one decreased and the other stay similar to control conditions, two generalist taxonomic groups increased and two reduced their trophic niche. When warming was combined with acidification two specialists and two generalist increased their trophic niche whilst the remaining specialist and two generalist reduced their trophic niche.

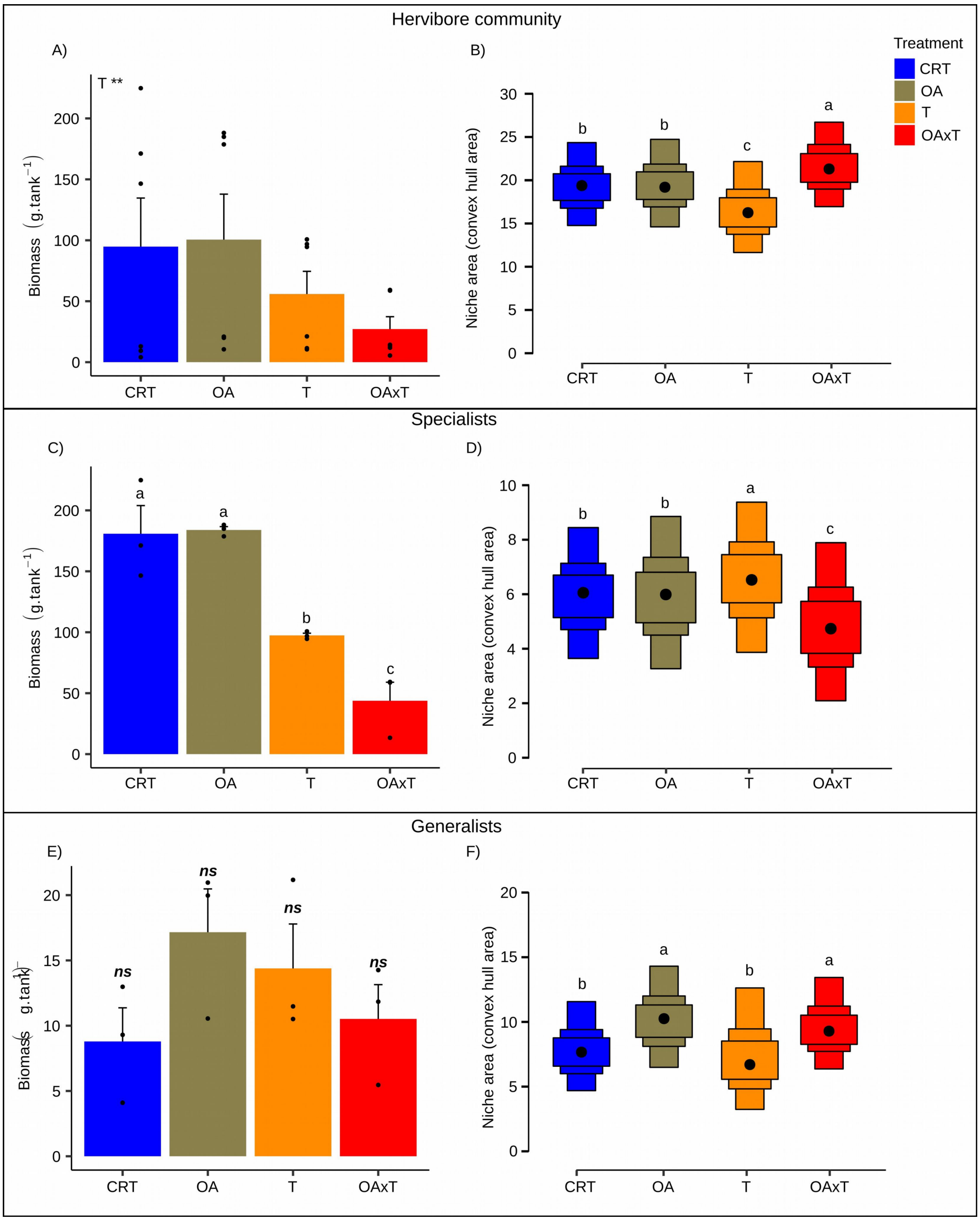

Figure 2. Illustrating biomass and niche area variation on (A,B) the herbivore community, (C,D) specialist and (E,F) generalist guilds between the simulated climate scenarios (CRT: current $p\text{CO}_2$ × current temperature; OA: future $p\text{CO}_2$ × current temperature; T: current $p\text{CO}_2$ × future temperature; OA × T: future $p\text{CO}_2$ × future temperature). (A,C,E) Data are represented as mean ± SEM. Different letters indicate significant differences ($p < 0.05$) and ns no significant differences ($p > 0.05$) based on a posteriori comparison of the means (shared letters indicate no difference). (B,D,F) Black circles in the centre represent the model total area (‰2), and grey boxes represent 50%, 75% and 95% credible intervals respectively. (B,D,F) Figures were produced from 105 Bayesian iterations of the total hull area (TA) of the Layman's metrics. Probability difference between TA within each treatment is demonstrated by small letters (see supplementary table 5 for its probability).

The overlap between trophic niches of specialists and generalists was reduced by climate change: from ~43% (control) to 36–37% (ocean acidification or warming in isolation) to 33% under combined stressors (supplementary table 4). Not only was trophic overlap reduced (i.e. potential competition for food), but also food availability for herbivores increased under acidification (25.6%) and warming (39.5%) in isolation, and even more when climate stressors were combined (138.8%), compared to controls (supplementary figure 3; supplementary table 5).

The random forest model explained 67.3% (p = 0.001) of the community biomass variability. Herbivore guild (specialist vs generalist) was the single-most important predictor variable of simulated community biomass (23% MSE, Figure 3A). The second and third most important predictor variables only explained a modest degree of variability: temperature (8% MSE) and trophic niche area (6% MSE). The random forest model explained 57% (p = 0.003) of specialist biomass with temperature being the single most important predictor variable (15% MSE) (Figure 3B), but was unable to explain variability for generalist biomass (-30%; p = 0.446) (Figure 3C).

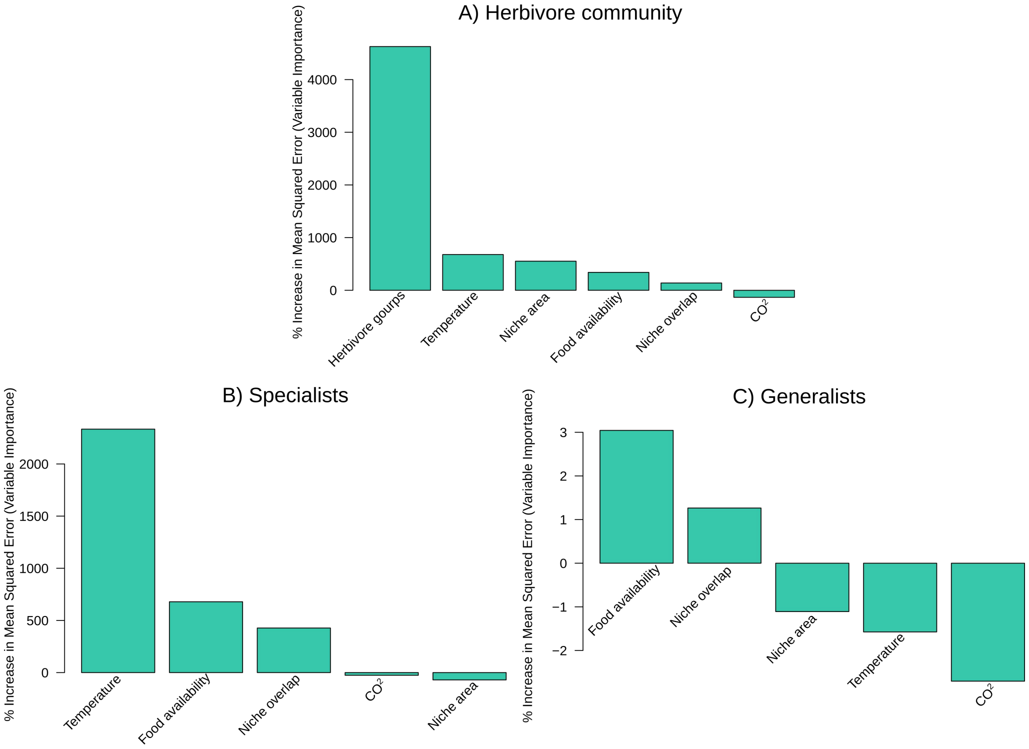

Figure 3. Showing the explanatory variable influence on (A) community, and herbivore guilds (B) specialist and (C) generalist biomass. Explanatory variables used were climate treatments (CO_2 and Temperature), ecological interactions (competition; niche overlap), and food availability.

We show that temperate coastal herbivore communities are able to modify their trophic niches under simulated future climate conditions in a relatively short period of time (six months). The idea that species are unable to change their ecological niches and resources to alternative ones without losing fitness (niche conservatism)[30] is well established and a cornerstone of theory describing species specialisation and evolution[3,31]. Yet, this theory is can be controversial and possibly be misleading in some cases[20,32] and possibly be misleading in some cases[7,21]. Indeed, we suggest that both herbivore guilds were able to modify their niche space under a future climate. However, whilst generalists were able to expand their niche and avoid population biomass losses (shifting niche[7]) under ocean acidification, specialists suffered the deleterious biomass effects (niche conservationism[33]) under elevated temperature, even though they were able to modify their niches. Because specialists were the largest contributor to the overall grazer community biomass, the maintenance of generalist biomass under all future climate treatments was insufficient to maintain overall community biomass. Thus, community biomass collapse would only be avoided if generalists could boost their biomass with the same magnitude as that of biomass collapse of specialists. While several studies in the laboratory and in nature have shown persistence or proliferation of generalists under future climate change, this may not necessarily translate to future maintenance of overall community biomass or biodiversity[34–36].

Specialists were able to expand the breath of their trophic niche under ocean warming as an adaptive response to increased stress, but under further increase of stress levels (i.e. ocean warming and acidification combined) their niche breadth collapsed. Even though specialists experienced relief from competition under this combined stressor treatment (i.e. increased food availability and decreased niche overlap with generalists) this was insufficient to buffer the deleterious effect of temperature on their biomass. Whilst, specialists ability to display scope for acclimatization, principally under thermal stress, due to narrower niche which may minimize the maintenance costs[37-38], they are known to be more rigid and have a low capability to change their niches, and therefore in general may fail to sustain population persistence under environmental disturbance[4,8].

The generalist herbivore community showed no effects of climate disturbances on their biomass. Their ability to modify their niche breadth under both ocean acidification treatments was enough to maintain their individual and but increased their contribution to the community biomass (due to specialist decline), and even showed a trend of increase. Generalists are often stronger competitors[13] and when they are able to maintain or boost their densities a collapse in biodiversity is expected, leading to community homogenisation[8]. The homogenisation of species communities may lead to weakened species interactions, diminishing the recovery capacity of natural systems39 after disturbance and altering the functioning and energy flows within ecosystems [34,35,39]. For example, similar experiments of similar communities showed that the positive effect of CO_2 enrichment on primary production is not propagated within the food web under ocean warming[40] and showed a reduction on energy flow from primary producers to secondary and tertiary consumers[18]. Thus, even though generalist species are able to partly buffer species community biomass, this is still likely to lead to deterioration of ecosystem goods and services.

In conclusion, whilst generalists maintained their biomass by maintaining (Fig. 1Ba) or expanding their trophic niche (Fig. 1Bb), specialists were only able to maintain biomass under ocean acidification in isolation (Fig. 1B1) but collapsed under ocean warming irrespective of whether they increased (Fig. 1B5) or decreased their trophic niche (Fig. 1B6). Hence, because climate change represents a continuous transformation of the environment, which reduces or liberates resources, it creates novel opportunities for those species that can adjust to exploit them to their adaptive advantage.

METHODS

We built and maintained a long-term (six months) mesocosm system at the South Australian Research and Development Institute (SARDI). The system was created to simulate a complex shallow temperate marine ecosystem under future climate change conditions (ocean acidification and warming) scaling up the understanding of abrupt climate change from individuals and organism to community-level responses with the incorporation of multiple drivers, acting alone or in combination[5,41-43]. Increasing the ecological complexity of mesocosm experiments enable the likelihood of buffering processes[44] to be incorporated, contrasting simplified species mixtures that do not include strong interactions that can counter-balance the direct effects of climate change (for further information on the mesocosm set up see the section methods into the supplementary information).

CLIMATE TREATMENTS

Ocean acidification and warming treatments simulated future conditions based on the Representative Concentration Pathway (RCP) 8.5, with a business-as-usual CO_2 emission scenario for the year 2100[28]. We used 12 mesocosm tanks in a crossed design using current water chemical properties with a ~400 ppm pCO_2 concentration equivalent to a pH of ~8.19 units (Control) and predicted future concentration (~900 ppm) with a pH of ~7.89 units (Ocean acidification, OA). Physical water parameters (temperature) were set based on the average Gulf of St. Vincent (South Australia) summer seawater temperatures (21°C) (Control) and a predicted future temperature increase of + 2.8°C (24 °C) (T). The combined interaction of ocean warming and acidification (OAT) used predicted future pCO_2 concentration (~900 ppm) with a pH of ~7.89 units and temperature increase of + 2.8°C (24 °C) ($n = 3$ replicate mesocosm per treatment).

Ocean acidification conditions were maintained for ~6 months to allow for adequate acclimation to elevated temperature and CO_2, rather than measuring short-term shock response to altered water conditions. To achieve the future pCO_2 concentration, seawater was injected with pure CO_2 before flowing into the mesocosm tanks. The target pCO_2 concentration was further maintained by bubbling the seawater in the enrichment tank with CO_2-enriched air (900 ppm) using a gas mixer (PEGAS 4000MF, Columbus Instruments, USA). The 24-hour variation in pH of seawater in each mesocosm was recorded in 30 min intervals using an automated pH logger (Control Units ACQ110, Aquatronica, Italy) for five consecutive days. These measurements were obtained to demonstrate that pH tends to have a small diurnal variation due to community metabolism, similar to subtidal variation found in natural ecosystems (supplementary figure 4). The heaters inside the enrichment bins were used to maintain the target elevated seawater temperature. During the experimental period, the pH and temperature (supplementary figure 5) of seawater were measured daily at a fix time (midday) to avoid pH variability due to community metabolism (respiration/photosynthesis) using a portable pH meter (SG2 SevenGo™, Mettler Toledo, Australia). We measure the alkalinity and salinity using an automated titrator (888 Titrando, Metrohm, Switzerland) and a handheld refractometer (SR6, Vital Sine, China) ($n = 8$ replicates per mesocosm), respectively, every fortnight. The pCO_2, carbonate (CO_{32-}), bicarbonate (HCO_3–) ions, and saturation state (Ω) of calcite and aragonite concentrations were calculated using the CO_2SYS program for Excel24[45] with dissociation constants from Mehrbach et al. (1973)[46] refit by Dickson & Millerro (1987)[47] (supplementary table 8).

PRIMARY PRODUCERS BIOMASS

We used rocky reef as the main benthic structural component and its sessile communities as food source (primary producers) of our mesocosm system. Rock reef was used due to its importance to the formation of coastal habitat around the world and for been the predominant formation on coastal areas of the Gulf St. Vincent. The rocky reef and their sessile biota were randomly collected *in situ* from natural shallow rocky reefs at 0.5–4 m depth. Upon collection, rocky reef rocks were transported fully submerged in seawater to

SARDI facility. At the facility rocks with similar size and algal assemblage composition were positioned on circular (42.5 cm in diameter) plastic modules. The use of modules were preferred to facilitate the sampling of primary producers at the end of the experiment. This modules were then randomly assigned to each mesocosm (*n* = 4 per tank, *n* = 12 per treatment) and positioned on a sand bed.

At the end of the experiment all rocks were scraped to remove all primary producers which were categorized into three major groups: (1) fleshy macro-algae; (2) turf algae (low-growing species less than 2 cm in height); and (3) cyanobacteria. Additionally, sediment organic matter (SOM) was collected from the sand surface (1 mm) of an undisturbed area to maximize the contribution of microalgae (*n* = 2 per tank). Particulate organic matter (POM) was collected by filtering ~500 l (*n* = 2 per tank) of mesocosm water through a 32 µm screen, thus comprising a mixture of phytoplankton, zooplankton and detritus. For the standing biomass estimation, all primary producers were oven-dried at 60 °C until constant weight be reached.

HERBIVORE COMMUNITIES

A few herbivores were introduced in the mesocosm tanks through the construction of the habitat (seven gastropods *Bulla quoyii*, *Thalotia conica*, *Phasianella australis*, *Cantharidus* sp., *Clanculus* sp., and *Turbo undulatus*; two species of top-shell gastropods, S*tomatella impertusa* and *Granata imbricata*; crabs; chitons; and limpets) and the continuous inflow of unfiltered seawater during the experiment (amphipods; copepods; and tanaids). Two herbivore taxon were also introduced in equal numbers in each tank before the experiment start, two fish species *Girella zebra* and *Acanthaluteres vittiger* (*n* = 5 per tank of each species); and shrimps (*n* = 10 per tank).

Due to the high variability and reduced biomass of some taxon induced by the climate treatments, the organism above were aggregated when possible into eight groups following their taxonomic and habitat affinities as follow: (1) amphipods; (2) copepods; (3) crabs; (4) tanaids; (5) shrimps; (6) gastropods^1 (*Bulla quoyii*, *Thalotia conica* and *Phasianella australis*); (7) gastropods^2 (*Cantharidus* sp., *Clanculus* sp., S*tomatella impertusa, Granata imbricata* and *Turbo undulatus*); (8) gastropods^3 (limpets and chitons); and (9) fish (*Girella zebra* and *Acanthaluteres vittiger*).

At the end of the experiment (August 2015), all larger-bodies (< 0.5 cm) individuals were collected and had their size and wet weight measured. Smaller-bodied animals were subsampled through various techniques including sediment cores, artificial habitat units and their mass was estimated using biovolume and their biomass was then extrapolated to entire tank. All organism collected and weighted was oven dry at 60 °C until constant weight be reached and stored desiccated in silica-gel.

ISOTOPES SIGNATURES

Samples for the isotopes signatures were obtained from desiccated organisms (oven-dried at 60 °C until constant weight be reached) collected at the end of the experiment. Small organisms such as micro primary producers (SOM and POM), turf algae, cyanobacteria, copepods, amphipods and tanaids, multiple individuals were aggregated in the same isotope sample to obtain sufficient organic material to perform the isotope analysis. Due to the high variability and low biomass of some taxon induced by the climate treatments, we were unable to balance the sampling effort among the tanks and treatments (see supplementary table 9 for the complete list of the sampling effort).

The isotope samples of small calcifiers (e.g. copepods, amphipods and tanaids) consisted of the entire animal body briefly homogenized in a ball mill. The samples were them divided in two groups, one was decalcified (1 M HCl) for an unbiased estimate of $\delta^{13}C$ and the other remained unmodified to estimate $\delta^{15}N$. For all other animals a small muscle tissue sample was used to obtain the isotopes signatures. All samples were weighed into a tin capsule (0.15-2.5 mg depending on sample type) and combusted in an elemental analyser (EuroVector, EuroEA) coupled to an isotope ratio mass spectrometer (Nu Instruments Horizon) at the University of Adelaide. After correction to internal standards (ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$) signatures were expressed in the conventional δ notation as parts per thousand deviation from international standards. The average error of the analysis was 0.079 ‰ for $\delta^{13}C$ and 0.068 ‰ for $\delta^{15}N$.

DATA ANALYSIS

To classify the herbivores taxonomic groups into two herbivores guilds (specialists and generalist) we first estimated the contribution of primary producers on the dietary proportion of each taxonomic group using a two-factor Bayesian tracer mixed model[50], with climate treatment as a fixed effect (4-levels: C, OA, T and OaxT) and herbivores taxonomic groups as a fixed effect nested in the climate treatments. The herbivores taxonomic groups diet diversity was then calculated using the Simpson's reciprocal diversity index (minimum value of 1 and the maximum value is equivalent to the total number of diet items available, 5). Taxonomic groups with the dietary diversity index values higher than 2 were classified as generalist's and those with values below 2 were grouped as specialists (see supplementary table 10 and supplementary figure 6).

To characterize herbivore community trophic niche breadth in each treatment we used total area for the convex hull (TA; Layman's metrics) based on $\delta^{15}N$-$\delta^{13}C$ bivariate space[49]. Metrics were estimated using Bayesian inference with 10^5 posterior draws – based on the replicate samples within each taxa and compared statistically between climate treatments. Trophic niche breadth of taxonomic groups were estimated through the standard ellipse area corrected for small sample sizes (SEA_c)[49] and compared statistically between climate treatments. Additionally, we calculated the trophic niche overlap between generalist and specialist within treatments to investigate the straighten and release of competitive interactions under climatic stressors.

Two-way ANOVAs with ocean acidification and temperature as fixed factors (each one with two levels, ambient and future conditions) were used to test the treatments effects at the end of the experiment in the (1) community biomass; (2) specialists biomass; and (3) generalists biomass. Additionally, another two-way ANOVA using the same factors was performed to evaluate differences among the treatments for each one of the taxonomic groups. A three-way ANOVA was used to test the variation on primary producers biomass (food availability) between the climate treatments. This analysis treated primary producers groups and climate treatments as fixed factors (CO_2 enrichment and temperature, each with two levels; ambient and future conditions) and mesocosms as a random block factor. Normality and homoscedasticity were improved by logarithmic or square root transformation in all parametric analysis. In case of a significant interaction, Student-Newman-Keuls (SNK) multiple comparisons of means followed.

A random forest regression model[50] was built to predict the overall herbivore community biomass. Using random forest, relationships were identified between the biomass sum of each taxonomic groups per mesocosm tank and seven covariates (temperature, pH, herbivore guilds, total convex hull, niche overlap and food availability). We also built two others random forest models to predict specialist and generalist biomass separately using six covariates (temperature, pH, herbivore guilds, total convex hull, niche overlap and food availability). A total of 1000 regressions trees were used during the random forest procedures and it was followed by a cross-validation using out-of-bag data allowing estimate the prediction performance (R^2) of the model. The regression significance test was performed using 5003 trees and 1000 permutations[50].

All test were performed using the R 3.4.1 and the packages MIXsiar[51], agricolae[52], randomForest[53], rfUnilities[54], SIBER[49] and vegan[55].

AUTHOR CONTRIBUTIONS

C.M.F, I.N., S.G. and S.D.C. designed the mesocosm and the experiments. C.M.F and S.G. built and maintained the mesocosms and performed the experiments. C.M.F analysed the data. C.M.F., I.N. and S.D.C. wrote the paper and all authors contributed to the writing of the manuscript.

DATA AVAILABILITY

The data that support the findings of this study are available from the authors on request; see author contributions for specific data sets.

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SUPPLEMENTARY INFORMATION

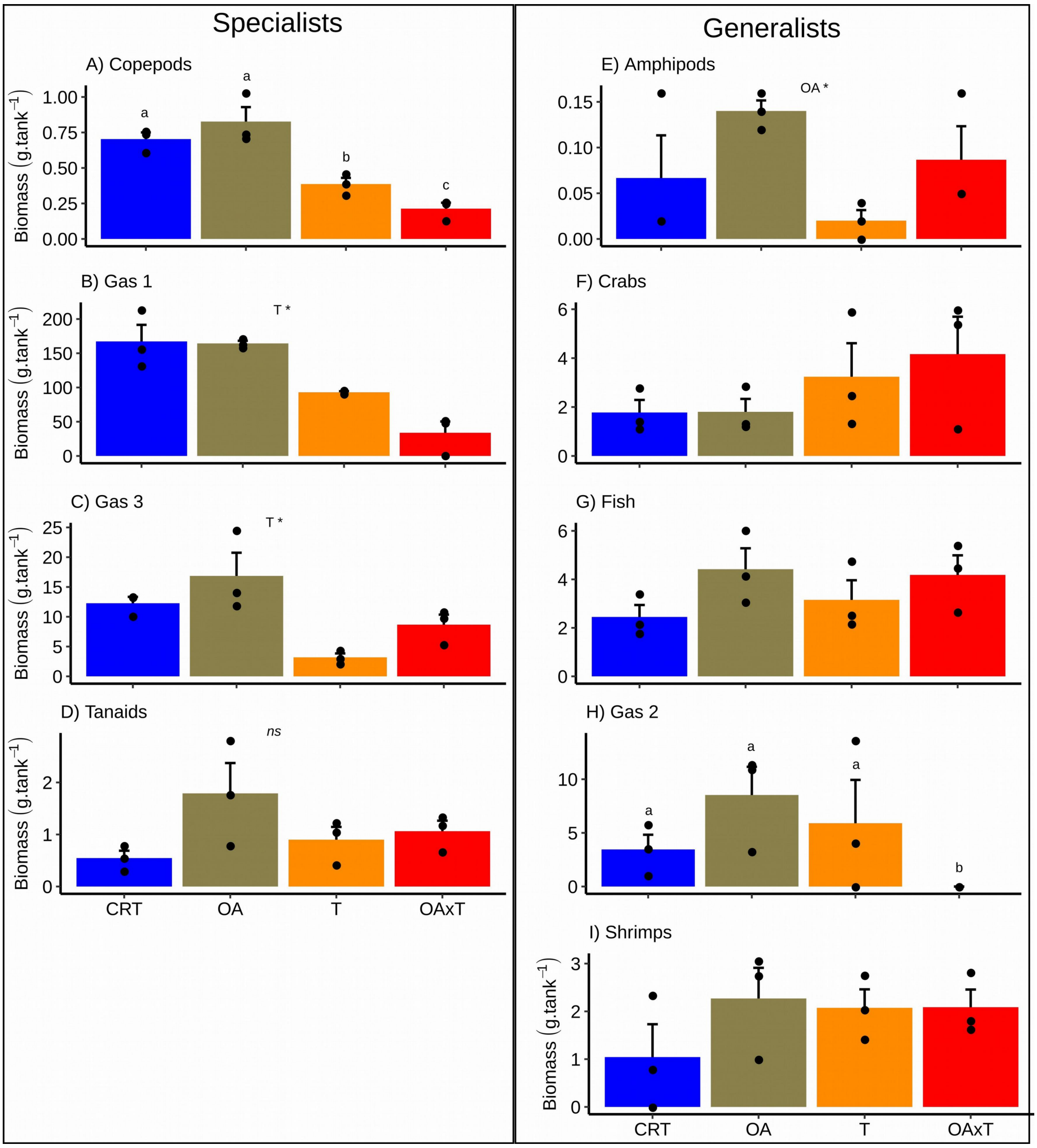
SUPPLEMENTARY RESULTS

Supplementary table 1. Two-way ANOVA with climate treatments as fixed factors demonstrating the difference in total biomass for the herbivore community (Community) and each guild (Specialist and Generalist) between treatments. Significant results are indicated in **bold**.

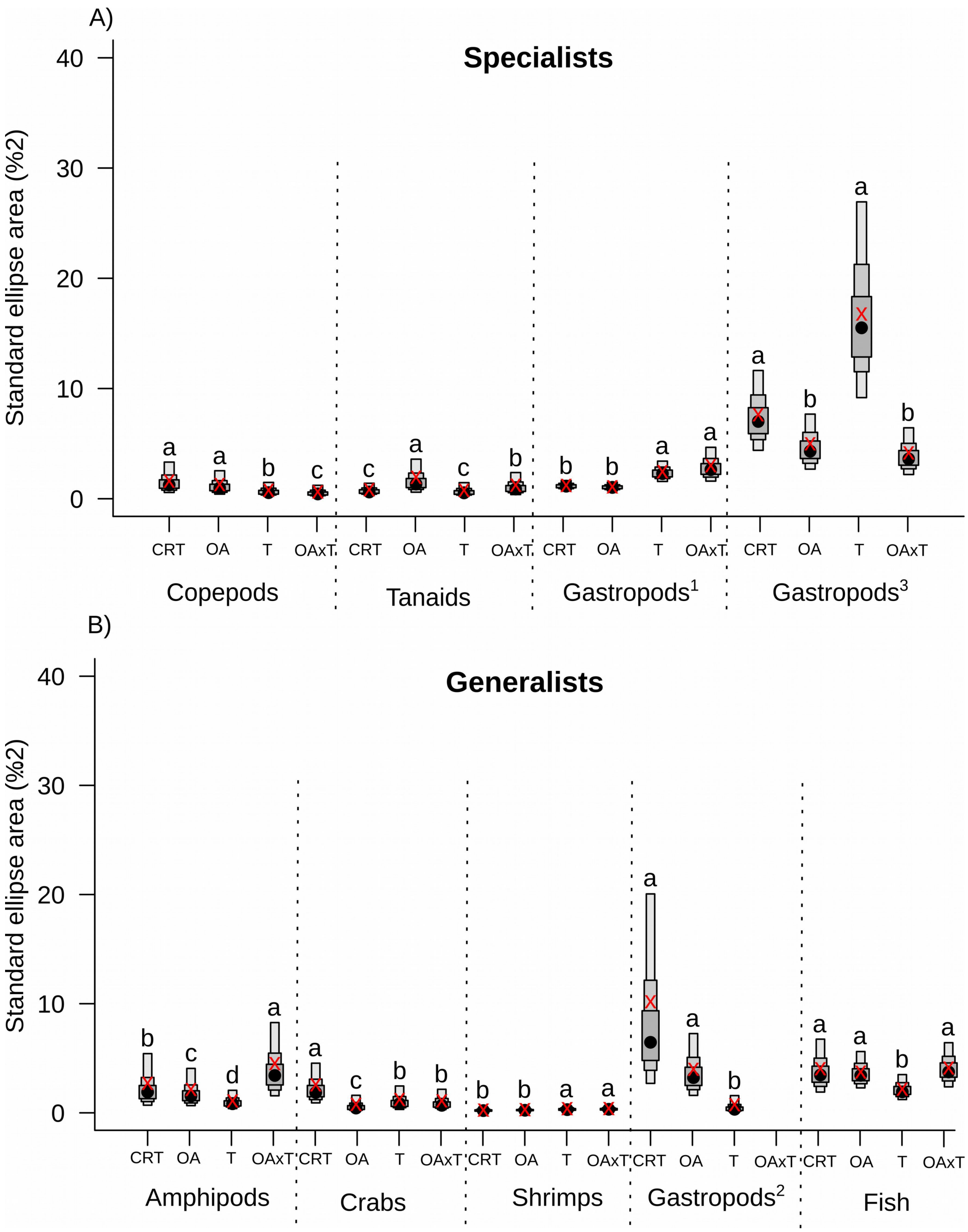
Biomass (g.tank^{-1})		*Df.*	*SS*	*MS*	F-value	p-value
Community	OA	1	6.300	6.300	3.941	0.0824
	Temp	1	76.680	76.680	47.969	**0.0001**
	OA:Temp	1	11.020	11.020	6.896	**0.0304**
	Residuals	8	12.790	1.600		
Specialist	OA	1	9.490	9.490	4.530	0.0660
	Temp	1	89.850	89.850	42.909	**0.0002**
	OA:Temp	1	13.090	13.090	6.251	**0.0369**
	Residuals	8	16.750	2.090		
Generalist	OA	1	0.314	0.3138	0.543	0.4821
	Temp	1	0.003	0.0029	0.005	0.9450
	OA:Temp	1	2.337	2.3366	4.046	0.0791
	Residuals	8	4.62	0.5776		

Supplementary table 2. Two-way ANOVA with climate treatments as fixed factors demonstrating the difference in the biomass of the lowest taxonomic groups of the herbivore community divided in each Specialists and Generalists between treatments. Significant results are indicated in **bold**.

			Df.	*SS*	*MS*	*F-value*	*p-value*
Specialists	Copepods	OA	1	0.0067	0.0067	1.2190	0.3016
		Temp	1	0.3336	0.3336	60.3700	**>0.0001**
		OA:Temp	1	0.0401	0.0401	7.2580	**0.0273**
		Residuals	8	0.0442	0.0055		
	Gas1	OA	1	16.1000	16.1000	4.2660	0.0727
		Temp	1	90.7100	90.7100	24.0400	**0.0012**
		OA:Temp	1	15.4400	15.4400	4.0930	0.0777
		Residuals	8	30.1900	3.7700		
	Gas3	OA	1	76.0500	76.0500	5.1730	0.0525
		Temp	1	223.3400	223.3400	15.1930	**0.0046**
		OA:Temp	1	0.6000	0.6000	0.0410	0.8446
		Residuals	8	117.6100	14.7000		
	Tanaids	OA	1	0.3327	0.3327	4.7990	0.0599
		Temp	1	0.0044	0.0044	0.0630	0.8077
		OA:Temp	1	0.1720	0.1720	2.4820	0.1538
		Residuals	8	0.5545	0.0693		
Generalists	Amphipods	OA	1	0.07419	0.07419	6.752	**0.0317**
		Temp	1	0.0315	0.0315	2.867	0.1289
		OA:Temp	1	0.00039	0.00039	0.035	0.856
		Residuals	8	0.0879	0.01099		
	Crabs	OA	1	0.04	0.04	0.131	0.727
		Temp	1	0.8099	0.8099	2.658	0.142
		OA:Temp	1	0.0336	0.0336	0.11	0.748
		Residuals	8	2.4376	0.3047		
	Fish	OA	1	0.489	0.489	4.188	0.0749
		Temp	1	0.0149	0.0149	0.128	0.7297
		OA:Temp	1	0.0489	0.0489	0.419	0.5355
		Residuals	8	0.9341	0.1168		
	Gas2	OA	1	0.532	0.532	0.454	0.5195
		Temp	1	5.452	5.452	4.653	0.0631
		OA:Temp	1	6.589	6.589	5.623	**0.0452**
		Residuals	8	9.375	1.172		
	Shrimps	OA	1	0.3364	0.3364	1.567	0.246
		Temp	1	0.2571	0.2571	1.197	0.306
		OA:Temp	1	0.3231	0.3231	1.505	0.255
		Residuals	8	1.7177	0.2147		



Supplementary figure 1. Biomass variation on Specialists taxonomic classes: (A) Copepods, (B)Gas^1 (most abundant gastropods), (C) Gas^3 (cryptic gastropods), and (D) Tanaids; and Generalists: (E) Amphipods, (F) Crabs, (G) Fish, (H) Gast^2 (less abundant gastropods) and (I) Shrimps; between the simulated climate scenarios (CRT*:* current pCO$_2$ × current temperature; OA: future pCO$_2$ × current temperature; T: current pCO$_2$ × future temperature; OA × T: future pCO$_2$ × future temperature). Different letters indicate significant differences ($p < 0.05$) and *ns* no significant differences ($p > 0.05$) based on *a posteriori* comparison of the means (shared letters indicate no difference). Main factors that showed a significant effect are highlighted (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Data are represented as mean ± SEM (n =3 per treatment) and individual data points are indicated by small circles.



Supplementary figure 2. Niche area of the smallest taxonomic classes based on corrected Standard Ellipse Areas (SEA_C) for (A) specialist guild: Copepods, Gastropods[1] (most abundant gastropods), Gastropods[3] (cryptic gastropods), and Tanaids; as well as (B) generalist: Amphipods, Crabs, Fish, Gastropods[2] (less abundant gastropods) and Shrimps. CRT = control, OA = ocean acidification, T = elevated temperature, OAT = ocean acidification and elevated temperature). Red x indicate the estimated maximum likelihood of the SEA_C.

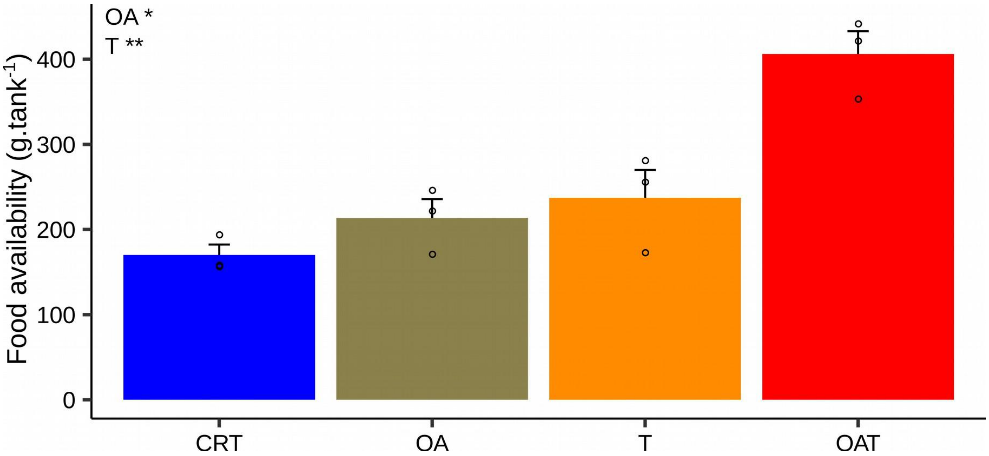
Supplementary table 3. Trophic niche breadth of the overall herbivore community, specialists and generalists guilds based on the distribution of the convex hull area (‰^{2}) based on the Layman's metrics (Niche area*). Additionally, we also provide information on the niche breadth variation between the climate treatments for smallest taxonomic classes of the specialist guild: Copepods, Gastropods^1 (most abundant gastropods), Gastropods^3 (cryptic gastropods), and Tanaids; as well as for generalist: Amphipods, Crabs, Fish, Gastropods^2 (less abundant gastropods) and Shrimps. The niche area ($^{\#}$) of the smallest taxonomic groups were based on corrected Standard Ellipse Areas for small samples (SEA_C), while community, specialists and generalist niche area (*) were based on the Total Convex Hull Area (TA) based on the Layman's metrics. Probability differences between the Bayesian iterations (10^5) of the Standard ellipses Areas (SEA_B) and TA within each treatment are demonstrated by its probability of expansion or retraction. Numbers higher than 0.6 denotes higher expansion or retraction probability and are indicated in **bold**. CRT = control, OA = ocean acidification, T = elevated temperature, OAT = ocean acidification and elevated temperature).

			Area expansion probability			
			CRT	OA	T	OAT
Community		Niche Area*	18.994	18.513	15.372	20.751
		CRT		0.531	**0.7747**	**0.748**
		OA			**0.795**	**0.724**
		T				**0.914**
Specialist	Overall	Niche Area*	6.041	6.015	6.633	4.732
		CRT		0.501	**0.630**	**0.718**
		OA			**0.621**	**0.708**
		T				**0.801**
	Copepods	Niche Area#	1.590	1.282	0.756	0.607
		CRT		**0.700**	**0.914**	**0.957**
		OA			**0.818**	**0.886**
		T				**0.624**
	Gastropods1	Niche Area#	1.199	1.072	2.990	2.442
		CRT		0.369	**0.999**	**0.875**
		OA			**0.999**	**0.918**
		T				0.089
	Gastropods3	Niche Area#	7.611	4.977	16.751	4.150
		CRT		**0.900**	**0.998**	**0.992**
		OA			**1.000**	0.130
		T				**1.000**
	Tanaids	Niche Area#	0.810	1.939	0.752	1.223
		CRT		**0.930**	0.422	**0.766**
		OA			**0.934**	0.239
		T				**0.802**

			CRT	OA	T	OAT
Generalist	Overall	Niche Area	7.084	9.450	6.411	9.095
		CRT		**0.815**	0.569	**0.775**
		OA			**0.822**	0.579
		T				**0.793**
	Amphipods	Niche Area#	2.697	2.128	1.084	4.505
		CRT		**0.641**	**0.885**	**0.769**
		OA			**0.813**	**0.881**
		T				**0.978**
	Crabs	Niche Area#	2.557	0.766	1.216	1.090
		CRT		**0.974**	**0.905**	**0.823**
		OA			**0.776**	**0.737**
		T				0.446
	Fish	Niche Area#	4.031	3.724	2.159	4.096
		CRT		0.467	**0.907**	0.474
		OA			**0.886**	0.516
		T				**0.902**
	Gastropods2	Niche Area#	10.165	3.982	0.736	n/a
		CRT		**0.918**	**0.999**	n/a
		OA			**0.994**	n/a
	Shrimps	Niche Area#	0.247	0.282	0.374	0.383
		CRT		0.582	**0.800**	**0.687**
		OA			**0.786**	**0.625**
		T				0.319

Supplementary table 4. Trophic niche overlap (‰^{2}) between the herbivore guilds, Specialist and Generalist, within the four treatments.

		Trophic niche overlap (‰2)			
		Generalist			
		CRT	OA	T	OAT
Specialist	CRT	42.55			
	OA		37.41		
	T			35.78	
	OAT				32.8



Supplementaty figure 3. Overall effect of climate treatments (CRT: current $p\text{CO}_2$ × current temperature; OA: future $p\text{CO}_2$ × current temperature; T: current $p\text{CO}_2$ × future temperature; OA × T: future $p\text{CO}_2$ × future temperature) on food availability (primary producers biomass) (n =3 per treatment). Data are represented as mean ± SEM and the main factors that showed a significant effect are highlighted (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Individual data points are indicated by small circles.

Supplementary table 5. Three-way split-plot ANOVA following Altman and Krzywinski 2015, with mesocosm tanks (Tank) as a block factor, and climate treatments and primary producers groups (PP) as fixed factors demonstrating the difference in food availability (biomass) between the treatments. Significant results are indicated in **bold**.

		Df.	*SS*	*MS*	F-value	p-value
Food availability (g.tank^{-1})	OA	1	17.864	17.864	10.603	**0.0116**
	Temp	1	42.386	42.386	25.157	**0.0010**
	OA:Temp	1	6.696	6.696	3.974	0.0813
	Residuals[Tank(OA:TEMP)]	8	13.479	1.685		
	PP	4	848.520	212.131	278.014	**<0.0001**
	OA:PP	4	10.520	2.630	3.447	**0.0189**
	Temp:PP	4	126.490	31.622	41.443	**<0.0001**
	OA:Temp:PP	4	28.850	7.213	9.453	**<0.0001**
	Residuals[Tank(OA:TEMP):PP]	32	24.420	0.763		

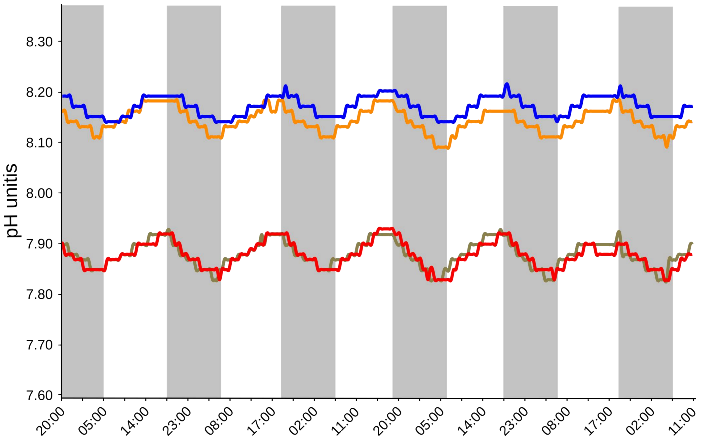
Supplementary table 7. Random forest model (1000 trees with 3 nodes) showing the influence of climate treatments (CO_2 and Temperature), ecological interactions (niche overlap) and food availability on the community and guilds biomass. MSE = Mean Square Error; *MSR* = mean of the square residues. Significance test based on 1000 permutations of 5000 trees. Significant results are indicated in **bold**.

Response variable	Explanatory variable	%MSE	Node Purity	% Variability explained	MSR	Model R^2	Random R^2	Randon R^2 variance	*p*
Community	Herbivore guilds	24.474	50770.985	67.33	1693.968	0.6728505	-0.2512374	0.04135698	**0.001**
	Temperature	8.015	14586.403						
	Niche area	5.934	21716.388						
	Food availability	5.012	11198.651						
	Niche overlap	2.573	8485.231						
	CO_2	-3.697	4296.56						
Specialist	Temperature	15.424	18155.153	56.75	1674.285	0.5510859	-0.3396718	0.07759594	**0.003**
	Food availability	5.906	7216.219						
	Niche overlap	5.472	9360.681						
	Niche area	-0.559	3136.867						
	CO_2	-1.346	1596.07						
Generalist	Food availability	5.077	44.983	-29.64	37.26324	-0.2988213	0.07283376	0.01339848	0.446
	Niche overlap	2.327	45.579						
	Niche area	-1.24	116.977						
	Temperature	-2.736	27.449						
	CO_2	-3.703	45.799						

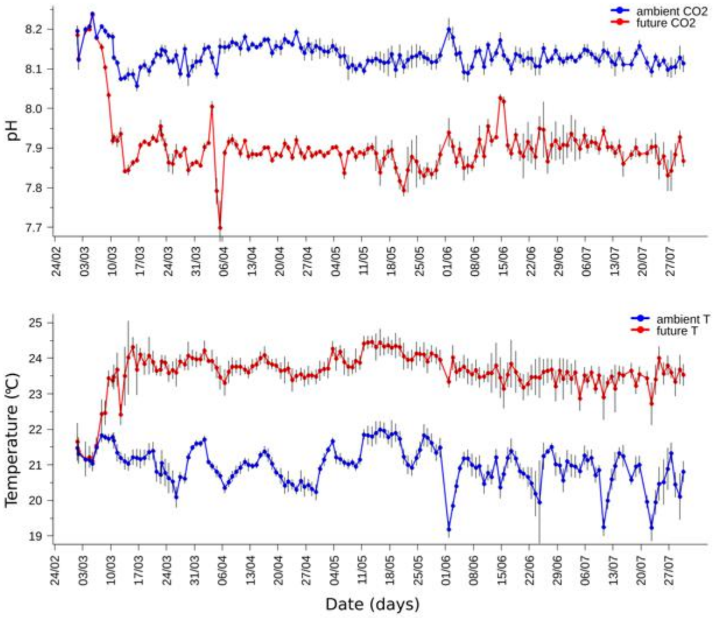
SUPPLEMENTARY METHODS

MESOCOSM DESIGN

The mesocosm system consisted of 12 mesocosm tanks (~1,800 L) held in a controlled temperature room with ambient air temperature set at 23°C, and operated and maintained from February 2015 to August 2015. Water physical and chemical parameters were maintained by 2 CO_2 enriched/Ambient CO_2 header tanks (800 L) and 12 CO_2/temperature enrichment bins (60 L). The two header tanks delivered unfiltred seawater from an offshore pipeline to all mesocosms at a rate of ~2.300 L day^{-1} , while the enrichment bins maintained target temperature and CO_2 values in the mesocosms tanks. Each mesocosm was illuminated by a 250 Watt high-pressure metal halide lamp (Powerstar HQI-T 250 W/D PRO, Osram, Germany), which was mounted at1 m above the mesocosm water surface, with a photoperiod of 14/10 hours of daylight simulating South Australia natural day light conditions in summer (Bureau of Meteorology). This lamp emits similar radiation and light wave length to sunlight, and each mesocosm benthic community received an irradiance of ~60 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR), which corresponds to an average PAR in subtidal areas (~7 m depth) at the Gulf St. Vincent in South Australia[2]. Excess seawater flowed out of the mesocosm through a central filter column (mesh size: ~20 µm) by gravity, and was collected in the adjacent enrichment bin which allowed maintenance of target pCO_2 and temperature in the mesocosm tanks. In the enrichment bin excess water flowed out (~2.300 L day^{-1}) to a drain. Each enrichment bin had two submersible titanium heaters (1 × 300 W, 1 × 500 W) and two pumps (~1.8 m^3 h^{-1}). The pumps were set to turn on and off alternately every six hours so that the seawater was pumped from the enrichment bin back to the mesocosm in opposite directions. The change in the direction of water circulation in the mesocosm simulates a tidal current change mimicking the natural environment, and allowing the entire mesocosm to receive the same water quality over experimental period.



Supplementary figure 4. 24-hr variation in pH of seawater in one mesocosm per treatment for five consecutive days, resulting from community metabolism (respiration and photosynthesis), showing how the tanks mimicked natural diurnal variability. The grey areas indicate night-time.



Supplementary figure 5. The daily variation in (a) pH and (b) temperature across treatments over a 6-month period (mean ± SDM).

Supplementary table 8. Carbonate system parameters of seawater during the experimental period (mean ± SDM). Control: current *p*CO_2 × current temperature; OA: future *p*CO_2 × current temperature; T: current *p*CO_2 × future temperature; OA × T: future *p*CO_2 × future temperature.

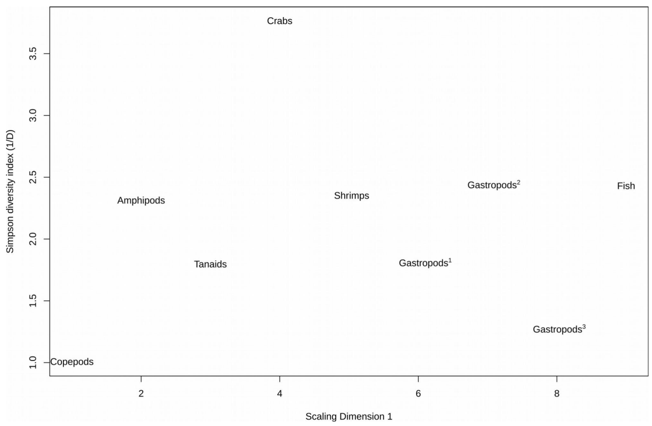
Parameter	Control	OA	T	OA × T
Temperature (°C)	21.0 ± 0.14	20.9 ± 0.04	23.7 ± 0.19	23.7 ± 0.08
pHNBS	8.14 ± 0.004	7.89 ± 0.009	8.12 ± 0.002	7.89 ±0.009
Salinity (ppt)	36.3 ± 0	36.3 ± 0	36.3 ± 0	36.3 ± 0
Total alkalinity (µmol kg–1)	2482 ± 4	2485 ± 5	2486 ± 6	2493 ± 3
pCO_2 (ppm)	465 ± 5	905 ± 6	500 ± 8	915 ± 25
HCO_{3-} (µmol kg–1)	1995 ± 6	2186 ± 3	1985 ± 2	2166 ± 9
CO_{32-} (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

Supplementary table 9. Number of isotopes signature replicates for herbivore and primary producers taxon among each tank of the four climatic treatment. Control: current $p\mathrm{CO_2}$ × current temperature; OA: future $p\mathrm{CO_2}$ × current temperature; T: current $p\mathrm{CO_2}$ × future temperature; OA × T: future$p\mathrm{CO_2}$ × future temperature. SOM = sediment organic matter and POM = particulate organic matter. Total of 543 samples.

Treatment		CRT			OA			T			OAT		
Tank		1	2	3	1	2	3	1	2	3	1	2	3
	Taxon												
Primary producers	Canopy	2	2	4	4	2	2	2	2	4	2	2	2
	Cyanobacteria	2	2	4	2	2	2	2	2	4	2	2	2
	POM	2	2	2	2	2	2	2	2	2	2	2	2
	SOM	2	2	2	2	2	2	4	4	2	2	2	2
	Turf	2	2	2	2	2	2	2	4	4	2	2	2
Herbivore Community	Amphipods	1	2	2	2	2	2	3	0	4	1	2	4
	Copepods	2	2	2	2	2	2	2	2	2	2	2	2
	Crabs	2	1	4	2	1	1	1	2	2	1	3	1
	Fish	6	2	3	5	8	7	8	4	3	3	7	7
	Gastropods1	9	13	9	11	11	9	6	12	9	6	9	0
	Gastropods2	3	0	2	2	2	4	2	1	0	0	0	0
	Gastropods3	5	10	3	5	5	5	4	6	5	7	5	3
	Shrimp	5	0	2	3	5	4	3	3	3	3	3	5
	Tanaids	4	2	2	2	2	2	2	2	2	2	2	2

Supplementary table 10. Simpson's reciprocal diversity index of herbivores taxonomic groups' diet diversity in crescent order. Minimum value of 1 and the maximum value of 5, which is equivalent to the total number of diet items available (primary producers groups).

Guild	Taxon	Simpson's diversity index (1/D)
Specialist	Copepods	1.002
	Gastropods^3	1.264
	Tanaids	1.798
	Gastropods^1	1.801
Generalist	Amphipods	2.307
	Shrimps	2.346
	Fish	2.432
	Gastropods^2	2.439
	Crabs	3.767



Supplementary figure 6. Simpson's reciprocal diversity index dimensional scaling showing herbivores taxonomic groups' dietary diversity.

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CHAPTER V

FUNCTIONAL LOSS IN HERBIVORES DRIVES RUNAWAY EXPANSION OF WEEDY SPECIES IN A NEAR-FUTURE OCEAN

Statement of Authorship

Title of Paper	Functional loss in herbivores drives runaway expansion of weedy species in a near-future ocean.
Publication Status	☐ Published ☐ Accepted for Publication ☑ Submitted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	Submitted to Proceedings of the Royal Society B on 24/09/2018. Status: Under review.

Principal Author

Name of Principal Author (Candidate)	Camilo Moitinho Ferreira		
Contribution to the Paper	Designed, built, maintained and performed the experiment; Analysed the data; Wrote the paper		
Overall percentage (%)	80%		
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		ite	22/10/2018

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.

Name of Co-Author	Ivan Nagelkerken		
Contribution to the Paper	Help designing the experiment; Supervised and helped to write the manuscript.		
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Name of Co-Author	Silvan U. Goldenberg		
Contribution to the Paper	Designed, built, and maintained the experiment; Helped revising the manuscript.		
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Name of Co-Author	Georgia A. C. Walden		
Contribution to the Paper	Maintained the experiment; Helped revising the manuscript.		
Signature		Date	21.11.2018

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Contribution to the Paper	Maintained the experiment; Helped revising the manuscript.		
Signature		Date	21-11-2018

ABSTRACT

The ability of a community to absorb environmental change without undergoing structural modification is a hallmark of ecological resistance. The recognition that species interactions can stabilize community processes, has led to the idea that the effects of climate change may be less than what most considerations currently allow. Here we tested whether herbivory can compensate for the expansion of weedy algae triggered by CO_2 enrichment and warming. Using a long-term mesocosm experiment, we show that increasing per capita herbivory by gastropods absorbs the boosted effects of CO_2 enrichment on algal production in temperate systems of weak to moderate herbivory. However, under the combined effects of acidification and warming this compensatory effect was eroded by reducing the diversity, density and biomass of herbivores. This loss of functionality combined with boosted primary productivity drove a fourfold expansion of weedy algae species. Our results demonstrate capacity to buffer ecosystems against CO_2 enrichment, but loss of this capacity through ocean warming, driving significant algal turf expansion. Identifying compensatory processes and the circumstances under which they prevail could potentially help manage the impacts of ocean warming and acidification, which are further amplified by local disturbances such as habitat loss and herbivore over-exploitation.

INTRODUCTION, RESULTS AND DISCUSSION

Natural systems tend to persist over long periods of time (e.g. kelp forests and coral reefs) despite near continuous environmental change[1–3], but where they collapse, change is likely to favour faster growing and opportunistic competitors, often considered as 'weedy' species[4]. A major research challenge centres on identifying stabilising mechanisms[5] that could adjust to variation in strength and persistence of environmental change allowing natural systems to resist collapse[6]. As an internal dynamic of ecosystems, stabilizing mechanisms gravitate around compensatory processes that generally involve species interactions that are able to stabilize environmental productivity and diversity[7]. Compensatory dynamics may not only stabilize ecosystem properties by adjusting species densities (i.e. density compensation)[8] or replacing lost species by functional equivalents (i.e. functional compensation)[9] but also via changes to interaction strengths among species that have disproportionate control over community processes (i.e. trophic compensation).

Ocean warming and CO_2 enrichment can increase the interaction strength between herbivores and plants[10–12] so that an increase in one (i.e. production) is compensated by the other (i.e. consumption). This intensification of consumption occurs through an increase in per capita feeding rates[13] and abundance of herbivores[14], which can stabilize productivity[6]. Yet, where such compensation is weak, ocean change can drive over-consumption or runaway-production[11,15,16] which trigger regime-shifts in marine systems[17,18].

In the marine realm, ocean warming and CO_2 enrichment are considered to favour faster growing and opportunistic algae (e.g. algal turfs and cyanobacteria), which allows them to turn from subordinates to dominants (e.g. kelp forests and coral reefs)[19–21]. As carbon emissions are set to intensify[22], it is crucial to understand whether compensatory dynamics can buffer natural environments against such shifts to turfs. Can the CO_2-boosted expansion of algal turfs[17] be counter-balanced, such that these systems are stabilized against global change? Herbivores are a renowned functional group that can compensate for increases in turf production[13] to stabilise ecosystem level processes.

In temperate marine systems, herbivory can range from substantial[18] to insubstantial[23]. Whilst the most celebrated examples of herbivory tend to focus on urchin-dominated systems (i.e. intensely grazed, urchin barrens), large parts of the world's coast experience negligible urchin grazing[24]. Understanding the strength of trophic compensation, therefore, in systems of weak to moderate grazing pressure (i.e. non-urchin dominated systems[23]) provides much needed insight into their vulnerability to ocean change.

We tested the strength of compensatory dynamics in a marine system of weak to moderate herbivory (i.e. a coast free of urchin barrens). Using a large complex of species (1,800 l tanks with >100 species) over a long-term (six months) we simulated the effects of future ocean warming and acidification. We assessed whether the various mechanisms of stability (i.e. trophic compensation, density compensation, and functional redundancy) could counter-balance an anticipated boost to primary production by ocean warming and acidification. These tests would indicate the vulnerability or robustness of coasts of lower herbivory to expansion of turfs under future ocean climate.

Gastropods were the major grazers in the mesocosms (Fig. 1). Stable isotope analysis showed that they were the main consumers of turf algae (supplementary figure 1), with other grazer taxa showing less dependence on turf as a food source. We observed a strong negative relationship between total consumption by gastropods and cover of turf algae ($R^2 = 0.75$; $p < 0.001$) (Fig. 2a). Only under ambient and elevated CO_2 conditions, in the absence of warming, gastropods were able to prevent the expansion of the turf cover over time (Fig. 2b; supplementary table 1). This outcome was driven by a combination of mechanisms whose strength varied among climate treatments.

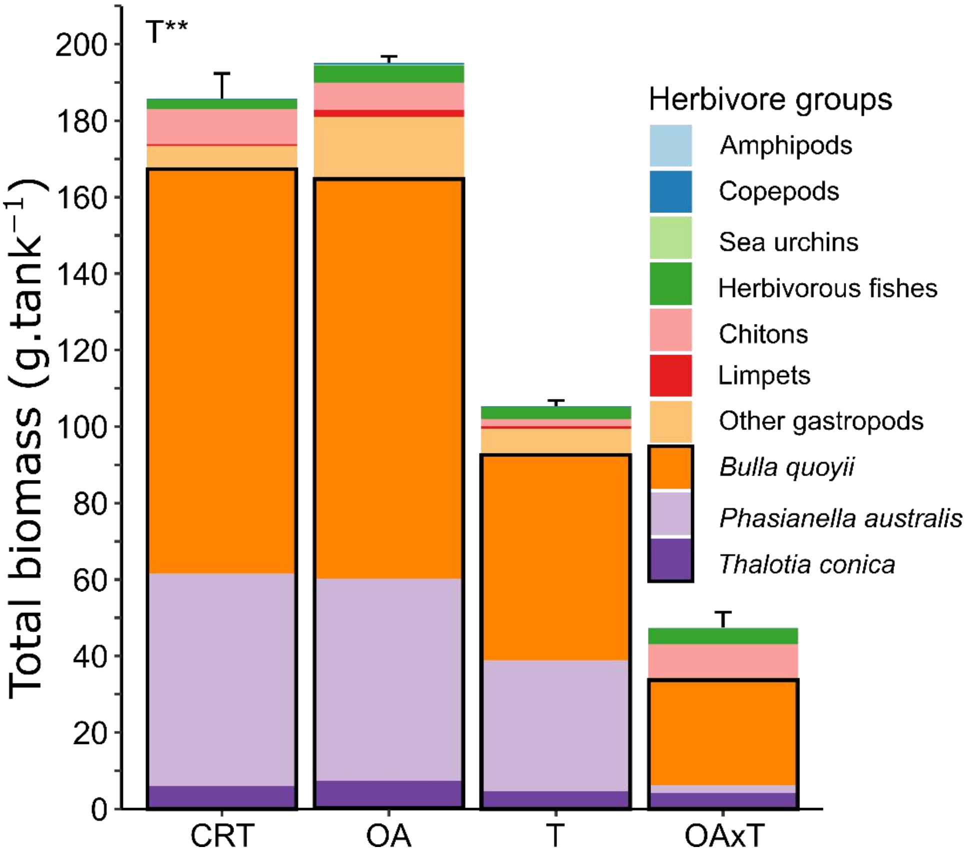
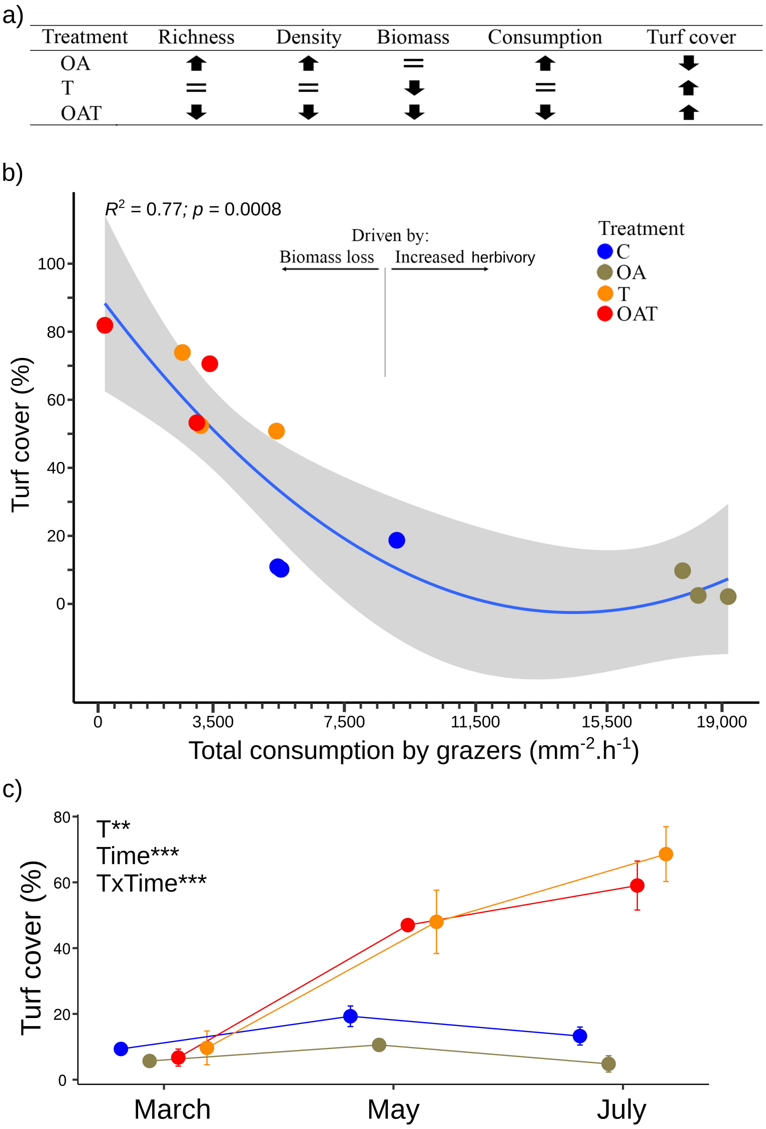


Figure 1. Biomass of herbivores among the four climate treatments (n = 3 mesocosm per treatment) (mean ± SEM). The lower three species of gastropod (see legend) represented the three most abundant species in the field and were used for the feeding trial (highlighted by black contours). (CRT: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature).

We experimentally tested whether changes in weedy turf cover were due to alterations in the gastropods' grazing activity, increased accumulation of algal biomass (net biomass accumulation), or a combination of the two under the different climate treatments. In the presence of grazers, turf-forming algae increased their cover fourfold in the mesocosms at elevated temperature, irrespective of acidification ($F_{1,8} = 77.5$, $p < 0.0001$; Fig. 3a, supplementary table 2), compared to the control treatment. Additionally, under CO_2 enrichment turf cover was lower than that in the controls at the end of the experiment (CO_2 enrichment × elevated temperature interaction; $F_{1,8} = 6.45$, $p = 0.035$). In the absence of grazers within the mesocosms, net algal biomass accumulation increased as a result of CO_2 enrichment ($F_{1,52} = 4.08$, $p = 0.048$) and elevated temperature ($F_{1,52} = 11.59$, $p = 0.001$), and their combined effect led to a nearly two-fold increase in turf biomass production compared to controls (Fig. 3b). Not only food resource (turfs) increased under elevated temperature, but also food nutritional value ($F_{1,20} = 19.31$, $p = 0.003$), as indicated by a higher relative nitrogen content of turf algae (Fig. 3f).



a)

Treatment	Richness	Density	Biomass	Consumption	Turf cover
OA	⬆	⬆	=	⬆	⬇
T	=	=	⬇	=	⬆
OAT	⬇	⬇	⬇	⬇	⬆

Figure 2. Influence of gastropod grazing on cover of turf algae across the climate treatments (CRT: current $p\text{CO}_2$ × current temperature; OA: future $p\text{CO}_2$ × current temperature; T: current $p\text{CO}_2$ × future temperature; OA × T: future $p\text{CO}_2$ × future temperature); (a) summary of the directions of change for herbivore responses (i.e. gastropod species richness, density, biomass, and per capita grazing rates) and cover of weedy turf algae, (b) scatterplot of the relationship between turf cover and herbivore consumption (each data point represents a single mesocosm). The fitted regression (grey area) indicates 95% confidence interval, (c) development of turf cover showing the positive influence of temperature on turf cover, but not CO_2 in isolation which was countered by herbivory (*n* = 3 mesocosms per treatment). Data are represented as mean ± SEM and the main factors that showed a significant effect are highlighted (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Data points are offset for clearer visual representation of treatments. Individual data points are indicated by small circles.

Grazing on turfs was affected through two different pathways: (1) an alteration in total grazer biomass (Fig. 3c), and (2) a change in the per capita grazing rate (Fig. 3d). The elevated temperature treatments had at least two times lower total gastropod biomass than under CO_2 enrichment alone or control conditions ($F_{1,8} = 6.6$, $p = 0.033$; Fig. 3c, supplementary table 2; supplementary figure 2b). This resulted from the impairment of biomass growth over time in four abundant gastropods species (supplementary figure 3). The main species driving the overall collapse in gastropod total biomass over time under elevated temperature were *B. quoyii* and *P. australis* ($F_{1,8} = 31.52$, $p = 0.0005$ and $F_{1,8} = 18.1$, $p = 0.0028$, respectively; supplementary table 3).

Likewise, the gastropod community showed the sharpest decline in densities in the combined treatment (CO_2 enrichment × elevated temperature interaction; $F_{2,16} = 14.48$, $p < 0.001$; supplementary figure 6a; supplementary table 4). Only one species, *T. undulatus*, showed a pattern of increased density under the combined elevated CO_2 and temperature treatment ($F_{1,16} = 4999.0$, $p = 0.005$). All other abundant gastropod species showed an impaired density under elevated temperature over time (supplementary figure 4, supplementary table 5). Gastropods not only suffered a decline in biomass and density, but also in their species numbers. Gastropod species richness was lowest under elevated temperature conditions ($F_{1,8} = 0.19$, $p = 0.005$; Fig. 2e), showing a sharp decrease over time ($F_{2,16}= 11.3$, $p = 0.0009$; supplementary table 4; supplementary figure 2c). Species loss was intensified with the addition of CO_2 enrichment as a stressor, leading to the disappearance of almost 80% of the gastropod species in the combined climate treatment (supplementary figure 2c). Finally, compared to ambient conditions, gastropod per capita grazing rates as measured in grazer enclosure cages increased three-fold under elevated CO_2 alone ($F_{2,69} = 7.08$, $p < 0.001$; supplementary table 6), but showed no change for the elevated temperature treatment (Fig. 2d).

We show that grazers can compensate for CO_2 enrichment by consuming the additional growth of turfs (i.e. counter the expansion of turfs). CO_2 enrichment can act as a resource to weedy species whose boosted growth displaces competitors[10]. For example, turfs are able to increase their cover and grow faster under CO_2 enrichment[25], leading benthic communities to undergo phase shifts towards domination by turf algae[20] and cyanobacteria[21]. Whilst marine grazers have the capacity to compensate for the higher productivity of algal turf under CO_2 enrichment (i.e. trophic compensation[13]), we observed consumption that reduced turf cover below that of ambient conditions (i.e. overconsumption), reducing the probability of turf expansion. The strength of such consumptive responses to CO_2 enrichment would be expected in the ocean since the energetic value of food often increases[26], opposite to observed responses on land[11]. Yet, we did not find a CO_2 related changes to food quality and consider our observation of overconsumption as a response to the increased metabolic demands of elevated CO_2[27,28]. Irrespective of the mechanism, our study shows the capacity of grazers to halt, or even reduce, runaway expansion of turfs under CO_2 enrichment.

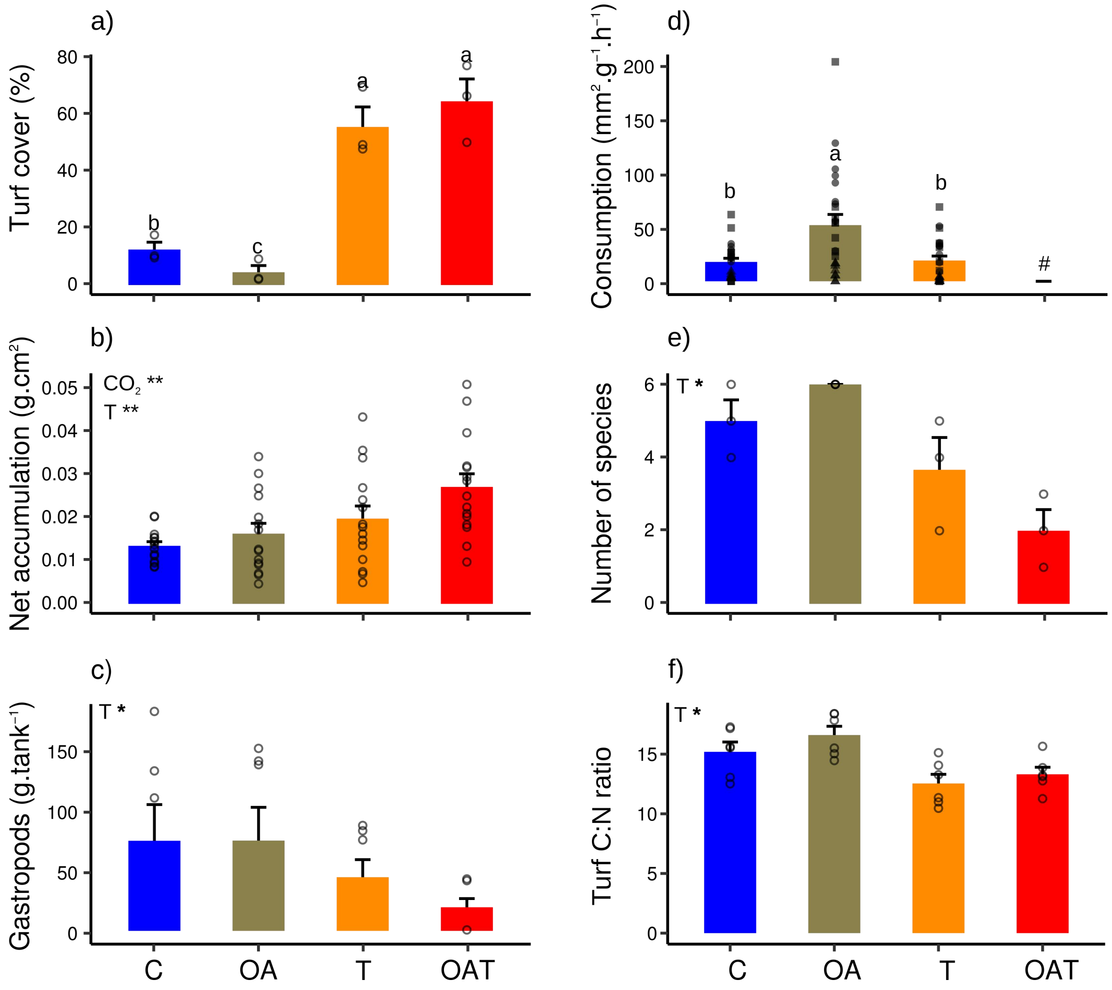


Figure 3. The overall effect of climate treatments (CRT: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature) on; (a) percentage cover of turf algae (grazers present) (n = 3 mesocosms per treatment); (b) net biomass accumulation of turf algae (grazers excluded) (n = 5 quadrats per tank); (c) total gastropod biomass (n = 3 mesocosms per treatment); (d) gastropod per capita feeding rates (n = 24 individuals per treatment); (e) gastropod species richness (n = 3 mesocosms per treatment); and (f) carbon to nitrogen ratios of turf algae (n = 2 samples per tank). Data are represented as mean ± SEM and different letters above bars represent significant differences ($p < 0.05$) based on an SNK test. For (b), (c) and (e) the main factors that showed a significant effect are highlighted (* = $p < 0.05$, ** = $p < 0.01$). (d) # = Feeding rates were not measured for the combined effect of ocean acidification and warming (OAT) because the number of surviving individuals in this treatment was too small (supplementary figure 2). Individual data points are indicated by small circles, with exception of (d) where squares, circles and triangles shapes represent the individual data points for *Thalotia conica, Phasianella australis,* and *Bulla quoyii*, respectively.

Trophic compensation failed when temperature was combined with CO_2 enrichment. Indeed, strong herbivorous responses to CO_2 enrichment are often reduced by warming[29]. Models about animal homeostasis during warming predict an intensification of foraging activity through increased metabolic demands and modification of food quality[30]. Whilst intensifying herbivory compensated for CO_2 boosted primary production in our study, the additional boost by temperature was not matched by an increase in herbivory. Grazing intensity remained invariant to warming, for which we speculate, occurred as an offset between nutritional benefits (i.e. enhanced energetic quality of food) and metabolic costs (i.e. elevated demands of warming). Critically, the difference in thermal tolerance between producers and their consumers can increase expansion of weed-like turfs[16]. Such boosts to production may outpace consumption, predicting ecosystem level effects via trophic interactions (i.e. as contingent on the relative increases in warming and CO_2 enrichment[31]. Runway expansion of turfs, therefore, is more likely when CO_2 enrichment and warming boosts their productivity, but consumers fail to compensate for warming.

Similar to trophic compensation, functional and biomass compensation failed to stabilise runaway production of turfs. We found that the mismatch between production and consumption was reinforced by a collapse in gastropod biomass, density and species richness under warming. This loss of grazers was not likely to have resulted from mortality due to captivity as individual species persisted and some species increased in density over time in mesocosms simulating current day climate. Also, there was an increase in grazer biomass but not density across all treatments, indicating a lack of density compensation despite growth of individual herbivores. Changes to grazer community was not driven by collapse of a single species, but was due to a decline across almost all species, both by warming alone and its combination with acidification. Only one species (*Turbo undulatus*) showed an increase in density under future climate, but due to its relatively low contribution to the total community density and biomass, this response did not compensate for turf expansion. Importantly, the stabilising mechanisms to elevated CO_2 seem to fail in circumstances where multiple stressors combine to overwhelm compensatory consumption of boosted production.

The present study however, has overlooked how seasonal variation (drop in water temperature during winter) or abiotic changes (decrease in nutrients discharge) may slow the pace of turf expansion. For example, cooler water temperature during the winter could give time to canopy algae to recover after long periods of elevated temperature enable them to compete for space displacing turf algae[32-35]. Additionally, the reduction of nutrient discharge could help maintain low levels of sedimentation, turbidity and nutrients, which generally trigger the loss of canopy algae and boost turf growth[36-37]. Because this caveat new studies with enhanced complexity, such as the inclusion of seasonality, sedimentation and nutrient as factors might provide an accurate picture of future ocean scenarios.

In conclusion, we show that ocean warming erodes the capacity of herbivores to stabilise an increase in primary production in a system of moderate intensity of grazing. The various mechanisms of stability (i.e. trophic compensation, density compensation, and functional redundancy) were not detected to counter-balance boosted primary production. Whilst both warming and acidification have been independently predicted to increase interaction strength between herbivores and plants, the compensatory responses to CO_2 enrichment was overwhelmed by the loss of consumer control under warming. The runaway expansion of weedy turfs suggests that the identification of compensatory mechanism and the circumstances under which these prevail could potentially help manage climate impacts in a changing ocean.

METHODS

A large mesocosm system consisting of 12 tanks (~ 1,800 L per tank) was built and maintained for six months at the South Australian Research and Development Institute (SARDI) to simulate a complex shallow temperate rocky reef marine ecosystem. Our aim was to understand how complex systems would behave under the effect of persistent climatic stressors. In contrast to most experimental studies, the increased ecological complexity based on multiple species interactions tend to increase the likelihood of incorporating buffering processes. This approach contrasts more simple mixtures of species, including those that do not include strong interactions that can counter-balance the main effects and create noticeable change (for further information on the mesocosm set up see the section methods into the supplementary information).

CLIMATE TREATMENTS

The seawater chemical and physical parameters (CO_2 enrichment and temperature) were set to mimic predicted future conditions based on the Representative Concentration Pathway (RCP) 8.5 for the year 2100, which represents a business-as-usual CO_2 emission scenario[22]. The experiment was conducted in a crossed design using current concentration of $p\mathrm{CO_2}$ (~400 ppm) equivalent to a pH of ~8.19 (Control) and predicted future concentration (~900 ppm) with a pH of ~7.89 (OA) in combination with average Gulf of St. Vincent (South Australia) summer seawater temperatures (21°C) (Control) and a predicted future temperature increase of + 2.8°C (24 °C) (T) and the combined interaction of ocean warming and acidification (OAT) ($n = 3$ replicate mesocosm per treatment).

Future seawater chemical and physical conditions were maintained for ~6 months to allow for adequate acclimation to elevated temperature and CO_2, rather than measuring short-term shock response to altered water conditions. To achieve the future $p\mathrm{CO_2}$ concentration, seawater in the header tank (supplementary figure 5) was injected with pure CO_2 before flowing into the mesocosms. The target $p\mathrm{CO_2}$ concentration was further maintained by bubbling the seawater in the enrichment tank with CO_2-enriched air (900 ppm) using a gas mixer (PEGAS 4000MF, Columbus Instruments, USA). The 24-hour variation in pH of seawater in each mesocosm was recorded in 30 min intervals using an automated pH logger (Control Units ACQ110, Aquatronica, Italy) for five consecutive days. These measurements were obtained to demonstrate that pH tends to have a small diurnal variation due to community metabolism, similar to subtidal variation found in natural ecosystems (supplementary figure 6). The heaters inside the enrichment bins were used to maintain the target elevated seawater temperature. During the experimental period, the pH (supplementary figure 7a) and temperature (supplementary figure 7b) of seawater were measured daily at midday using a portable pH meter (SG2 SevenGo™, Mettler Toledo, Australia).This daily measurement was fixed in time to avoid measurement of pH variability solely due to community metabolism (respiration/photosynthesis).

Total alkalinity and salinity were measured fortnightly using an automated titrator (888 Titrando, Metrohm, Switzerland) and a handheld refractometer (SR6, Vital Sine, China) ($n = 8$ replicates per mesocosm), respectively. The concentrations of $p\mathrm{CO_2}$, carbonate ($\mathrm{CO_3^{2-}}$) and bicarbonate ($\mathrm{HCO_3^-}$) ions, and saturation state (Ω) of calcite and aragonite were calculated using the $\mathrm{CO_2}$SYS program for Excel24[38] with dissociation constants from Mehrbach et al.[39] refit by Dickson & Millerro[40] (supplementary table 7).

BENTHIC COMMUNITIES

Rocky reef was selected as the main benthic structural component of our mesocosm system, because it is one of the predominant coastal habitat of the Gulf St. Vincent. Rocky reef habitats were created using four circular habitat modules (42.5 cm in diameter) per mesocosm with a total of 12 rocky reef modules per treatment. The modules were used to facilitate the sampling of species at the end of the experiment as well as to increase the numbers of subsamples inside each mesocosm. The modules consisted of rocks and their sessile biota, which were randomly collected *in situ* from natural shallow rocky reefs at 0.5–4 m depth. The rocks were colonized by a diverse assemblage of algae, dominated by *Sargassum* spp., *Cystophora* spp., a number of calcareous algae, and low growing fleshy algae (e.g. *Exallosorus* spp. and *Zonaria* spp.). Sessile animals included sponges, tunicates, calcareous worms and bivalves. Upon collection, rocky reef rocks were transported fully submerged in seawater to the mesocosms. Rocks with similar size and algal assemblage composition were positioned on the plastic modules. The four rocky reef modules were randomly assigned to each mesocosm and were positioned on a mixed bed of artificial and natural sand.

The benthic assemblages of the rocky reef modules in our mesocosms were photographed monthly (i.e. $n = 288$, during the course of the experiment) using high-resolution images at a fixed distance from a top view (supplementary figure 8). The benthic algae were identified to the lowest taxonomic level possible and subsequently categorised into four major groups: (1) fleshy canopy-forming algae; (2) fleshy sub-canopy algae; (3) calcareous algae (including crustose coralline algae); (4) weedy algae. Weedy algae were defined as a mix of turf algae (low-growing species less than 2 cm in height) and cyanobacteria. The relative cover of these four groups of algae was estimated using the Coral Point Count with Excel Extensions (CPCe) Software[41], through the identification of 100 randomly distributed points per module.

GRAZER COMMUNITIES

Prior to placing herbivorous gastropods into the mesocosms, their individual sizes and weights were measured using a digital Vernier calliper and an electronic balance, respectively. A fixed number of individuals of each species (10 *Bulla quoyii*, 12 *Thalotia conica*, 20 *Phasianella australis*, 10 *Cantharidus* sp., 1 *Clanculus* sp., and 1 *Turbo undulatus* per mesocosm) of similar size and weight were randomly transferred into each mesocosm. This proportion among species roughly represented their relative abundance on the rocks collected to build the rocky reef modules, and reflected their abundance in the natural environment. The gastropod abundance on the rocky reefs modules was visually counted in the middle (May 2015) of the experiment to determine the temporal variation in community structure. At the end of the experiment (August 2015), all individuals were collected and had their size and weight measured. Other major grazer groups were also present in the mesocosms tanks, such as fish (*Girella zebra* and *Acanthaluteres vittiger*), limpets, chitons, amphipods, copepods, sea-urchins, and two species of top-shell gastropods (*Stomatella impertusa* and *Granata imbricata*). However, their combined biomass contributed less than one third to the total grazer biomass (see Fig. 1 for the contribution of each major group to total grazer biomass) and they also show a much smaller use of weedy algae as food sources as show in their isotopic space (supplementary figure 1; see supplementary table 8 for the number of isotopes signature replicates used to construct the isotopic space for each grazer functional group).

The loss of grazers (i.e. a reduction in their densities, biomass and richness) in our study is not likely to be a result of mortality due to captivity, yet the exact mechanisms responsible for mortality (e.g. natural mortality, disease, competition, or starvation) in the elevated temperature treatments remain to be assessed. Despite the reduction in grazer densities in all treatments this did not prevent an overall gain in their biomass, whilst their species richness remained unaltered under control conditions (supplementary figure 2). Additionally, variation in grazer community structure was not driven by collapse of a single species, but due to a decline across all species (supplementary figure 4; supplementary table 5).

FEEDING TRAILS

To conceptualize the impacts of climate change on the balance between production and consumption we compared the grazing performance of herbivorous gastropods as well as primary production in the absence of grazers across treatments. We measured per capita feeding rates to understand how climate treatments affected the feeding physiology of gastropod species in the treatments. This was then combined with changes in total grazer biomass to understand the overall changes to standing algal biomass as observed in the mesocosms after 6 months. To measure the grazers' per capita consumption rates, the three most abundant species (*B. quoyii*, *T. conica* and *P. australis*) were used (*n* = 8 individuals per species per treatment). Gastropods with similar size and weight were starved for 24 h before the feeding trials. Then, each individual was transferred into a clean (devoid of algae) experimental cage (*n* = 1 individual per cage, 12 cm × 12 cm × 5 cm) and maintained in the mesocosm and climate treatment where they originated from until the start of the feeding trials.

The weedy algae used as food were grown on plates (50 cm × 10 cm) under each of the treatment conditions for one month prior to the feeding trials. This ensured that the composition and structure of the turf forming algae on the tiles to be similar to those found in the mesocosms of each climatic treatment, and to assure that differences in feeding performance were not only due to differences in herbivore traits but also to algal traits. The mesocosms were covered with a tarp to simulate night-time, as many grazing gastropods are nocturnal feeders. The colonized plates were cut in smaller pieces (5 x 10 cm) and only pieces with 100% of turf cover were used during the feeding trail. The trial started by placing each small plate into an experimental cage with a gastropod. The gastropods were allowed to feed for three hours, and then the tiles were removed from the cages and photographed using a high-definition camera (Canon EOS 1100D, 12.2 megapixels) at a fixed distance of 37 cm. Feeding rate was calculated as the surface area of turf removed per hour, based on the open spaces on the tile cover. The turf area was measured using the trial version of the software eCognition 9 (Trimble, Germany), which provides a high accuracy of measuring landscape areas and a great analytical capacity to measure environmentally complex objects[42].

TURF ACCUMULATION

To determine the net accumulation of the turf community in the mesocosms, a mesocosm-scale exclusion experiment (rather than herbivore-free cages) was performed at the end of the experimental period. All grazers including the gastropods were removed from the mesocosms and open patches (20 × 20 cm) on the tank walls were created by scrapping off all existing algal overgrowth. This allowed algal species to recolonise the substratum free of herbivory. After one week, the selected patches were scraped clean again and all newly colonised algae were collected (*n* = 5 replicate areas per mesocosm). Net accumulation was then calculated by measuring the wet and dry weight of newly grown algae, after blotting and oven-drying at 60°C for 24 hours, respectively.

DATA ANALYSIS

To test the temporal variation in the gastropod total density, biomass and species richness between the climate treatments we used a three-way permutational split-plot ANOVA for a randomized complete block design, for repeated measures over time as proposed by Altman and Krywinski[43]. This analysis treated time (two levels for biomass, March (begin) and June (end) of the experiment; and three levels for density and richness, March (begin), May (middle) and June (end) of the experiment) and climate treatments as fixed factors (CO_2 enrichment and temperature, each with two levels; ambient and future conditions) and mesocosms tanks were used as a block factor, since it was the experiment unit and one hierarchy level above the individual responses. Additionally, a three-way split-plot ANOVA's were performed using the same factors and design to evaluate differences among the treatments over time for each one of the six most abundant gastropod species, relative turf cover and gastropods species richness. To reduce inflation of Type I error, a Bonferroni adjustment of the *p*-value was used. All analyses were ran using 4999 permutations.

Two-way permutational split-plot ANOVAs with ocean acidification and temperature as fixed factors (each one with two levels, ambient and future conditions) were used to test the treatments effects at the end of the experiment in the (1) percentage of weedy species cover; (2) weedy net accumulation; (3) gastropod density; (4) total gastropod biomass; and (5) gastropods richness. In the two-way permutational split-plot ANOVA of weedy net accumulation, mesocosm tanks and replicates within the tanks were used as a block factors.

The per capita feeding rate within the cages was calculated by dividing the surface area of turf algae consumed by the individual weight of each respective grazer and time spent grazing. Normality and homoscedasticity were improved by logarithmic or square root transformation of percent cover and gross productivity of turf forming algae, as well as gastropod species richness, biomass and per capita feeding rate. Differences in grazer per capita feeding rates were evaluated by two-way ANOVA, with climate treatment as a fixed effect (3-levels: C, OA, T) and gastropod species as a random effect due to extremely low grazer abundances. In case of a significant interaction, Student-Newman-Keuls (SNK) multiple comparisons of means followed. All test were performed using the R 3.4.1 and the packages lmPerm[44] and agricolae[45] (De Mendiburu 2014).

Linear regression was performed with total consumption as the explanatory variable and turf cover as the dependent variable to elucidate the relationship between feeding pressure and turf cover. Total consumption was calculated by multiplying the average of the per capita feeding rate of each studied species in each treatment with their respective biomass in each mesocosm. To estimate the total consumption for the ocean acidification × temperature treatment (OAT; which could not be performed due to low numbers of gastropods), we used the highest per capita feeding rate from the other three treatments for each species and then multiplied these with the gastropod biomass from the ocean warming × ocean acidification treatment (This provided an overestimation rather than underestimation of grazing pressure in this treatment and in such way reduced a Type I error). Furthermore, because total consumption rate of the ocean acidification × temperature treatment was the lowest of all treatments (even if overestimated) the data points were located at the far left-hand portion of the graph depicting turf cover vs total consumption graph (Fig. 2b). If total consumption for this treatment had indeed been overestimated, data points would have been located even further to the left on the x-axis, but this would not have significantly affected the orientation and shape of the curve.

AUTHOR CONTRIBUTIONS

C.M.F, I.N., S.G. and S.D.C. designed the mesocosm and the experiments. C.M.F and S.G. built and maintained the mesocosms. C.M.F, S.G., G.W. and J.Y.S.L performed the experiments. C.M.F analysed the data. C.M.F., I.N. and S.D.C. wrote the paper and all authors contributed to the writing of the manuscript.

DATA AVAILABILITY

The data that support the findings of this study are available from the authors on request; see author contributions for specific data sets.

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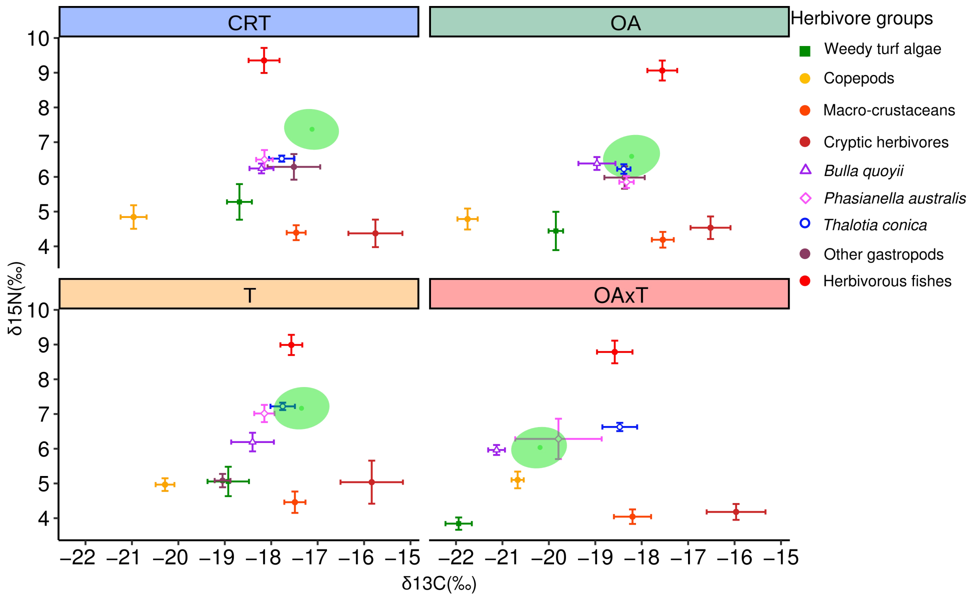
SUPPLEMENTARY INFORMATION

SUPPLEMENTAL DATA ITEMS



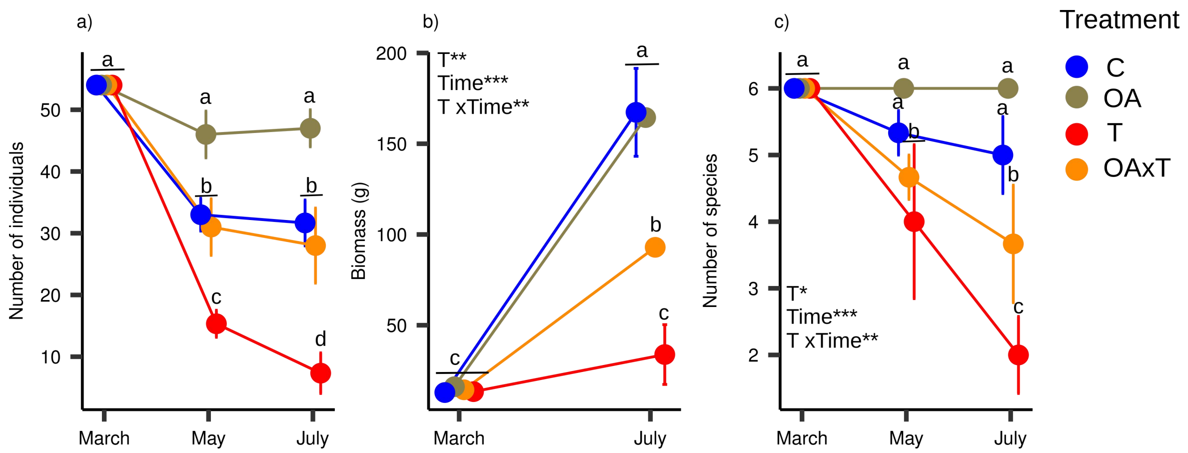
Supplementary figure 1. Stable carbon and nitrogen isotope signatures (mean ± SEM) of the main herbivore taxa (in terms of biomass, see Fig. 1) found in each treatment (C = control, OA = ocean acidification, T = elevated temperature, OAT = ocean acidification and elevated temperature). Enrichment between food source and consumers is on average +1.3 ± 0.3‰ for carbon and +2.2 ± 0.3‰ for nitrogen for consumers raised on plant and algal diets[1]; the green ellipses indicate these average enrichment values for turf algae and demonstrate that gastropods are the main grazers on weedy turf algae in our mesocosm system. Cryptic herbivores = limpets, chitons, and the two species of top-shell gastropods *(Stomatella impertusa* and *Granata imbricata*); herbivorous fishes (*Girella zebra* and *Acanthaluteres vittiger*).

Supplementary table 1. Three-way split-plot ANOVA for repeated measurements over time following Altman and Krzywinski 2015, with mesocosm tanks as a block factor, and climate treatments and time as fixed factors demonstrating the difference in turf benthic cover between the treatments over time. Significant results are indicated in **bold**. Subscript show the transformation used to improve the variable normality, sqrt = Square root

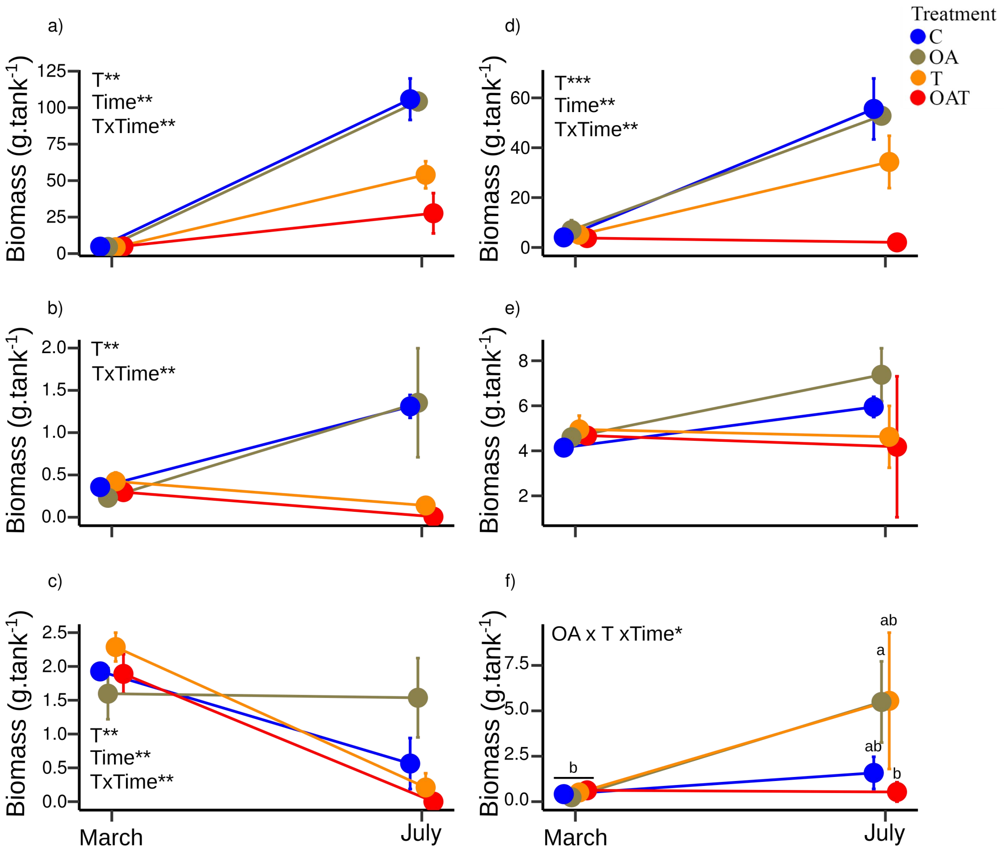
		df	*MS*	*Pseudo F*	*p*
Turf cover$^{\text{sqrt}}$	OA	1	1.409	1.446	0.2635
	TEMP	1	65.981	67.736	**<0.0001**
	OA × TEMP	1	4.547	4.668	0.0627
	Residuals[Tank(OA × TEMP)]	8	0.974		
	TIME	2	28.842	51.970	**<0.0001**
	OA × TIME	2	0.133	0.240	0.7897
	TEMP × TIME	2	20.360	36.687	**<0.0001**
	OA × TEMP × TIME	2	0.299	0.538	0.5941
	Residuals[Tank(OA × TEMP) × TIME]	16	0.555		

Supplementary table 2. Two-way split-plot ANOVA results demonstrating the difference in turf cover, net accumulation productivity, and grazer biomass richness, and turf C:N ratio between the four treatments. Significant results are indicated in **bold.** Superscript show the transformation used to improve the variable normality: sqrt = Square root (x); and log = Log$_{10}$(x + 1) was applied.

		df	*MS*	*Pseudo F*	*p*
Turf cover^{log}	OA	1	0.111	3.632	0.0931
	TEMP	1	2.370	77.500	**<0.0001**
	OA × TEMP	1	0.197	6.445	**0.0348**
	Residuals [Tank(OA × TEMP)]	8	0.031		
Net accumulation^{log}	OA	1	0.0000003	4.084	**0.0485**
	TEMP	1	0.0000008	11.589	**0.0013**
	OA × TEMP	1	0.0000006	0.805	0.3738
	Residuals [Samples(Tank(OA × TEMP)]	4	0.0000003		
	Residuals [Tank(OA × TEMP)]	52	0.0000007		
Grazer biomass^{log}	OA	1	0.405	2.374	0.1620
	TEMP	1	1.127	6.615	**0.0330**
	OA × TEMP	1	0.407	2.387	0.1610
	Residuals [Tank(OA × TEMP)]	8	0.170		
Grazer richness^{log}	OA	1	0.011	0.826	0.3899
	TEMP	1	0.193	14.707	**0.0050**
	OA × TEMP	1	0.052	3.928	0.0828
	Residuals	8	0.013		
Turf C:N ratio^{sqrt}	OA	1	0.006	2.705	0.0673
	TEMP	1	0.042	19.311	**0.0036**
	OA × TEMP	1	0.000	0.091	0.8076
	Residuals [Tank(OA × TEMP)]	20	0.008		



Supplementary figure 2. Temporal variation in (a) number of gastropods per tank, (b) grazer biomass (grams) per tank, and (c) grazer species richness per tank among the four treatments (mean ± SEM). Different letters represent significant difference based on Tukey HSD *a posteriori* comparisons of the means ($p < 0.05$). (CRT: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature). *A posteriori* tests for grazer biomass and richness were performed using the interaction term T × Time.



Supplementary figure 3. Differences in the biomass for each of the six most abundant gastropod species: a) *Bulla quoyii*, b) *Clanculus* sp., c) *Cantharidus* sp., d) *Phasionella australis*, e) *Thalotia conica*, and f) *Turbo undulatus* between the treatments (CRT: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature). Data are represented as mean ± SEM and the main factors that showed a significant effect are highlighted after the *P*-values were corrected by a Bonferroni adjustment, significance cut-off at $p < 0.0083$ (* = $p < 0.008$, ** = $p < 0.0008$, *** = $p < 0.00008$).

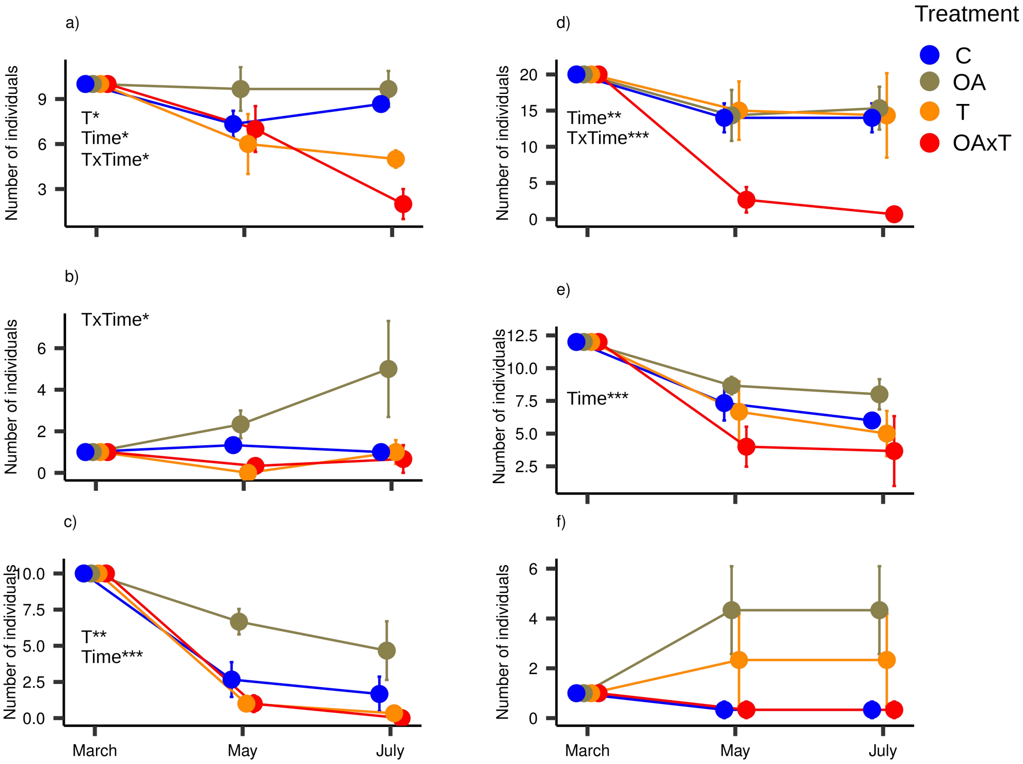
Supplementary table 3. Three-way split-plot ANOVA results for repeated measurements over time following Altman and Krzywinski 2015 demonstrating the difference in biomass for each of the six gastropods grazer species (*Bulla quoyii*, *Clanculus* sp., *Cantharidus* sp., *Phasionella australis*, *Thalotia conica,* and *Turbo undulatus*) between the treatments over time, tank was used as block factor. *P*-values were corrected by a Bonferroni adjustment, significance cut-off at $p < 0.0083$. Significant results are indicated in **bold.** Superscript show the transformation used to improve the variable normality: log = Log$_{10}$(x + 1); and nt = no transformation was applied.

		df	*MS*	*Pseudo F*	*p*
Bulla sp.^{nt}	OA	1	284.200	1.491	0.2568
	TEMP	1	6177.000	32.410	**<0.0001**
	OA × TEMP	1	217.400	1.141	0.3167
	Residuals[Tank(OA × TEMP)]	8	190.600		
	TIME	1	27949.100	142.351	**<0.0001**
	OA × TIME	1	301.000	1.533	0.2508
	TEMP × TIME	1	6189.800	31.526	**0.0005**
	OA × TEMP × TIME	1	244.700	1.246	0.2967
	Residuals[Tank(OA × TEMP) × TIME]	8	196.300		
Cantharidus spp.^{nt}	OA	1	0.001	0.005	0.9462
	TEMP	1	0.602	4.285	0.0722
	OA × TEMP	1	0.276	1.961	0.1990
	Residuals[Tank(OA × TEMP)]	8	0.141		
	TIME	1	4.501	60.600	**<0.0001**
	OA × TIME	1	0.143	1.931	0.2022
	TEMP × TIME	1	1.156	15.565	**0.0043**
	OA × TEMP × TIME	1	0.279	3.751	0.0888
	Residuals[Tank(OA × TEMP) × TIME]	8	0.074		
Clanculus spp.^{nt}	OA	1	0.104	219.000	0.3151
	TEMP	1	1.196	4999.000	**0.0024**
	OA × TEMP	1	0.013	110.000	0.4818
	Residuals[Tank(OA × TEMP)]	8	0.037		
	TIME	1	0.043	51.000	0.9608
	OA × TIME	1	0.002	51.000	0.8039
	TEMP × TIME	1	1.492	4999.000	**0.0020**
	OA × TEMP × TIME	1	0.018	51.000	0.7059
	Residuals[Tank(OA × TEMP) × TIME]	8	0.061		

		df	*MS*	*Pseudo F*	*p*
Pha. australis^{log}	OA	1	0.578	10.838	0.0110
	TEMP	1	1.095	20.525	**0.0019**
	OA × TEMP	1	0.769	14.418	**0.0053**
	Residuals[Tank(OA × TEMP)]	8	0.053		
	TIME	1	1.981	36.182	**<0.0001**
	OA × TIME	1	0.562	10.258	0.0126
	TEMP × TIME	1	0.991	18.108	**0.0028**
	OA × TEMP × TIME	1	0.391	7.134	0.0283
	Residuals[Tank(OA × TEMP) × TIME]	8	0.055		
Tha. conica^{nt}	OA	1	0.515	51.000	0.6863
	TEMP	1	4.976	358.000	0.2207
	OA × TEMP	1	2.551	115.000	0.4696
	Residuals[Tank(OA × TEMP)]	8	4.441		
	TIME	1	5.287	51.000	0.6863
	OA × TIME	1	0.242	51.000	0.8039
	TEMP × TIME	1	10.984	336.000	0.2321
	OA × TEMP × TIME	1	0.481	51.000	0.8627
	Residuals[Tank(OA × TEMP) × TIME]	8	5.901		
Turbo spp.^{nt}	OA	1	0.514	0.062	0.8104
	TEMP	1	0.097	0.012	0.9167
	OA × TEMP	1	27.933	3.342	0.1049
	Residuals[Tank(OA × TEMP)]	8	8.359		
	TIME	1	48.485	7.072	0.0288
	OA × TIME	1	0.419	0.061	0.8109
	TEMP × TIME	1	0.802	0.117	0.7411
	OA × TEMP × TIME	1	31.814	4.640	0.0634
	Residuals[Tank(OA × TEMP) × TIME]	8	6.856		

Supplementary table 4. Three-way split-plot ANOVA for repeated measurements over time following Altman and Krzywinski 2015 with mesocosm tanks as a block factor, demonstrating the difference in gastropods total density, total biomass and richness between the treatments over time. Significant results are indicated in **bold.** No transformation was used.

		df	MS	Pseudo *F*	*p*
Grazer density	OA	1	16.000	51.000	0.8039
	TEMP	1	1444.000	4999.000	**0.0032**
	OA × TEMP	1	1045.440	4999.000	**0.0034**
	Residuals [Tank(OA × TEMP)]	8	54.140		
	TIME	2	2344.110	4999.000	**<0.0001**
	OA × TIME	2	5.330	66.000	0.7273
	TEMP × TIME	2	382.330	4999.000	**<0.0001**
	OA × TEMP × TIME	2	271.440	4999.000	**<0.0001**
	Residuals [Tank(OA × TEMP) × TIME]	16	17.060		
Grazer biomass	OA	1	1406.100	315.000	0.2413
	TEMP	1	16584.100	4999.000	**<0.0001**
	OA × TEMP	1	1864.600	1115.000	0.0825
	Residuals [Tank(OA × TEMP)]	8	389.100		
	TIME	1	62760.000	4999.000	**0.0074**
	OA × TIME	1	1515.000	1641.000	0.0579
	TEMP × TIME	1	16605.000	4999.000	**<0.0001**
	OA × TEMP × TIME	1	1463.000	3114.000	**0.0312**
	Residuals [Tank(OA × TEMP) × TIME]	8	354.000		
Grazer richness	OA	1	0.111	63.000	0.6191
	TEMP	1	16.000	4999.000	**0.0124**
	OA × TEMP	1	4.000	950.000	0.0958
	Residuals [Tank(OA × TEMP)]	8	1.306		
	TIME	2	10.111	4999.000	**0.0070**
	OA × TIME	2	0.111	55.000	0.7818
	TEMP × TIME	2	5.333	4999.000	**0.0066**
	OA × TEMP × TIME	2	1.333	2083.000	0.1128
	Residuals [Tank(OA × TEMP) × TIME]	16	0.472		



Supplementary figure 4. Difference in the total number of individuals for each of the six most abundant gastropod species (mean ± SEM): a) *Bulla quoyii*, b) *Clanculus* sp., c) *Cantharidus* sp., d) *Phasionella australis*, e) *Thalotia conica*, and f) *Turbo undulatus* between the treatments (CRT: current $p\mathrm{CO}_2 \times$ current temperature; OA: future $p\mathrm{CO}_2 \times$ current temperature; T: current $p\mathrm{CO}_2 \times$ future temperature; OA × T: future $p\mathrm{CO}_2 \times$ future temperature). The main factors that showed a significant effect are highlighted after the *P*-values were corrected by a Bonferroni adjustment, significance cut-off at $p < 0.0083$ (* = p < 0.008, ** = p < 0.0008, *** = p <0.00008)

Supplementary table 5. Three-way ANOVA results demonstrating the difference in density for each of the six grazer species (*Bulla quoyii*, *Clanculus* sp., *Cantharidus* sp., *Phasionella australis*, *Thalotia conica*, and *Turbo undulatus*) between the treatments over time. *P*-values were corrected by a Bonferroni adjustment, significance cut-off at $p < 0.0083$. Significant results are indicated in **bold.** Superscript show the transformation used to improve the variable normality: sqrt = Square root (x); log = Log$_{10}$(x + 1); and nt = no transformation was applied.

		df	*MS*	*Pseudo F*	*p*
Bulla sp.^{nt}	OA	1	0.444	51.000	0.902
	TEMP	1	58.778	4999.000	0.012
	OA × TEMP	1	7.111	644.000	0.135
	Residuals[Tank(OA × TEMP)]	8	3.444		
	TIME	2	42.111	4999.000	**0.006**
	OA × TIME	2	5.444	1099.000	0.197
	TEMP × TIME	2	24.778	4999.000	0.022
	OA × TEMP × TIME	2	3.111	460.000	0.448
	Residuals[Tank(OA × TEMP) × TIME]	16	2.819		
Cantharidus spp.^{sqrt}	OA	1	0.572	603.000	0.143
	TEMP	1	6.259	4999.000	**0.001**
	OA × TEMP	1	1.651	4999.000	0.019
	Residuals[Tank(OA × TEMP)]	8	0.177		
	TIME	2	17.276	4999.000	**<0.0001**
	OA × TIME	2	0.147	66.000	0.697
	TEMP × TIME	2	1.591	4999.000	0.036
	OA × TEMP × TIME	2	0.417	1581.000	0.162
	Residuals[Tank(OA × TEMP) × TIME]	16	0.314		
Clanculus spp.^{sqrt}	OA	1	0.510	278.000	0.266
	TEMP	1	4.193	4999.000	0.012
	OA × TEMP	1	0.510	297.000	0.253
	Residuals[Tank(OA × TEMP)]	8	0.376		
	TIME	2	0.394	2544.000	0.039
	OA × TIME	2	0.128	278.000	0.489
	TEMP × TIME	2	1.093	4999.000	**0.004**
	OA × TEMP × TIME	2	0.493	517.000	0.174
	Residuals[Tank(OA × TEMP) × TIME]	16	0.160		

		df	*MS*	*Pseudo F*	*p*
Pha. australis^{log}	OA	1	0.704	4405.000	0.022
	TEMP	1	0.808	4999.000	0.011
	OA × TEMP	1	0.745	4999.000	0.005
	Residuals[Tank(OA × TEMP)]	8	0.050		
	TIME	2	0.569	4999.000	**<0.0001**
	OA × TIME	2	0.183	4999.000	0.014
	TEMP × TIME	2	0.227	4999.000	**0.006**
	OA × TEMP × TIME	2	0.200	4999.000	0.009
	Residuals[Tank(OA × TEMP) × TIME]	16	0.029		
Tha. conica^{nt}	OA	1	0.111	51.000	1.000
	TEMP	1	28.444	856.000	0.105
	OA × TEMP	1	13.444	470.000	0.177
	Residuals[Tank(OA × TEMP)]	8	6.778		
	TIME	2	139.111	4999.000	**0.002**
	OA × TIME	2	0.778	95.000	0.905
	TEMP × TIME	2	7.111	832.000	0.215
	OA × TEMP × TIME	2	3.444	592.000	0.269
	Residuals[Tank(OA × TEMP) × TIME]	16	4.653		
Turbo spp.^{sqrt}	OA	1	0.657	180.000	0.361
	TEMP	1	0.657	155.000	0.394
	OA × TEMP	1	5.972	2461.000	0.039
	Residuals[Tank(OA × TEMP)]	8	0.973		
	TIME	2	0.012	51.000	0.941
	OA × TIME	2	0.164	100.000	0.700
	TEMP × TIME	2	0.164	134.000	0.627
	OA × TEMP × TIME	2	1.493	4999.000	**0.005**
	Residuals[Tank(OA × TEMP) × TIME]	16	0.243		

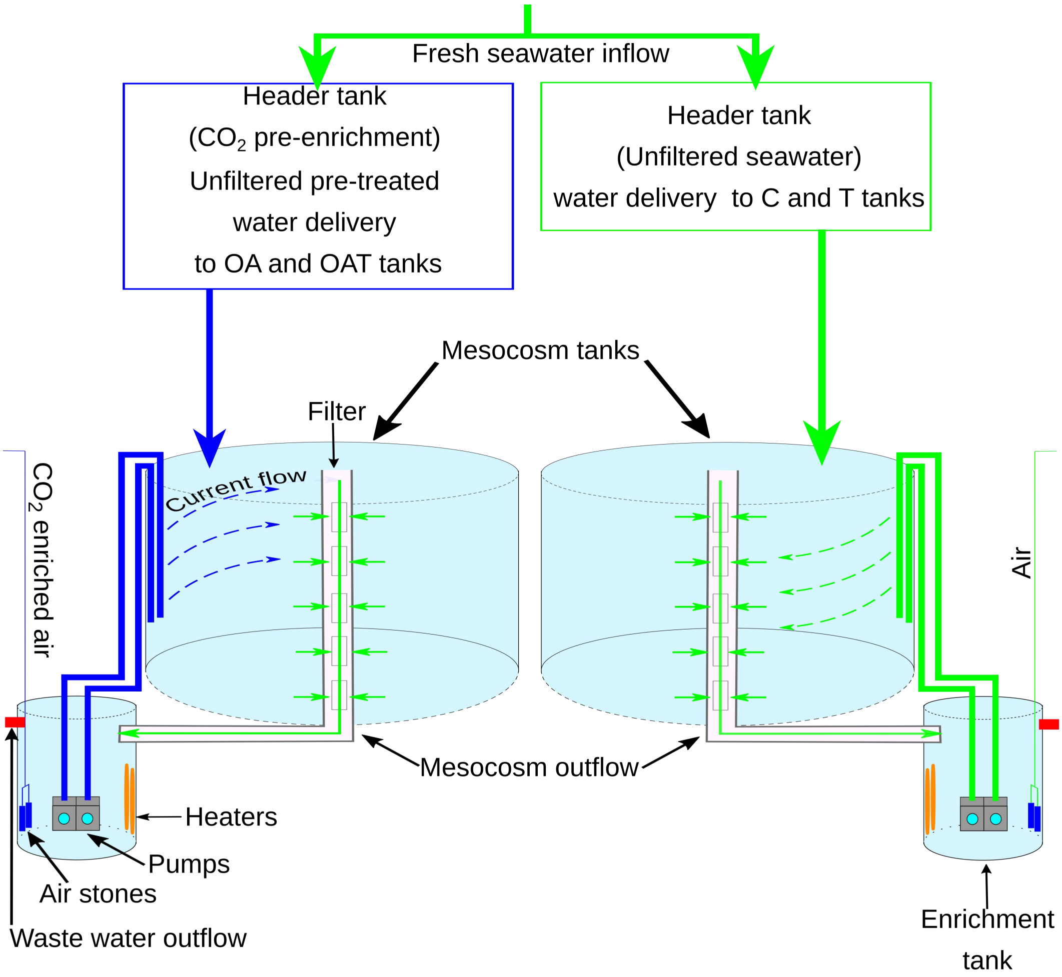
Supplementary table 6. Two-way ANOVA of per capita consumption rates under control, ocean acidification and ocean warming treatments. Feeding rates could not be examined under the combined effects of ocean acidification and warming as the abundance of surviving herbivores was too low. Significant results are indicated in **bold.** Data was Square root transformed to improve normality.

		df	MS	*F value*	*p*
Per capita consumption	Treatments	2	2.0435	6.8689	**0.0108**
	Species	2	6.6488	22.3493	**0.0001**
	Treatment × Species	4	0.5320	1.7883	0.1985
	Residuals	62	0.342		

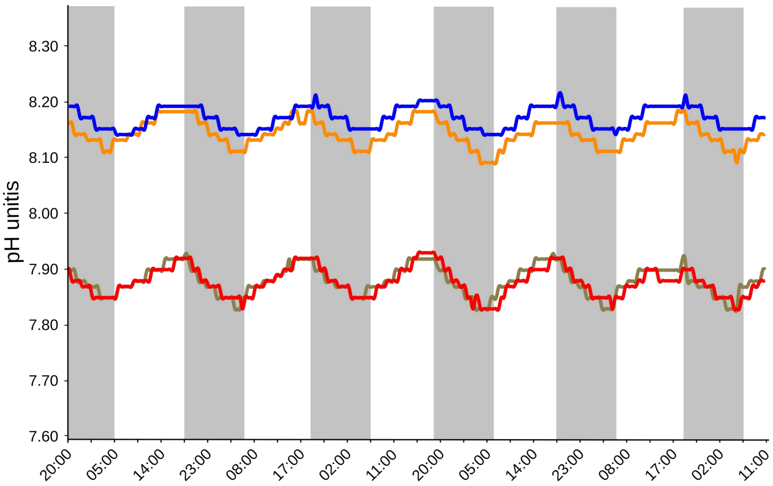
SUPPLEMENTARY METHODS

MESOCOSM DESIGN

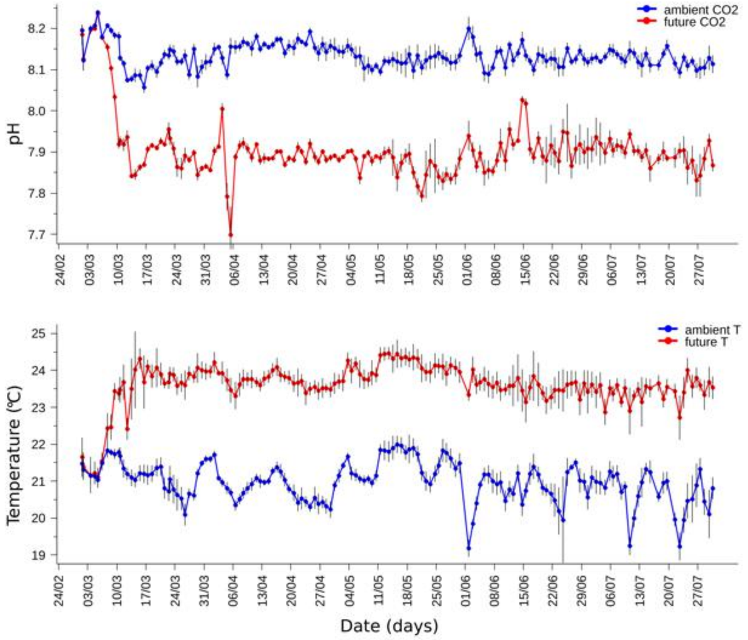
The mesocosm system consisted of 12 mesocosm tanks (~1,800 L) held in a controlled temperature room with ambient air temperature set at 23°C, and operated and maintained from February 2015 to August 2015. Water physical and chemical parameters were maintained by 2 CO_2 enriched/Ambient CO_2 header tanks (800 L) and 12 CO_2/temperature enrichment bins (60 L). The two header tanks delivered unfiltered seawater from an offshore pipeline to all mesocosms at a rate of ~2.300 L day^{-1}, while the enrichment bins maintained target temperature and CO_2 values in the mesocosm tanks. Each mesocosm was illuminated by a 250 Watt high-pressure metal halide lamp (Powerstar HQI-T 250 W/D PRO, Osram, Germany), which was mounted at1 m above the mesocosm water surface, with a photoperiod of 14/10 hours of daylight simulating South Australia natural day light conditions in summer (Bureau of Meteorology). This lamp emits similar radiation and light wave length to sunlight, and each mesocosm benthic community received an irradiance of ~60 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR), which corresponds to an average PAR in subtidal areas (~7 m depth) at the Gulf St. Vincent in South Australia[2]. Excess seawater flowed out of the mesocosm through a central filter column (mesh size: ~20 µm) by gravity, and was collected in the adjacent enrichment bin which allowed maintenance of target pCO_2 and temperature in the mesocosm tanks. In the enrichment bin excess water flowed out (~2.300 L day^{-1}) to a drain. Each enrichment bin had two submersible titanium heaters (1 × 300 W, 1 × 500 W) and two pumps (~1.8 m^3 h^{-1}). The pumps were set to turn on and off alternately every six hours so that the seawater was pumped from the enrichment bin back to the mesocosm in opposite directions. The change in the direction of water circulation in the mesocosm simulates a tidal current change mimicking the natural environment, and allowing the entire mesocosm to receive the same water quality over experimental period.



Supplementary figure 5. Showing a schematic drawing of the mesocosm system. (C: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature).



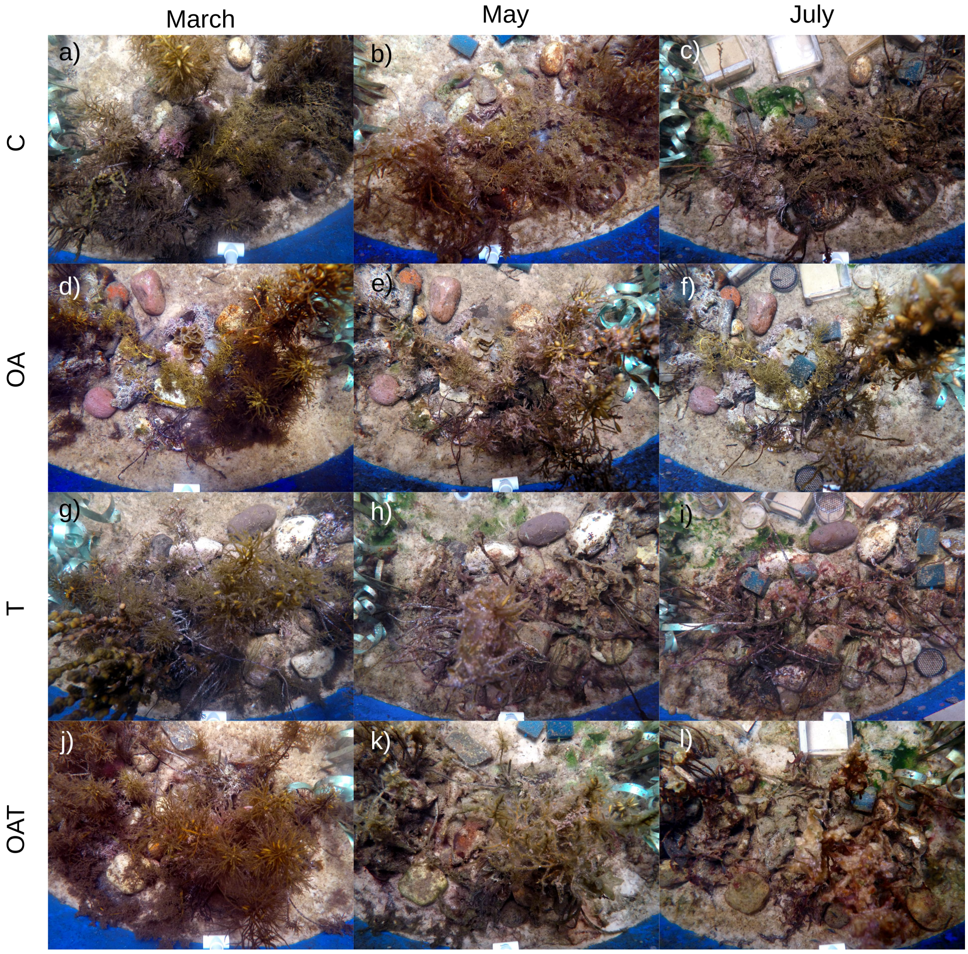
Supplementary figure 6. 24-hr variation in pH of seawater in one mesocosm per treatment for five consecutive days, resulting from community metabolism (respiration and photosynthesis), showing how the tanks mimicked natural diurnal variability. The grey areas indicate night-time.



Supplementary figure 7. Daily variation in (a) pH and (b) temperature across treatments over a 6-month period (mean ± SDM).

Supplementary table 7. Carbonate system parameters of seawater during the experimental period (mean ± SDM). Control: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature.

Parameter	Control	OA	T	OA × T
Temperature (°C)	21.0 ± 0.14	20.9 ± 0.04	23.7 ± 0.19	23.7 ± 0.08
pHNBS	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^{2-} (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



Supplementary figure 8. Photo sequence showing turf cover during three different periods, beginning (March), middle (May) and end (July) of the experiment for control (photos a, b and c), ocean acidification (d, e and f), elevated temperature (g, h and i) and the combination of ocean acidification and elevated temperature (j, k and l). (C: current pCO_2 × current temperature; OA: future pCO_2 × current temperature; T: current pCO_2 × future temperature; OA × T: future pCO_2 × future temperature).

Supplementary table 8. Number of isotopes signature replicates for the major herbivore groups among the four climatic treatment. Control: current $p\mathrm{CO_2}$ × current temperature; OA: future $p\mathrm{CO_2}$ × current temperature; T: current $p\mathrm{CO_2}$ × future temperature; OA × T: future $p\mathrm{CO_2}$ × future temperature.

Herbivore group	Control	OA	T	OA × T
Copepods	6	6	6	6
Macrocrustaceans	11	12	11	11
Cryptic gastropods	11	12	10	11
Others gastropods	8	9	4	0
Bulla quoyii	9	9	9	5
Phasionella australis	9	9	8	3
Thalotia conica	9	9	6	5
Herbivorous fishes	11	16	13	15

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CHAPTER VI

GENERAL DISCUSSION

GENERAL DISCUSSION

The maturing of ecological theories is characterised by exploration of limits to their explanatory power and the development of pluralistic approaches, findings and interpretations. My contribution to ocean acidification research has been to rebalance a shift from the predominance of reporting of negative effects and ecological change to assessments of stabilizing mechanisms that buffer environmental change. The long-term consequences of ocean acidification might be dampened where organisms are able to adapt rapidly enough to keep pace with changing conditions (e.g. generalists), whereas others may fail to adapt (e.g. specialists). My thesis focuses on a key functional group of marine consumers (herbivores) and their response to climate change at two levels of biological organisation (population and community levels). My findings represent an advance into forecasting the effects of changing climatic on the organisation of marine communities and their components. By scaling up the propagating effects of behavioural changes from the individual level through to their populations and communities, I show how ecosystems might resist or succumb to climate change. Incorporation of such complexity is considered one of the most vexing challenges to forecasting future natural systems[1–6].

The combination of individual response to climate change and its propagation to population, community and ecosystem levels allow the observation of dampening and buffering interactions that might counterbalance the deleterious effect of the abrupt environmental change on all ecological levels of natural systems[6–9]. It also may provide insights under which circumstances these buffering interactions might prevail, and where they fail. For example, in my thesis, I show how herbivores individual behaviour plasticity allowed species to capitalize on the continuous novelty of opportunity created by climate change leading to boosted population density (Chapter 2). The adjustments on both individual and population level altered bottom-up and top-down processes leading to community reshuffling and enhanced food webs under future climate disturbance (Chapter 3). However, when behavioural plasticity cannot ensure population homeostasis, the likelihood of herbivore community collapse is enhanced (Chapter 4), and when herbivores collapse they lose functionality, diminishing ecosystem resistance under ocean warming and acidification (Chapter 5).

The creation of models that forecast climate change effects on marine ecosystems are useful and comprehensively account all complex interrelationships among processes that operate at different spatial and temporal scales[10]. However, no single model can address how changes in single species have implications on the overall community and by consequence on their systems[11]. Thus, they should not be interpreted without caution, particularly with regard to the limitations involved[12]. In order to build accurate forecast models, modellers need strong linkages and a hierarchical and parameterized set of data[13,14]. Currently, there are only few studies that have scaled up the effects of climate change from individual responses in a complex natural environment to the consequences at ecosystem level[l9,15,16]. This thesis might address this gap and may potentially help modellers to create more accurate predictions since accounting for long-term, multiscale responses to single and multiple stressors, in an ecosystem context is critical. I show how mechanisms and processes that operate at the individual and population levels propagate onto the community and ecosystem levels, facilitating the incorporation of these mechanisms and processes in future models to improve their accuracy.

In specific terms, I show that: (1) specialized herbivores might modify their behaviour, and such change allows them to exploit novel environmental conditions (triggered by increasing anthropogenic CO_2 emissions) to increase the carrying capacity of the environment and consequently densify their populations (Chapter 2); (2) this specialized herbivore not only increased the carrying capacity of the environment but also mediated bottom-up and top-down processes simultaneously, facilitating the population densification of other herbivores, and consequently fuelling local food webs under ocean acidification (Chapter 3); (3) despite having behavioural plasticity (ability to change their trophic niche breadth), boosted food availability and release of negative interactions (e.g. competition), specialist herbivore may still fail to prevent sharp declines in their populations. With decreasing specialist biomass collapse of the overall herbivore community is expected, since generalists cannot boost their biomass with similar or higher magnitude as that of the specialist decline under ocean warming (either in isolation or combined with ocean acidification) (Chapter 4); and (4) when herbivore communities collapse, runaway expansion of weedy turf algae is followed with possibly dire consequences for the entire ecosystem (Chapter 5).

I show that in complex experiments and field conditions herbivores can take advantage of the positive effects that high CO_2 enrichment has on primary production[9,16–18] and even increase their population size. CO_2 enrichment functions as a natural fertilizer in some marine plants by acting as a resource and increasing bottom-up forces in natural systems [19,20], and may drive changes in algal communities[18]. The enhanced resources boost the carrying capacity of the system which can support larger population sizes at higher trophic levels[15,21], including herbivores that directly benefit from elevated primary productivity[22]. It may lead to the increase in the interaction strength between herbivores and plants[23–25] in such a way that it may lead to intensification of consumption which may occur through an increase in per capita feeding rates[26] and herbivore population densification[27], which can then stabilize excess productivity[28]. However, I show that this plant – herbivore relationship can go beyond what has been established in the literature. I show that herbivores acted in synergy with CO_2 enrichment to enhance their crop yields by enforcing a range of techniques that boost production rates[29–32] and extend the carrying capacity of the system enabling the densification of their population. Thus, increasing bottom-up processes fuelled and propagated through the food web[15,16] boosting the biomass of herbivores. The effects of climate on mesopredators was weak, but detectable. By weakening top-down control, the biomass of herbivores might also be boosted in the absence of mesopredator control levels similar to those found under ambient CO_2. Additionally, I show that herbivores have the capability to control weedy algae expansion under ocean acidification in isolation, avoiding their expansion and strengthening compensatory process that stabilizes natural environments in a high-CO_2 ocean.

The emergence of positive interactions under climate change revealed in the present thesis may help the incorporation of positive interactions in community structure models allowing scientists to better understand the spatial distribution, population dynamics of species, and environmental diversity[36–38] under future climatic conditions. Ecological theory has heavily focused on understanding the effects of negative interactions (e.g. competition and predation) and how they propel processes in natural systems[39]. Yet, positive interactions neglected by many ecologists may have effects of similar magnitude to negative interactions[40,41] and may occur under disturbance strengthening, resulting in changes to the environment[42–44]. Such complex species positive interactions can significantly enhance our understanding of the inherent capacity of nature to buffer ecological change under a changing climate.

In contrast to ocean acidification, elevated temperature (in isolation or combined with high CO_2) led to decline in the overall abundance of herbivores, triggered by reductions in specialists. Specialists have a more rigid adherence to their feeding niches and have a lower capability to adapt to changes in trophic resources, and therefore in general fail to sustain population persistence under environmental disturbance[45–48]. Generalists, in contrast, were able to maintain their abundances. My innovation on how generalists adapt to abiotic change and specialists fail to meet abiotic change is a major contribution to studies seeking to understand the concept of ecological forcing. While several studies in the laboratory and in nature have shown persistence or proliferation of generalists under future climate change, this may not necessarily translate to future maintenance of overall community biomass or biodiversity[33,47,49,50]. I show that this is because specialist species generally are the ones the most contribute to the total diversity and abundance of natural ecosystems[51–53] and are most likely to fail to adapt, whereas generalists appear able to compensate at the community level.

Whilst compensatory mechanisms can stabilise natural systems against change, where they fail change might be substantial. I show that the different types of compensation (i.e. density, functional and trophic compensation by herbivores[26,58–60] fails under ocean warming in isolation or when combined with ocean acidification. The consequences of collapse and functional loss of herbivores can go beyond habitat modification (dominance alteration from canopy algae to weedy algae[18,20]) which is already known to drive diversity loss in marine systems[21,61–63]. Herbivore collapses can have deeper implications than the dominance alteration in benthic communities, for example, the collapse of similar communities under similar conditions could not propagate the positive effect of CO_2 enrichment on primary production within the food web under ocean warming[15] and showed a reduced energy flow from primary producers to secondary and tertiary consumers in marine food webs[16]. This is very likely to lead to simplified systems similar to those found during past climatic events which drove mass extinctions[64–66].

FUTURE DIRECTIONS

In my thesis, I studied the functional role of some temperate marine herbivores under climatic stressors. I used a set of field and complex laboratory experiments which added layers of natural complexity, necessary to move beyond responses in simple aquarium experiments[2–6]. However, there is still room to further advance the concepts, mechanisms and processes studied here. Some future research in this field includes:

(1) Execution of experiments at natural CO_2 vents, similar to the ones performed in this study with the incorporation of more trophic levels. CO_2 vents are considered to be important in situ labs to understand the effects of ocean acidification over multiple generations despite the few caveats67 related to their size and fluctuations in CO_2 release. Recent studies at CO_2 vents have so far revealed the possible effects of ocean acidification in calcifier metabolic responses[18,22,68,69], species behaviour[21,33], competition[70–72], and the overall consequences on species diversity. However, there are still many unanswered questions, principally on how

ocean acidification may alter the trophic structure and the energetic flow in complex food webs;

(2) The continuation of mesocosm experiments with enhanced complexity (as the one presented here) should be preferred over simple designs, increasing when possible the diversity of species and their interactions, and adding more trophic levels to the food web[2–6]. I also suggest, that despite the maintenance cost, mesocosms should be cared out over multiple generations. Such procedures would allow the incorporation of adaptive and evolutionary responses that may grant species persistence under pressing[73–76] disturbances and presents a fundamental limit to predictive modelling in climate change[12]. Such inclusion might ensure the establishment of better wildlife management and creation of policies that would assure the maintenance of the good and services provided by natural systems;

(3) The integration of natural CO_2 vent studies and mesocosm experiments should be attempted in future studies, to incorporate multiple stressors rather than exclusively with ocean acidification. I also suggest the integration of a layer, for those working with ocean warming, that would be the use of areas that have been suffering from changes in ocean currents and a sharp increase in ocean temperatures due to climate change (tropicalization hotspots), such as the East Australian coast[77–79]. Such an approach using the integration of natural CO_2 and tropicalization hotspots would be a strong confirmatory tool of mesocosm experiments9 and may improve the generalization and extrapolations that is observed in controlled mesocosms studies;

(4) I pioneer new thinking into climate change on specialist herbivores and forecast their sharp decline, relative to generalist species. Despite generalists not showing collapses in their densities under simulated climatic conditions, we should better understand the effect of climate change on generalist herbivores as they are often stronger competitors[47,52,53] and when they are able to maintain or boost their densities biodiversity may collapse[33]. They also may hold the key to understand specialisation under future climatic conditions[46,47] and could

potentially mitigate the deleterious effects of climate change on natural systems stabilising it against the runaway expansion of weedy algae when specialist species collapse;

(5) Species niches are multidimensional[80,81], and in this thesis I only focused on the trophic niche. Incorporating the integration of more dimensions, such as trophic, habitat and thermal niche and test them in isolation and combination under future climatic conditions could help to answer pressing questions about species tolerance niche threshold and enable the identification of tipping points that can lead to decline in population persistence.

GENERAL CONCLUSION

This thesis has addressed a vexing ecological challenge that is scaling up the understanding of climate change (ocean warming and acidification) effects from individual to the community level. Early literature was heavy on negative reporting of ocean acidification that aligned with gloomy predictions for future marine ecosystems. My research shows how to move on from these readily detectable direct effect on individual organisms to include tests of species interactions that underpin community dynamic. I not only reveal how these interactions are not only drivers of community change, but also stabilizers against such change. Whilst stabilizers involve processes that dampen the effects of disturbance or hasten recovery, my research showed these processes are weak. Unlike pulse disturbances that eventually relax (e.g. storms), CO_2 emissions act as a ramp disturbance that increase in intensity over time. Hence, understanding how communities might persist during ramp disturbances puts focus on mechanisms that resist community change. Hence, my assessment of the propagation of bottom-up (resource) and top-down (consumption) responses is a key step forward.

My assessment of climate change goes beyond testing the predominant direct and indirect pathways of ecological stability and change. I join the nexus between the changing forces of primary production and trophic structure by consumers to demonstrate how anticipate how altered trophic processes can propagate or counter ecological change. I demonstrated that some species will not be demographically impaired by elevated CO_2, and indeed can increase their crop yields to densify their populations under future climate, by replacing naturally diverse vegetation with productive monocultures of food; a benefit that is shared with human populations. Likewise, this species will modify bottom-up and top-down processes driving alterations to food-web interaction strengths and changes in community structure. The likelihood of herbivore collapse will sharp increase driven by loss of specialists, and the inability of generalist to increment community abundances in the same pace as specialists vanish. As a consequence, herbivore functionality might erode and all together ecosystem may lose their capacity to resist persistent and ramping disturbances, such as ocean acidification and warming. Therefore, climate change represents a continuous transformation of the environment, creating novel conditions and opportunities for those species that can adjust to exploit the new and open spaces to their adaptive advantage. My pioneering thinking about how to consider community change as a function of generalist and specialist responses offers new insights into community stability and vulnerability to abiotic change. Simply put, I show that the future for nature is not all doom and gloom my contribution is to help future researches to perceive alternative routes of understanding, and comprehend that natural systems are subject to continual change.

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