ECOLOGICAL RESPONSES TO OCEAN ACIDIFICATION AND WARMING: SCALING UP FROM INDIVIDUALS TO COMMUNITIES

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Presented for the degree of Doctor of Philosophy

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The University of Adelaide

February 2018

THE UNIVERSITY of ADELAIDE

DECLARATION

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I acknowledge the support I have received for my research through the provision of an Australian Government Research Training Program Scholarship.

Silvan Urs Goldenberg

14.02.2018

CONTENTS

ACKNOWLEDGMENTS

Great thanks goes to

my supervisors Ivan Nagelkerken and Sean Connell for all their patience and advice that lead to a slow but steady progress in my skills to write more absorbable papers,

my two fellow PhD students Camilo Ferreira and Hadayet Ullah for all the hard work we did together and their friendship,

all the students and volunteers who were invaluable for the construction, maintenance and sampling of the mesocosms: Emma Marangon, Angelique Bonnet, Robbert Geertsma, Laurene Merillet, Mariel Adan, Marco Brustolin, Georgia Walden, Nick Innes, James Jacob, Tim Lynch, Jonathon Leung, Thomas Hue, Nicole Stubing, Erica Gibbs, Gus Pawson, Maddy Coutts, Brigitta Torma, Kimberley Day and Cara McMeel,

Wayne Hutchinson and Mark Gluis from SARDI for their helpfulness when it came to technical questions throughout the mesocosm project,

and also all the other students from the marine biology group including Jennifer Pistevos, Tullio Rossi, Shannon Lauchlan, Ericka Coni, Almendra Dominguez, Katherine Heldt, Giulia Ghedini and Kelsey Kingsbury for the great company over the past 3.5 years.

ABSTRACT

Impacts of human CO_2 emissions on ecosystems and their services are inherently difficult to predict, as ecosystem responses emerge from complex and dynamic networks of organisms and their interactions. Yet, our understanding of the ecological imprint of future climate remains largely based on tests of single species in the laboratory. Here I show how the responses of individual organisms to ocean acidification and ocean warming scale-up to species communities and reveal the underlying ecological dynamics. This was accomplished through the study of behaviour, bottom-up and top-down forcing, food web architecture, and functional composition in 1,800 L mesocosms that harboured a temperate near-shore community including various species of algae, invertebrates and fishes.

The negative effects of ocean acidification were buffered effectively through stabilizing processes at both simple and complex levels of biological organisation. Consequently, acidification primarily acted as a resource (via CO_2-enrichment) that increased productivity throughout the food web. In contrast, ocean warming shifted the balance in key ecological processes leading to a novel community structure that would likely undermine ecosystem services. Dynamics with the potential to compensate for the uneven sensitivities between functions failed to engage – given the fundamental influence of temperature on physiology – which allowed impacts to cascade through the community. This stress through warming also negated any positive effects of acidification.

My findings bridge the gap between the simplicity of the laboratory and species communities in nature, by revealing how impacts of future climate can be countered or accelerated through ecological processes. A predictive understanding of stability or change in ecosystems is key to the management of natural resources in a future ocean.

CHAPTER I

GENERAL INTRODUCTION

HUMAN CO_2 EMISSIONS AND THE OCEANS

Human population growth and technological advances over the past two centuries have been made possible through the burning of fossil fuels [1]. Yet, the effects of the resulting CO_2 emissions on the earth system are pervasive [2]. Physical consequences of the increased greenhouse effect such as warming climate, sea level rise and weather extremes (i.e. storms, floods and droughts) are forecast to cause socio-economic issues globally [2]; in fact, it may prove to be humanity's greatest challenge [3]. In addition to these more direct and predictable impacts, goods and services provided by ecosystems including food, natural materials and recreational opportunities are at risk [4,5]. However, predicting ecosystem responses to elevated CO_2 concentrations is inherently difficult, as these responses emerge from complex and dynamic networks of organisms and their interactions.

Several decades of intense scientific research have not only provided an understanding of the abiotic processes that result from human CO_2 emissions [2,6,7] but also identified a range of biological responses [8-12]. The most prominent impacts on ocean ecosystems are expected from the warming and acidification of sea surface waters [4,13,14]. The latter process termed ocean acidification refers to the absorption of anthropogenic CO_2 by the ocean, which reacts to lower seawater pH [15]. An increase in CO_2 partial pressure from todays 400 ppm to 900 ppm – as projected for the end of this century under a business-as-usual emission scenario – would lead to an average sea surface temperatures rise and pH decrease of approximately 3 °C and 0.3 units, respectively [6]. These rapid changes in physical and chemical environment will affect the physiology of many marine organisms. As such, warming increases metabolic rates in all ectotherms [16], exceeding the thermal limits of some species [17,18]. Acidification impairs ecologically relevant behaviours [19-21] and raises the costs of calcification [22-24] and acid-base balance [25]. Yet, primary producers can utilize the additional CO_2 as a nutrient [26,27]. Whilst these direct effects have been studied in great detail in isolated species under laboratory conditions, we know surprisingly little about how they scale up to the level of species communities and ecosystems [28].

Abiotic change can be countered or accelerated through the collective response of the lower-level processes that characterize ecosystems [29-33]. The emerging structure and function of ecosystems - not altered physiology or species loss *per se* – then drive change or stability in natural resources and services [34-40]. Indeed, these basic ecosystem properties were observed to shift or degrade significantly under rapid ocean acidification and warming in Earth's history [41-43] or at natural analogues of ocean acidification [44-46] or warming [47,48] today. Experimentation has revealed some of the mechanisms that explain how the impacts may propagate through communities [49-53] or how they may be buffered by compensatory processes [54-57]. Whilst such studies that incorporate higher levels of ecological complexity

through species interactions and larger spatio-temporal scales are limited, they are seen as missing link towards our ability to foresee change in future ecosystems [19,28,58-61].

RESEARCH AIMS

The aim of my PhD was to understand how the responses of individual organisms to ocean acidification and warming scale-up to species communities. The thesis is based on three research chapters (II, III and IV), written in the formats of the journal in which they are published or intended to be published. The ecological parameters studied in each of these chapters are illustrated in Figure 1, as part of the global interaction between humans (via CO_2 emissions) and ocean ecosystems (via ecosystem services). Each chapter links specific individual-level effects of future climate to specific properties of species communities. Jointly, the specialised chapters investigate several of the key ecological processes through which the effects of future climate may propagate or may be countered from low to high levels of biological organization.

Chapter II focuses on the changes to bottom-up and top-down forcing under future climate. The key role of these trophic forces in structuring food webs has been demonstrated through decades of ecological research [62-66]. In particular, eutrophication via nutrient run-off [67,68] and top-down degradation via over-exploitation [69,70] have served as prime examples of the vulnerability of trophic dynamics to human activities [33,71]. Yet, we are only beginning to understand how human CO_2 emissions may alter existing trophic theory [30,51,72-74] and the services provided by future food webs such as fisheries production [9,75]. By studying growth and population sizes within individual trophic levels, Chapter II aims to unravel the balance of production and consumption across trophic levels, which ultimately underpins food web structure. The chapter is published in Global Change Biology (doi: 10.1111/gcb.13699).

Chapter III examines compensatory processes inherent in the complexity of nature that can buffer direct effects of future climate. Individuals, populations and species communities possess a remarkable flexibility in order to adjust to variable environmental conditions [76-81]. Understanding the underlying ecological processes is a difficult yet critical quest for modern ecology, as they may provide ecosystems with some capacity to withstand the pressure of human activities [29,31,58,82,83]. Using motile consumer species, Chapter III aims to contrast the negative effects of future climate on isolated behavioural traits to the performance during more complex tasks and to the longer-term viability of populations. Several lower-level processes are identified, particularly under ocean acidification, that shape ecological responses from the organismal to community level. The chapter is published in Nature Climate Change (doi: 10.1038/s41558-018-0086-0).

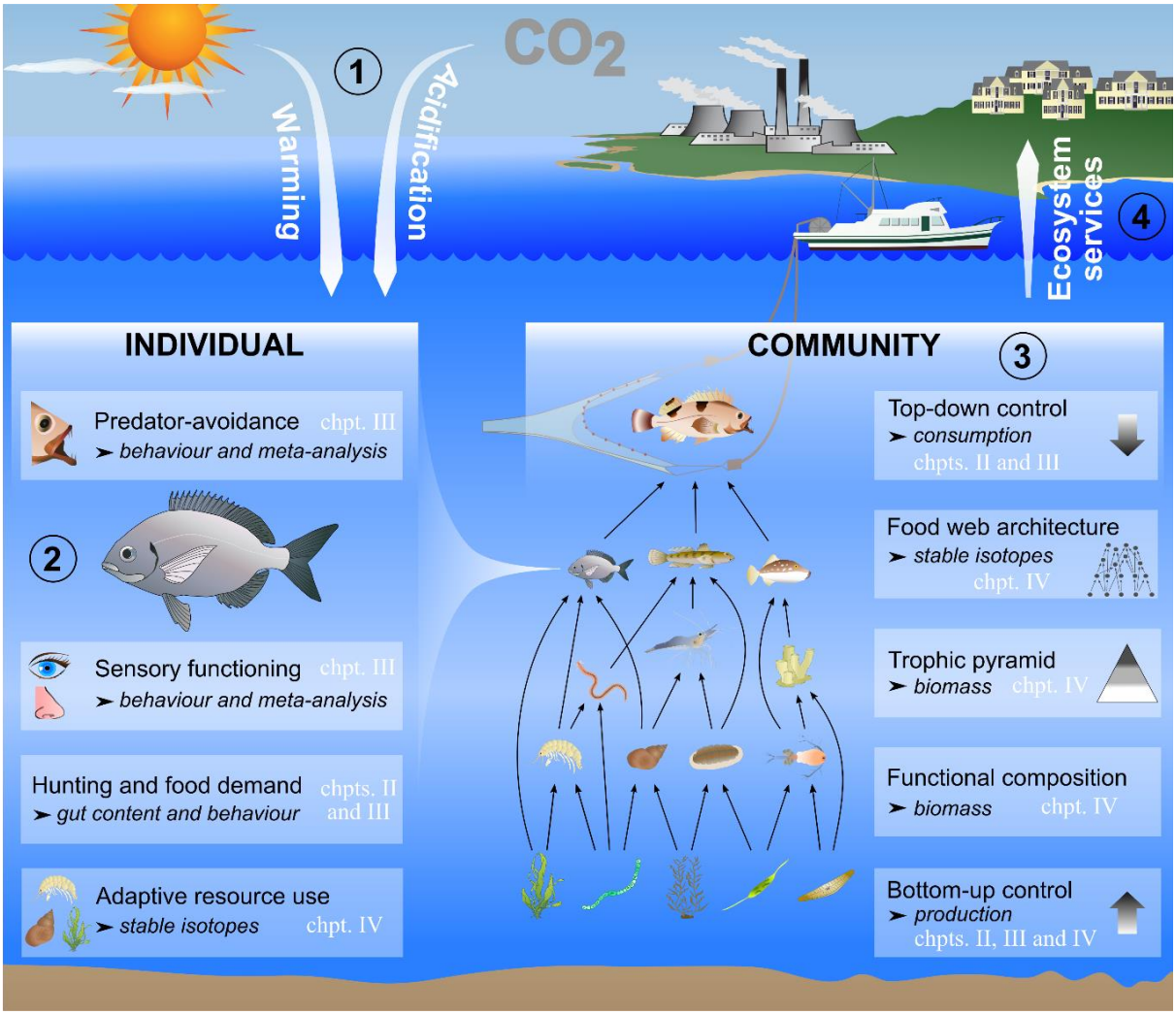

Figure 1: Study system: Human CO_2 emissions cause ocean acidification and warming (**1**), affecting individual organisms (**2**) whose responses may be buffered or reinforced by species interactions leading to stability or change in community structure and function (**3**) which loop back to humans via ecosystem services (**4**). Principle methodologies are given in *italic* and PhD chapters (chpt.) in white. Artwork by Silvan Goldenberg and Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

Chapter IV centres on the architecture, composition and function of food webs under future climate. Consumer species are able to adapt their foraging strategy to match changing patterns in their resources [84] or competitors [85], in accordance with optimal foraging theory [86]. Such adaptive trophic behaviour of consumers gives food web architecture, which represents all feeding relationships between species, dynamic characteristics that can stabilize against natural abiotic variability [32,81]. However, it is less well understood how food web architecture may respond to intense abiotic change due to human activities and whether it may be able to prevent a radical shift in the basic structure of food webs [33,87]. Chapter IV aims to understand the adaptive potential of food web architecture in response to future climate and the consequences for the fundamental composition and function of food webs. This chapter is currently prepared for submission to a journal.

These research chapters represent a critical link between the responses to future climate measured in the simplicity of the laboratory and their consequences for ecosystems. They show that organisms and ecological processes can be affected through various pathways

which have opposing consequences for species communities. Whilst future climate is in some cases compensated effectively and even acts as a resource that increases food web productivity, impacts propagate unrestrained in other cases leading to community degradation. Understanding stability and change in species communities is key to the mitigation of ecological impacts of human CO_2 emissions and the management of natural resources in a future ocean.

EXPERIMENTAL APPROACH

The research in chapter II, III and IV was based on a large mesocosms with a mosaic of rocky reef, seagrass and sandy habitat that harboured a temperate shallow-water community. The mesocosms were exposed to present day and future levels of ocean acidification and warming according to end-of-century projections in a crossed 2-factor design. Due to their high taxonomic and functional diversity, the mesocosms provided an ideal environment to not only conduct detailed investigations into the physiology and behaviour of organisms but also to study species interactions and emerging community properties. Mesocosms have become increasingly popular to test various ecological responses to future climate [51,52,74,88-91], as they seem a good compromise between costs and realism [59,92-94]. Mesocosms also allow to manipulate several environmental variables simultaneously and are thus useful to study stressor-interactions [95-97]. This is a critical advantage in respect to ocean acidification and warming which will co-occur globally and are forecast to act synergistically, additively and antagonistically [98,99]. Although progress in this field is rapid, the system presented in this thesis remains – to the best of my knowledge – the ecologically most realistic and complex mesocosm on benthic marine communities to date.

To answer my research questions, I focus on specific information derived from the mesocosm community through direct sampling of ecological parameters and/or through additional experimental manipulations. The different methodologies used in each chapter are illustrated in Figure 1. Chapter II is based on an isolated compartment of the mesocosm community comprising three distinct trophic levels including microalgae, invertebrate prey and one species of predatory fish. The simplicity of this model food web allowed for the sophisticated manipulations required to parameterize production and consumption across trophic level; the key to a mechanistic understanding of bottom-up and top-down forces. Chapter III centres on all larger and highly motile consumers of the mesocosm community including eight species of fish and shrimp. A behavioural experiment on sensory functioning and predator avoidance combined with gut content analysis and long term growth provided an estimate of performance of these consumers at different levels of ecological complexity. A global meta-analysis was then used to relate our findings to other study systems. Chapter IV incorporates the full taxonomic diversity of the mesocosm community with the aim to

unravel the trophic architecture, composition and functioning of a complex food web. Here, all habitats within the mesocosms were sampled thoroughly to obtain C and N stable isotope signatures of 29 taxa and the standing biomass of the 14 major functional groups. Throughout chapter II to IV processes are generally studied within whole food webs, while special focus is given to fishes and their role as one of the ocean's key consumers.

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CHAPTER II

BOOSTED FOOD WEB PRODUCTIVITY THROUGH OCEAN ACIDIFICATION COLLAPSES UNDER WARMING

Statement of Authorship

Title of Paper	Boosted food web productivity through ocean acidification collapses under warming
Publication Status	☑ Published ☐ Accepted for Publication ☐ Submitted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	Goldenberg SU, Nagelkerken I, Ferreira CM, Ullah H, Connell SD (2017) Boosted food web productivity through ocean acidification collapses under warming. Global Change Biology 23:4177-4184 DOI: 10.1111/gcb.13699

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Contribution to the Paper	study design, conducting experiment, data analysis and writing		
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.		
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Co-Author Contributions

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

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

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

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

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ABSTRACT

Future climate is forecasted to drive bottom-up (resource-driven) and top-down (consumer-driven) change to food web dynamics and community structure. Yet, our predictive understanding of these changes is hampered by an over-reliance on simplified laboratory systems centred on single trophic levels. Using a large mesocosm experiment, we reveal how future ocean acidification and warming modify trophic linkages across a 3-level food web: i.e. primary (algae), secondary (herbivorous invertebrates) and tertiary (predatory fish) producers. Both elevated CO_2 and elevated temperature boosted primary production. Under elevated CO_2, the enhanced bottom-up forcing propagated through all trophic levels. Elevated temperature, however, negated the benefits of elevated CO_2 by stalling secondary production. This imbalance caused secondary producer populations to decline as elevated temperature drove predators to consume their prey more rapidly in the face of higher metabolic demand. Our findings demonstrate how anthropogenic CO_2 can function as a resource that boosts productivity throughout food webs, and how warming can reverse this effect by acting as a stressor to trophic interactions. Understanding the shifting balance between the propagation of resource enrichment and its consumption across trophic levels provides a predictive understanding of future dynamics of stability and collapse in food webs and fisheries production.

INTRODUCTION

Ecosystems are rapidly degrading from an increasing intensity and range of human activities (Halpern *et al.*, 2008; Vitousek *et al.*, 1997). Many organisms are directly affected by human driven change to their physical and chemical environment, and their responses propagate across communities through altered species interactions (Rosenblatt & Schmitz, 2016; Wootton, 1994). To understand the modifications to ecosystem function and services, we need to identify common principles through which these organism-level impacts scale-up to ecosystem-level effects (Riebesell & Gattuso, 2015). Trophic interactions are ideal proxies for the study of this propagation as they incorporate complex networks connecting organisms to communities. Bottom-up (i.e. resource-driven) and top-down forces (i.e. consumer-driven) act along these pathways to maintain or drive ecosystem structure and function (Estes *et al.*, 2011; Heath *et al.*, 2014) and thereby often dominate over direct effects (Ockendon *et al.*, 2014).

Ocean acidification and warming can affect organisms both negatively (i.e. stressor) and positively (i.e. resource) either directly or through altered trophic forcing. As a stressor, warming generally increases metabolic rates in ectotherms (Dillon *et al.*, 2010), whilst ocean acidification raises the energetic costs involved with calcification and acid-base regulation (Kroeker *et al.*, 2013; Portner, 2008). Even neural functioning can be impaired due to elevated CO_2 causing a reduced performance in behaviours relevant for trophic energy flow (Clements & Hunt, 2015; Nagelkerken & Munday, 2016). Such stress can create a mismatch between consumption and energy demand reducing fitness and weakening the functionality of affected food web components (Lemoine & Burkepile, 2012). Increased food demand in consumers can also intensify top-down control of their prey populations (Nagelkerken & Connell, 2015), leading to a strengthening of trophic cascades (Kratina *et al.*, 2012; Provost *et al.*, 2016). In contrast, as a resource, primary producers can benefit from future climate by utilizing the enriched CO_2 as a nutrient and elevated temperature to boost physiology (Ainsworth & Long, 2005; Connell & Russell, 2010). Such enhancement of primary production has the capacity to strengthen the bottom-up control of food webs (Gruner *et al.*, 2008). Thus, alterations to top-down and bottom-up forcing can create trophic imbalances that propagate through different trophic levels and thereby alter food web structure (Heath *et al.*, 2014; O'Connor *et al.*, 2011), with prominent effects for ecosystem services (Smith, 2003).

Our understanding of how ocean acidification and warming alter resource propagation and its consumption within food webs is hampered by an over-reliance on simplified laboratory systems centred on single trophic levels and stressors (Riebesell & Gattuso, 2015; Wernberg *et al.*, 2012). Critical advances regarding the trophic relationship between primary producers and herbivores under future climate have already been made using mesocosm food webs

(e.g. Alsterberg *et al.*, 2013; O'Connor *et al.*, 2009). Although individual components of predator-prey interactions were also addressed (e.g. Ferrari *et al.*, 2015; Pistevos *et al.*, 2015; Provost *et al.*, 2016), functioning food webs that include all major interdependencies between prey and predators have not yet been investigated in the context of ocean acidification and warming. Principles from plant-herbivore interactions have limited applicability for higher trophic interactions due to the fundamentally different effects of CO_2 and temperature on primary producers versus animals. Therefore, as central element of natural food webs, predator-prey interactions remain the key to a comprehensive understanding of future ecological change (Estes *et al.*, 2011; Ockendon *et al.*, 2014).

Here, we reveal how future ocean acidification and warming individually and interactively modify trophic linkages across a 3-level food web and uncover the shifting balance between bottom-up versus top-down forcing. We studied a temperate benthic food web consisting of primary (microalgae), secondary (herbivorous invertebrates) and tertiary (predatory fish) producers using 1,800 l mesocosms with various habitats and a diverse species community, manipulated according to end-of-century climate projections. Our findings demonstrate a shift in balance between the propagation of resource enrichment and its consumption across trophic levels and provide a predictive understanding of future dynamics of stability and collapse in food webs.

METHODS

Mesocosms

Our mesocosm simulated a shallow temperate coastal ecosystem with high level of realism. Twelve circular mesocosms each with a volume of 1,800 l were maintained indoors at a research station (February-July 2015), and habitats and organisms were collected in the vicinity between 1-5 m depth. The mesocosms comprised a mosaic of the three principle local habitat types (Fig. S1, S2; Gulf St. Vincent, South Australia; Bryars & Rowling, 2009): 1) 'artificial seagrass' with epiphytes planted into fine silica sand 6 cm deep, 2) 'open sand' composed of the same sand 6-25 cm deep, and 3) 'rocky reef' made of natural rocks including associated macrophytes and invertebrates. The two soft-bottom habitats were additionally seeded with 25 l natural sediment collected amongst seagrass meadows and including all infauna and flora. In the flow-through system, unfiltered seawater from 1.5 km off-shore (~8 m depth) continuously supplied nutrients and planktonic propagules to each mesocosm at 2,300 l day^{-1}. To simulate tidal water movement, a diffuser formed a light circular current in the mesocosms alternating direction in 6 h intervals. A lamp was mounted above each mesocosm with a spectrum close to sunlight and an irradiance corresponding to a local water depth of ~6-7 m (14/10 light-dark cycle, 30 min dawn and dusk dimming).

Climate treatments

Ocean acidification (levels: ambient and elevated CO_2) was manipulated in crossed combination with ocean warming (levels: ambient and elevated temperature), using three replicate mesocosms per treatment combination (see Table S1 for details on water parameters). We achieved a mean elevated pCO_2 of 900 ppm (pH = 7.89) and temperature rise of +2.8 °C, which represented the conditions predicted for the end of this century following a business-as-usual emission scenario (RCP8.5; Bopp *et al.*, 2013). We applied an ambient temperature of 21 °C, corresponding to average summer temperature based on a five year dataset of two local loggers (5 m depth, 2010-2015, SA Water). For the ocean acidification treatment, the incoming seawater was pre-conditioned to elevated pCO_2 levels with pure CO_2 in a header tank. Additionally, water was continuously circulated between each mesocosm and a separate bin heavily bubbled with enriched air at 1000 ppm pCO_2. Submersible titanium heaters were used in the elevated temperature treatments. Temperature and pH were measured daily and alkalinity fortnightly in each mesocosm. As typical for shallow coastal systems, community metabolism produced diurnal variability in pH and reduced pCO_2 to 900 ppm due to net autotrophy.

Food web assessment

We studied a sediment-associated 3-level food web including predatory fish, herbivorous invertebrates and microalgae. Longfin gobies (*Favongobius lateralis*) were the principle predators on the soft-bottom habitat, where they took bites at the sand to catch small invertebrates (see supplementary methods - predators). Seven juveniles caught with seine nets were introduced to each mesocosm (mean ± SD total length = 22 ± 4 mm) and first habituated to captivity for 1 month. Then, the mesocosm communities were progressively acclimatized to their respective climate treatment over one week and kept at treatment levels for 3.5 months. This duration was considered as sufficiently long to reach an extended level of acclimation in the predators and allowed for potentially ~1-10 (depending on taxa) herbivore and ~100 microalgae generations. Predators tripled in body mass confirming that the mesocosms provided ample food and habitat. Finally, predator production was estimated as the combined gain in mass of all gobies within each mesocosm over the entire study period.

To assess production and standing biomass of herbivores, three different sampling units were built using the bottom part of plastic vials (6.5 cm diameter, 2 cm depth): 1) covered by mesh (~5 mm mesh size) to exclude predators for measurement of production, 2) entirely open and accessible to predators for measurement of standing biomass, and 3) covered by an elevated mesh allowing predators to enter as a procedural control for the presence of the

mesh. The units were filled with 1.5 cm of mesocosm sand, which had been washed superficially to remove any excess organic matter while retaining low levels of herbivores. Then, units were placed on the 'open sand' habitat and herbivore populations allowed to grow out for one month at the end of study period.

Herbivores were sampled within two units per mesocosm for each production, standing biomass and the procedural control. The replicate units for each measure were then pooled prior to sample processing. Herbivores were extracted from the sand via floatation with Ludox TM colloidal solution with a specific gravity of 1.18 and collected on a 120μm sieve. The three dominant invertebrate taxa, which also corresponded to the principle prey found in the predators' stomachs (see supplementary methods – predators), were counted under a stereo-microscope (see supplementary methods – herbivores). A subsample of the two smaller taxa, copepods (~0.2-1 mm) and annelids (~0.6-5.3 mm), was photographed to determine average individual mass based on biovolume estimates, which was then applied to the count of each sample. The considerably larger tanaid shrimps (~2-5 mm) were instead weighed on a microscale (±0.1 mg). The combined wet mass of these three taxa was finally calculated (~830 individuals per sample). There was no main effect of the mesh (ANOVA: df(1,8), $p = 0.54$) or interaction between the effect of the mesh and climate treatments (ANOVA: df(1,8), $p > 0.11$ for all interactions), and thus procedural control and standing biomass units were pooled. Finally, the estimates from the units were extrapolated to the area of the entire soft-bottom habitat resulting in one replicate of both herbivore production and standing biomass per mesocosm.

Microalgae were assessed using sampling units for production, standing biomass and the procedural control which were identical to those used for the herbivores. Prior to placement into the mesocosms, herbivores had however been removed in the covered units for microalgae production (n = 2 per mesocosm) using boiling water. Herbivores (and predators) were instead present in the open units for microalgae standing biomass (n = 4 per mesocosm) and the procedural control (n = 4 per mesocosm). Microalgae were allowed to recolonize the sand surface inside the units over one month at the end of the study period.

Chlorophyll *a* served as a proxy for microalgae biomass. It was extracted from each unit with 90 % acetone, measured spectrophotometrically (6405 UV/Vis, Jenway) and its concentration calculated (Jeffrey & Humphrey, 1975). There was no interaction between the effect of the mesh and climate treatments (ANOVA: df(1,8), $p > 0.30$ for all interactions), and thus units for standing biomass and the procedural control were pooled. For the data analysis, the average across units was calculated and then extrapolated to the area of the entire soft-bottom habitat resulting in one replicate for both microalgae production and standing biomass per mesocosm.

Predator behaviour and food demand

To assess the predators' response to an olfactory food cue, a behavioural experiment was conducted within the mesocosm. A food cue disperser containing a food mix of various invertebrates was placed on the 'open sand' habitat to start the test. Then, the surrounding area was video recorded from the top and side for 7 min (Fig. S2). A target was overlayed during the subsequent video analysis and the behaviour of each predator manually recorded using the software Solomon Coder. We interpreted the number of line crosses into and within the target as food search activity. This behavioural test was conducted on two different days in the final month of the study, each day at a different area within the mesocosm. The behaviour during all individual predator observations during both days was summed and the response variable 'line crosses per minute' calculated. A procedural control preceding each trial showed identical foraging activity for all climate treatments in the absence of a food cue (Fig. S4a), suggesting that any difference in behaviour during the trials was due to the presence of the olfactory food cue.

To determine food demand, the predators were captured and starved for 20 h (i.e. gastric evacuation). Then, before being sacrificed, they were released back into their original mesocosm to forage freely for 4 h. The prey in their stomach was counted under a stereo microscope and the average mass of prey organisms estimated applying the taxa-specific mass obtained from the herbivore units. The temperature sensitivity of digestion rate, however, made a direct comparison of stomach contents between levels of warming less reliable. Therefore, the predators' attack rate at the benthos was determined by video recording an area of each mesocosm from the top for 10 min on each of 3 different days. The consumption of prey relative to the predator's mass was calculated for each mesocosm as follows: feeding rate = attack rate of predators × average mass of prey organisms / predator mass.

Statistical analysis

Normality and homogeneity of variance were improved by transformation if appropriate and assumptions met for all analyses (Shapiro-Wilk test, Levene's test and visual examination of residuals). To assess the effect of future climate on the different response variables measured, two-way ANOVAs were conducted with ocean acidification and warming as fixed factors. These were followed by Student–Newman–Keuls post-hoc tests in case a significant interaction was found between the climate treatments. For a more detailed assessment of how future climate may affect the propagation of secondary to tertiary production, a linear model with ocean acidification and warming as fixed factors, herbivore production as covariate and predator production as response variable was examined. As there was no evidence for an altered relationship between secondary and tertiary production under future climate (Table S3), a final linear regression was fitted across all climate treatments.

Data analyses were performed with the software package R version 3.2.3 (R Core Team, 2015).

Ethics

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

RESULTS

Elevated CO_2, elevated temperature and their combined effect boosted primary production (Fig. 1a, Table S2a). The successive propagation of the enhanced bottom-up forcing, however, depended on warming. Under elevated CO_2 alone, secondary production increased in the same fashion as primary production (Fig. 1b, Table S2b). In contrast, under elevated temperature, secondary production remained unaltered compared to controls (Fig. 1b, Table S2b). At the next level of trophic transfer, a strong positive relationship was observed between secondary and tertiary production independent of climate treatments (Fig. S3, Table S3). Consequently, tertiary production remained unchanged under elevated temperature but nearly doubled under elevated CO_2 alone (Fig. 1c, Table S2c).

Tertiary-level predation by fish on secondary producers increased under both climate treatments. Under elevated CO_2 alone, however, the feeding rates of predators corresponded to that of controls once relativized for predator biomass (Fig. 1d, Table S2d). Despite the enhanced production of secondary producers under elevated CO_2 alone, their standing biomass remained unchanged to controls (Fig. 1e, Table S2e) given the stronger top-down control due to increased predator biomass (Fig. 1c). In contrast, under elevated temperature, predators showed higher feeding rates, while maintaining growth rates equal to controls (Fig. 1d, Table S2d, Fig. 1c). Accordingly, the standing biomass of secondary producers dropped in the presence of predators (Fig. 1e, Table S2e). Primary producer standing biomass, in the presence of secondary producers and predators, increased through both elevated CO_2 and temperature (Fig. 1f, Table S2f).

The sensory capability of predators was impaired by elevated CO_2 as they failed to show an increased foraging activity when exposed to an olfactory food cue compared to no cue (Fig. S4, Table S2g). In the absence of elevated CO_2, predators instead considerably intensified their food search behaviour upon the introduction of a food cue.

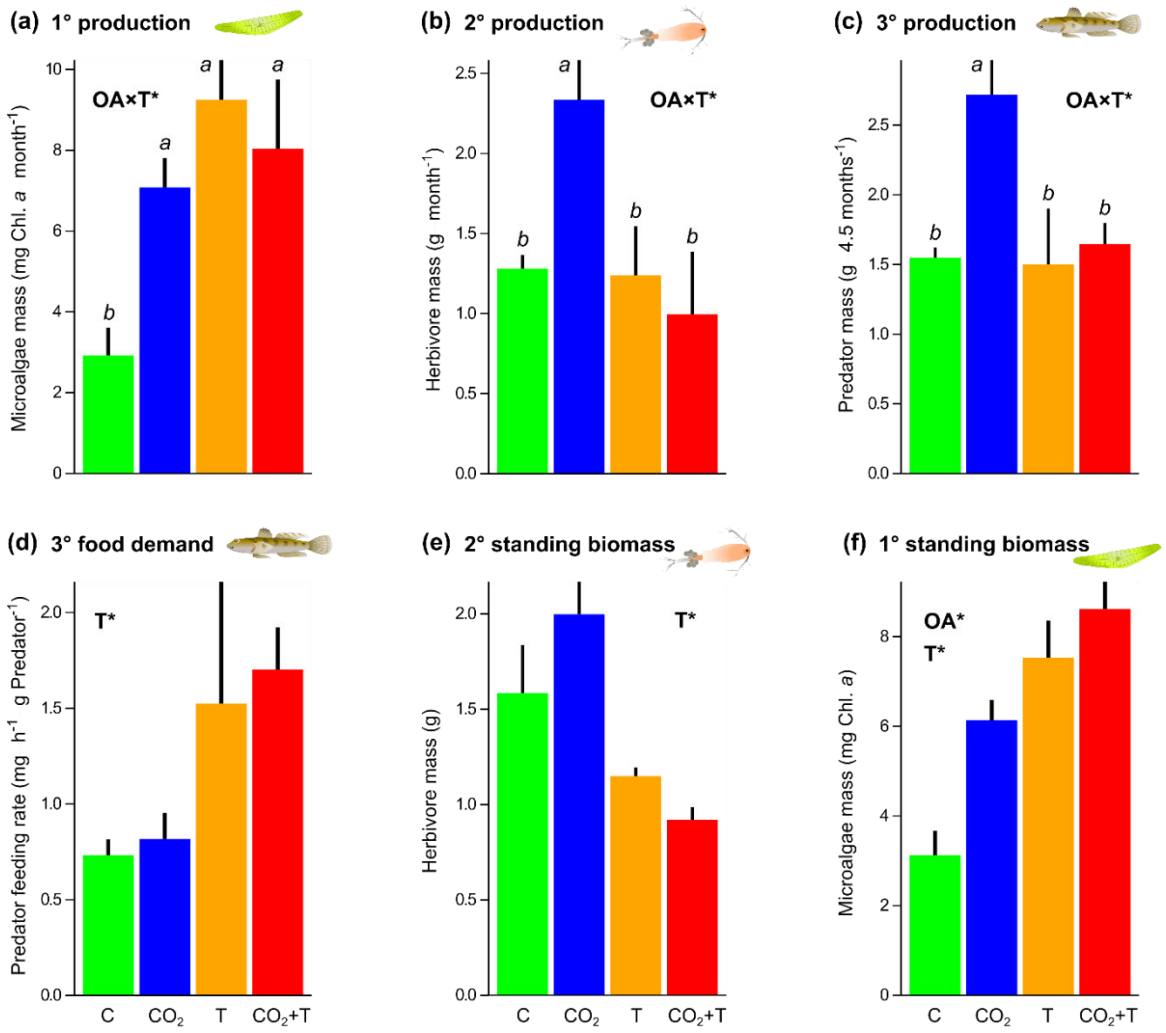

Figure 1: Effects of ocean acidification (OA) and warming (T) on trophic processes. Mean + SE are based on n = 3 mesocosms per treatment, each extrapolated from several subsamples. * marks significant effects. For interactions, means with different lower case letters differ significantly based on SNK post-hoc tests.

DISCUSSION

We demonstrate that elevated CO_2 can function as a resource boosting productivity across multiple trophic levels (Fig. 2). This result is striking because it contrasts the majority of previous studies on single trophic levels, which predict a reduced secondary and tertiary production under future acidification (see meta-analysis of Nagelkerken & Connell, 2015). The overall performance of both herbivores and predators was likely to have been positively affected since we focused on taxa more tolerant to ocean acidification stress (Kroeker *et al.*, 2013; Wittmann & Portner, 2013). Likewise, at CO_2 vents generalist herbivores and meso-predators that are exposed to elevated CO_2 over long-term showed increases in their population sizes (Connell *et al.*, 2017; Nagelkerken *et al.*, 2016). Thus, the propagation of enhanced bottom-up forcing to higher food web levels as shown in our study provides a mechanistic understanding of why generalist consumers can experience increases, rather than decreases, in their population sizes in nature.

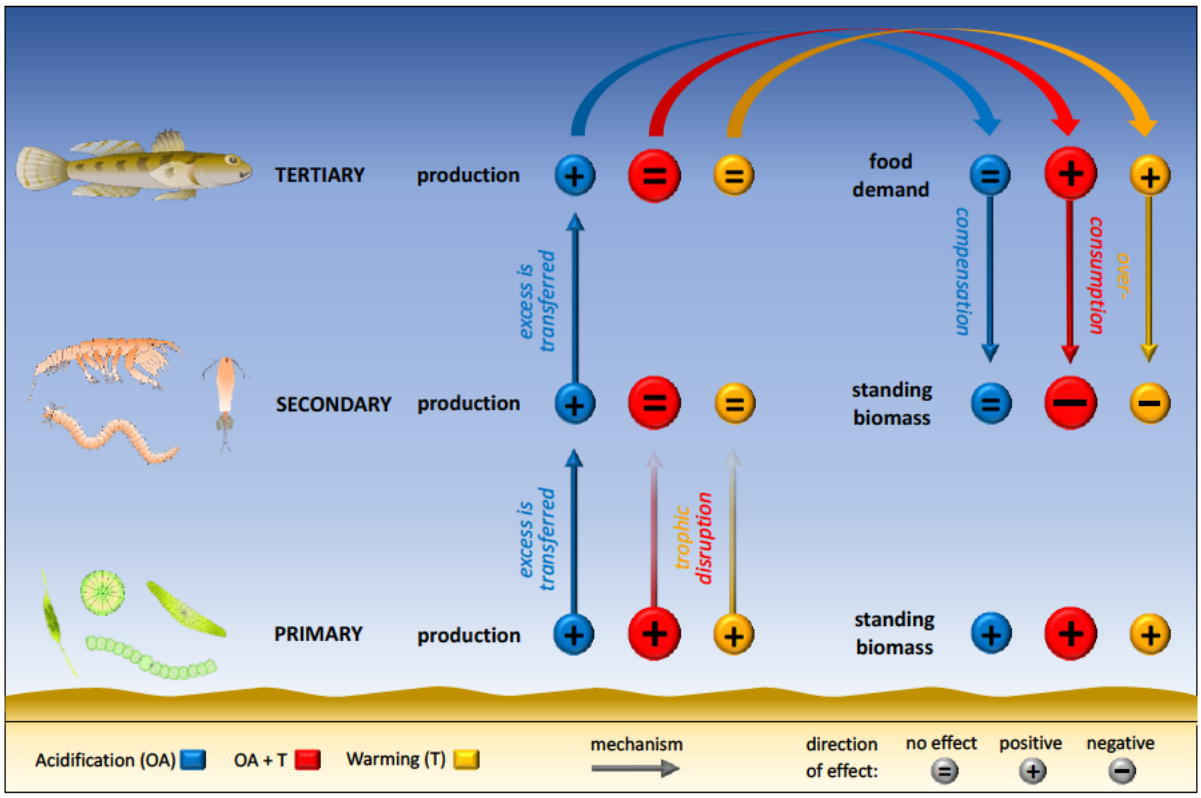

Figure 2: Conceptual diagram of how future climate can modify bottom-up and top-down forcing across a 3 level food web. The effects on each trophic level as well as changing linkages between trophic levels are contrasted to present day conditions (≙ control treatment), as measured in mesocosms.

Neither top-down control by predators nor their ability to capitalize on proliferating prey populations was weakened by acidification, even though the predators' olfactory capability was disturbed. Hence, the stressor component of ocean acidification, i.e. increased acid-based regulation (Portner, 2008) and impaired behaviour (Nagelkerken & Munday, 2016), seems to be insignificant for the long-term growth and survival of these meso-predators under ecologically more complex conditions. By maintaining their trophic functionality, our predators could also prevent an outbreak in herbivore abundances under elevated CO_2 through trophic compensation (Ghedini *et al.*, 2015): that is, the excess secondary productivity was consumed by the predators resulting in no change in herbivore abundances but enhanced predator growth. These dynamics resulted in an overall food web structure which matched trophic theory predicting that an energy supplement to primary producers mainly increases biomass at the top trophic level (here predators) and every second level below it (here primary producers) (aquatic: Heath *et al.*, 2014; terrestrial: Oksanen & Oksanen, 2000). Therefore, the essential role of meso-predators in mediating bottom-up and top-down processes appears to be a foundation by which some food webs may retain their function under ocean acidification.

Ocean warming, in contrast, acted as a stressor and negated the resource driven benefits of elevated CO_2. It disrupted the bottom-up propagation of resource enrichment during the

trophic transfer from primary producers to herbivores, while strengthening top-down control by predators (Fig. 2). The lack of enhanced secondary production under warming might be explained by reduced nutritional quality in algae food (e.g. blooming of toxic cyanobacteria, O'Neil *et al.*, 2012) or higher metabolic demands in herbivores that could not be met by their consumption. Such a temperature-driven mismatch can lower ingestion efficiency and lead to reduced fitness in herbivores, as the raised costs for basic maintenance leave less energy for growth and reproduction (Lemoine & Burkepile, 2012). In contrary, warming can benefit herbivores when tested within their natural thermal range (i.e. in colder seasons) (O'Connor *et al.*, 2009). This emphasizes that some aspects of the metabolic theory of ecology might not apply once the optimal thermal ranges of species are surpassed (Angilletta *et al.*, 2002; Portner & Farrell, 2008). Understanding food web dynamics during summer warming, as tested in our study, is essential since temperature extremes have become key drivers of species loss and community structure (e.g. Wernberg *et al.*, 2016).

A possible mismatch between herbivore production and food demands of carnivores may occur under future climate (Nagelkerken & Connell, 2015). Indeed, our predators required larger amounts of prey to sustain equal growth rates under warming. Consequently, herbivore populations declined as warming drove predators to intensify their top-down control in the face of elevated metabolic demand (Dillon *et al.*, 2010; Pistevos *et al.*, 2015). The trophic compensation we observed under acidification was evidently reversed through temperature stress into an imbalanced relationship between prey and predators. These dynamics may cascade further down the food web, as enhanced primary producers are facing herbivores with lower biomass and fitness, leading to a runaway expansion of primary producers (Mertens *et al.*, 2015). Accordingly, in our mesocosms, primary producer biomass under warming was more than twice that under present day conditions after only one month of re-growth. By hindering compensatory processes that counterbalance the effects of human disturbances (Connell & Ghedini, 2015), warming may destabilize ecological communities in future oceans. The predicted imbalance between production and consumption under warming possibly also applies to linkages at higher trophic levels and may lead to a systematic degradation of food webs.

The changes to future food webs predicted here will be shaped by the complexity of ocean processes. The potential for food web enhancement through anthropogenic CO_2 is for example limited by other resources for primary producers (i.e. nutrients and light) and might thus be entirely absent in extremely nutrient deficient systems (Verspagen *et al.*, 2014). Although the general decrease of secondary producer biomass with increasing temperature has been detected through modelling in accordance with our results (O'Connor *et al.*, 2011), positive effects of warming may also be observed if trophic levels are not at equilibrium state (e.g. O'Connor *et al.*, 2009). Given this context dependency, it is not surprising that opposing results were found by Alsterberg *et al.* (2013), who tested similar food web

components (sediment-associated microalgae and invertebrates) in a different scenario (competing with larger primary producers and herbivores for resources). Finally, secondary impacts resulting from rising sea surface temperatures, e.g. increased stratification or expansion of oxygen minimum zones (Boyce *et al.*, 2010; Schmidtko *et al.*, 2017), will likely cause further degradation of the already metabolically stressed food webs.

Making predictions about the fate of fisheries under future climate is challenging, in particular due to the uncertainty over future primary productivity and its propagation through food webs to fisheries species (Brander, 2007). Our findings suggest that there is the potential of ocean acidification to increase yields of particular species through the transfer of resource enrichment across multiple trophic levels, in cases where the species responsible for trophic energy flow are less susceptible to the direct effects of acidification. Yet, trophic inefficiency under warming may negate any bottom-up forcing through elevated CO_2 and reduce future fisheries production. By assessing the shifting balance between the propagation of resource enrichment and its consumption across trophic levels, we provide a predictive understanding of future dynamics of stability and collapse in food webs and fisheries.

Authors' contribution

All authors designed the research, S.U.G., C.M.F. and H.U. performed the research, S.U.G. analysed the data, S.U.G., I.N. and S.D.C. wrote the manuscript and all authors contributed to writing of the manuscript.

Acknowledgements

We thank W. Hutchinson and M. Gluis for technical advice, all the students helping with construction and maintenance of the mesocosms, T. Kildea for providing local temperature data and three anonymous reviewers for their constructive comments on the manuscript. Organism-symbols were either drawn by S.U.G. or modified from Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). This study was financially supported by an Australian Research Council Future Fellowship Grant to I.N. (FT120100183) and S.D.C. (FT0991953) and by a grant from the Environment Institute (the University of Adelaide). C.M.F. was supported by a Science Without Borders PhD scholarship through CAPES (Coordination for the Improvement of Higher Education Personnel) Brazil (scholarship no. 13058134).

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SUPPLEMENTARY METHODS

Table S1 and Figures S1-2

Technical set-up and habitat

The study was conducted in a flow-through system. All incoming seawater was first transferred to two 800 l header tanks and from there gravity fed to each mesocosm **(1**, Fig. S1**)**. The header tank supplying water to the six acidified mesocosms was pre-conditioned to elevated pCO_2 levels with pure CO_2 (control system ACQ110 Aquatronica, Italy). Each mesocosm continuously exchanged water (~1,800 l per h) with its individual 60 l bin to maintain treatment levels. These bins were heavily aerated with enriched air at 1000 ppm pCO_2 (PEGAS 4000 MF Gas Mixer, Columbus Instruments, Columbus, Ohio) or ambient air at 400 ppm pCO_2 depending on the acidification treatment, and contained submersible titanium heaters (800 W) to achieve elevated temperature. Two diffuser pipes **(2)** used this water circulation to form a mild circular current inside the mesocosms alternating direction every 6 h. Water flowed back to the 60 l bin through gravity after passing a filter column with a ~20 μm screen **(3)**, which ensured that larger organisms were retained within the mesocosms. Overall, our complex set-up ensured an environment free of unnatural disturbances such as pump noise, air bubbles or electrical currents.

A 250W metal halide lamp (Osram Powerstar HQI-T 250/D/PRO) was mounted above each mesocosm **(4**, Fig. S1**)**. The lamp had a colour temperature of 5500 K, a colour rendering index of 92 and a wave length distribution similar to sunlight as the spectrum provided by the manufacturer showed. The mean ± SD irradiance at the mesocosm bottom was 3833 ± 1304 lux, derived by measures in 5 cm intervals from the centre to the tank wall. Applying attenuation coefficients from the literature, this irradiance corresponds to approx. 6-7 m depth in Gulf St. Vincent (Phillips *et al.*, 1981). For these estimations, the local average daily summer irradiance over the past 20 years was used (Bureau of Meteorology, www.bom.gov.au, location Adelaide).

The research was conducted at the South Australian Research and Development Institute (SARDI; 34°57'10"S, 138°30'20"E), and all habitats and organisms used were collected within 60 km of the facility. The benthic habitat in our mesocosms comprised four patches of each 'rocky reef' **(5**, Fig. S1**)** and 'artificial seagrass' **(6)** arranged in pairs and 'open sand' surrounding these patches **(7)**. The artificial seagrass was designed after the most abundant local seagrass *Posidonia* spp. (Bryars & Rowling, 2009) and was incubated for 2 weeks in the subtidal close to seagrass meadows to allow for epiphytic colonization before being transplanted into the mesocosms. The silica sand was chosen according to the sediment found at local beaches and seagrass meadows with the main grain size fraction between 0.21 - 0.85 mm (type N30, Sloans Sand, Australia). An assemblage of six species of juvenile

fish was also introduced, based on their high abundances in shallow coastal water during summer locally. Of these fish species, the longfin goby was the principle predator on the sand in our mesocosm.

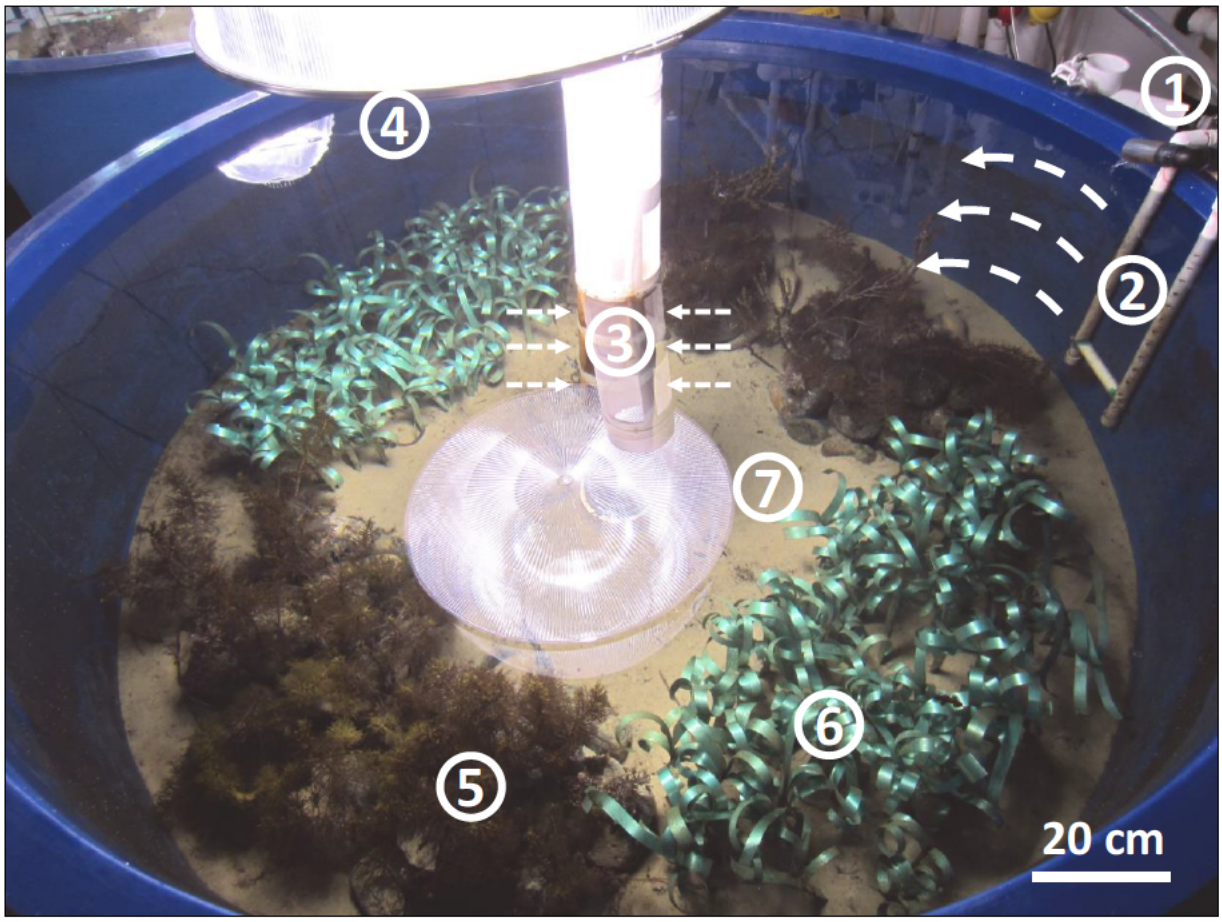

Figure S1: Mesocosm at the beginning of the experiment showing the technical set-up and the arrangement of the three habitat types.

Seawater parameters

Refer to Table S1 for an overview of the seawater properties under the different climate treatments. Temperature and pH were measured daily at midday (Mettler Toledo SevenGo™ SG2, calibrated daily). Fortnightly, salinity was measured with a SR6 refractometer (Vital Sine) and total alkalinity estimated by Gran titration from water samples (888 Titrando, Metrohm, Switzerland), with a total of eight estimates per mesocosm. Alkalinity measures were accurate within 1 % of certified standards (reference material from A. Dickson, Scripps Institution of Oceanography). Average seawater pCO_2, bicarbonate, carbonate and the saturation states of calcite and aragonite were calculated using CO2SYS for Excel (Pierrot *et al.*, 2006) with constants from (Mehrbach *et al.*, 1973) refit by (Dickson & Millero, 1987).

Table S1: Overview of water parameters during the 3.5 months treatment period (mean ± SD). Standard deviations represent the variability between mesocosms.

Parameter	control	elevated CO_2	elevated T	elevated CO_2 + T
Temperature (°C)	21.1 ± 0.13	20.9 ± 0.05	23.8 ± 0.18	23.8 ± 0.08
pH_{NBS}	8.14 ± 0.004	7.88 ± 0.004	8.12 ± 0.002	7.89 ±0.009
Salinity (ppt)	36.3 ± 0	36.3 ± 0	36.3 ± 0	36.3 ± 0
Total Alkalinity (μmol kg^{-1})	2482 ± 4	2485 ± 5	2486 ± 6	2493 ± 3
pCO_2 (ppm)	465 ± 5	905 ± 6	500 ± 8	915 ± 25
HCO_3 (μmol kg^{-1})	1995 ± 6	2186 ± 3	1985 ± 2	2166 ± 9
CO_3 (μmol kg^{-1})	200 ± 2	123 ± 1	206 ± 2	135 ± 3
Ω Calcite	4.74 ± 0.05	2.91 ± 0.02	4.90 ± 0.05	3.20 ± 0.07
Ω Aragonite	3.09 ± 0.04	1.90 ± 0.01	3.22 ± 0.03	2.10 ± 0.05

Food web

Herbivores

Four dominant taxa were identified in the herbivore units with the following biomass composition (mean ± SD based on n = 12 mesocosms): tanaids 33.8 ± 13.1 %, copepods 20.0 ± 7.5 %, annelids 35.5 ± 8.9 % and nematodes 10.6 ± 2.8 %. These taxa have high abundances in the top layer of coastal sediments and are recognized as major consumers of sediment-associated microalgae (Buffan-Dubau & Carman, 2000; Davis & Lee, 1983; Montagna, 1984; Montagna *et al.*, 1995). They thus represent a crucial link between benthic primary production and higher trophic levels. Nematodes contributed less than 0.01 % to the predator's diet and were excluded from this study. To estimate the herbivore biomass in the sampling units, for small herbivores (i.e. copepods, small annelids and nematodes), only a subsample of 7.5 % was counted for each sample by randomly selecting 30 out of the 400 cells on the counting tray. In contrast, the entire sample was assessed for large herbivores (i.e. tanaids and larger annelids). We calculated the biovolume of the smaller herbivore taxa based on photographs and measurements with ImageJ: n = 159 copepods, n = 65 annelids and n = 138 nematodes. The taxa specific average mass across climate treatments was then used to obtain the total herbivore mass for each sample. Only for copepods, the treatment specific average mass was used since it differed between climate treatments (ANOVA: $F_{(1,155)} = 4.13$, $p = 0.044$).

Predators

The predatory fish used in this study, *Favonigobius lateralis*, inhabits shallow soft-bottom habitats (seagrass and non-vegetated) and is amongst the most abundant species locally (Bloomfield & Gillanders, 2005; Connolly, 1994; Gomon *et al.*, 2008; Wear & Tanner, 2007). The behavioural observations confirmed their strong association with the soft-bottom habitat in the mesocosms, as they spent over 80 % of time and performed 90 % of their foraging over soft-bottom during 275 min of individual tracking. They were observed

foraging within the herbivore units frequently, and stomach content analysis identified the herbivore taxa found in these units as principle food source. The mass of each herbivore taxa in the predator stomachs was calculated using their count and the taxa-specific average mass from the herbivore sampling units, resulting in the following mean ± SD diet composition (based on n = 12 mesocosms, each represented by 5-7 fish): tanaids 44.3 ± 13.4 %, copepods 39.1 ± 15.9 %, annelids 5.0 ± 5.2 % and other taxa 10.5 ± 8.8 % (i.e. molluscs, ostracods, nematodes and unidentified invertebrates). This composition should not be interpreted in detail due to the large difference in digestibility between prey taxa as a consequence of size and the presence or absence of an exoskeleton. For example, the contribution of annelids was likely considerably underestimated because they were small and lacked an exoskeleton and the contribution of tanaids overestimated as they were large and heavily armoured.

The physical condition of the predators, based on Fulton's condition factor (Bolger & Connolly, 1989), remained unaltered by future climates (ANOVAs: df(1,8), $p > 0.7$ for OA, T and OA×T). The only 5 fish that died, out of the total of 84 individuals, were distributed among the mesocosms with elevated temperature. Contrasting this 10 % loss in abundance under elevated temperature to the 75 % gain in average individual mass under elevated CO_2 alone suggests that the patterns in predator productivity (≙ abundance x average growth) and top-down forcing were mainly a result of differential predator growth rates, rather than a change in predator numbers or physical condition. To note, our experiment did not allow for predator reproduction. Over long-term in nature, predator populations would also be expected to respond to changing food availability and metabolic demands by altered abundances.

Predator behaviour

Each individual predator was tracked from entering until exiting the field of view (Fig. S2) of the top camera (GoPro™ Hero4 Silver). These predators typically sit motionless on the bottom and inspect the sand around them. They either strike at the sand or hop a few cm forward to evaluate a new spot. The chances of finding a lucrative prey source hence increase with the number of cycles of hopping and evaluating. Therefore, we interpreted the number of line crosses into and within the target centred on the cue disperses as food search activity. The food cue disperser was built with a transparent 50 ml vial with nine windows cut into sides and top and covered by fine mesh. A smaller opaque tube inside the vial contained 4.5 g food mix (defrosted bloodworms and various kinds of marine molluscs and crustaceans; Fish Fuel and Co., Australia). Tests with food dye indicated a slow and continuous dispersion out of the opaque tube and finally vial. A food cue disperser not containing food mix was located at the exact same site for the 24 h prior to each behavioural trial to allow for habituation. Preceding each trial, a procedural control video recording was

conducted for three minutes where the dummy disperser was exchanged by another dummy disperser and not by a disperser containing food mix like in the later trial.

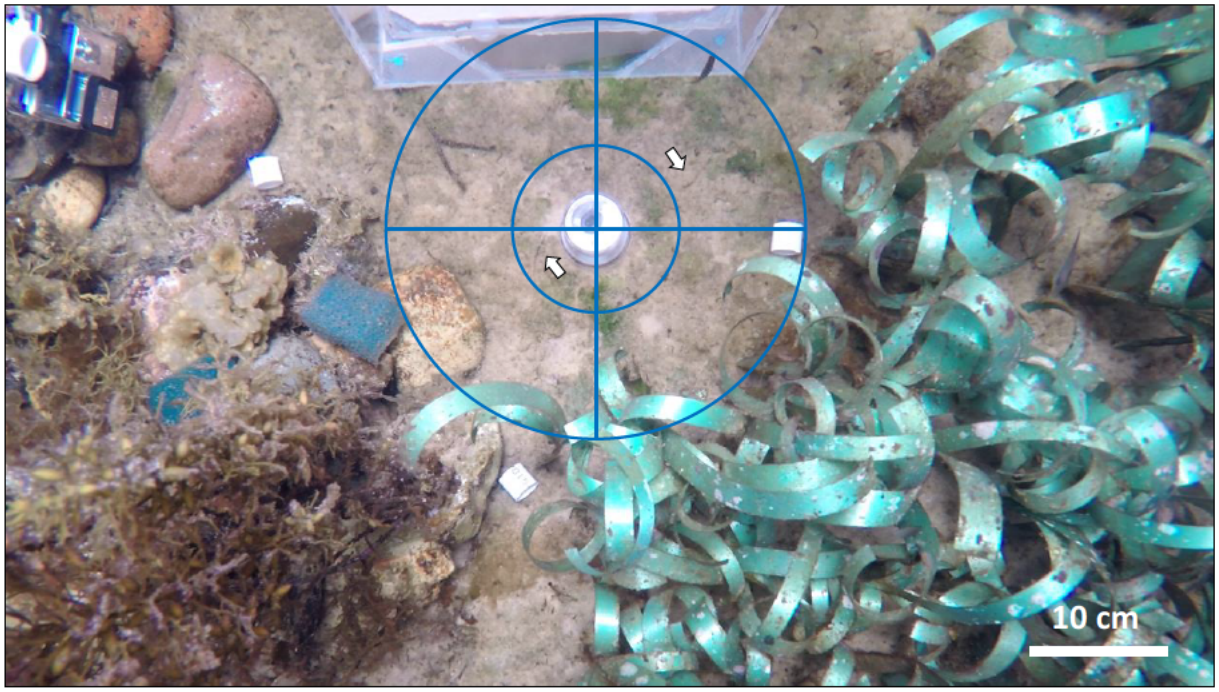

Figure S2: Field of view of the top camera during behavioural trials testing the response of the predatory fish to an olfactory food cue. The target of 30 cm diameter was overlayed for the video-analysis. White arrows point out predators. Photo shows mesocosm habitat 3.5 months into the experiment.

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SUPPLEMENTARY RESULTS

Tables S2-3 and Figures S3-4

Table S2: ANOVAs testing the effects of ocean acidification (OA), warming (T) and their interaction on alternate trophic levels. Significant effects relevant for further interpretation are indicated in **bold**.

Response variable (transformation)	**Source of variation**	**df**	**MS**	**F-ratio**	**P-value**
a) Microalgae production 	OA	1	6.5	1.76	0.221
	T	1	39.7	10.82	0.011
	OA×T	1	21.7	5.90	**0.041**
	Residuals	8	3.7		
b) Herbivore production ($x^{1.5}$) 	OA	1	2.46	3.43	0.101
	T	1	4.70	6.55	0.034
	OA×T	1	4.64	6.47	**0.035**
	Residuals	8	0.72		
c) Predator production ($x^{1.5}$) 	OA	1	5.75	7.94	0.023
	T	1	4.20	5.80	0.043
	OA×T	1	4.30	5.94	**0.041**
	Residuals	8	0.72		
d) Predator feeding rate ($x^{1.5}$) 	OA	1	0.04	0.04	0.854
	T	1	6.81	6.43	**0.035**
	OA×T	1	<0.01	<0.01	0.987
	Residuals	8	1.06		
e) Herbivore standing biomass 	OA	1	0.03	0.34	0.576
	T	1	1.72	23.33	**0.001**
	OA×T	1	0.31	4.17	0.075
	Residuals	8	0.07		
f) Microalgae standing biomass 	OA	1	12.6	10.78	**0.011**
	T	1	35.6	30.52	**<0.001**
	OA×T	1	2.8	2.38	0.162
	Residuals	8	1.2		
g) Predator number of line crosses 	OA	1	23.5	10.28	**0.013**
	T	1	1.4	0.61	0.459
	OA×T	1	0.7	0.29	0.602
	Residuals	8	2.3		

df = degrees of freedom; MS = mean squares

Table S3: Model selections to derive the most parsimonious model for the relationship between secondary and tertiary production. The global model included ocean acidification (OA) and warming (T) as fixed factors, herbivore production (H) as covariate and predator production as response variable ($x^{1.5}$-transformed). Sub-models with all possible combinations of OA, T and H were compared using the Akaike information criterion corrected for small sampling size (AIC*c*; Hurvich & Tsai, 1989). Each row represents one sub-model with shaded cells marking the effects included. Sub-models are ranked from the most parsimonious (lowest AIC*c*) to the least parsimonious, and only the five best sub-models are shown. The 'relative importance' of each effect across all possible sub-models is provided by the sum of Akaike weights over all sub-models that included the particular effect.

H	OA	T	H×OA	H×T	OA×T	H× OA×T	df	AIC*c*	delta	weight
■	■						4	25.6	0	0.60
■							3	27.5	1.88	0.24
■		■		■			5	30.4	4.75	0.06
■	■		■				5	30.5	4.83	0.05
■	■	■					5	31.9	6.22	0.03
1.00	0.69	0.11	0.06	0.06	<0.01	<0.01	relative importance			

df = number of model parameters; delta = increase in AIC*c* compared to the most parsimonious sub-model; weight = probability that the sub-model is the best among all candidate sub-models

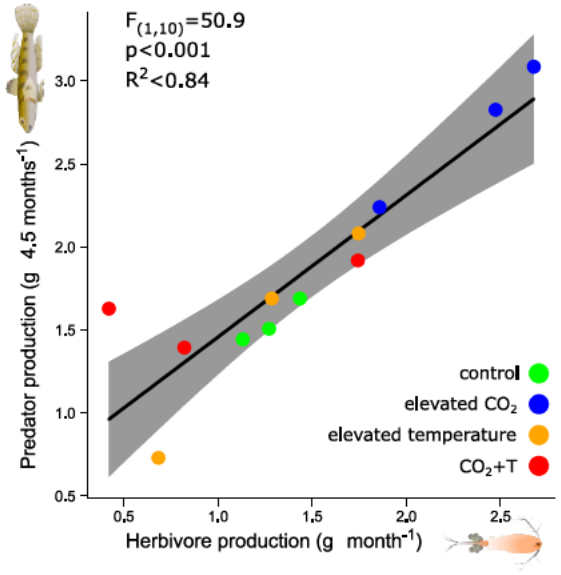

Figure S3: Trophic transfer from secondary to tertiary producers. The regression (incl. 95 % confidence belt) is applied across climate treatments based on the model selection in Table S3.

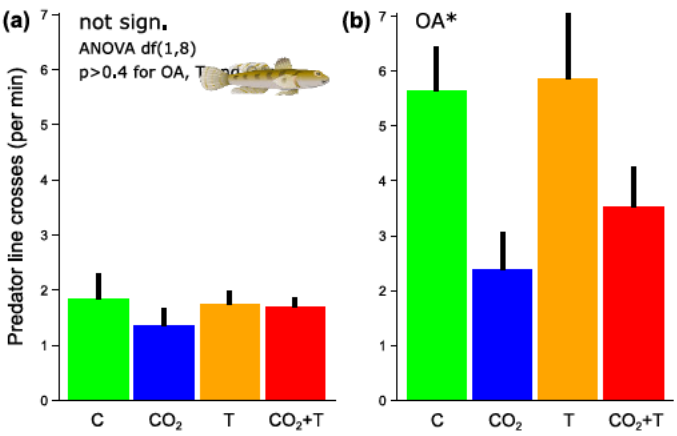

Figure S4: Food search activity of predators in the **(a)** absence and **(b)** presence of an olfactory food cue. Mean + SE are based on n = 3 mesocosms per treatment combination. * marks significant effect.

Reference: Hurvich CM, Tsai C-L (1989) Regression and time series model selection in small samples. Biometrika, **76**, 297-307.

CHAPTER III

ECOLOGICAL COMPLEXITY BUFFERS THE IMPACTS OF FUTURE CLIMATE ON MARINE CONSUMERS

Statement of Authorship

Title of Paper	Ecological complexity buffers the impacts of future climate on marine consumers
Publication Status	☐ Published ☒ Accepted for Publication ☐ Submitted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
Publication Details	Goldenberg SU, Nagelkerken I, Marangon E, Bonnet A, Ferreira CM, Connell SD (2018) Ecological complexity buffers the impacts of future climate on marine consumers. Nature Climate Change

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Name of Principal Author (Candidate)	Silvan U Goldenberg		
Contribution to the Paper	study design, conducting experiment, data analysis, meta-analysis and writing		
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	2/02/2018

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

Ecological complexity represents a network of interacting components that either propagate or counter the effects of environmental change on individuals and communities [1-3]. Yet, our understanding of the ecological imprint of ocean acidification (elevated CO_2) and climate change (elevated temperature) is largely based on reports of negative effects on single species in simplified laboratory systems [4,5]. By combining a large mesocosm experiment with a global meta-analysis, we reveal the capacity of consumers (fishes and crustaceans) to resist the impacts of elevated CO_2. Whilst individual behaviours were impaired by elevated CO_2, consumers could restore their performances in more complex environments that allowed for compensatory processes. Consequently, consumers maintained key traits such as foraging, habitat selection and predator avoidance despite elevated CO_2 and sustained their populations. Our observed increase in risk-taking under elevated temperature, however, predicts greater vulnerability of consumers to predation. Yet, CO_2 as a resource boosted the biomass of consumers through species interactions and may stabilise communities by countering the negative effects of elevated temperature. We conclude that compensatory dynamics inherent in the complexity of nature can buffer the impacts of future climate on species and their communities.

INTRODUCTION, RESULTS AND DISCUSSION

The web of life is classically considered as a network of organisms interlinked to each other and their environment through biotic and abiotic processes [1]. These networks not only drive population dynamics but also shape the ecological imprint of human activities at multiple levels of biological organisation [2,3]. Individuals possess remarkable plasticity in using the complexity of their environment to persist through abiotic stress [6-9]. Yet, their interactions with other species can propagate [10,11] or stabilize against change [12], giving rise to strong and complex indirect effects [13,14]. In turn, species diversity enhances function [15] and stability within ecosystems [16,17]. Consequently, as it manifests from individuals to ecosystems, ecological complexity has the potential to alter or stabilize local communities during global change.

Predictions of ecological responses to future ocean acidification and warming remain largely based on simplified laboratory systems and species in isolation [4]. The metabolic rates of marine ectotherms are directly affected by warming [18], which accelerates growth in some species when sufficient food is provided [19]. However, in nature, temperature driven regime-shifts can negate such direct benefits by eroding the resources on which they rely [20]. Ocean acidification can raise the energetic costs involved with calcification and acid-base regulation [21,22] and impair neural functioning causing disturbed responses in ecologically relevant behaviours [5]. An intensification of these direct effects from ocean acidification might be expected when animals are exposed to the pressures and complexities of nature. In contrast, fishes, crustaceans and calcifying herbivores can flourish at natural analogues of ocean acidification [23,24]. These counter-intuitive findings suggest the existence of mechanisms that reverse the direction of change within the complexity of ecological communities.

Understanding the response of actively foraging animals to global change is particularly challenging because, compared to plants or sedentary animals, they consume a diversity of biological resources [25] and are able to react through their mobility and complex behaviour [7,26]. Interactions between an individual and its environment are mediated by behaviour; acting as a first line of defence against rapid human-induced change [27]. Exceptional plasticity in behaviour draws upon building blocks of ecological complexity such as space, time or environmental information to initiate compensatory responses [6,7]. For example, animals that are impaired in one sense through abiotic change (e.g. olfaction impaired by ocean acidification) may retain their capacity for relevant decision making when provided with more complete information about their environment through additional sensory cues [28,29]. Therefore, a deeper understanding of the role of behavioural plasticity and the indirect effects that operate within communities is critical to bridge the gap between the effects of future climate in the laboratory and their consequences in nature [3-5].

The first step of our investigation experimentally tested whether ecological complexity can modify the effects of ocean acidification and warming on active consumers. In 1,800 l mesocosms harbouring a mosaic of habitats, we assessed the response of an assemblage of eight species of omnivorous and carnivorous fish and shrimp (Table S10) at the organism to community levels. The consumers were supported by a self-sustaining and highly diverse food web including microflora and fauna, macrophytes (20+ species) and macroinvertebrates (70+ species). Elevated CO_2 (910 μatm, pH=7.89) and temperature (+2.8 °C, baseline 21 °C) were maintained for 4.5 months according to end-of-century projections (RCP 8.5) [30]. Warming was simulated based on summer temperatures because climate extremes are key drivers of community structure [20]; temperatures remained nevertheless within the thermal limits of the consumer species (see Table S12).

This mesocosm approach showed that the direct negative effects of elevated CO_2 can be buffered and even reversed by ecological complexity. Consumers under elevated CO_2 were less attracted to either olfactory or visual food cues in isolation – the simplest level of complexity (Fig. 1a, Table S1, S2). However, when both olfactory and visual cues were present, consumers fully restored their attraction to food cues under elevated CO_2 (Fig. 1a). Accordingly, the success of consumers during hunting was not affected by elevated CO_2, estimated through the number of live prey captured while foraging freely amongst structured habitats (Fig. 1b, Table S3a). Consumer-resource interactions operated over long-term in the mesocosms, as consumers had to search and compete for the self-replenishing resources. At this ecologically more complex level, resource availability was boosted by elevated CO_2 (Fig. 1c, Table S3b), and correspondingly, consumer assemblages showed higher biomass (Fig. 1d, Table S3c). This response was not altered by the identity of consumer species (Table S4).

Whilst elevated temperature did not affect cue sensing in consumers (Fig. 1a, Table S1), it intensified risk-taking behaviours that could increase their exposure to predators in nature. Consumers invested more effort in acquiring food under elevated temperature (Fig. 2a, Table S3d), but this was not converted to increased biomass (Fig. 1d, Table S3c). In the absence of a predator, consumers of all climate treatments aggressively competed for food in unsheltered habitat (Fig. 2b, Table S5, 6). Only consumers under ambient temperature reduced these interactions when facing a live predator, while consumers under elevated temperature maintained high levels of risk-taking. In contrast, CO_2 did not affect the response of consumers to a live predator that provided the full range of predator cues (Fig. 2b, Table S5).

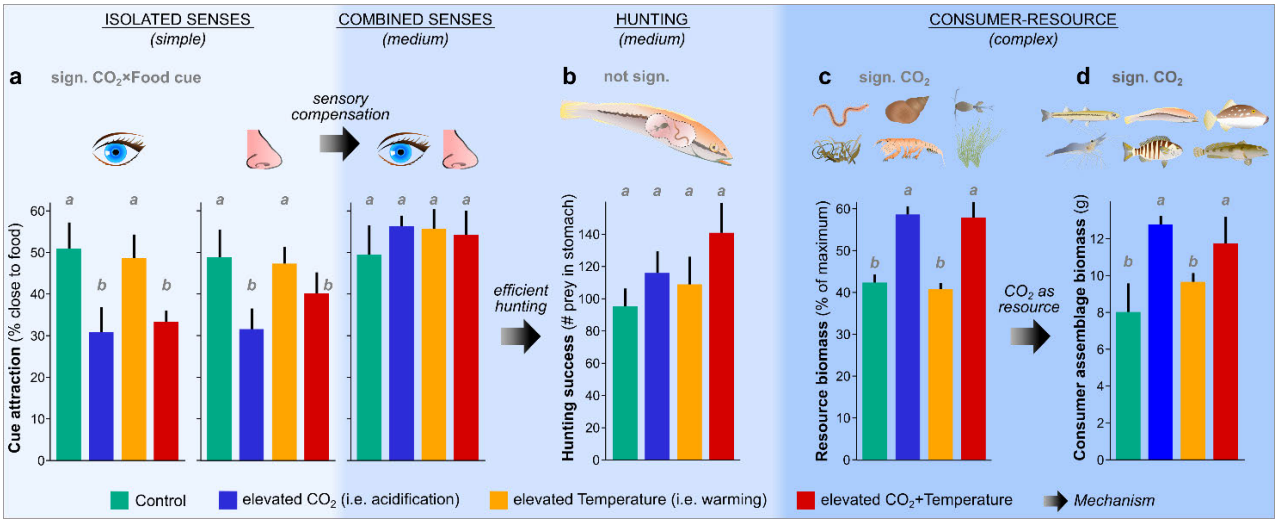

Figure 1: Mesocosm study showing how the negative effects of ocean acidification on consumers can be buffered and reversed through ecological complexity (mean + SE). **a)** Sensing of visual, olfactory and combined visual-olfactory food cues (n = 6 behavioural trials from 3 mesocosms). **b)** Invertebrate prey captured during foraging (n = 53, 62, 49 and 54 fish). **c)** Availability of resources and **d)** overall performance of consumers estimated as biomass after long-term exposure (n = 3 mesocosms). Different superscripts mark significantly different groups of means following main effects (via ANOVA, plot b-d) or interaction (via post-hoc tests, plots in a).

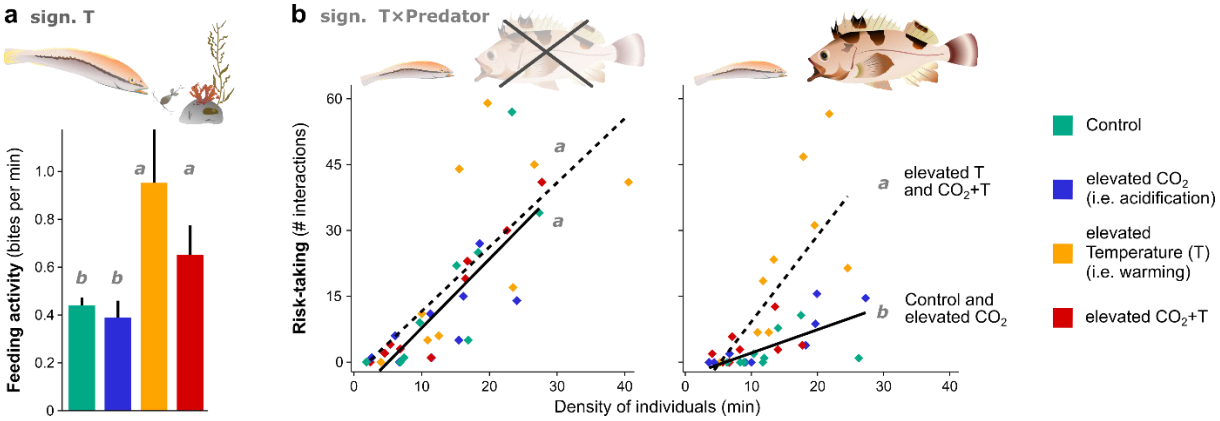

Figure 2: Mesocosm study showing how warming can increase risk-taking behaviour in consumers. **a)** Hunting effort (mean + SE) required to meet food demand (n = 3 mesocosms). **b)** Willingness to take risks in the absence and presence of a live predator (n = 18 behavioural trials per regression line from 6 mesocosms). Different superscripts mark significantly different groups of means following main effect (via ANOVA, plot a) or interaction (via post-hoc tests, plots in b).

The second step of our investigation related these experimental responses to ocean acidification with responses of other study systems (n = 102 experiments) that similarly included fishes or decapod crustaceans. The performance of consumers was considered in three key ecological traits – predator avoidance, habitat selection and foraging – under different levels of ecological complexity. Meta-analysis suggested a steady reduction of the impacts of ocean acidification on consumers from ecologically simple to complex experiments (Fig. 3, Table S8a), which is in agreement with our mesocosm study. Elevated

CO_2 had a strong negative effect on multiple behaviours in simpler experiments (Table S9a). However, negative effects on behaviour, growth or survival were less severe (for predator avoidance) or absent (for habitat selection and foraging) in experiments with medium complexity (Table S9a). While we defined these two levels of complexity through the presence of sensory cues – 'simple' for an isolated cue and 'medium' for multiple cues – they were likely representative of ecological complexity in a broader context (see Table S16). At natural CO_2 vents, the most complex level that integrated ecological traits and allowed for biotic interactions, population densities of consumers remained on average unaffected (Fig. 3, Table S9a), but showed an increase for several individual experiments (Fig. S1).

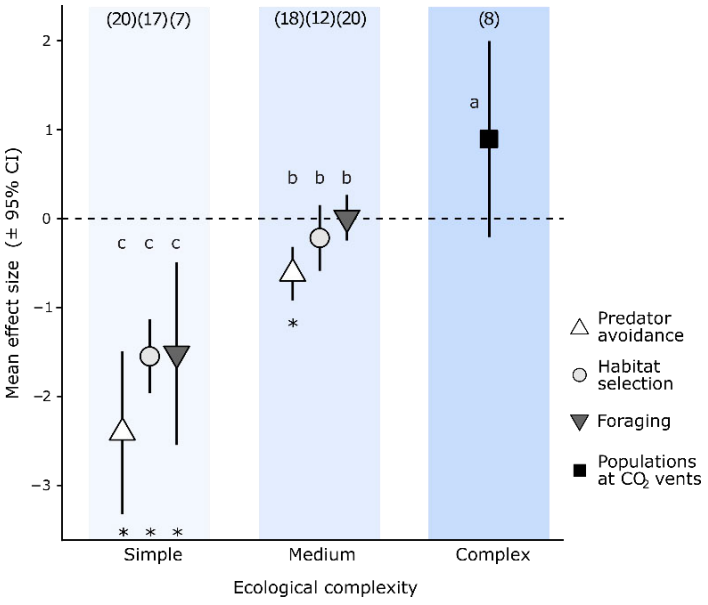

Figure 3: Meta-analysis on the effects of ocean acidification on the performance of fishes and decapods at different levels of ecological complexity. Effect sizes are standardised mean differences (Hedges' g) and should be interpreted as multiples of standard deviations. Within each of the three ecological traits, different superscripts mark effect sizes that differ significantly between levels of complexity. Asterisks mark significant differences from 0 and parentheses give the number of experiments included.

After accounting for ecological traits and levels of complexity in the meta-analysis, the amount of remaining heterogeneity indicated that responses of consumers to elevated CO_2 differed substantially among experiments (I^2 and Q statistics in Table S9a). Whilst the CO_2-effect appears to be variable across species and contexts, the consumer responses from our mesocosm are close to the mean effect sizes from the literature and may thus be seen as representative (Fig. S1).

We show that ecological complexity buffers the influence of future climate on marine consumers and highlight the importance of compensatory processes within complex communities. We not only provide an experimental demonstration for this phenomena, but also show how widely spread it may occur across multiple systems. Physiological responses to ocean acidification were compensated at the organismal level, and indirect effects subsequently acted as principle pathways towards negative (via ocean warming) or positive change (via ocean acidification) (Fig. 4). Such successive incorporation of increasing ecological complexity may explain why global change can be dampened at larger spatio-temporal scales [2]. It may also assist us in understanding the widespread nature of

observations in the stability-biodiversity debate: e.g. why plant diversity reinforces the resistance of grassland productivity to abiotic stress [17], and why increasing trophic diversity provides stability to food webs[16] and enhances ecosystem services [15]. From homeostasis within individuals to interactions among species, these lower-level processes may contribute to emergent properties of stability and resistance at the scale of complex food webs and ecosystems [12].

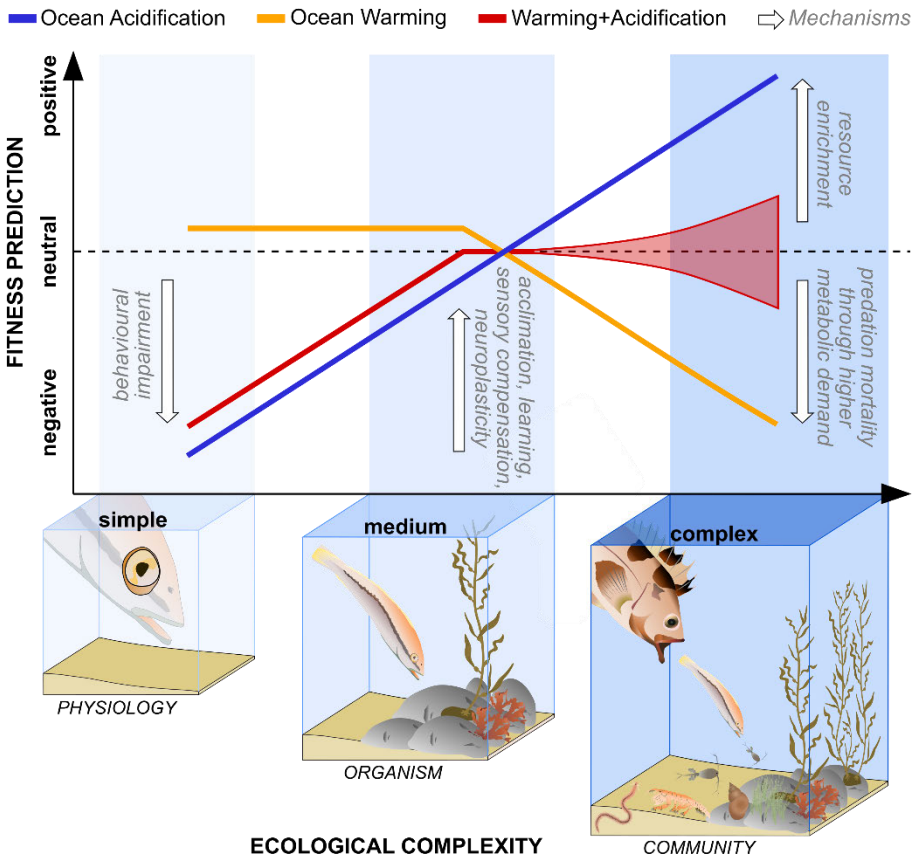

Figure 4: Conceptual framework of how increasing ecological complexity can buffer the direct negative effects of future climate on marine consumers and drive community dynamics through biotic interactions. Fitness predictions are based on a multi-species assemblage tested in a foraging context in mesocosms (acidification and warming) and on a global meta-analysis considering multiple ecological traits (acidification only).

Whilst isolated sensory modalities were often compromised by ocean acidification – a results that on its own would predict population decline – consumers could restore their performances through compensatory responses at the organism level. For instance, sensory compensation may occur via two mechanisms based on the cognitive flexibility of animals [6,28,29]: an impaired sensory modality is replaced by a functioning one (i.e. sensory redundancy) or, as demonstrated in our mesocosms with vision and olfaction, two impaired modalities complement each other (i.e. sensory complementation). In the broad ecological context of our meta-analysis, neuroplasticity and learning may also form part of the repertoire of processes that buffer against the negative effects of ocean acidification [7,31]. However, the full compensatory potential may only be accomplished if animals are offered

choices (e.g. in resources and habitat) under long-term selective pressure (e.g. competition and survival). These criteria are met at natural CO_2 vents and in our mesocosms and might have favoured the development of behavioural strategies to maintain increasingly difficult tasks such as hunting. By drawing upon the complexity that characterises ecological niches, behavioural plasticity can improve the fitness of animals during unprecedented environmental change including ocean acidification and buy genetic adaptation time for physiological recalibration [8,27,32].

At the community level in our mesocosms, an increase in resources supported greater consumer biomass reversing the direct negative effect of ocean acidification. Primary producers can utilise anthropogenic CO_2 as a nutrient [33] that propagates to secondary [24] and tertiary producers [23,34]. Alterations to consumer-resource interactions are generally regarded as powerful drivers of food web structure and function [3,11], and we show that CO_2 enrichment can benefit an entire assemblage of consumers, including eight species of omnivores and carnivores. CO_2 enrichment may similarly be responsible for the increase in fish numbers at CO_2 vents in the Mediterranean, the tropical Pacific and the temperate Pacific as documented by several studies in our meta-analysis. Whilst our findings provide a broader framework in which to consider ocean acidification – a field dominated by reports on negative effects – ecosystems as a whole still seem likely to experience losses in species and functional diversity [18]. As such, ocean acidification may I) impair other life stages including reproduction and early life-history that are not fully considered at CO_2 vents due to the subsidy of individuals from nearby control areas, II) enable generalist species to displace specialist species [14], III) threaten calcifying consumers including molluscs and echinoderms [22], and IV) impact foundation species such as corals causing degradation of habitats and the species they support [35].

Ocean warming may counter the positive effects of acidification on consumers by increasing their vulnerability to higher order predation. In our mesocosms, the rising metabolic demand at elevated temperature [18] may have favoured competition for food over vigilance in the trade-off between growth and survival [36,37]. Through increased risk-taking in consumers and raised food demands in their predators [18,19], warming would intensify predator-prey interactions. These findings are unlikely to reflect short-term stress-responses, as the thermal niche of our consumer assemblage was not exceeded by the warming treatment. This possibly explains the absence of any negative effects of warming on foraging behaviours and biomass. In contrast, species loss and a substantial re-organisation is forecast for consumer assemblages closer to their upper thermal limits, which is more often the case in the subtropics [38]. Trophic complexity that incorporates resources (i.e. gain) and predators (i.e. loss) [11,25] propagates change via indirect effects [3,10,34] that may dominate over direct effects of human stressors [13]. Accordingly, our findings suggest that changes in consumer assemblages in future oceans can depend on the relative balance between the negative effect of predation through warming and the positive effect of resource enhancement

through acidification (Fig. 4). This consideration challenges the view of ocean acidification as an overwhelming stressor and, instead, indicates its potential to buffer some impacts of coinciding ocean warming. Consumers may consequently maintain function under future climate to support some ecosystem services, such as the trophic transfer of benthic production towards fisheries.

We here bridge the knowledge gap between direct effects of future climate and the dynamics of species assemblages in natural environments. Our findings reveal processes that counter the propagation of change, both at simple (via sensory compensation) and elevated levels of complexity (via resource enrichment and interacting stressors). Therefore, we highlight the potential of ecological complexity to buffer or reverse the responses of species to future climate and mediate change or stasis in ecological communities.

Authors' contribution

S.U.G., I.N. S.D.C and C.M.F designed the study, S.U.G., E.M., A.B. and C.M.F. performed the research, S.G. analysed the data, S.U.G. conducted the meta-analysis, S.U.G., I.N. and S.D.C. wrote the manuscript and all authors contributed to writing the manuscript.

Acknowledgements

We thank all the students, W. Hutchinson, M. Gluis, T. Kildea and M. Brustolin for their help with the mesocosm project. Organism-symbols were drawn by S.U.G. or from Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Financial support was received by the Australian Research Council Future Fellowship Grant FT120100183 (to I.N.) and FT0991953 (to S.D.C.) and by a grant from the Environment Institute (the University of Adelaide). C.M.F. was supported by a Science Without Borders PhD scholarship through CAPES (Coordination for the Improvement of Higher Education Personnel) Brazil (scholarship no. 13058134).

METHODS

MESOCOSM STUDY

Mesocosms

We simulated a shallow temperate coastal ecosystem with enhanced level of realism using twelve circular mesocosms of 1,800 l each (see Fig. S2 and S5 for photos; width = 169 cm and depth = 80 cm), maintained indoors from February to July 2015. Each mesocosm comprised a mosaic of the three dominant local habitats (Gulf St. Vincent, South Australia) [39]: I) 'Rocky reef' made of natural rocks collected from the sea and including associated macrophytes and invertebrates, II) 'artificial seagrass' colonized by epiphytes and planted into fine silica sand, and III) 'open sand' composed of the same sand. Natural sediment collected among seagrass meadows and including all infauna and flora was used to seed the soft-bottom habitats (25 l per mesocosm). Primary production was fuelled by a lamp that simulated a local water depth of ~6-7 m (14/10 light-dark cycle, 30 min dawn and dusk dimming). A flow-through of unfiltered seawater provided each mesocosm with nutrients and planktonic propagules at 2,300 l day^{-1}.

Climate treatments

CO_2 (levels: ambient and elevated) was crossed with temperature (levels: ambient and elevated) using three replicate mesocosms per treatment combination. Climate manipulations followed end-of-century projections under a business-as-usual emission scenario (RCP8.5) [30] (see Table S13 and Fig. S3 for details on water parameters). An ambient temperature of 21 °C was applied corresponding to local summer conditions (average over two loggers: 5 m depth, 5 year dataset 2010-2015, SA Water). To achieve elevated CO_2, the seawater was pre-conditioned with pure CO_2 to treatment levels (1000 μatm pCO_2) and then continuously circulated between each mesocosm and an associated bin heavily aerated with CO_2-enriched air (at 1000 μatm pCO_2). These bins also contained heaters in the elevated temperature treatments. As expected from shallow coastal systems, community metabolism produced diurnal variability in pH and reduced pCO_2 to 910 μatm due to net autotrophy (Fig. S4).

Consumer assemblage

We studied an assemblage of highly mobile omnivorous and carnivorous consumers, including juveniles of six species of fish and two species (same genus) of shrimp (Table S10). To start, 7-10 individuals of each fish species and 10 shrimps (total of n = 55 per mesocosm, 10-40 mm in length) were introduced to each mesocosm, which was then exposed to the

climate treatments for 4.5 months. This long-term exposure not only ensured an advanced level of acclimation in the consumers but also allowed trophic and competitive forces to act on the consumer assemblage. Correspondingly, the consumers adjusted to their specific environmental conditions through growth and survival, with an average of 25.1 ± 4.4 (± SD) individuals remaining per mesocosm at the end of the experiment (Table S11).

The effects of ocean warming on ecological communities is forecast to vary considerably between regions depending on the specific thermal niches of component species [38]. As indicated by latitudinal distributions, the 8 consumer species used in our mesocosm likely differ in their thermal niches (Table S12). While all species also occur in considerably colder regions relative to the location of our study, their ranges extend differently towards warmer regions. Yet, we found no evidence for a species-specific effects of warming on biomass or abundance after long-term exposure in the mesocosms (Table S4). A change in composition was possibly not observed as our study location is not at the upper thermal limit of any of the consumer species.

Consumer behaviour

Cue sensing and decision making in the context of foraging and predation were tested inside the mesocosms after 2.5 months of exposure to the climate treatments. To study potential sensory compensation, the attraction of the consumers to three distinct food cues was tested: I) isolated visual cue, II) isolated olfactory cue and III) combined visual and olfactory cue. A 'food cue provider' provided the visual (highly active brine shrimps, 2-5 mm length), olfactory (mix of various invertebrates), and combined cues without a change in appearance (Fig. S5). To study consumers under predation risk, a live predator (*Gymnapistes marmoratus*, ~9 cm total length, n = 3 per treatment, for thermal niche see Table S12) was presented in a cage emitting the natural range of predator cues (Fig. S5). The predators were acclimated to the climate treatments for one month in separate tanks and fed daily *ad libitum* with a mix of local prey fishes and shrimps.

Behavioural trials with all combinations of 'food cue' (levels: visual, olfactory and visual + olfactory) and 'predator' (levels: absent and present) were conducted in each mesocosm in random order on different days, totalling 6 trials per mesocosm. The food cue provider was placed in front of the predator cage to start the trials and the surrounding area video recorded from the top (field of view 90×50 cm) for 7 min. During the subsequent video analysis, a circular overlay centred on the provider divided the field of view into an area 'close' and 'distant' to the food cue (Fig. S5). The behaviour and location of individuals was manually recorded for every second from entering until exiting the field of view using the software Solomon Coder. Hardyheads were not considered because they often stayed in the water column out of camera view. For each trial, the sum across all individual observations was used as consumer response.

Three response variables were derived for further analysis. I) 'Cue attraction' was estimated as the percentage of time spent 'close' to the food cue relative to the time spent in the entire field of view. A procedural control preceding each trial showed no effect of the climate treatments on the attraction to the provider in the absence of a food cue (see supplementary methods – consumer behaviour). II) 'Risk-taking' was determined by counting all clearly identifiable competitive interactions between individuals in the area close to the food cue (i.e. attacks, fights and chases). This area faced the predator cage and provided no habitat structure. III) 'Hunting activity' was measured as bite rate at the benthic habitat by the carnivorous fish (i.e. little weed whiting, blue weedy whiting and longfin goby). To represent the general effort invested into hunting in the mesocosm environment, only the area distant to the food cue and trials without predator were considered here and pooled to obtain one replicate per mesocosm.

Consumer biomass, hunting success and diet

Over the final month of the study, the actual foraging outcome was assessed through stomach content analysis. Consumers were captured, starved for 20 h (i.e. gastric evacuation), and then released back into their mesocosm to forage freely for 4 h. Finally, the stomachs of fishes were assessed under a stereo microscope to identify their principle resources using biovolume estimation and to determine 'hunting success' through the number of prey invertebrates captured (see Supplementary information – resources). Due to temperature sensitivity of digestion rates, hunting success under elevated temperature was likely underestimated and should thus only be compared between levels of CO_2. As shrimps masticate larger prey, we derived their diet from the literature. For each mesocosm, consumer biomass and abundance was calculated as the sum over all individuals. Both these responses showed no evidence for a species-specific climate treatment effect (Table S4), which validates the use of responses across a species assemblage in this study.

Resource availability

A large species and functional diversity of resources was introduced with the habitats and unfiltered flow-through seawater. This increased the likelihood of species more tolerant to low pH or high temperature which are essential for community dynamics that buffer against the loss of sensitive taxa such as density compensation and functional redundancy. Moreover, the long-term exposure allowed for advanced acclimation in larger and multiple generations in smaller-bodied resource taxa (see Supplementary information – resources). Over the final month of the study, the principle resources of the consumers were sampled thoroughly in all habitats: small molluscs, annelids, copepods, macrofaunal crustaceans, matt-forming algae, and detritus. The measures for each resource were then standardized to the maximum value observed for the respective resource in any mesocosm. The average

across the different standardized resources provided a relative measure of resource availability for each mesocosm.

Data analysis

I) Two-way ANOVAs were conducted with CO_2 and Temperature as fixed factors for response variables with mesocosm as lowest level of replication. II) For 'hunting success', which was instead based on individuals as replicates, linear mixed models were fit incorporating CO_2 and Temperature as fixed factors and Mesocosm as random factor. III) The behavioural responses 'cue attraction' and 'risk-taking' were tested within each mesocosm under all six possible combinations of Food cue and Predator. Thus, linear mixed models were fit based on a conventional split-block design employing Mesocosm as random blocking factor [40]. The fixed effects included CO_2 and Temperature as between block factors, Food cue and Predator as within block factors and all their interactions. Competition was expected to be influenced by the density of individuals in each behavioural trial. Thus, for the response 'risk-taking', the time individuals were present close to the food cue (i.e. density) was added as covariate. To identify the key drivers of behaviour, sub-models with all possible combinations of the fixed effects were compared using the Akaike Information Criterion corrected for small sampling sizes (AIC*c*) [41], while retaining the random model structure. The fixed effects of the most parsimonious sub-models were also tested using ANOVA.

In case of a significant ($\alpha = 0.05$) interaction, post hoc multiple comparisons adjusted by false discovery rate were conducted [42]. The testing of multiple responses in the same mesocosms did likely not alter our interpretation of the results through an inflation of Type I error (Table S7). Deviations from normality of residuals and random effects were assessed with normal Q-Q plots and Shapiro-Wilk tests, homogeneity of variance with residual versus fitted plots and Levene's tests, and sphericity with Mauchly's tests. The heteroscedasticity and/or positive skewness in several response variables were corrected by transformation. More information on model diagnostics and transformations can be found in the corresponding statistic tables in the Supplementary information. All data analyses were performed with R version 3.4.1 [43].

Ethics

Research was conducted under approval of the University of Adelaide animal ethics committee (projects: S-2012-193A). The collection of organisms and habitat was permitted by the Minister for Transport and Infrastructure and the Government Department of Primary Industry and Regions SA (exemptions: 9902676 and 9902752).

META-ANALYSIS

Literature search

We searched for studies published between 2008-2017 in the field of ocean acidification that included experiments or observations on fishes or decapod crustaceans in the laboratory or at CO_2 vents in the field (see Supplementary information – search protocol). The primary search with Web of Science was complemented by scanning recent reviews/meta-analyses and unpublished data. Only experiments simulating realistic future scenarios were considered with a pCO_2 of on average ~1000 μatm (range 600 - 2100 μatm), but extreme values were accepted for environments with naturally high pCO_2. Finally, we identified 102 experiments from 57 studies (Figure S6) that matched one of seven categories following the general framework of the mesocosm study. A detailed list of all experiments is provided by Table S19 (this Excel table is unfortunately too large to be printed in the thesis).

Experiments at CO_2 vents that measured population sizes were classified as being ecologically 'complex' as they integrate over various ecological traits and include biotic interactions over long term allowing for potential indirect effects. Experiments at 'simple' or 'medium' complexity could instead be assigned to either of the ecological traits 'predator avoidance', 'habitat selection' or 'foraging'. 'Simple' was used for experiments on isolated sensory modalities typically tested with short-term behaviours and 'medium' for experiments in which individuals could use two or more sensory modalities in short-term behavioural tests or during longer term growth or survival. More detail on the types of experiments that were considered in the meta-analysis are given in Table S14. Although increasing complexity was categorized based on sensory modalities and the presence/absence of long-term biotic interactions, it represented also an increase in other potential measures of complexity (Table S16).

Effect sizes and analysis

Information was extracted for each experiment from supplementary data or from figures through data-mining (web plot digitizer 3.12). We calculated the standardized mean difference as effect size for each experiment, which represented the mean difference in performance of consumers in control and elevated CO_2 conditions standardized by standard deviations (Hedges' g) [44]. Standardized mean difference is popular in modern meta-analysis [45], and better suited for our study than the log-transformed response ratio as it can be applied to a wider range of data (but see Table S8b, 9b).

For each of the 7 categories defined by trait and complexity, we conducted a random-effects meta-analysis [45,46] to estimate an overall mean effect size and to test its significance. These models were fitted with restricted maximum likelihood and weighed the effect sizes of

individual experiments according to their uncertainty. The conservative Knapp-Hartung approach was employed for hypothesis tests and to construct confidence limits [47]. The heterogeneity statistics I^2 and Cochran's Q-test [48] were calculated to quantify and test for the variability in the data that is due to differences between individual effect sizes (i.e. experiments) beyond what could be expected by chance alone. A substantial amount of unexplained heterogeneity was found for all mean effect sizes (Table S9a), which was however not related to the specific degree of acclimation or pCO_2 increase that characterized individual experiments (Table S17). A discussion on other factors that may have influenced the effect of elevated CO_2 can be found in the Supplementary information under 'potential moderators'.

In addition, for each of the three ecological traits, we conducted a mixed-effects meta-analysis [45,46] that employed ecological complexity as moderator with its levels 'simple', 'medium' and 'complex'. Although the 'complex' level did not distinguish between ecological traits, it was included in all three analyses as the comparison of population responses at CO_2 vents with the performance in specific traits at 'simple' and 'medium' complexity is meaningful. A significant moderator test was followed by post hoc multiple comparisons adjusted by false discovery rate [42]. The meta-analysis was conducted with the R package metafor (version 2.0-0) [46].

Data diagnostics

Forest plots, normal Q-Q plots, residual versus fitted plots, and Cook's distance were used to assess data properties and extreme outliers were subsequently winsorized (see Supplementary information – data analysis and Table S15). A 'leave-one out' analyses was conducted in which one individual effect size at a time was removed before retesting the significance of the model. This sensitivity analysis confirmed that our interpretation of the results was not driven by the presence of single, particularly influential experiments (Table S9). Publication bias was assessed with funnel plots and 'trim and fill' analysis to test for funnel plot asymmetry [49]. Although this analysis indicated publication bias for some of the mean effect sizes, augmenting the data with the hypothetically missing experiments did not alter the significances (Table S9).

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SUPPLEMENTARY RESULTS

Tables S1-9 and Figure S1

MESOCOSM STUDY

Table S1: Model selection to derive the most parsimonious mixed model for cue sensing in the consumers. The global model included CO_2, Temperature, Predator (P) and Food cue (F) and all their interactions as fixed effects and Mesocosm as random effect (maximum likelihood fit [1,2]). Sub-models with all possible combinations of the fixed effects were compared using AIC*c* [3], of which only the five best sub-models are shown here. Each row represents one sub-model, ranked from the most parsimonious (lowest AIC*c*) to the least parsimonious, and shaded cells mark the effects included. The 'relative importance' of each effect across all possible sub-models is provided by the sum of Akaike weights over all sub-models that included the particular effect. Model diagnostics: After square root transformation, data was approximately normally distributed and the assumptions of homogeneity and sphericity met.

CO_2	T	P	F	CO_2 ×T	CO_2 ×P	CO_2 ×F	T×P	T×F	P×F	CO_2× T×P	CO_2× T×F	CO_2× P×F	T×P ×F	CO_2×T ×P×F	df	AIC*c*	delta	weight
■		■	■			■			■						13	-119.3	0.00	0.26
■			■			■									10	-117.5	1.81	0.11
■		■	■			■									11	-116.9	2.37	0.08
■	■	■	■			■			■						14	-116.8	2.49	0.07
■	■	■	■			■	■	■	■				■		19	-116.5	2.74	0.06
0.99	0.39	**0.83**	**1.00**	0.07	0.17	**0.87**	0.16	0.13	**0.66**	<0.01	<0.01	0.02	0.12	<0.01	relative importance			

df = number of model parameters; delta = increase in AIC*c* compared to the most parsimonious sub-model;
weight = probability that the sub-model is the best among all candidate sub-models

Table S2: ANOVA on cue sensing in the consumers based on the most parsimonious sub-model identified in Table S1 (sqrt-transformed). The mixed model included CO_2 as fixed between block factor, Predator and Food cue as fixed within block factor and Mesocosm as random blocking factor (restricted maximum likelihood fit [1,2]). The more conservative approach was used not assuming additivity and using the Kenward-Roger approximation for degrees of freedom.

Source of variation	df_{Num}	df_{Den}	MS	F-ratio	P-value
CO_2	1	10	0.049	7.0	0.024
Predator	1	11	0.017	2.4	0.147
Food cue	2	20	0.064	9.1	0.002
CO_2 × Food cue	2	20	0.037	5.3	**0.015**
Predator × Food cue	2	22	0.029	4.1	**0.030**

MS = mean squares; df_{Num} and df_{Den} = numerator and denominator df

Table S3: ANOVAs testing the effects of CO_2, Temperature and their interaction on hunting of consumers and on biomass of resources and consumers. (b), (c) and (d) are based on the sum over all individuals of each mesocosm (n = 3 per treatment). For (a) instead, replicates were based on individuals, and thus mixed models were first fit including Mesocosm as random factor (restricted maximum likelihood fit [4]). Mesocosm was then removed following highly insignificant likelihood ratio tests (L<0.001, p=0.99) [1]. (a) is based on fishes only due to the difficulty of stomach content analysis in shrimp. (d) is based on zoobenthivorous fishes only since it was not possible to identify bites in the zooplanktivores or assign bites to either algae grazing or hunting in the omnivores. Model diagnostics: a) One fish was identified as extreme outlier by Cook's distance with very few prey items in its stomach. This suggested that the fish has not been in a foraging mode – the behaviour of interest here – and it was thus removed from the analysis. The strongly right-skewed raw data was successfully normalized through log_{10}-transformation, which also lead to homogeneous variances. b) and c) Raw data met assumptions of normality and homogeneity. d) Data was square root transformed to achieve homogeneity of variance, and residuals were approximately normally distributed.

Response variable	Source of variation	df	MS	F-ratio	P-value
a) Hunting success	CO_2	1	0.059	0.36	0.551
	T	1	0.047	0.29	0.593
	$CO_2 \times T$	1	0.071	0.43	0.512
	Residuals	214	0.165		
b) Resource biomass	CO_2	1	0.0781	47.6	**<0.001**
	T	1	0.0013	0.2	0.645
	$CO_2 \times T$	1	0.0001	<0.1	0.862
	Residuals	8	0.0028		
c) Consumer biomass	CO_2	1	35.0	9.47	**0.015**
	T	1	0.3	0.07	0.793
	$CO_2 \times T$	1	5.3	1.44	0.264
	Residuals	8	3.7		
d) Hunting activity	CO_2	1	0.032	1.82	0.214
	T	1	0.174	9.94	**0.014**
	$CO_2 \times T$	1	0.011	0.60	0.460
	Residuals	8	0.017		

df = degrees of freedom; MS = mean squares

Table S4: Model selection to derive the most parsimonious mixed models for consumer biomass and abundance based on replicates at the species level. The global model was structured according to a conventional split-block design with Mesocosm as random blocking factor, CO_2 and Temperature as between block factors, and Species (S) as within block factor (maximum likelihood fit [1,2]). Here, the most parsimonious models did not include the effects of interest, namely an interaction between Species and the climate treatments, and hence follow-up ANOVAs were not run. To improve data properties due to low and variable abundances, the ecologically and morphologically similar species little weed whiting and blue weedy whiting were pooled, which lead to 6 different taxa (here Species) for the analysis. Sub-models with all possible combinations of the fixed effects were compared using AIC*c* [3], of which only the five best sub-models are shown here. Each row represents one sub-model, ranked from the most parsimonious (lowest AIC*c*) to the least parsimonious, and shaded cells mark the effects included. Finally, the 'relative importance' of each effect across all possible sub-models is provided by the sum of Akaike weights over all sub-models that included the particular effect. Model diagnostics: a) Data was $\log_{10+1}$-transformed to improve normality and sphericity, which were still slightly violated. However, no further steps were taken, as 1) homogeneity was met, 2) all effects of interest here showed clear cut results, i.e. the interactions of Species with any of the climate treatments (relative importance <0.01), and 3) the main analysis based on the biomass of the entire consumer assemblage met the model assumptions well. b) Raw data met the assumptions of normality, homogeneity and sphericity.

a) Biomass per species

CO_2	T	S	CO_2×T	CO_2×S	T×S	CO_2×T×S	df	AIC*c*	delta	weight
■		■					9	-73.4	0.00	0.60
■	■	■					10	-71.4	1.98	0.22
		■					8	-69.2	4.15	0.08
■	■	■					11	-69.0	4.43	0.07
	■	■					9	-67.1	6.32	0.03
0.90	0.32	**1.00**	0.07	<0.01	<0.01	<0.01	relative importance			

b) Abundance per species

CO_2	T	S	CO_2×T	CO_2×S	T×S	CO_2×T×S	df	AIC*c*	delta	weight
■		■					9	288.0	0.00	0.34
		■					8	288.1	0.12	0.32
■	■	■					10	290.4	2.42	0.10
	■	■					9	290.5	2.51	0.10
	■	■			■		14	291.6	3.64	0.05
0.53	0.35	**1.00**	0.05	<0.01	0.11	<0.01	relative importance			

df = number of model parameters; delta = increase in AIC*c* compared to the most parsimonious sub-model; weight = probability that the sub-model is the best among all candidate sub-models

Table S5: Model selection to derive the most parsimonious mixed model for risk-taking in consumers. The global model included CO_2, Temperature, Predator (P) and Food cue (F) and all their interactions as fixed effects, Density of individuals (D) as covariate and Mesocosm as random effect (maximum likelihood fit [1,2]). A prior analysis showed no interactions between the covariate and the fixed effects confirming its use as main effect only. Sub-models with all possible combinations of the fixed effects were compared using AIC*c* [3], of which only the five best sub-models are shown here. Each row represents one sub-model, ranked from the most parsimonious (lowest AIC*c*) to the least parsimonious, and shaded cells mark the effects included. Finally, the 'relative importance' of each effect across all possible sub-models is provided by the sum of Akaike weights over all sub-models that included the particular effect. Model diagnostics: Normality, homogeneity and sphericity were all improved and met through square root transformation.

CO_2	T	P	F	D	CO_2 ×T	CO_2 ×P	CO_2 ×F	T×P	T×F	P×F	CO_2× T×P	CO_2× T×F	CO_2× P×F	T×P ×F	CO_2×T ×P×F	df	AIC*c*	delta	weight
	■	■		■				■								9	257.2	0.00	0.33
■	■	■		■				■								10	258.6	1.40	0.16
■	■	■		■	■			■								11	259.7	2.44	0.10
■	■	■		■	■	■		■			■					13	259.7	2.50	0.09
	■	■		■												8	261.0	3.78	0.05
0.55	**0.98**	**0.97**	0.11	**1.00**	0.26	0.20	<0.01	**0.84**	0.01	0.01	0.10	<0.01	<0.01	<0.01	<0.01	relative importance			

df = number of model parameters; delta = increase in AIC*c* compared to the most parsimonious sub-model;
weight = probability that the sub-model is the best among all candidate sub-models

Table S6: ANOVA on risk-taking in consumers based on the most parsimonious sub-model in Table S5 (sqrt transformed). The mixed model included Temperature as fixed between block factor, Mesocosm as random blocking factor, Predator as within block factor and Density of individuals as covariate (restricted maximum likelihood fit [1,2]). The more conservative approach was used not assuming additivity and using the Kenward-Roger approximation for degrees of freedom.

Source of variation	df_{Num}	df_{Den}	MS	F-ratio	P-value
T	1	9.6	6.8	5.9	0.037
Predator	1	10.2	10.3	8.9	0.013
Density	1	64.4	95.0	82.2	**<0.001**
T × Predator	1	10.1	8.0	6.9	**0.025**

MS = mean squares; df_{Num} and df_{Den} = numerator and denominator

Table S7: P-value adjustment across the different responses of the mesocosm study to control for inflation of type I error. The p-values of the effects of interest were extracted for each response variable, followed by a p-value adjustment by false discovery rate. Significant effects did not turn non-significant.

Response variable	Effect of interest	ANOVA p-value	P-value adjusted by FDR
Cue attraction	CO_2×Food	0.0146	0.0228
Hunting success	CO_2	0.5507	0.5507
Resource biomass	CO_2	0.0001	0.0007
Consumer biomass	CO_2	0.0152	0.0228
Hunting activity	T	0.0135	0.0228
Risk-taking	T×Predator	0.0252	0.0302

META-ANALYSIS

Table S8: Weighted mixed-effects meta-analyses on the response of consumers to elevated CO_2 with ecological complexity as moderator. Ecological traits were analysed separately but always in combination with 'complex' ecological complexity. **a)** Principle effect size measure used in this study and **b)** alternative effect size measure which could only be calculated for foraging. The more conservative Knapp-Hartung approach was used for moderator and post-hoc tests. The latter were adjusted for multiple comparison by false discovery rate.

Ecological trait	# Experiments	Heterogeneity		Moderator (≙ ecological complexity)			Post-hoc tests		
		Q_E	P-value	df	F-ratio	P-value	simple vs. medium	simple vs. complex	medium vs. complex
a) Standardized mean difference:									
Predator avoidance	46	379	<0.001	2, 43	15.55	**<0.001**	<0.001	<0.001	0.016
Habitat selection	37	170	<0.001	2, 34	20.16	**<0.001**	<0.001	<0.001	0.023
Foraging	35	110	<0.001	2, 32	10.44	**<0.001**	0.002	<0.001	0.048
b) Ln response ratio:									
Foraging	35	134	<0.001	2, 32	5.92	**0.007**	0.021	0.006	0.150

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

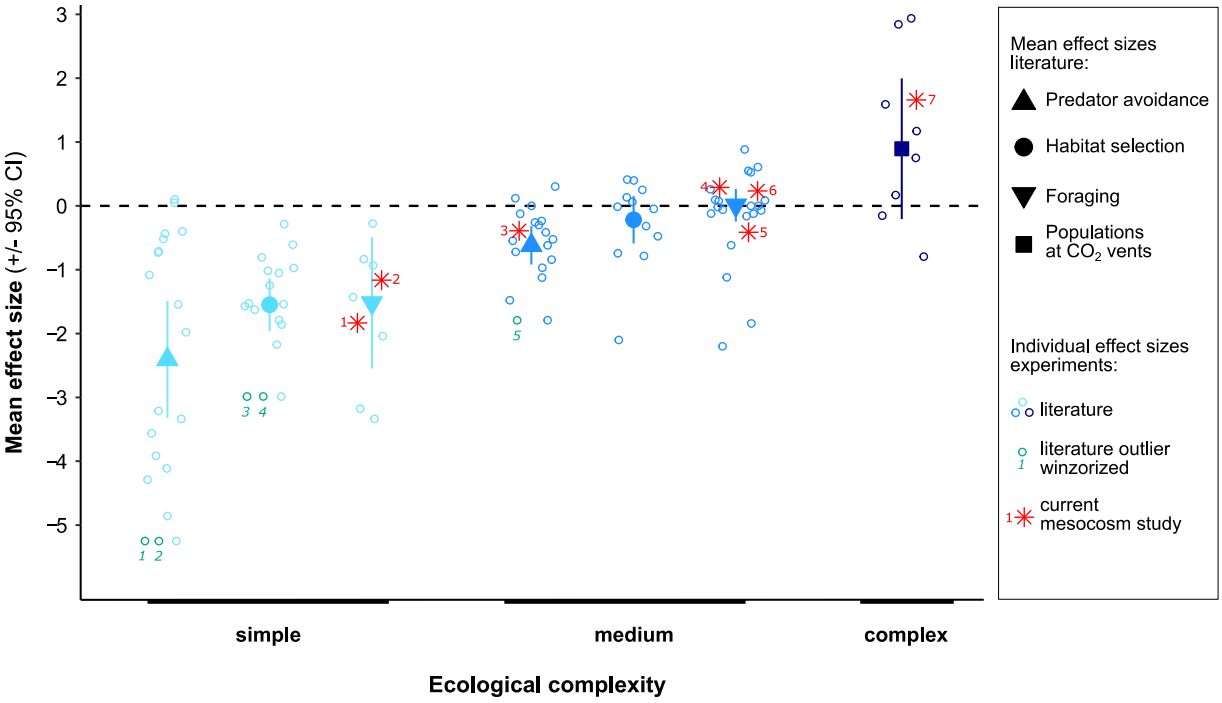

Figure S1: Overall mean effect sizes and effect sizes of individual experiments illustrating the variability and range of consumer responses to elevated CO_2. The corresponding effect sizes from the mesocosm study are overlayed in **red** but not considered in the overall mean effect sizes (1 = vision, 2 = olfaction, 3 = risk-taking, 4 = vision+olfaction, 5 = hunting activity, 6 = hunting success and 7 = biomass). Extreme outliers that were winsorized are highlighted in **green** (original values: *1* = -26.0, *2* = -25.8, *3* = -10.1, *4* = -8.2 and *5* = -2.76).

Table S9: Weighted random-effects meta-analyses on the response of consumers to elevated CO_2. Combinations of trait and complexity were analysed separately. **a)** Principle effect size measure used in this study and **b)** alternative effect size measure which could only be calculated for foraging and for populations at CO_2 vents. Estimates based on ln response ratio are given as proportional change centred on zero (i.e. back-transformed and minus 1). In all analyses, the more conservative Knapp-Hartung approach was used to test significances of mean effect sizes. Publication bias: Effect sizes of hypothetically missing experiments were added using 'trim and fill' analysis until funnel plot symmetry was restored. No publication bias was assumed if '0' experiments had to be added. In case of publication bias, the mean effects size of the hypothetical model including the missing experiments was estimated and tested. The potential influence of publication bias is indicated by the difference in estimate and significance between hypothetical and original model. In any case, further interpretation should be based on the original model. Sensitivity: A 'leave-one out' analysis retested the model after removing the effect size of one experiment at a time. The significance compared to the full model may or may not (yes/no) change through the exclusion of any of the individual experiments. The most extreme change in significance through this procedure is given. The change from non-significant to significant for populations at CO_2 vents was not further considered as it was favoured by the detected publication bias and as the alternative effect size ln response ration remained non-significant.

			Mean effect size			**Heterogeneity**				**Publication bias**			**Sensitivity**	
Complexity	**Ecological trait**	**# Experi-ments**	Esti-mate	T-value	P-value	I^2 (%)	Q	df	P-value	Experi-ments	Esti-mate	P-value	sign. change	max. P-value
a) Standardized mean difference:														
Simple	Predator avoidance	20	-2.41	-5.50	**<0.001**	95.1	262	19	<0.001	5	-1.64	0.003	no	<0.001
	Habitat selection	17	-1.55	-7.92	**<0.001**	79.4	78	16	<0.001	0	NA	NA	no	<0.001
	Foraging	7	-1.52	-3.62	**0.016**	73.1	19	6	0.005	0	NA	NA	no	0.030
Medium	Predator avoidance	18	-0.62	-4.35	**<0.001**	72.0	56	17	<0.001	0	NA	NA	no	<0.001
	Habitat selection	12	-0.22	-1.30	0.220	63.1	31	11	0.001	0	NA	NA	no	0.156
	Foraging	20	0.01	0.08	0.938	23.8	31	19	0.044	4	0.16	0.378	no	0.442
Complex	CO_2 vent	8	0.89	1.92	0.097	94.5	61	7	<0.001	2	0.37	0.532	yes	0.047
b) Ln response ratio:														
Simple	Foraging	7	-0.52	-3.38	**0.015**	91.2	36	6	<0.001	1	-0.38	0.023	no	0.037
Medium	Foraging	20	-0.04	-0.46	0.648	62.8	50	19	<0.001	4	-0.09	0.371	no	0.409
Complex	CO_2 vent	8	0.37	0.95	0.373	94.8	48	7	<0.001	0	NA	NA	no	0.103

I^2 = heterogeneity to total variability; Q-test for heterogeneity with associated Q-statistic (Q), degrees of freedom (df) and p-value

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SUPPLEMENTARY METHODS

Table S10-18 and Figures S2-7

MESOCOSM STUDY

Habitat and Technical set-up

The study was conducted at the South Australian Research and Development Institute (SARDI; 34°57'10"S, 138°30'20"E), and all organisms and habitats were collected between 1-5 m depth from within 60 km of the facility. Each mesocosm contained four patches of each 'rocky reef' **(# 1,** Fig. S2**)** and 'artificial seagrass' **(# 2)** arranged in pairs and surrounded by 'open sand' **(# 3)**. The rocks harboured associated biota as found at the collection site including macrophytes (naturally attached), matt-forming algae, small macrofauna and meiofauna. The artificial seagrass resembled the dominant local genus (*Posidonia* spp.) [1]. Prior to being transplanted into the mesocosms, it was incubated for 2 weeks in the ocean close to natural seagrass habitats for epiphytic colonization. The fine silica sand, which made the base of the soft-bottom habitats (depth: seagrass 6 cm and open sand 6-25 cm), had a grain size between 0.21 - 0.85 mm (type N30, Sloans Sand, Australia) similar to sediment found at local beaches and seagrass meadows.

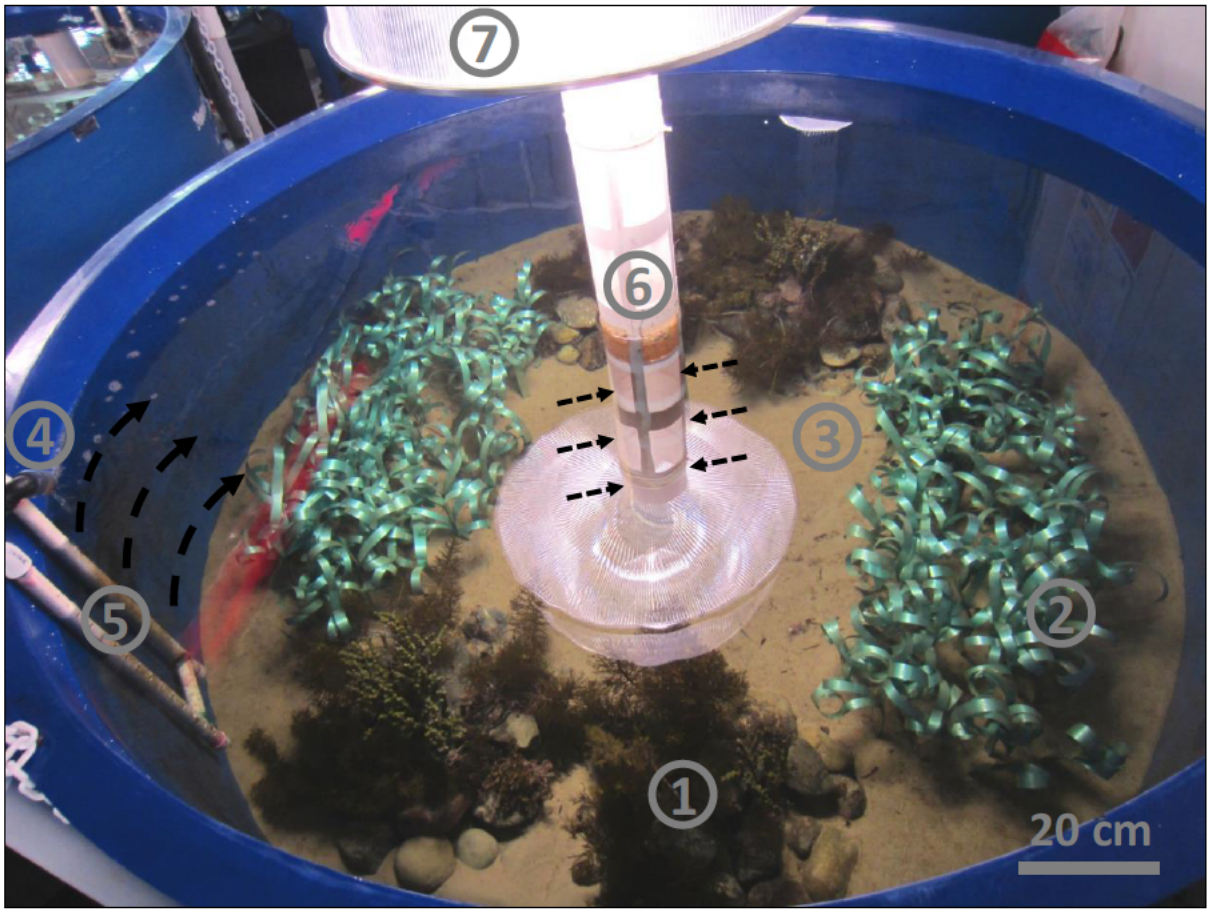


Figure S2: A mesocosm at the start of the experiment showing habitat arrangement and technical set-up.

The study was conducted in a flow-through system supplied by water from 1.5 km offshore and ~8 m depth. The incoming seawater was first transferred to two 800 l header tanks and from there gravity fed to the mesocosms **(# 4**, Fig. S2**)**. One of these header tanks provided water for the mesocosms with elevated CO_2 and was pre-conditioned to elevated pCO_2 levels using pure CO_2 (control system ACQ110 Aquatronica, Italy). To maintain the climate treatments, each mesocosm continuously exchanged water (~1,800 l per h) with an associated 60 l bin (a separate bin for each mesocosm). These bins were heavily aerated with enriched air at 1000 μatm pCO_2 (PEGAS 4000 MF Gas Mixer, Columbus Instruments, Columbus, Ohio) or ambient air at 400 μatm pCO_2 depending on the CO_2 treatment, and contained submersible titanium heaters (800 W) to achieve elevated temperature. This circulation was diverted by two diffuser pipes **(# 5)** to create a mild circular current inside the mesocosms, which alternated direction every 6 h similar to tidal water movement. The water returned to the 60 l bins through gravity while passing a filter column (~20 μm mesh size) **(# 6)** to retain animals within the mesocosms. Overall, this elaborate technical set-up provided an environment free of unnatural disturbances such as air bubbles, electrical currents or pump noise.

Primary production was fuelled by a 250 W metal halide lamp (Osram Powerstar HQI-T 250/D/PRO) mounted above each mesocosm **(# 7**, Fig. S2**)**. The lamp had a colour temperature of 5500 K, a colour rendering index of 92 and a wave length distribution similar to sunlight (according to the spectrum provided by the manufacturer). Measures in 5 cm intervals from the centre to the tank wall suggested an irradiance of 3833 ± 1304 lux (mean ± SD) at the level of the benthic habitat. This irradiance corresponds to ~6-7 m depth in Gulf St. Vincent based on previously published attenuation coefficients [2]. Estimations were made using the local average daily summer irradiance (Bureau of Meteorology, www.bom.gov.au, location Adelaide, past 20 years of data).

Consumer Assemblage

The species were selected based on their high juvenile abundances in local shallow coastal waters during summer. They were caught with seine and hand nets and habituated to the mesocosms under ambient conditions for 3-4 weeks. Then, the mesocosms were progressively acclimatized to their respective climate treatment over a period of one week and kept at treatment levels for 4.5 months. The high initial abundances (Table S10) ensured resource limitation, which in turn ensured that consumers were under constant pressure from consumer-resource interactions and from intra- and interspecific competition. We expected lower intra-specific competition for the shrimps and hardyheads due to their more isolated ecological niches and thus raised their initial abundances to 10 individuals.

Table S10: Consumers introduced to each mesocosm at the beginning of the study. The shrimps comprised a random mix of *Palaemon intermedius* and *Palaemon serenus*. The classification into feeding guilds and principle foraging habitats followed the extensive behavioural observations and stomach content analyses.

Species	Common name	# introduced	Total length ± SD (mm)	Feeding guild and principle habitat
Neoodax balteatus	little weed whiting	7	30 ± 8	zoobenthivore hard bottom and vegetation
Haletta semifasciata	blue weedy whiting	7	31 ± 4	zoobenthivore hard bottom and vegetation
Favonigobius lateralis	longfin goby	7	22 ± 4	zoobenthivore soft bottom
Girella zebra	zebrafish	7	17 ± 2	omnivore hard bottom and vegetation
Acanthaluteres vittiger	toothbrush leatherjacket	7	30 ± 8	omnivore hard bottom and vegetation
Atherinosoma microstoma	small-mouthed hardyhead	10	24 ± 5	zooplanktivore water column
Palaemon spp.	caridean shrimp	10	10 - 30	omnivore all benthic habitats

Table S11: Abundance of consumers per mesocosm at the end of the study (mean ± SD). The replication shown here is exact for the analyses related to biomass and abundance. Instead, we can assume slightly higher abundances during the behavioural trials as these were conducted several weeks before animal collection. The two closely related and ecologically similar species 'little weed whiting' and 'blue weedy whiting' were pooled as 'whiting'.

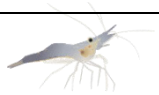
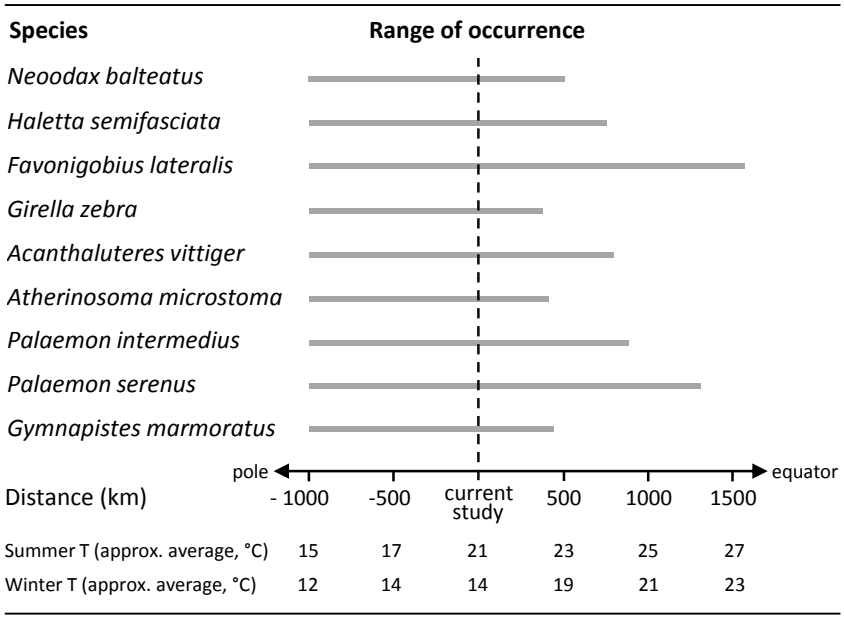
TREATMENT	 Whiting	 Longfin goby	 Zebrafish	 Leather jacket	 Hardyhead	 Shrimp	Consumer assemblage total
control	4.0 + 0.0	7.0 ± 0.0	3.0 ± 1.7	1.0 ± 0.0	3.7 ± 0.6	3.0 ± 3.0	21.7 ± 5.0
elevated CO_2	5.3 ± 1.2	7.0 ± 0.0	4.3 ± 2.9	2.3 ± 1.5	2.7 ± 2.5	6 ± 2.0	27.3 ± 5.0
elevated T	3.0 ± 1.7	6.3 ± 1.2	3.3 ± 2.1	1.3 ± 1.2	3.7 ± 1.5	7.3 ± 2.1	24.7 ± 0.6
elevated CO_2+T	3.7 ± 0.6	6.0 ± 1.0	3.7 ± 1.5	2.0 ± 1.0	4.7 ± 1.2	6.7 ± 2.1	26.7 ± 4.9

Table S12: Realized thermal distributions of the consumers and the predator, which indicate that the latitude of the mesocosm system did not represent the upper or lower thermal limit for any of the species. Ranges are based on occurrence maps from the Atlas of Living Australia (http://bie.ala.org.au, accessed Oct. 2017, extreme outlier occurrences not considered), additionally verified through fishbase (http:/aquamaps.org, accessed Oct. 2017). The lower limit was confined by the southern end of Tasmania, explaining the same limit across species. Average winter and summer sea surface temperatures are based on maps provided by the Australian Bureau of Meteorology (http://bom.gov.au, accessed Oct. 2017, across years 1961-1990), except for the current study for which the locally employed temperature loggers were used. As seasonal averages of broad coastal regions, these temperatures do not consider seasonal maxima or smaller scale geographical features (e.g. shallow bays) which can be several degrees above/below the averages. Hence, the provided temperatures likely underestimate the species' realized thermal ranges. In particular, higher thermal tolerances can be expected for the two consumer species with the most restricted occurrence ranges *G. zebra*, which also inhabits rock pools as young juvenile, and *A. microstoma*, which also inhabits shallow mangrove creeks.



Seawater Parameters

An overview of seawater properties is provided in Table S13, a trajectory of pH and temperature throughout the entire study period in Figure S3, and the diurnal variability in pH produced by community metabolism by Figure S4. For each mesocosm, temperature and pH were measured daily at around midday (Mettler Toledo SevenGo™ SG2, calibrated daily) and salinity (SR6 refractometer, Vital Sine) and total alkalinity (total of n = 8 per mesocosm; Gran titration; 888 Titrando, Metrohm, Switzerland) fortnightly. Alkalinity measures were accurate within 1% of certified standards (reference material from A. Dickson, Scripps Institution of Oceanography). Finally, pCO_2, bicarbonate, carbonate and the saturation states of calcite and aragonite were calculated using CO2SYS for Excel [3] with constants from Mehrbach et al. [4] refit by Dickson and Millero [5].

Table S13: Average seawater properties during the 4.5 months treatment period. Standard deviations indicate the variability between mesocosms.

Variable	control	elevated CO_2	elevated T	elevated CO_2+T
Temperature (°C)	21.0 ± 0.14	20.9 ± 0.04	23.7 ± 0.19	23.7 ± 0.08
pH_{NBS}	8.14 ± 0.004	7.89 ± 0.009	8.12 ± 0.002	7.89 ±0.009
Salinity (ppt)	36.3 ± 0	36.3 ± 0	36.3 ± 0	36.3 ± 0
Total Alkalinity (μmol kg^{-1})	2482 ± 4	2485 ± 5	2486 ± 6	2493 ± 3
pCO_2 (μatm)	465 ± 5	905 ± 6	500 ± 8	915 ± 25
HCO_3 (μmol kg^{-1})	1995 ± 6	2186 ± 3	1985 ± 2	2166 ± 9
CO_3 (μmol kg^{-1})	200 ± 2	123 ± 1	206 ± 2	135 ± 3
Ω Calcite	4.74 ± 0.05	2.91 ± 0.02	4.90 ± 0.05	3.20 ± 0.07
Ω Aragonite	3.09 ± 0.04	1.90 ± 0.01	3.22 ± 0.03	2.10 ± 0.05

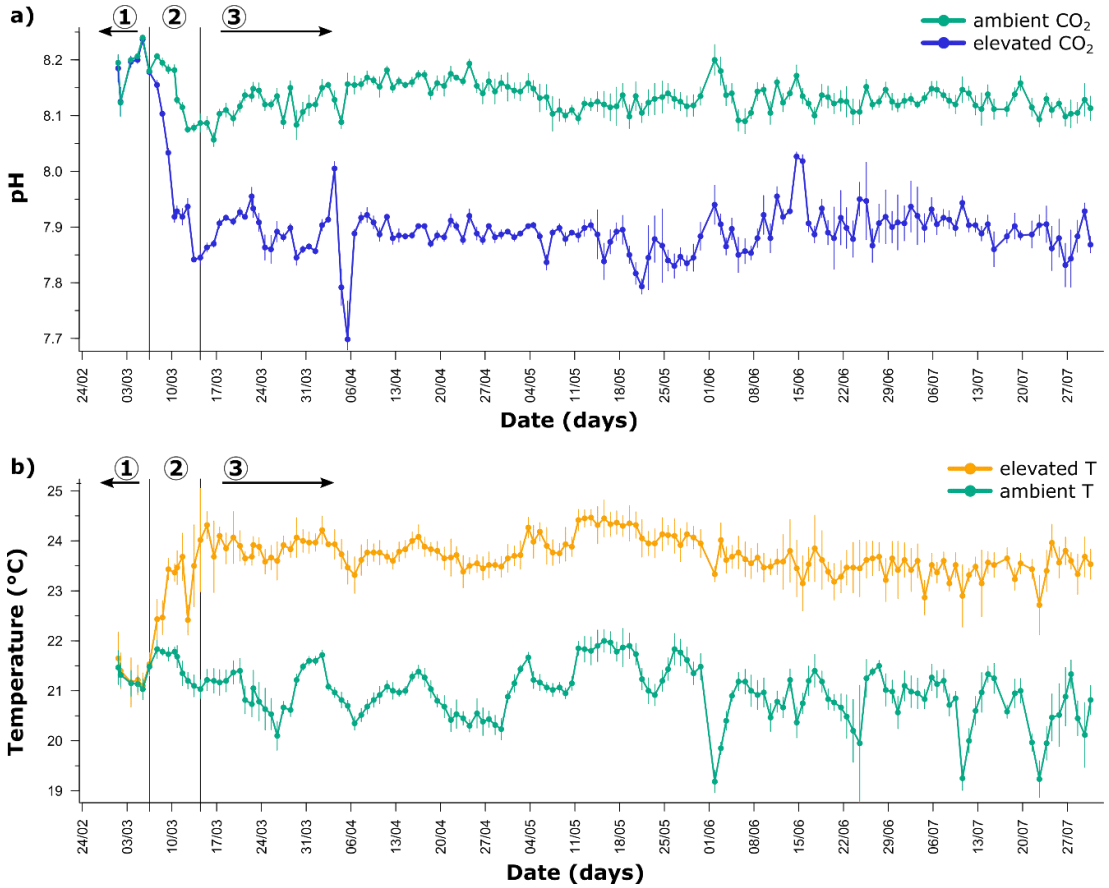


Figure S3: Achieved ocean acidification **(a)** and warming **(b)** over the study period, including the last week of the acclimation period under ambient conditions **(# 1)**, the progressive elevation to treatment levels **(# 2),** and the 4.5 months at treatment levels **(# 3)**. Mean ± SD are based on the daily measurements of the n = 6 mesocosms at ambient or elevated treatment levels.

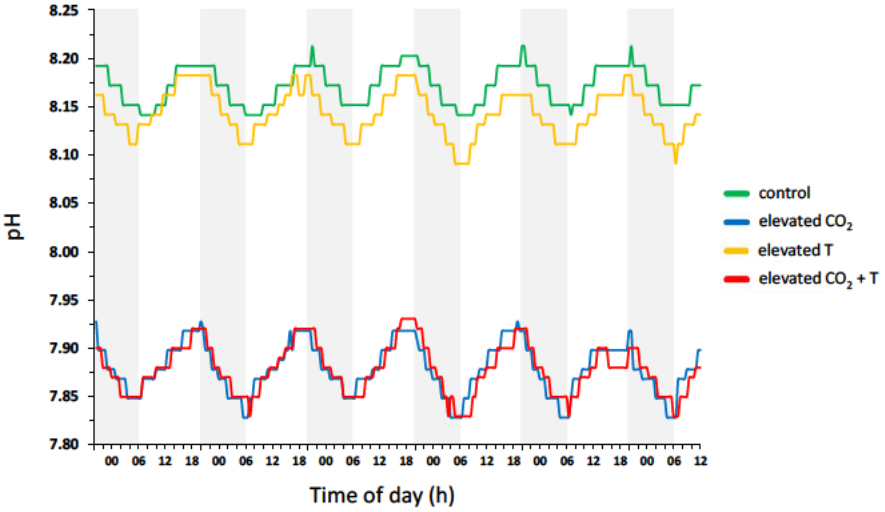


Figure S4: Daily variability in pH measured over a 5 day period in the middle of the study period. This analysis was only done for one mesocosm per treatment combination, serving as an example. For these 4 mesocosms in parallel, pH was recorded in 30 min intervals with a pH logger (control system ACQ110 Aquatronica, Italy). Grey bands mark night-time and white bands day-time hours.

Consumer Behaviour

The food cue providers were built with a transparent 50 ml vial with 9 windows on sides and top covered by fine mesh and containing a smaller opaque tube (Fig. S5). For the olfactory cue, the opaque tube contained 4.5 g crushed food mix (defrosted bloodworms and various kinds of marine molluscs and crustaceans, Fish Fuel and Co., Australia). Tests with food dye suggested a slow and continuous cue dispersion out of the tube and finally vial. For the visual cue, the space between the tube and the vial contained ~25 highly active brine shrimps (*Artemia salina*). For the trials with isolated visual cue, the windows in the vial were sealed. For the combined olfactory and visual cue, the provider simply contained both food mix and brine shrimps.

The scorpionfish *Gymnapistes marmoratus* was used to simulate a high predation risk environment because it is abundant locally and feeds on both crustaceans and fish [6]. While the consumers were exposed to the predators only during the 7 min behavioural tests in the mesocosm, they were likely familiar with it from their early juvenile life in the wild given the omnipresence of this predator at the collection sites. The obvious change in behaviour of the consumers upon introduction of the predator and the significant effect of the predator on all response variables confirmed that they experienced the predator as a threat. In parallel to the placement of the food cue provider marking the start of the trial, the predator was placed into its cage using two hand nets. For the trials without predator, the same procedure was performed but with empty nets. The predator cage was positioned in the centre of the mesocosm. It was made of transparent acrylic and fine mesh but was covered on the sides and back to ensure that both visual and olfactory predator cues were only emitted through the front side directly towards the area 'close' to the food cue.

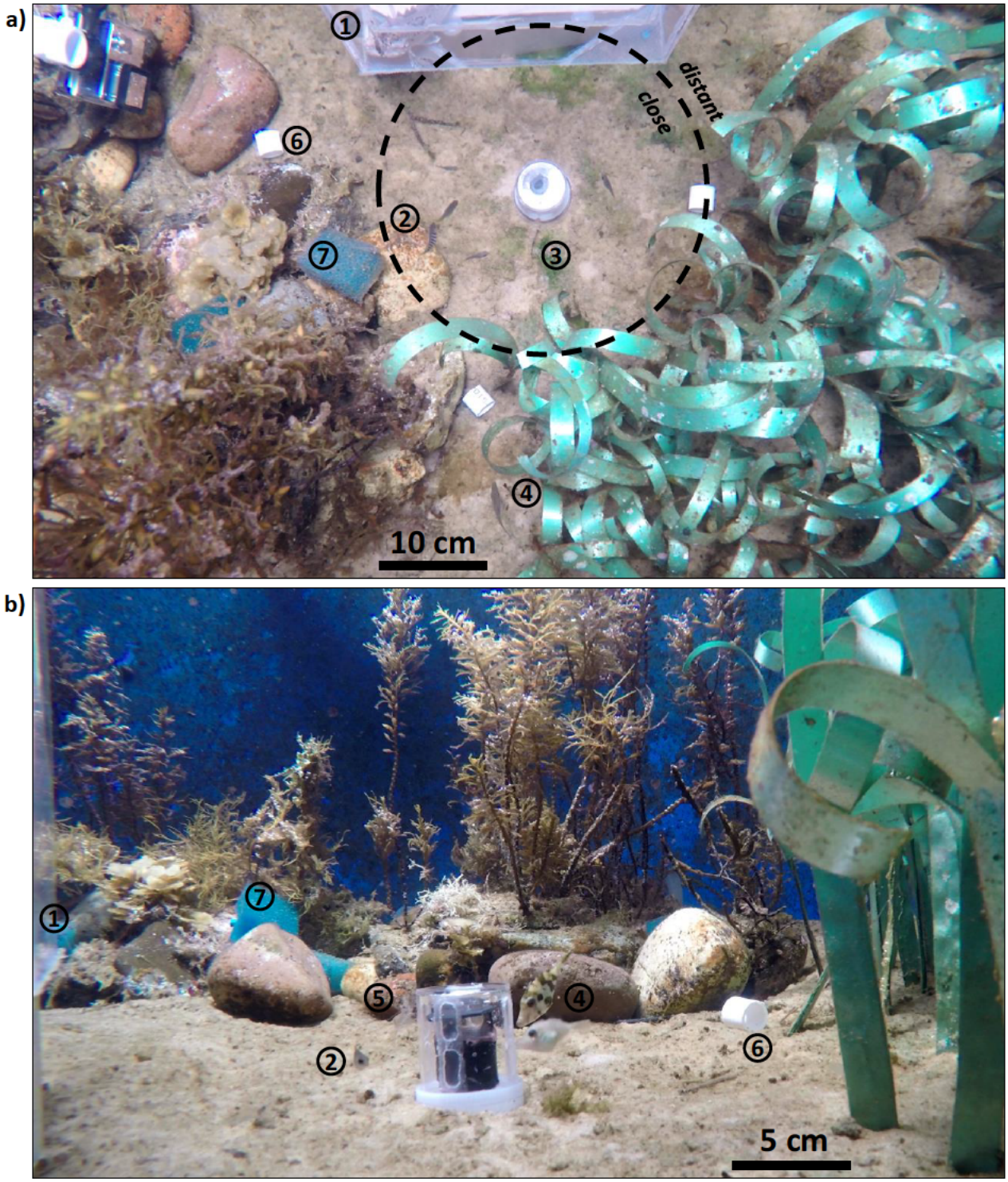


Figure S5: Set-up during behavioural trials testing the response of the consumers to a live predator and food cues. **a)** Field of view of the top camera, with a circle centred on the food cue provider to categorize the individuals' location as 'close' (within circle) or 'distant' (outside of circle) to the food cue. **b)** View of side camera with close-up of the food cue provider. Two out of the nine windows covered by mesh for odour dispersion are visible. The tiny white dots on the black background inside the provider are live brine shrimps. Pictures show mesocosm habitat 3.5 months into the experiment. **(# 1)** Predator cage, **(# 2)** zebrafish, **(# 3)** longfin goby, **(# 4)** leather jacket, **(# 5)** shrimp, **(# 6)** size reference, and **(# 7)** artificial habitat unit to assess copepod resources.

One behavioural trial was conducted daily in each mesocosm over 6 consecutive days, including all possible combinations of food cue and predator presence. The distinct experimental set-up, including open sand, rocky reef and seagrass habitat (Fig. S5a), was randomly re-located daily to one of three possible sites to cover the entire mesocosm. A circle of 30 cm diameter was chosen for the area 'close' to the food cue as it matched approximately the open area between predator cage and the habitats (Fig. 5a). Each individual was tracked from entering until exiting the field of view of the top camera (Fig. S5a), whereas the side camera (Fig. S5b) was only used in situations requiring an alternative viewing angle (GoProTM Hero4 Silver). For each trial, an average of 19.8 ± 11.1 (± SD) observations of individuals were made across species which totalled to 27.9 ± 9.7 min (± SD) of behavioural observation.

Several measures were taken to minimize or test for potential effects related to the methodology used. Firstly, a dummy food cue provider not containing any food was located at the exact same site for the 24 h prior to each behavioural trial to allow for habituation. The consumers were also acclimatized to the empty predator cage, the camera frame and cameras for 15 min before the trials started. Secondly, directly preceding each trial, a procedural control video recording was conducted for 3 min. Here, the dummy provider was exchanged by another dummy provider and not by a provider containing food like in the later trial. This procedural control showed no effect of the climate treatments on the attraction to the provider in the absence of a food cue (ANOVA: df(1,8), $p>0.46$ for CO_2, T and $CO_2 \times T$). It also showed that the consumers were generally attracted by the food cue, as evident when comparing their proximity to the food cue provider between procedural controls and trials (ANOVA: $F_{(1,11)}=38.8$, $p<0.001$).

Resources

To identify potential food resources of the consumers, the biovolume contribution of major resource categories was estimated for each individual fish after inspecting the stomach content under a stereo microscope. The relative contribution of each resource was then standardized according to the mass of the fish, which resulted in the following stomach composition across all fish species and climate treatments (mean ± 95 % CI, n = 218 stomachs analysed): algae and detritus 41.3 ± 2.5 %, copepods 39.3 ± 1.1 %, macrofaunal crustaceans 10.9 ± 0.9 %, small molluscs 3.9 ± 0.3 %, and other invertebrates 4.6 ± 0.5 % (annelids, ostracods and unidentified). These estimates inform about the general presence or absence of certain resources. They should, however, not be used to evaluate the relative importance of these resources for the fishes since their characteristics differed considerably: prey items size (e.g. tanaid vs. copepod), general appearance and energetic value (e.g. fauna vs. flora) and digestibility (e.g. presence or absence of exoskeleton). According to the

literature, the shrimp species we studied (*Palaemon* spp.*)* feed on detritus, small molluscs, annelids and other crustaceans [7].

Resource availability in each mesocosm was assessed through the relative biomass of six resource categories: Small molluscs on rocky reef; Annelids on rocky reef and soft bottom; Copepods on rocky reef and soft bottom; Macrofaunal crustaceans on rocky reef and soft bottom; Detritus on rocky reef; Matt-forming algae on rocky reef, tank wall and seagrass leaves. For the resources that were sampled in multiple habitats, biomasses were combined according to the relative area of each habitat in the mesocosms. In more detail:

1) All small molluscs (chitons, limpets, bivalves, slugs and small gastropods), annelids (polychaetes and oligochaetes), and macrofaunal crustaceans (amphipods) were collected from each rocky reef via picking and sieving through a 1 mm sieve (wet mass, n = 4 subsamples per mesocosm).

2) Copepods on the rocky reef were extracted from artificial habitat units made of aquarium filter sponges (length x height x width = 60 x 25 x 40 mm, pore size 2-5 mm) incubated on the rocky reefs for 1 month (biovolume wet mass, n = 2 subsamples per mesocosm).

3) Copepods, annelids (polychaetes and oligochaetes), and macrofaunal crustaceans (tanaids) on the soft bottom habitat were assessed through sediment cores (65 mm diameter, 15 mm depth) followed by floatation extraction with Ludox TM colloidal solution with a specific gravity of 1.18 and collection on a 45 μm sieve (biovolume wet mass, n = 4 subsamples per mesocosm). While the larger organisms were weighed directly, the annelids from the soft-bottom and all copepods were counted under a stereo microscope on a counting tray. Their wet mass was then calculated using biovolume averages based on photographs and measurements with ImageJ of a subset of individuals (across climate treatments: n = 159 copepods, n = 65 small annelids). For copepods, the treatment-specific average biovolume was used since it differed between climate treatments (ANOVA: $F_{(1,155)}$ = 4.13, p = 0.044).

4) Detritus was estimated as organic matter remaining on the rocky reefs after removing live algae and animals (dry mass, n = 4 subsamples per mesocosm).

5) Matt-forming algae were scraped from the rocky reef, tank wall and seagrass leaves (dry mass, n = 13 subsamples per mesocosm).

An advanced level of acclimation could be expected for larger resource taxa with longer generation times as they had spent the majority of their life in the mesocosms (e.g. molluscs). In contrast, transgenerational acclimation and adaptation was possible for smaller-bodied resource taxa. Our exposure time to the climate treatments of 140 days compares as follows to potential generation times of these taxa: benthic microalgae 0.4-6 days [8,9], benthic copepods 9-26 days [10], tanaids 42 days [11], amphipods 35-49 day [12,13], and annelids 17-55 days [14,15].

META-ANALYSIS

Search Protocol

We followed a protocol that aimed to identify existing evidence to answer the question 'Do ocean acidification impacts on highly mobile consumers depend on the level of ecological complexity at which performances are tested?'. Web of Science databases were filtered by research field, methodology and taxa (Fig. S6). The search was limited to studies published in 2008 or later as it represents the beginning of the uprising of ocean acidification research, in particular for the taxa that are of interest here [16]. The studies returned by the literature search subsequently underwent a step-wise screening from title, to abstract and full text (Fig. S6). At each step, the following criteria were assessed and studies retained that could not be excluded with certainty:

1) Approach:
- Empirical data from either experiments or observations including a control and elevated CO_2 group
- Excluded: modelling or theoretical studies

2) Taxa:
- Teleost fishes, elasmobranches and decapod crustacean (shrimps and crabs)

3) Life-stage:
- Settlement stage larvae, juveniles and adults
- Excluded: embryos, yolk sack stage larvae

4) Environment:
- Marine or brackish

5) Ecological trait:
- Responses directly related to the detection of or escape from predators, the detection or use of habitat and the detection, manipulation, or capture of food resources (Table S14)
- Excluded: A) purely physiological responses, with the exception of two studies due to their direct implication for foraging – one on claw strength and one on temporal resolution of vision; B) more basic behaviours such as activity, lateralization or boldness in the absence of a stimulus (e.g. predator); C) growth or survival when being fed (unnatural resources: rotifers, artemia, defrosted fish, pellets, etc.)

6) Acidification:
- Corresponds to realistic future scenario and reduced pH is reached through elevated pCO_2
- Excluded: acidification through other means such as HCl

The remaining studies were complemented by screening recent reviews/meta-analysis in the field [16,17,18,19]. Only 5 studies were added through this process indicating that our literature search was comprehensive. Three studies conducted at CO_2 vents which were unpublished

at the time but known to the authors were also included (Table S19 studies # 22, 23 and 37). Finally, for reasons of independence, 5 studies were removed which tested the same species with the same design as studies already considered in the meta-analysis.

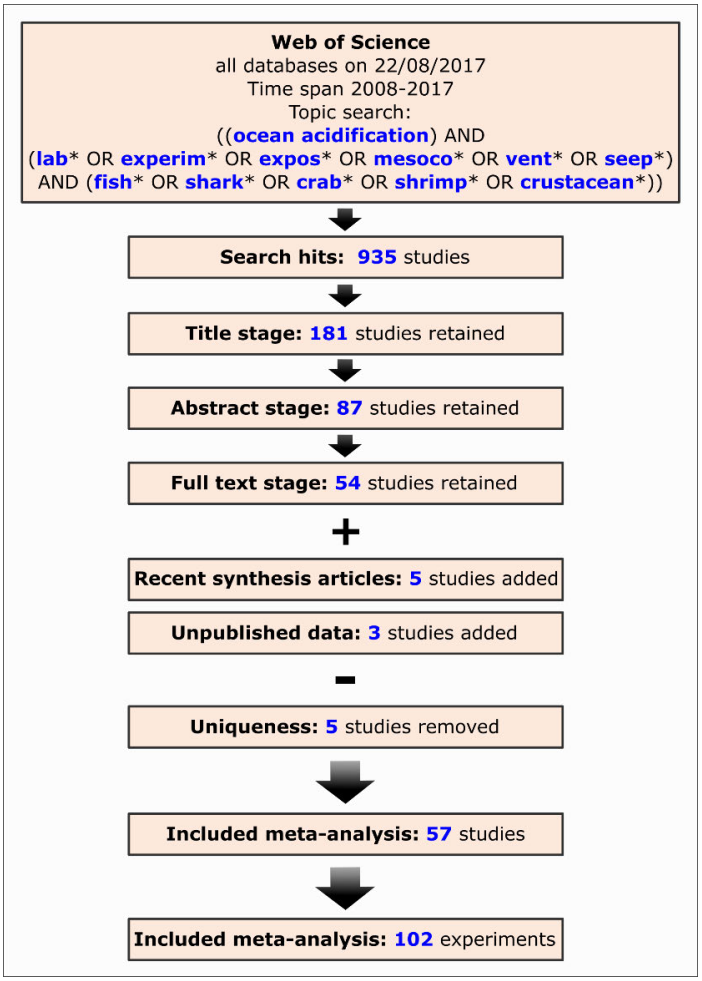


Figure S6: Overview of the selection process for the experiments included in the meta-analysis. The Boolean operator 'AND' narrows the search by specifying criteria that have to be met simultaneously, while 'OR' broadens the search by providing alternative criteria of which only one needs to be met. The asterisk * allows search terms to vary in their endings.

From the 57 selected studies, 102 experiments were extracted for inclusion in the meta-analysis based on the following guidelines (see Table S19 for list of all experiments; this Excel table is unfortunately too large to be printed in the thesis):

1) Multiple experiments were considered from the same study in case they a) were related to different ecological traits or levels of ecological complexity, b) were from the same combination of trait and complexity but differed considerably in their design c) or if they could be seen as sufficiently independent to be published as separate articles. This ensured that larger studies supported by multiple species, systems or methodologies had more influence on the overall results relative to smaller studies.

2) If multiple response variables were available for the same experiment, only the most meaningful one was selected based on the context of the study or on general ecological

theory. If several species were tested together in the same tank or at the same CO_2 vent (i.e. multiple responses are equally relevant), an aggregate effect size was calculated across the responses of individual species (R package Mad [20], method according to Borenstein et al. [21] using 100 % correlation between species).

3) If a system was tested at several elevated levels of pCO_2, only the experiment closest to 936 μatm was considered (emission scenario RCP8.5 [22]).

4) If a system was tested at several points in time, only the experiment with the longest exposure time was considered.

5) The results of 4 experiments that used fishes as both prey and predator were considered for both traits predator avoidance and foraging, just from opposite perspectives.

Table S14: Examples of typical experiments considered in the meta-analysis for each combination of ecological complexity and ecological trait.

Complexity *(inclusion criteria)*	**Trait**	**Typical experiments**
Simple *(1 sensory cue)*	**Predator avoidance**	choice flume chamber with olfactory predator or alarm cue, behavioural change in aquaria after introducing visual or olfactory predator cues, response to approaching visual threat
	Habitat selection	choice flume chamber with olfactory habitat cues, habitat choice test in simple set-up based on isolated olfactory, visual or auditory habitat cues
	Foraging	choice flume chamber with olfactory food cues, ability to find food in simple set-up based on olfactory food cues, ability of visual sense to detect fast moving objects
Medium *(2+ sensory cues)*	**Predator avoidance**	behavioural change in aquaria after introducing both visual and olfactory predator cues, response to approaching threat that includes multiple cues (visual + auditory + water motion), survival/escape performance when exposed to real predator over short-term (in small aquaria, in larger tanks with shelter or in the field)
	Habitat selection	choice test in small aquaria or larger tanks including several habitat cues (olfactory + visual + auditory), use of natural habitat in the laboratory or in the field
	Foraging	ability to find food in simple set-up based on combined visual-olfactory food cues, success in catching live prey in small aquaria or larger tanks with shelter, hunting success on natural live prey amongst structured habitats in the field, long-term growth when having to hunt on natural live prey in the laboratory
Complex *(populations at CO_2 vents)*	**All traits integrated**	abundances of either individual species or species communities that could potentially be influenced by indirect effects of elevated CO_2

Data Analysis

The majority of experiments were reported with continuous response variables with a natural zero point – the requirements for the use of log-transformed response ratio as effect size. However, 24 relevant experiments that were unevenly distributed across traits and complexities did not fit these criteria. Their exclusion would have led to reduced power, potential bias and an incomplete representation of the literature. Therefore, standardized mean difference was chosen as effect size for the meta-analysis because it applies to a wider range of data types [21] and because estimation methods are available in case it cannot be derived directly [23,24]. As such, 13 experiments were based on binary responses (e.g. survival yes/no) with underlying traits in which individuals could be expected to vary continuously (e.g. ability to avoid predators). Here, the probit-transformed risk difference was used as estimate of the standardized mean difference [23]. It should be noted that our findings were unlikely to be driven by the choice of effect size measure as the same general pattern was found with log-transformed response ratio for the categories to which it applied (see Table S8b, 9b).

The effect sizes of five experiments were identified as extreme outliers through sudden gaps in forest plots, a large influence on the overall mean effect size estimates and heterogeneity statistics, and through Cook's distance. These extremely negative effect sizes were manually raised to the value of the next smallest non-outlier effect size (i.e. winzorizing, Table S15, Fig. S1). The direction of these effect sizes was therefore considered in the meta-analysis, while reducing their influence on the data properties and the overall results. Excluding them entirely would cause bias as they were more likely real than due to chance given that effects of elevated CO_2 differed truly and considerably between experiments (see heterogeneity statistics table S9a). Also, this approach to outlier treatment made the overall results only more conservative, as four out of the five extreme values represented experiments at simple levels of complexity.

Table S15: Identification and winzorizing of extreme outlier effect sizes. Extreme values were raised to the next smallest non-outlier effect size. The next largest non-outlier Cook's distance is given for comparison. The numbers of the outlier experiments are associated with Table S19.

Category (complexity / trait)	**Outlier effect size**	**Next smallest effect size**	**Outlier Cook's distance**	**Next largest Cook's distance**	**Outlier experiment #**
Simple / Predator avoidance	-26.0	-5.3	0.87	0.033	51
	-25.8	-5.3	0.73	0.033	101
Simple / Habitat selection	-10.1	-3.0	1.03	0.043	57
	-8.2	-3.0	0.30	0.043	53
Medium / Predator avoidance	-2.8	-1.8	0.40	0.15	102

Potential Moderators

Table S16: Association analyses showing that our specific categorization of ecological complexity is also reflective of ecological complexity in a broader context. We correlated our two levels 'simple' and 'medium' – defined by the availability of sensory cues – to three other potential measures of complexity that could easily be extracted for each experiment: 1) the presence or absence of natural habitat, 2) the presence or absence of the opportunities and pressures needed to learn adaptive behavioural strategies, and 3) the presence or absence of a social environment. The association coefficient Yule Q ranges from -1 (≙ perfect negative association), to 0 (≙ no association) and 1 (≙ perfect positive association) [25].

Potential measure of complexity	**Association with our measure** (sensory cues)			
	Yule Q	X^2	**df**	**P-value**
Habitat	0.914	28.5	1	<0.0001
Learning	0.642	7.90	1	0.0050
Social Environment	0.933	17.1	1	<0.0001

Pearson's X^2 test with associated X^2 statistic, degrees of freedom (df) and p-value

Table S17: Weighed random-effects meta-regressions on the response of consumers to elevated CO_2 with pCO_2 level (in μatm) or exposure time (in days) as continuous moderators. The two moderators and the three ecological traits were analysed separately but always across simple and medium complexity. Populations at CO_2 vents were excluded here as their pCO_2 levels typically vary in space and time and as the exposure time could not be specified. The more conservative Knapp-Hartung approach was used for moderator tests. Both covariates were log10-transformed to reduce the influence of a few very large values.

Ecological trait	**# Experiments**	**df**	**Level pCO_2**			**Acclimation**		
			slope	F-value	P-value	slope	F-value	P-value
Predator avoidance	38	1, 34	2.65	3.21	0.082	0.009	0.00	0.982
Habitat selection	29	1, 25	0.53	0.37	0.549	0.167	0.63	0.435
Foraging	27	1, 23	0.42	1.19	0.287	0.017	0.01	0.931

df = nominator and denominator degrees of freedom; slope = regression slope

The substantial amount of unexplained heterogeneity in the meta-analysis (Table S9a) raises the question about other factors that may have influenced the effect of elevated CO_2 (for acclimation and pCO_2 level see Table S17).

We could unfortunately not account for specific characteristics of experiments such as ecosystem, taxa or life-stage because of insufficient replication. As such, young coral reef fishes were over-represented at simple complexity for the traits 'predator avoidance' and 'habitat selection'. To investigate for potential bias, the association between performance and complexity can be assessed directly for some of these coral reef species. In many but not all instances, these comparisons within species and life stage show, just like the overall pattern of the meta-analysis, a strong effect at simple but a reduced or absent effect at medium or complex levels of complexity: Chivers et al. [26] and Ferrari et al. [27] vs. Allan et al. [28]

and Ferrari et al. [29]; within Devine et al. [30]; within Munday et al. [31] but see also Devine and Munday [32].

Predator avoidance at medium complexity appeared to be influenced by the specific predation scenario (weighted mixed-effects meta-analysis with predator manipulation as moderator: $F_{(2,15)} = 5.49$, $p = 0.016$). While the negative effect on survival was evident when only the consumers but not the predators had been maintained in captivity and exposed to elevated CO_2, no effect was detected, on average, in experiments that treated both consumers and predators equally (Table S18 and Fig. S7). That is, the negative effect of elevated CO_2 on predator avoidance was buffered most under the most realist predation scenario, which did not advantage the predator. However, this concept requires further testing as the same predator species was used, though in different designs, in the experiments that exposed both the consumer and predator to elevated CO_2 in captivity (e.g. see Allan et al. [28], Ferrari et al. [29]).

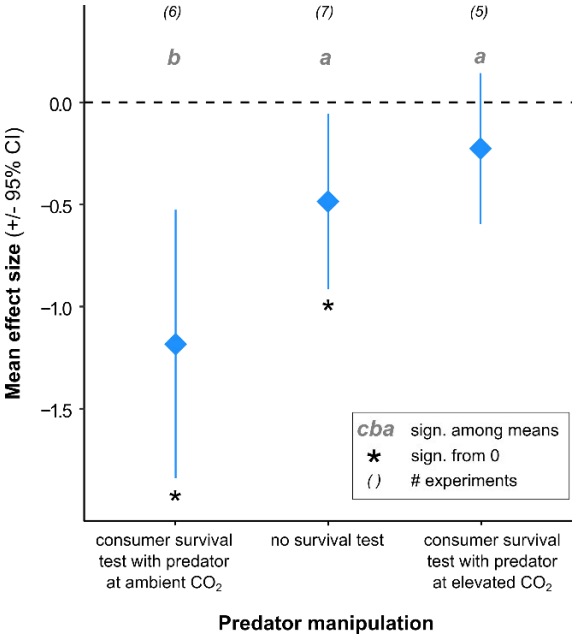


Figure S7: Influence of the specific predation scenario on the ability of consumers to avoid predation at medium complexity. In all cases, consumers had been maintained in captivity and exposed to elevated CO_2 before testing. Here, experiments were assigned to one of three categories according to the predator treatment: predators were neither exposed to elevated CO_2 nor held captive and predators actively hunted the consumers (left), predation risk was simulated (centre), and predators were exposed to elevated CO_2 and handled in the laboratory similarly to the consumers and predators actively hunted the consumers (right). Lower case letters mark mean effect sizes that differ significantly following post-hoc tests adjusted by false discovery rate.

Table S18: Weighted random-effects meta-analyses on the predator avoidance of consumers at medium complexity.

Predator	# Experiments	Mean effect size			Heterogeneity				Sensitivity	
		Esti-mate	T-value	P-value	I^2 (%)	Q	df	P-value	sign. change	max. P-value
ambient CO_2	6	-1.18	-4.63	0.006	62.09	13.35	5	0.020	no	0.021
no survival test	7	-0.49	-2.76	0.033	64.39	17.06	6	0.009	yes	0.086
elevated CO_2	5	-0.23	-1.70	0.165	0.00	3.16	4	0.531	no	0.083

I^2 = heterogeneity to total variability; Q-test for heterogeneity with associated Q-statistic (Q), degrees of freedom (df) and p-value

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CHAPTER IV

STABLE TROPHIC INTERACTIONS REINFORCE THE DEGRADATION OF FOOD WEBS UNDER FUTURE CLIMATE

Statement of Authorship

Title of Paper	Stable trophic interactions reinforce the degradation of food webs under future climate
Publication Status	☐ Published ☐ Accepted for Publication ☐ Submitted for Publication ☑ Unpublished and Unsubmitted work written in manuscript style
Publication Details	

Principal Author

Name of Principal Author (Candidate)	Silvan U Goldenberg
Contribution to the Paper	study design, conducting experiment, stable isotope analysis, data analysis and writing
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 2/02/2018

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
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Contribution to the Paper	study design, conducting experiment and revising manuscript
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Contribution to the Paper	study design and writing
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ABSTRACT

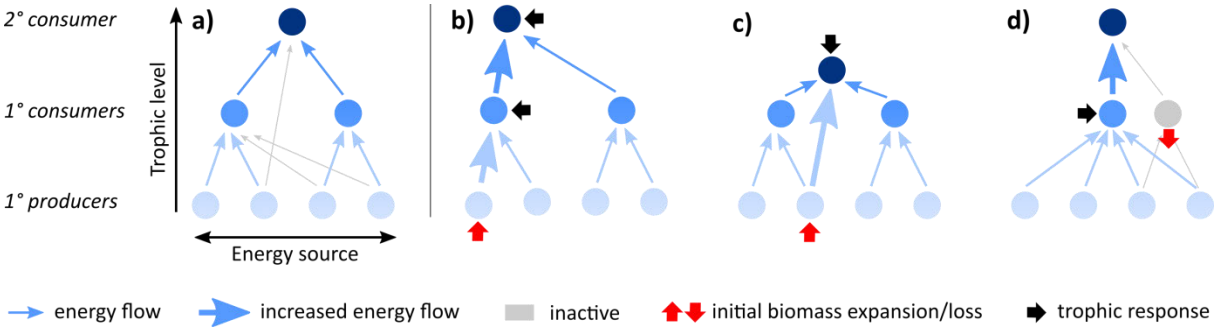
Ecosystems globally are experiencing an ever accelerating taxonomic re-organisation due to pervasive anthropogenic pressures. One of the central questions is whether food webs can adapt their architecture – that is, the feeding relationships between organisms – to counter such changes and maintain ecosystem structure and function. Using a diverse mesocosm community and stable isotope analysis, we reveal that food web architecture can be surprisingly stable under future climate and thus unable to compensate for the decline of sensitive or proliferation of benefiting taxa. Key ecological processes that stabilize communities against environmental change such as functional redundancy, trophic compensation or species substitution were largely absent under elevated temperature. Consequently, a novel trophic pyramid emerged with substantial expansion of biomass at the base (i.e. primary producers) and top (i.e. secondary consumers) and contraction in the centre (i.e. primary consumers). This imbalance may characterize a transitionary state before the collapse into short, bottom-heavy food webs that has been observed in prehistoric and modern ecosystems when severe abiotic stress persists long-term. We conclude that food webs may be less adaptive than previously thought and limited in their capacity to prevent degradation of ecosystems and their services in a warming ocean.

INTRODUCTION

Our livelihood and life-style are sustained by complex yet inherently adaptive systems that can provide goods and services in a variable world [1,2]. For example, self-organising networks of specialised cells enable immune systems to maintain health against novel pathogens [3], and the dynamic behaviour of individual businesses allows economies to satisfy an ever-changing demand [4]. While similar principles apply to ecosystems [5], the preservation of their services into the future depends on how lower-level ecological processes adjust to intensifying human activities [6]. On the one hand, an unrestrained expansion or loss of ecological functions can destabilize food webs [7] and lead to the degradation of entire ecosystems [8,9]. Such changes in basic composition of food webs are commonly studied using trophic pyramids – based on biomass, abundance or energy – as they not only inform about food web health but also about underlying ecological processes [10-12]. On the other hand, the complex network of feeding interactions between organisms that characterizes food webs (i.e. trophic architecture) may be able to effectively counter environmental change and maintain functional diversity [13,14].

The adaptive capacity of trophic architecture is rooted in the flexible trophic behaviour of consumers [15] (see Box 1). As consumers tend to focus their foraging on resources that are plentiful [16], they play a critical role in the regulation of proliferating and recovery of rare resources [14]. The adaptive potential is further extended through redundancy amongst functionally similar consumer species [17]; that is, the loss of sensitive species can be compensated through niche expansion and density substitution by less sensitive species now liberated from competition [18]. Whilst the potential of such adaptive trophic behaviours is limited and highly variable [19-21], they are considered key to the resistance and resilience of ecosystems by reinforcing prey population control and the continuation of energy flow [8,15,22].

Species naturally differ in their responses to future climate, as the life-strategies of some are disadvantaged and others benefited [24]. Ocean acidification threatens calcifiers [25] and impairs key behaviours in many consumers [26,27], and yet primary producers may use the excess CO_2 as a nutrient [28,29]. Similarly, ocean warming can cause severe metabolic stress in species near their upper thermal limits [30], whilst others may gain from the accelerated physiology [31] and expand their ranges [32]. Undoubtedly, these climate stressors will cause the loss of species globally. However, it is not species richness *per se* but the functional structure of ecosystems that provides natural resources and services [17,33,34]. One of the key questions is whether the fundamental structure of ecosystems can be preserved through mechanisms that stabilize against the taxonomic re-organisation under future climate.



Box 1: Hypothetical adaptations of trophic architecture to changes in composition, here exemplified trough the expansion or loss of species, that are driven by abiotic change. The architecture is based on feeding interactions (arrows) between species (nodes) that can intensify, weaken, activate or inactivate depending on the foraging strategy that is currently optimal for consumers [14,23]. The trophic niches of consumers (position in trophic space) reflect the origin of energy, in terms of basal resources (horizontal axis) and the number of trophic steps (vertical axis).

a) Baseline where each consumer has a horizontally centered position indicating equal contribution of its two resource species. **b)** The over-expansion of a primary producer that benefits from abiotic change is countered by higher consumption. Its increased contribution to the energy flow within the food web is represented by the horizontal shift in consumers. **c)** An optional omnivore initiates feeding on an expanding primary producer, leading to a decrease in trophic level of the omnivore and shortening of the food web. **d)** A consumer replaces the trophic function of its competitor that became extinct (i.e. redundancy), which is indicated by the approach of their trophic niches.

In contrast to these examples, a constant architecture would lead to severe changes in biomass composition and associated functions. In **b-d**, biomass would accumulate at the bottom of the food web and in form of a few dominating primary producer species. Additionally in **d**, the energy flowing through the extinct consumer would be lost entirely leading to lower primary and secondary consumer biomass.

Here we test the ability of trophic architecture to compensate for increasing climatic stress and investigate shifts in trophic pyramids and the functional composition of species communities. In 1,800 L mesocosms, we exposed a model community to simulated ocean acidification (elevated CO_2: 910 μatm, pH=7.89) and ocean warming (elevated temperature: +2.8 °C, baseline 21 °C ≙ summer average) for 4.5 months according to end-of-century projections (RCP 8.5 [35]). We assessed the performance of functional groups at different trophic levels through their standing biomass and used stable isotope analysis to unravel trophic architecture. Stable isotope ratios provide time-integrated estimates about feeding relationships based on energy flow, where the trophic position of a consumer is approximated by $\delta^{15}N$ and the basal resources that support it by $\delta^{13}C$ [36], following the same logic as in Box 1. Our study demonstrates how maintenance of a stable trophic architecture under climatic stress can lead to the functional and trophic degradation of communities.

RESULTS

A transformation in the biomass structure of communities occurred as a result of the strong but opposing responses of trophic levels to temperature (Fig. 1). We structured communities into 14 major functional groups including five groups of micro- or macroalgae (primary producers), five of herbivores, one of detritivores and two of filter feeders (primary consumers), and one of each predatory invertebrates and fishes (secondary consumers) (Table S8). Both CO_2 and temperature enhanced bottom-up forcing through increased community primary production (Fig. 2a, Table S1a). Under elevated CO_2 alone, taxa across all trophic levels benefited from this resource enrichment (Figs. 1b, S1a), and communities maintained a functional composition close to that of controls (Fig. 2b-c, Table S1b). In contrast, under elevated temperature irrespective of CO_2, mainly primary producers and secondary consumers increased in biomass while primary consumers systematically declined by >40 % on average (Figs. 1c-d, S1b-c). The functional composition of these communities was clearly distinct to that of the controls (Fig. 2c). Under the combined effect of elevated CO_2 and temperature, the expansion of biomass at the bottom of the food web was particularly pronounced due to the extreme proliferation of turf algae and cyanobacteria (Fig. S1c), and led to a 10-fold increase in dominance of autotrophic compared to heterotrophic organisms (Fig. 2b, Table S1b).

In contrast to biomass, trophic architecture across all taxa and the trophic niches of individual taxa remained largely unchanged, even under the combined pressure of elevated CO_2 and temperature (Fig. 1). Across taxa, the architectural extent (i.e. trophic level range, basal resource range and niche area) or the position of taxa relative to one another (i.e. trophic diversity, redundancy and evenness) were unaffected by the climate treatments (Fig. S2, Table S3). Likewise, individual taxa maintained their specific position in trophic space under all climate treatments (Fig. S3). Also, the niche breadth of taxa – representing between-individual diet specialisation – showed neither an overall change nor a collapse only in taxa that were sensitive to future climate (Fig. S4).

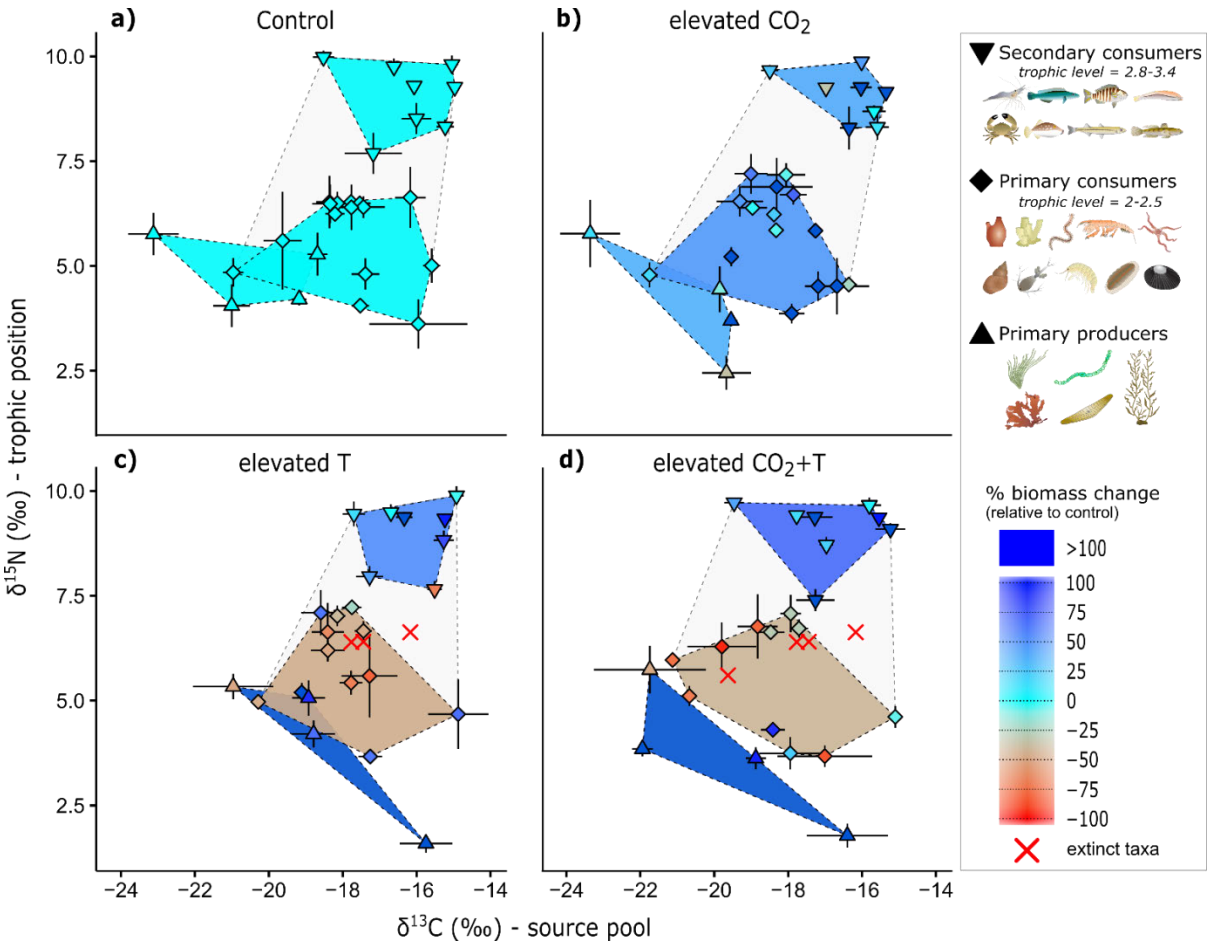


Figure 1: Trophic architecture and biomass composition of mesocosm communities under different climate treatments. Each symbol represents the stable isotope signature (mean ± SE) and change in biomass of one taxon. Coloured polygons show the average change in biomass of the three trophic levels. Light-grey polygons indicate the trophic niche of the consumer community. Taxa that were either entirely absent or not present in sufficient amount for stable isotope analysis are marked as (ecologically) extinct with a position corresponding to the signatures of the controls. Taxa labels and sample sizes are provided in Figure S10 and Table S11.

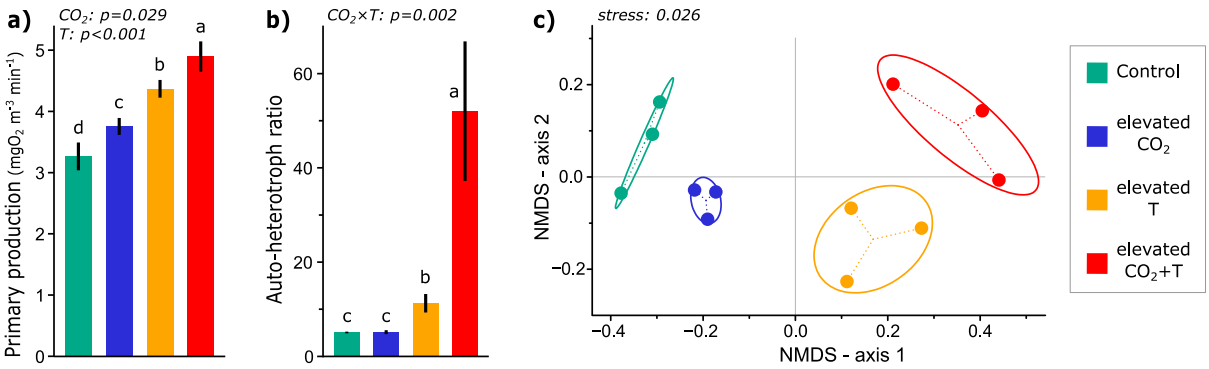


Figure 2: Basic community characteristics under different climate treatments across all functional groups. **a)** Primary production (± SE) estimated through gross O_2 production and **b)** biomass ratio (± SE) of autotrophic to heterotrophic organisms. Following 2-way ANOVAs with CO_2 and Temperature (T), letters above bars mark significantly different means according to main effects (a) or the interaction (via post-hoc tests, b). **c)** Functional composition using non-metric multidimensional scaling on the biomass of the 14 principle functional groups (see Figure S1). Given are mesocosms (data points), treatment centroids (intersection of dashed lines), and the 95% confidence ellipses for the centroids. Plots a-c are based on n = 3 mesocosms.

The stability of trophic architecture under elevated temperature implied impairment in compensatory processes that are mediated by the adaptive trophic behaviour of consumers. The absence of functional redundancy is best illustrated using herbivory. Two key herbivore groups – the largest in biomass (non-cryptic molluscs) and highest in abundance (copepods) – strongly declined under elevated temperature, in particular in combination with elevated CO_2 (Figs. S5a, S1b-c). However, none of the less sensitive herbivore groups re-occupied this opened-up trophic space; that is, functionality was lost (Fig. S5b, Table S4). Further, a lack of trophic compensation at the food web scale was apparent. Expected was an active shift of omnivorous taxa – tracking the availability of resources (Fig. S1b-c) – towards an increasingly herbivorous diet. Such adjustments in feeding choices at lower trophic levels would be reflected in an overall shorter food web. Yet, a reduction in trophic level at the top of the food web was not observed, neither in the entire assemblage of secondary consumers (Fig. S6) nor in any of its 8 taxa individually (Table S6).

DISCUSSION

We show that trophic architecture can remain unexpectedly stable under ocean warming, while the relative biomass among functional groups re-organises. The lack of an adaptive response in architecture to buffer environmental change mediated the emergence of a novel trophic pyramid with substantial expansion at the base and top and contraction in the centre (Fig. 3b); a pattern that was exaggerated in the combined stressor scenario (Fig. 3d). Warming likely caused an imbalance in multiple community dynamics at once including a shift towards 'weedy' [28] and less palatable primary producers [37,38], ingestion inefficiency in secondary producers [39], and over-consumption of prey by predators in the face of elevated metabolic demand [29,31]. The strong influence of temperature on physiology [24,40] may explain why consumers across the food web failed to adjust their feeding behaviour to the changing landscape of resources. In contrast, ocean acidification alone only represented a moderate stressor to our community, primarily in the form of CO_2 enrichment boosting primary production. Here, the enhanced bottom-up forcing propagated rather evenly to higher trophic levels (Fig. 3c), consistent with trophic theory [41] and implying some degree of trophic compensation [29,42]. An adaptation in trophic architecture was not required under ocean acidification alone, as the additional energy could be channelled upwards via the same feeding interactions.

Whilst our predators maintained their biomass and diversity under warming, natural food webs may become depleted at their top when the full complexity of ecosystems is considered. Food webs at larger spatial scales incorporate higher-order predators. These may either succumb the stress of warming and acidification [43,44] or deplete lower trophic

levels, including the predators that were studied here, due to elevated metabolic rates [31,45]. Independent of possible changes in top-down forcing, the small predators of the mesocosm – only tested within one generation – may not be able to resist long-term exposure to climatic stress or additional disturbances given the impoverishment in their prey. An ecological tipping point may be passed [7,46] beyond which higher trophic levels can no longer be supported, inevitable leading to a collapse into a shorter, more bottom-heavy trophic pyramid (Fig. 3e). This end state is common in ecosystems that are under intense pressure from overfishing [12,47], species invasions [48], nutrient enrichment [49], variation in river discharge [50], or experimental warming [51]. Clearly, many stressor-ecosystem interactions do not exhibit effective compensation. Our study may reveal one of the transitionary dynamics – an adjustment of biomass around a stable trophic architecture – that can lead to an imbalanced trophic pyramid with little capacity to resist further disturbance.

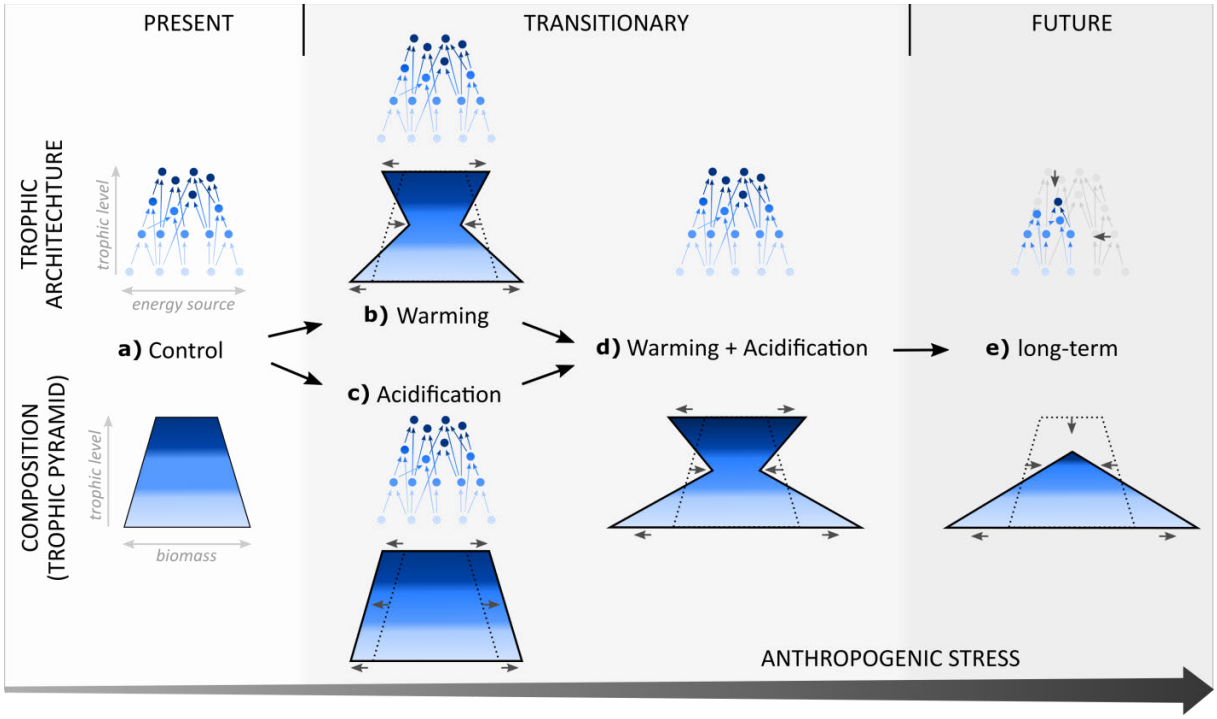


Figure 3: Theoretical diagram of how non-adaptive trophic architecture under anthropogenic stress can initially lead to altered trophic pyramids (our experiment) and bottom-heavy food webs and the degradation of higher-order consumers over the long term (literature).

Whilst the relative change in biomass between functional groups or trophic levels in our communities only represent the initial response to warming, it is likely to be followed by species extinction if the stressor persist [52]. The removal of nodes (i.e. species) in the architecture would ultimately force a simplification towards shorter food webs with fewer energy channels (Fig. 3d). Similarly, periods in Earth's history with extreme climate change, ocean acidification and hypoxia led to a simple architecture comprising lower trophic levels [53] and generalist interactions [54]. Following mass extinction events that occurred during these periods, species evolution over millions of years was required to rebuild – from the bottom up – ecosystems with more complex trophic architectures [53]. Indeed, evidence suggests that

a human-induced mass extinction may be imminent [55]. Only a deceleration of change by reducing CO_2 emissions and a removal of existing pressure through local environmental stressors may give food webs a chance to adapt and ecosystems the ability to provide critical services to future human generations.

Authors' contribution

S.U.G., I.N., C.M.F and S.D.C designed the study, S.U.G. and C.M.F. maintained the mesocosms, S.U.G. conducted the stable isotope analysis, S.U.G. analysed the data, S.U.G., I.N. and S.D.C. wrote the manuscript and all authors revised the manuscript.

Acknowledgements

We thank W. Hutchinson, M. Gluis, T. Kildea, M. Brustolin, M. Rollog and all the students for their help. Organism-symbols were drawn by S.U.G. or are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). Financial support was received by the Australian Research Council Future Fellowship Grant FT120100183 (to I.N.) and FT0991953 (to S.D.C.) and by a grant from the Environment Institute (the University of Adelaide). C.M.F. was supported by a Science Without Borders PhD scholarship through CAPES (Coordination for the Improvement of Higher Education Personnel) Brazil (scholarship no. 13058134).

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METHODS

Mesocosms

A temperate benthic coastal ecosystem was simulated indoors from February to July 2015 using twelve circular tanks of 1,800 l (see Fig. S7 for photos). Each of these mesocosms was provided with unfiltered seawater including nutrients and planktonic propagules at 2,300 l day^{-1}. They comprised a mosaic of the three dominant local habitats (Gulf St. Vincent, South Australia) [1]: i) 'Rocky reef' built of rocks from the sea with all associated macrophytes and invertebrates, ii) 'artificial seagrass' planted into fine silica sand, and iii) 'open sand' composed of the same sand. The artificial seagrass had been incubated for 2 weeks in the sea nearby natural seagrass for epiphytic colonization. The soft-bottom habitats (i.e. sand and seagrass) of each mesocosm were seeded with 25 l sediment collected among seagrass meadows and including all infauna and flora. A lamp simulated a local light regime of about 6-7 m water depth and supported primary production (14/10 light-dark cycle, 30 min dawn and dusk dimming).

Ecological community

The overall aim was to assemble a multi-trophic community that features high taxonomic and functional diversity while being as natural as possible. A variety of sessile and mobile organisms were passively introduced through the habitat at the start and the continuous inflow of unfiltered seawater during the experiment. In addition, a range of larger motile consumers were introduced to each mesocosm including 6 fish species (total of 45 individuals), two shrimp species (10 individuals), and 8 gastropod species (total of 56 individuals) (Table S7). Whilst specific thermal niches determine sensitivities to future climate [2], our temperature treatment did not surpass the upper thermal limits of any of the fish or shrimp species (see chapter III). This assessment was difficult for many of the other taxonomic groups, due to unknown thermal ranges and/or sampling at broader taxonomic level. Nevertheless, the high diversity in these groups increased the likelihood of more tolerant species that are critical for functional redundancy.

The longer term exposure not only allowed acclimation in larger and multiple generations in smaller species (see supplementary methods) but also enabled biotic interactions to shape community properties. Secondary consumers moved between various micro- and macro-habitats and maintained a varied diet (fish stomach content: crustaceans, molluscs, annelids and algae); behaviour that is required for the coupling of energy channels and the adaptive response to changing prey availability. Overall, communities adjusted to their specific environmental conditions through growth, mortality and – in case of species with short life cycles – reproduction. By the end of the experiment, they were likely close to their

equilibrium state as suggested by key functional groups at both the bottom and top of the food web. First, the cover of cyanobacteria and turf algae remained, after initially increasing rapidly in the mesocosms with elevated temperature, stable over the final month. Second, the unaltered physical condition of the fishes ^{3} across mesocosms and treatments (Tables S9) indicated certain continuity in trophic processes. That is, fishes responded to changes in resource availability through growth and mortality and not through rapid adjustments in physical condition that would be expected if trophic processes fluctuated strongly. The final taxonomic complexity, biomass and abundance of an average community are illustrated in Table S8.

Climate treatments

We crossed the factors CO_2 (levels: ambient and elevated) and temperature (levels: ambient and elevated) using three replicate mesocosms per treatment combination (see Table S10 for water parameters). To achieve elevated CO_2, the seawater was pre-conditioned to elevated pCO_2 levels with pure CO_2 and then circulated between each mesocosm and an associated bin heavily aerated with CO_2-enriched air. Community metabolism produced diurnal variability in pH; a characteristic of shallow coastal systems (Fig. S9). Ambient temperature was set according to average local summer conditions over the past 5 years (2 data loggers, 5 m depth, 2010-2015, SA Water), and heaters were used to achieve elevated temperature. The mesocosm communities were habituated to captivity for 3-4 weeks, progressively raised to their respective climate treatment over 1 week, and finally maintained at treatment levels for 4.5 months (Fig. S8).

Biomass and primary production

The community composition was assessed over the final month of the experiment, and the methodology is provided in detail in the supplementary information. In brief, all individuals of the larger-bodied taxa were collected by searching the entire mesocosm habitat thoroughly. Smaller-bodied taxa were instead subsampled through various techniques including sediment cores, artificial habitat units and chlorophyll *a* measures before being extrapolated to the entire mesocosm. Larger-bodied consumer taxa were weighed as wet mass on a micro scale after removal of excess water with a paper towel, while the mass of copepods and small annelids was estimated using biovolume. Due to the difficulty of removing excess water, primary producers were analysed as dry mass either by drying at 60 °C or extrapolation from chlorophyll *a* concentrations. For the data analysis, taxa were pooled into 14 functional groups and – based on the stable isotope signatures – into 3 trophic levels (see Table S8).

Community primary production was estimated at the end of the experiment. O_2 concentration was measured in 1 min intervals over at least 30 min (HQ40d Portable Meter, sensor LDO101, HachTM), while mesocosms were sealed off the atmosphere with a transparent plastic cover. This procedure was conducted once during daylight and once during night-time in each mesocosm. Linear regression were fitted (R^2 mean ± SD = 0.94 ± 0.04) to obtain a rate of O_2 production during daytime (net production) and consumption during night-time (respiration). Finally, gross primary production was calculated as the sum of net production and respiration.

Stable isotope samples

About 175 separate stable isotope samples from 28 distinct taxonomic groups were used to analyse trophic architecture under each climate treatment (~700 samples in total). Samples were derived from the biomass sampling described before or through the collection of additional material (see supplementary methods). In case of sessile or little motile taxonomic groups, these samples represented spatially separated areas within the mesocosm. To obtain sufficient organic material for isotope analysis, samples represented individuals (larger consumers), multiple individuals (smaller consumers and macrophytes) or an undefined number of individuals (smaller primary producers). While we aimed to collect an even number of samples for each taxon per mesocosm (2 or 3 samples) and climate treatment (6 or 9 samples), this was not always possible due to high variability or generally low biomass caused by a strong treatment effect. A complete list of the taxa included in the analysis and their replication is provided in Table S11.

Muscle tissue was used for larger, motile consumers (fishes, predatory invertebrates and all molluscs) and cleaned stomach sacks for ascidians. The entire body was instead used for smaller consumers and primary producers. Samples were dried at 60 °C and briefly homogenized in a ball mill except the smallest samples (e.g. copepods) that were used entirely. Samples of brittle stars contained considerable amounts of carbonate and were thus split in two: one part remained unmodified to estimate $\delta^{15}N$ and the other was decalcified (1 M HCl) for an unbiased estimate of $\delta^{13}C$. 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 $^{15}N/^{14}N$ 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 $\delta^{15}N$. Isotope signatures are integrated over days to months depending on metabolism and growth rate [4,5]. The duration of our mesocosm was likely sufficient for a near complete isotopic turnover in all taxa given that even the taxa with the largest body

size (*B. quoyii*) or highest trophic level (*F. lateralis*) showed a substantial mean (± SD, n = 12) per capita increase in mass with 2461 ± 414 % and 202 ± 53 %, respectively.

Stable isotope analysis has become a popular tool in ecology as it provides a unique insight into the stability or change of feeding interactions [6]. In brief, biological processes can discriminate between heavy and light C and N isotopes. A depletion of ^{13}C occurs during assimilation and this effect varies substantially between primary producers. Therefore, $\delta^{13}C$ may reflect the horizontal trophic architecture, given that it changes only slightly with increasing trophic level (approx. -1 to +2 ‰ [7]). In contrast, ^{15}N experiences a stronger enrichment through each trophic step (approx. +1.5 to +4.5 ‰ [7]), and thus $\delta^{15}N$ may reflect the vertical architecture. The variability in enrichment factor between species and systems [7] causes no issue for our study, as the entire stable isotope analysis is conducted in relative terms using the control mesocosms as reference.

The magnitude of possible shifts in stable isotope signatures of consumers in bivariate $\delta^{13}C$ and $\delta^{15}N$ space in response to environmental change is always bounded by the difference in signature of their resources (as illustrated in Box 1). In a hypothetical and simplified example, if the $\delta^{13}C$ signatures of the two potential resources of a consumer are 5 ‰ apart, then the consumer's signature may shift horizontally within these 5 ‰ depending on the relative contribution of the two resources. Similarly, if the consumer is an omnivore with potential resources from the first and second trophic level with $\delta^{15}N$ signatures 3.4 ‰ apart, then the consumer's signature may shift vertically within 3.4 ‰ reflecting the signature between a pure carnivore and herbivore. Accordingly in our study, the detection of a shift in consumer diet by stable isotope analysis was possible due to the distinct signature of the major resource groups (see distance and precision in Fig. 1).

Data analysis

Two-way ANOVAs with CO_2 and Temperature as fixed factors were conducted for gross primary production, auto-heterotroph ratio, and biomass of each of the 14 functional groups. These were followed by Student–Newman–Keuls (SNK) *post hoc* tests in case of a significant ($\alpha = 0.05$) interaction. Additionally, the difference in functional composition between communities was illustrated using non-metric multidimensional scaling based on the 14 functional groups (Bray-Curtis, Wisconsin standardization [7]).

All stable isotope analyses were conducted across mesocosms in order to employ the more sophisticated Bayesian approaches. This was appropriate because mesocosm as random factor did neither affect the isotope signatures of the entire assemblage of consumers (Fig. S11a, Table S12a) and basal resources (Fig. S11b, Table S12b) nor of individual taxa (Table S13).

To characterize trophic architecture based on $\delta^{15}N$-$\delta^{13}C$ bivariate space, six community-wide metrics were assessed for each climate treatment using all 23 consumer taxa: i) '$\delta^{15}N$ range' and ii) '$\delta^{13}C$ range' for the distance between taxa with smallest and largest values, iii) 'total area' for the convex hull encompassed by all taxa, iv) 'mean distance to centroid' for the distances of species to the community centroid, v) 'mean nearest neighbour distance', and vi) 'standard deviation of nearest neighbour distance' (see Fig. S2 for the ecological interpretation of these metrics) [8]. Metrics were estimated using Bayesian inference with 12,000 posterior draws – based on the replicate samples within each taxa – and compared statistically between climate treatments [9]. Additionally, to evaluate potential shifts in trophic niches of individual taxa, linear regressions were conducted with the average control $\delta^{15}N$ or $\delta^{13}C$ as explanatory and treatment $\delta^{15}N$ or $\delta^{13}C$ as dependent variable, respectively.

Trophic niche breadth of individual taxa was estimated through the standard ellipse area corrected for small sample sizes in $\delta^{15}N$-$\delta^{13}C$ bivariate space (SEA_c, includes ~40 % of the data) [9]. Only taxa sampled at the individual-level were considered, for niche breath to represent between-individual diet specialisation. Mean effect sizes were calculated across taxa for each climate treatment using log-transformed response ratios ($lnRR = ln(SEA_{c\ Treatment}/SEA_{c\ \ Control})$) [10]. Finally, changes in niche breath under future climate were related to changes in biomass using linear regression.

Trophic niches were compared between herbivore groups to evaluate the potential for functional redundancy within the broader function of herbivory. This analysis was only conducted for the herbivores as, unlike the other consumer functions, they comprised several distinct subgroups of which some declined under future climate while others did not. The average distances of niches between pairs of herbivores – i.e. distances between centroids of standard ellipses – was estimated using Bayesian inference with 12,000 posterior draws [9]. Then, it was tested whether less sensitive herbivores shift their niches towards those of sensitive herbivores under future climate. Further, a potential reduction in trophic level of the 8 taxa of secondary consumers under future climate was investigated based on $\delta^{15}N$ in a conventional split-block ANOVA. It included CO_2 and Temperature as between block factors, Taxon as within block factor and mesocosm as random blocking factor [11].

For ANOVAs and regressions, normality and homogeneity were assessed using normal Q-Q plots and Shapiro-Wilk tests and residual versus fitted plots and Levene's tests, respectively. Data was transformed if necessary. Analyses were performed with R version 3.4.1 [12] and Bayesian analysis with the R package SIBER version 2.1.3 [9].

Ethics

Research was conducted under approval of the University of Adelaide animal ethics committee (projects: S-2012-193A). The collection of organisms and habitat was permitted by the Minister for Transport and Infrastructure and the Government Department of Primary Industry and Regions SA (exemptions: 9902676 and 9902752).

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SUPPLEMENTARY RESULTS

Tables S1-6 and Figures S1-6

Table S1: ANOVAs on **a)** gross primary production of the mesocosm community and **b)** ratio between the biomass of all autotrophic (primary producers) and heterotrophic (all consumers) organisms included in this study. Both response variables were $\log_{10}$-transformed to improve normality and homogeneity.

	Source of variation	df	MS	F-ratio	P-value
a) Primary production	CO_2	1	0.0093	7.0	0.029
	T	1	0.0443	33.5	<0.001
	CO_2×T	1	0.0001	0.1	0.759
	Residuals	8	0.0013		
b) Auto-heterotroph ratio	CO_2	1	0.315	20.8	0.002
	T	1	1.292	85.3	<0.001
	CO_2×T	1	0.308	20.4	0.002
	Residuals	8	0.015		

df = degrees of freedom; MS = mean square

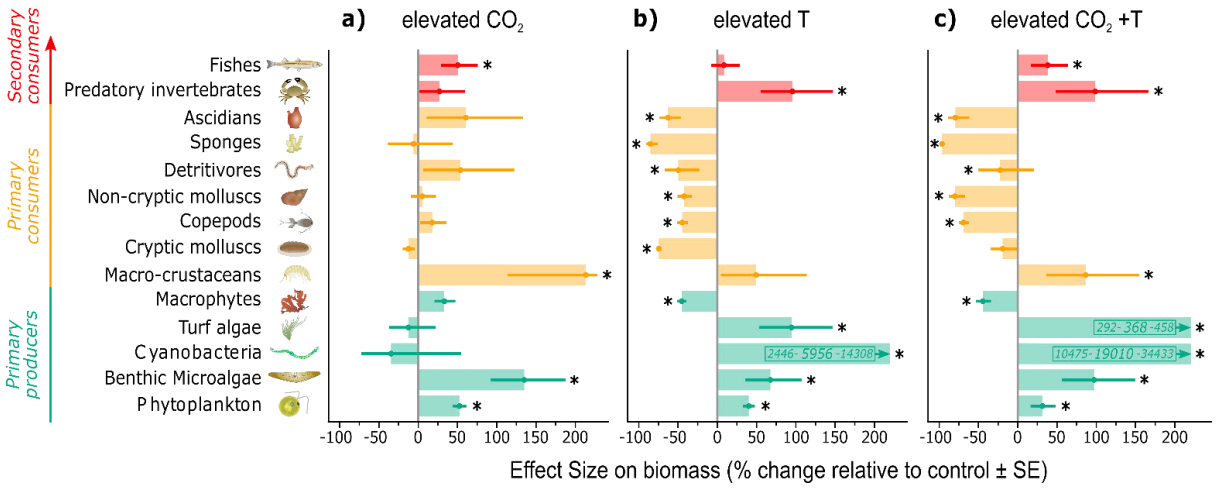

Figure S1: Effects of the climate treatments on the biomass of different functional groups and trophic levels. Effect sizes and standard errors were calculated as log-transformed response ratios of the respective climate treatment and the control (n = 3 mesocosms per treatment) [1], which were then back-transformed and centred on zero for graphical illustration. Statistical significances are marked by * and are not based on the effect sizes but on 2-way ANOVAs (see Table S2) due their superior power in the absence of interactions. Consumers are ranked from the bottom to the top according to their $\delta^{15}N$ signature (low to high) and primary producers according to their approximate size (small to large). Bars are limited to +200 % for the primary producers that showed a disproportionally large increase. Their effect sizes are still given with lower and upper limits of the standard error.

Table S2: ANOVAs on the biomass of the different functional groups. In case of an interaction, SNK post-hoc tests were used to determine differences between individual means.

	Functional group	Source of variation	df	MS	F-ratio	P-value	Effects
a) Secondary consumers	Fishes	CO_2	1	23.43	8.4	**0.020**	ambient < elevated
		T	1	0.05	0.0	0.901	
		$CO_2 \times T$	1	1.58	0.6	0.473	
		Residual	8	2.78			
	Predatory invertebrates	CO_2	1	0.81	0.4	0.560	
		T	1	25.23	11.5	**0.010**	ambient < elevated
		$CO_2 \times T$	1	0.52	0.2	0.639	
		Residual	8	2.20			
b) Primary consumers	Ascidians	CO_2	1	5.9	1.1	0.325	
		T	1	124.5	23.2	**0.001**	ambient > elevated
		$CO_2 \times T$	1	18.1	3.4	0.103	
		Residual	8	5.4			
	Sponges *(sqrt-transformed)*	CO_2	1	0.56	1.5	0.259	
		T	1	14.16	37.6	**<0.001**	ambient > elevated
		$CO_2 \times T$	1	0.14	0.4	0.561	
		Residual	8	0.38			
	Detritivores	CO_2	1	5.07	3.4	0.101	
		T	1	12.28	8.3	**0.020**	ambient > elevated
		$CO_2 \times T$	1	0.55	0.4	0.559	
		Residual	8	1.47			
	Non-cryptic molluscs	CO_2	1	2340	3.1	0.115	
		T	1	36347	48.6	<0.001	
		$CO_2 \times T$	1	4104	5.5	**0.047**	C = elevated CO_2 > elevated T > elevated CO_2+T
		Residual	8	748			
	Copepods *(sqrt-transformed)*	CO_2	1	0.0063	1.1	0.319	
		T	1	0.3300	59.5	<0.001	
		$CO_2 \times T$	1	0.0400	7.2	**0.028**	C = elevated CO_2 > elevated T > elevated CO_2+T
		Residual	8	0.0056			
	Cryptic molluscs	CO_2	1	15.95	5.6	0.045	
		T	1	57.75	20.3	0.002	
		$CO_2 \times T$	1	40.33	14.2	**0.005**	C = elevated CO_2 = elevated CO_2+T > elevated T
		Residual	8	2.84			
	Macro-crustaceans *(sqrt-transformed)*	CO_2	1	0.3734	5.7	**0.044**	ambient < elevated
		T	1	0.0122	0.2	0.678	
		$CO_2 \times T$	1	0.1612	2.5	0.156	
		Residual	8	0.0656			
c) Primary producers	Macrophytes	CO_2	1	293.9	4.3	0.071	
		T	1	3806.3	56.3	**<0.001**	ambient > elevated
		$CO_2 \times T$	1	264	3.9	0.084	
		Residual	8	67.7			
	Turf algae	CO_2	1	12635	35.0	<0.001	
		T	1	41778	115.6	<0.001	
		$CO_2 \times T$	1	15165	42.0	**<0.001**	C = elevated CO_2 < elevated T < elevated CO_2+T
		Residual	8	361			
	Cyanobacteria *(sqrt-transformed)*	CO_2	1	5.28	3.5	0.100	
		T	1	43.12	28.3	**<0.001**	ambient < elevated
		$CO_2 \times T$	1	6.15	4.0	0.079	
		Residual	8	1.53			
	Benthic microalgae	CO_2	1	0.1315	19.0	0.002	
		T	1	0.0044	0.6	0.451	
		$CO_2 \times T$	1	0.0538	7.8	**0.024**	C < elevated CO_2 = elevated T = elevated CO_2+T
		Residual	8	0.0069			
	Phytoplankton	CO_2	1	0.003851	6.2	0.037	
		T	1	0.000720	1.2	0.313	
		$CO_2 \times T$	1	0.007437	12.0	**0.009**	C < elevated CO_2 = elevated T = elevated CO_2+T
		Residual	8	0.000620			

df = degrees of freedom; MS = mean squares; C = Control; T = temperature

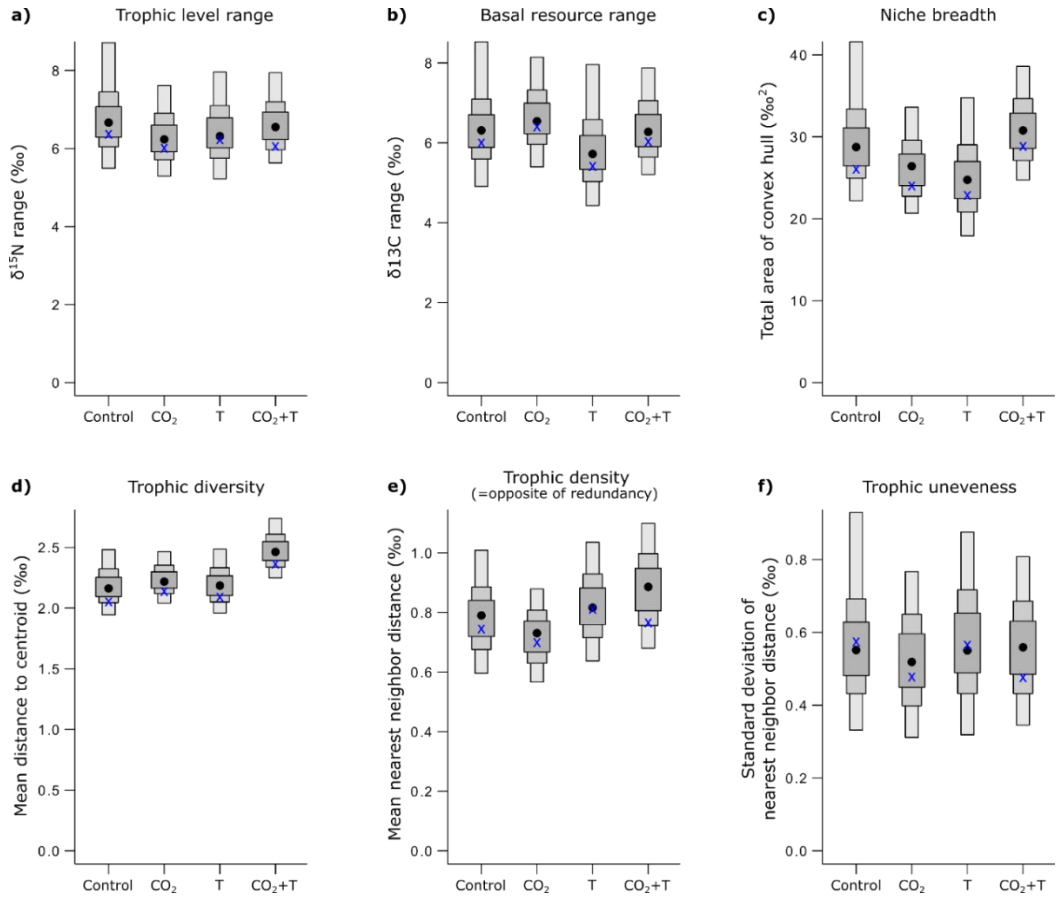

Figure S2: Metrics that characterize the isotopic space occupied by the community of primary and secondary consumers (**a**, **b**, **c**) and the position of individual consumer taxa relative to each another (**d**, **e**, **f**). Given are Bayesian estimates (• = mode) with 50%, 75% and 95% credible intervals (shaded boxes), and maximum likelihood estimates (x). CO_2 = elevated CO_2, T = elevated T, CO_2+T = elevated CO_2+T. See Table S11 for sample sizes.

Table S3: Comparison of the community metrics between climate treatments using Bayesian inference. Values represent the probability of one treatment to be larger than the other. Substantial evidence for a difference between treatments, which would be indicated by probabilities larger than 0.95 or smaller than 0.05, was not found. **a)** All consumer taxa are included corresponding to Figure 1 and S2. **b)** Only consumer taxa are included which were present in all 4 climate treatments, to confirm that the (ecological) extinction of some of the taxa in T and CO_2+T did not alter our interpretation of the community metrics.

Metric	**C > CO_2**	**C > T**	**C > CO_2+T**	**CO_2 > T**	**CO_2 > CO_2+T**	**T > CO_2+T**
a) All taxa						
δ^{15}N range	0.719	0.652	0.575	0.438	0.346	0.407
δ^{13}C range	0.386	0.707	0.509	0.791	0.623	0.293
Total area	0.760	0.797	0.390	0.594	0.156	0.136
Mean distance to centroid	0.371	0.477	0.062	0.597	0.071	0.067
Mean nearest neighbor distance	0.717	0.390	0.259	0.192	0.108	0.349
Standard deviation of nearest neighbor distance	0.626	0.501	0.531	0.379	0.410	0.539
b) Excluding extinct taxa						
δ^{15}N range	0.725	0.638	0.551	0.420	0.320	0.405
δ^{13}C range	0.323	0.678	0.434	0.796	0.609	0.273
Total area	0.728	0.765	0.281	0.590	0.125	0.127
Mean distance to centroid	0.268	0.783	0.164	0.904	0.315	0.059
Mean nearest neighbor distance	0.729	0.543	0.490	0.320	0.279	0.445
Standard deviation of nearest neighbor distance	0.564	0.573	0.739	0.512	0.682	0.666

C = Control, CO_2 = elevated CO_2, T = elevated T, CO_2+T = elevated CO_2+T

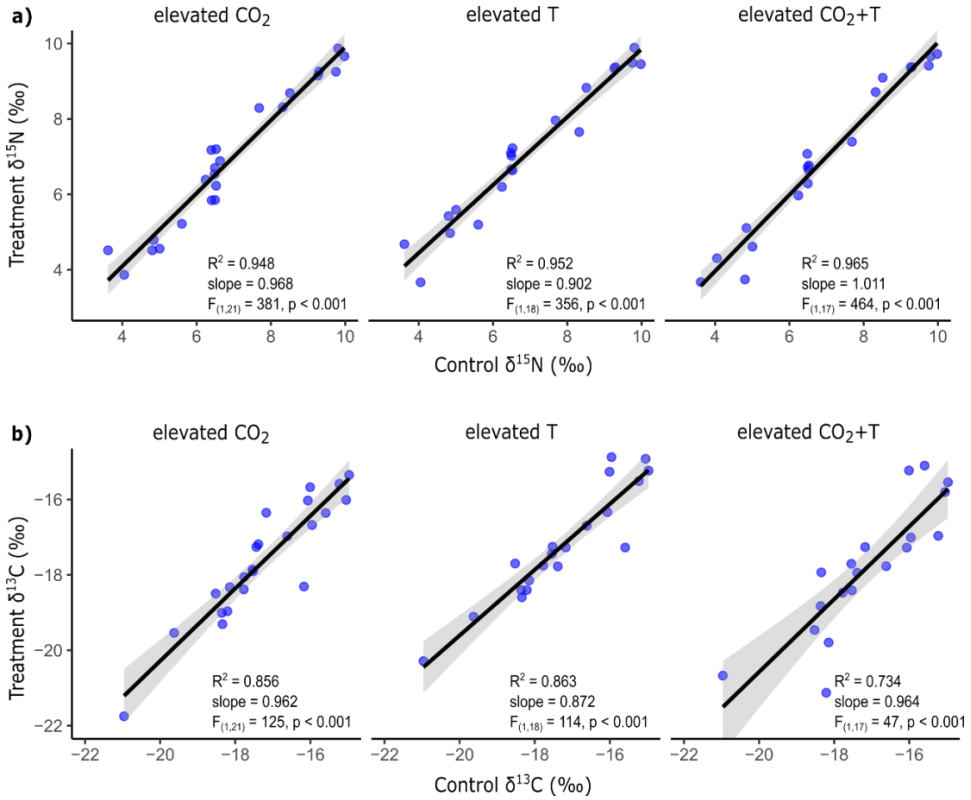

Figure S3: Comparison between the trophic niches of consumers under control and future climate based on their **a)** trophic position and **b)** source pools. Each data point represents the average isotopic signature of one taxon across the three replicate mesocosms. A slope and R^2 of 1 would indicate that future trophic niches perfectly match those under present-day conditions. The larger deviance from a perfect fit in (b) can at least partly be attributed to the change in isotopic signature of some of the source pools (i.e. primary producers) under future climate, rather than to a change in diet of the consumers. Statistical components of this figure should not be interpreted in detail as the individual data points, being the different taxa, originate from the same set of mesocosms and are thus not independent.

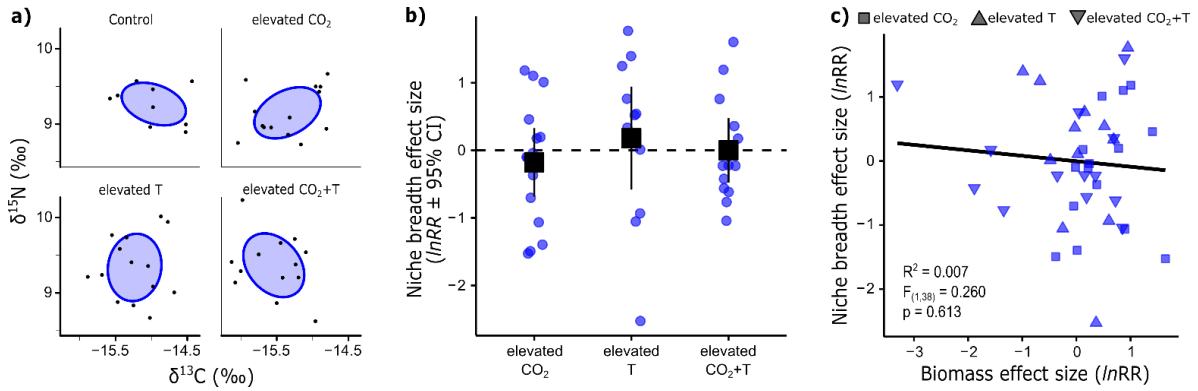

Figure S4: Trophic niche breadth of consumer taxa under future climate. **a)** The measure of niche breadth – standard ellipse area corrected for small sample size (SEA_c) – illustrated for one taxon. Data points represent isotopic signatures of individual shrimps. **b)** Mean effects sizes (black squares) of the climate treatments on niche breadth across all taxa. Confidence intervals not crossing 0 would indicate a significant effect. Each data point represents the individual effect size of one taxon. **c)** Test of whether changes in niche breath under future climate are related to changes in biomass. Each data point represents the individual effect size of one taxon. Here, we would expect a positive relationship if trophic niches collapse in taxa sensitive (i.e. reduced biomass) to future climate and no relationship if changes in niche breath are unrelated to sensitivities. For b and c, only taxa with isotope samples based on individuals and with more than three samples for both control and the respective climate treatment could be considered: elevated CO_2 n = 15 taxa, elevated T n = 12 taxa, elevated CO_2+T n = 13 taxa.

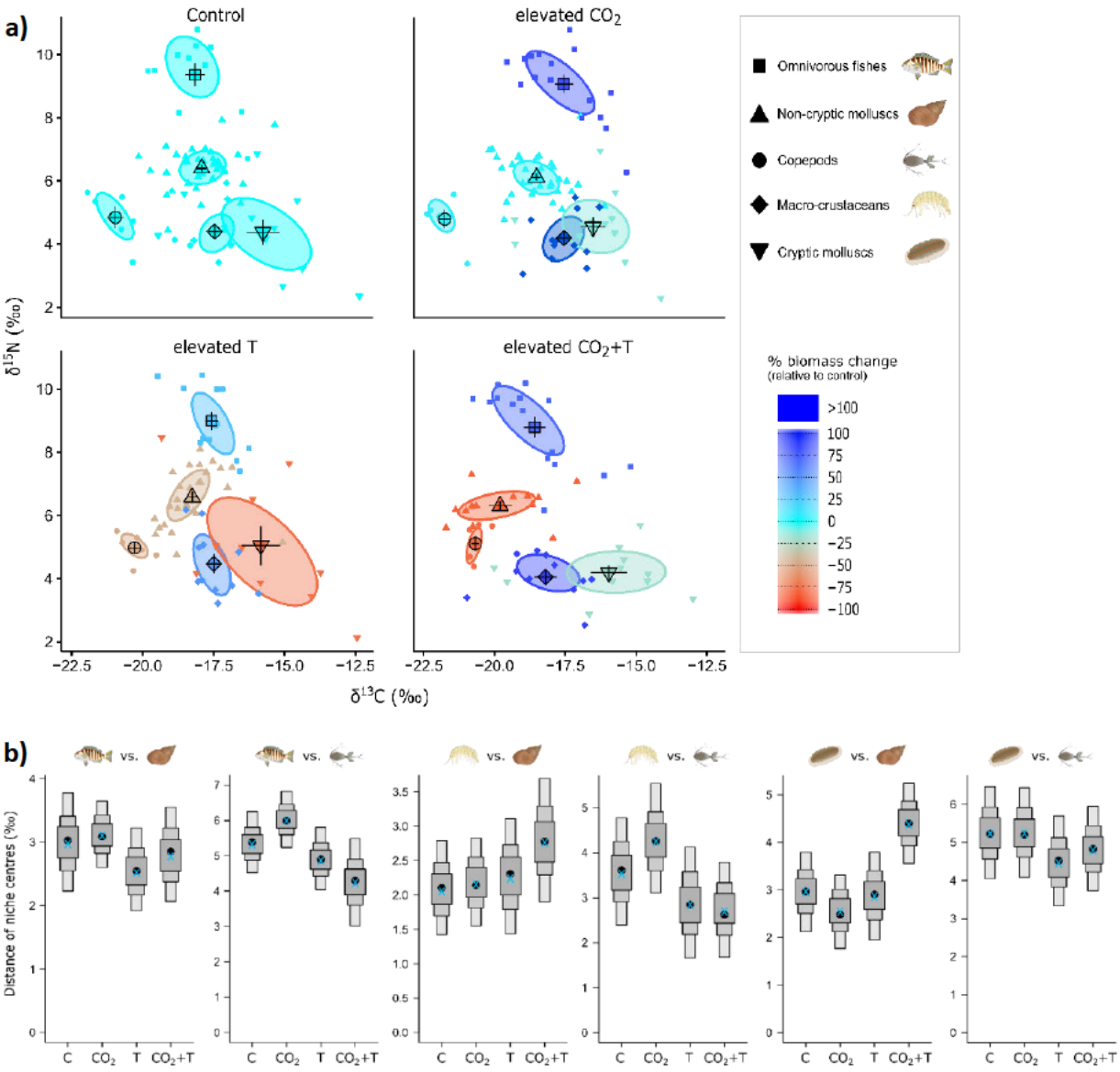

Figure S5: Analysis of functional redundancy within the herbivore community; that is, the tendency of less sensitive herbivores to occupy the trophic space opened up through the loss of sensitive herbivores under elevated T and elevated CO_2+T. **a)** Trophic niches and changes in biomass of different herbivores. Shown are stable isotope signatures of individual samples (small symbols), standard ellipse areas, centroids (larger symbols) with standard errors, and changes in biomass (colour). **b)** Distances of trophic niches between pairs of herbivores. Each plot represent the distances between centroids of one less sensitive (omnivorous fishes, macro-crustaceans or cryptic molluscs) and one sensitive herbivore (non-cryptic molluscs or copepods), classified according to their change in biomass. Given are Bayesian estimates (• = mode) with 50%, 75% and 95% credible intervals (shaded boxes), and maximum likelihood estimates (x). CO_2 = elevated CO_2, T = elevated T, CO_2+T = elevated CO_2+T. See Table S11 for sample sizes and Table S4 for statistical tests.

Table S4: Statistical analyses associated with Figure S5 for the distance of niches between less sensitive and sensitive herbivores under control and future climate. Values represent the probability for a smaller distance under future climate compared to controls. Substantial evidence for a reduction in distance – indicated by probabilities larger than 0.95 – was not found.

Herbivore pair	C > CO_2	C > T	C > CO_2+T
Omnivorous fishes vs. Non-cryptic molluscs	0.387	0.811	0.639
Omnivorous fishes vs. Copepods	0.117	0.784	0.936
Macro-crustaceans vs. Non-cryptic molluscs	0.414	0.369	0.102
Macro-crustaceans vs. Copepods	0.197	0.795	0.849
Cryptic molluscs vs. Non-cryptic molluscs	0.772	0.568	0.010
Cryptic molluscs vs. Copepods	0.493	0.824	0.702

C = Control, CO_2 = elevated CO_2, T = elevated T, CO_2+T = elevated CO_2+T

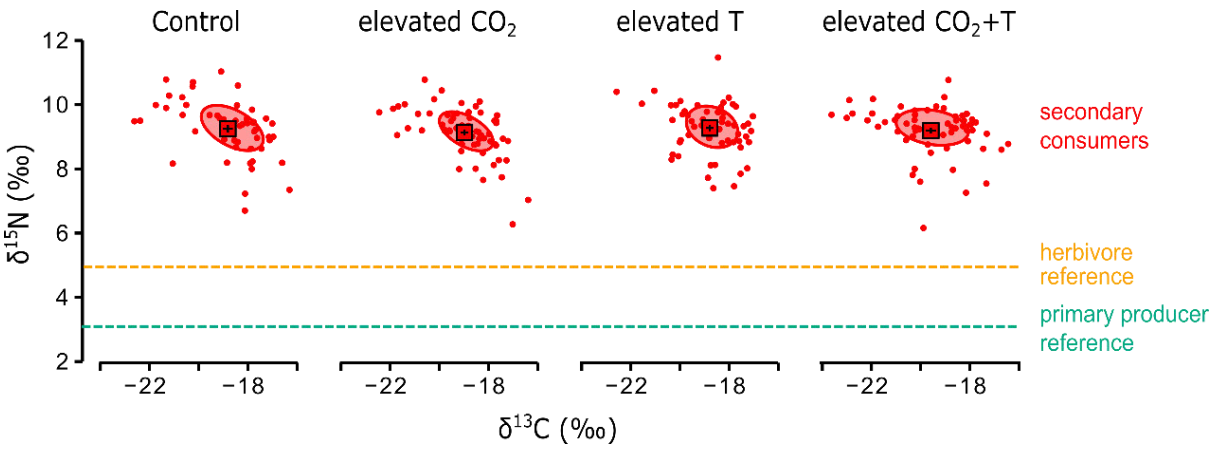

Figure S6: Trophic niche of the assemblages of motile secondary consumers including all fishes and larger predatory invertebrates. Shown are stable isotope signatures of individual organisms (small circles), standard ellipse areas, and centroids (larger squares) with standard errors. The reference lines represent the average $\delta^{15}N$ across all primary producers and all herbivore samples (non-cryptic molluscs, copepods, cryptic molluscs and macro-crustaceans), respectively, across the four climate treatments.

Table S6: ANOVA on the effects of future climate on $\delta^{15}N$ of secondary consumers, as a proxy for trophic level. The mixed model includes CO_2 and Temperature (T) as fixed between block factor, Taxon (fishes and predatory invertebrate, n = 8 taxa) as fixed within block factor and Mesocosm as random blocking factor. The model was fit by restricted maximum likelihood [2] and the Kenward-Roger approximation for degrees of freedom was used. The data was x^2-transformed to improve normality and homogeneity.

Source of variation	df_{Num}	df_{Den}	MS	F-ratio	P-value
CO_2	1	8.2	11.1	0.18	0.682
T	1	8.2	7.2	0.12	0.740
Taxon	7	51.6	1823.1	29.70	**<0.001**
CO_2 × T	1	8.2	8.9	0.15	0.713
CO_2 × Taxon	7	51.6	41.9	0.68	0.687
T × Taxon	7	51.6	34.2	0.56	0.788
CO_2 × T × Taxon	7	51.6	49.4	0.80	0.587

df_{Num} = numerator degrees of freedom; df_{Den} = denominator degrees of freedom; MS = mean squares

References

1. Viechtbauer W (2010) Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software* 36: 1-48

2. Zuur A, Ieno E, Walker N, Saveliev A & Smith G (2009) Mixed effects models and extensions in ecology with R. *New York: Springer*

SUPPLEMENTARY METHODS

Tables S7-13 and Figures S7-11

Habitat and Technical set-up

A flow-through mesocosm system was maintained at the South Australian Research and Development Institute (SARDI; 34°57'10"S, 138°30'20"E). All biological material was collected at 1-5 m depth within 60 km of the facility. Seawater from 1.5 km offshore and ~8 m depth was transferred to two 800 l header tanks. One of these tanks supplied the mesocosms with ambient pCO_2 and the other was pre-conditioned to elevated pCO_2 levels using pure CO_2 (control system ACQ110 Aquatronica, Italy) to supply the mesocosms with elevated CO_2 **(# 1**, Fig. S7**)**. The mesocosms themselves exchanged water (~1,800 l per h) with an associated 60 l bin; a separate bin for each mesocosm. To maintain the climate treatments, these bins were heavily aerated with ambient air at 400 μatm pCO_2 or enriched air at 1000 μatm pCO_2 (PEGAS 4000 MF Gas Mixer, Columbus Instruments, Columbus, Ohio) and contained submersible titanium heaters (800 W). Two diffuser pipes **(# 2)** made use of this water circulation to create a mild circular current inside the mesocosms, which alternated direction every 6 h to simulate tidal water movement. The water flew back to the bins through gravity while passing a filter column (~20 μm mesh size) **(# 3)** that retained the organisms within the mesocosm. This elaborate system assured that the mesocosms themselves were free of unnatural disturbances such as air bubbles, electrical currents or pump noise.

A 250 W metal halide lamp (Osram Powerstar HQI-T 250/D/PRO) mounted above each mesocosm **(# 4**, Fig. S7) provided the energy for primary production. The lamp had a colour temperature of 5500 K, a colour rendering index of 92 and a wave length distribution similar to sunlight, according to the spectrum provided by the manufacturer. Measures in 5 cm intervals from the centre to the tank wall suggested an irradiance of 3833 ± 1304 lux (mean ± SD) at the level of the benthic habitat. This corresponds to ~6-7 m depth in Gulf St. Vincent based on previously published attenuation coefficients [1] and the local average daily summer irradiance (Bureau of Meteorology, www.bom.gov.au, location Adelaide, past 20 years of data).

The habitat comprised four patches of each 'rocky reef' **(# 5,** Fig. S7**)** and 'artificial seagrass' **(# 6)** arranged in pairs and surrounded by 'open sand' **(# 7**). The rocks harboured associated biota as found at the collection site including macrophytes (naturally attached), matt-forming algae, small macrofauna and meiofauna. The artificial seagrass was designed after the dominant local genus (*Posidonia* spp.) [2]. Fine silica sand was used for the soft-bottom habitats (depth: seagrass 6 cm and open sand 6-25 cm), with a grain size between 0.21 - 0.85 mm similar to sediment found at local beaches and seagrass meadows.

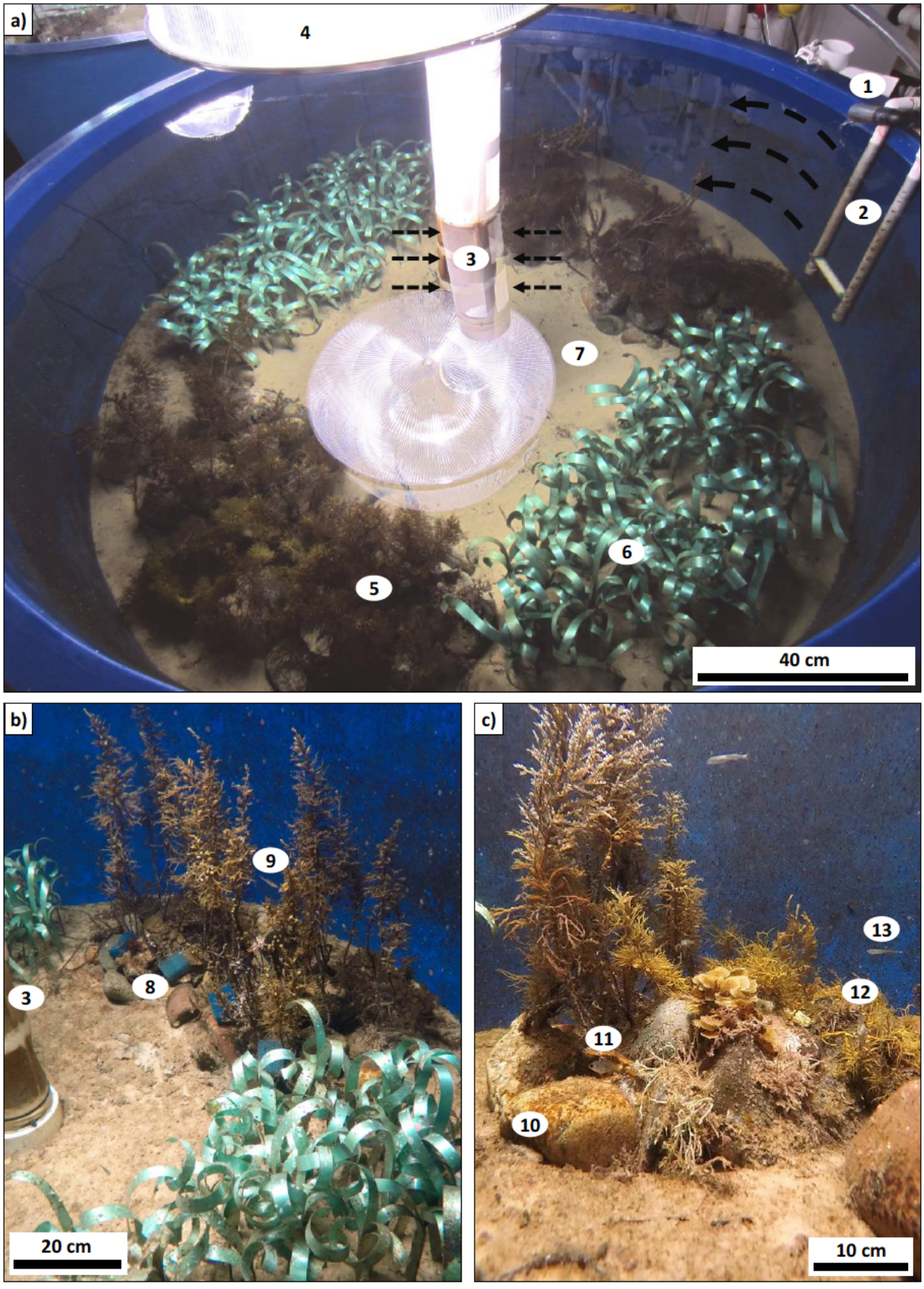

Figure S7: a) Mesocosm at the start of the experiment and **b)** ½ mesocosm and **c)** $^{1}/_{8}$ mesocosm 3.5 months into the experiment. Scales refer to the centre of the photo. (**# 1**) Inflow of fresh seawater, (**# 2**) diffuser pipes, (**3 #**) filter column, (**# 4**) lamp, (**# 5**) rocky reef, (**# 6**) seagrass, (**# 7**) open sand, (**# 8**) artificial habitat unit to sample copepods, (**# 9**) blue weedy whiting, (**# 10**) longfin goby, (**# 11**) zebrafish, (**# 12**) toothbrush leatherjacket, (**# 13**) small-mouthed hardyhead.

Ecological Community

The fish and shrimp species – comprising the majority of secondary consumers – were selected because of their high juvenile abundances in shallow coastal waters during summer. Their initial densities were set high (Table S7) as these taxa were unable to increase their numbers through reproduction in our mesocosms. This favoured resource limitation over the experimental period and thus natural trophic behaviour through the pressures of intra- and interspecific competition. The densities of the larger gastropods (Table S7) were instead based on the habitat that had been collected in the sea and introduced in the mesocosms. For this, all gastropods above approximately 0.5 cm were removed from the habitat and redistributed among all mesocosms to reach even abundances and species compositions. Whilst an advanced level of acclimation could be expected for secondary consumers and larger gastropods, transgenerational acclimation and adaptation was possible for smaller-bodied taxa. Our exposure time of 140 days compares as follows to potential generation times of some of these taxa: benthic microalgae 0.4-6 days [3,4], benthic copepods 9-26 days [5], tanaids 42 days [6], amphipods 35-49 day [7,8], and annelids 17-55 days [9,10].

Table S7: Larger-bodied consumers distributed to each mesocosm at the beginning of the experiment. The shrimps comprised a random mix of *Palaemon intermedius* and *Palaemon serenus*.

	Species (common name)	**# introduced**	**Total length / Mass ± SD**
Fishes	*Neoodax balteatus* (little weed whiting)	7	30 ± 8 mm
	Haletta semifasciata (blue weedy whiting)	7	31 ± 4 mm
	Favonigobius lateralis (longfin goby)	7	22 ± 4 mm
	Girella zebra (zebrafish)	7	17 ± 2 mm
	Acanthaluteres vittiger (toothbrush leatherjacket)	7	30 ± 8 mm
	Atherinosoma microstoma (small-mouthed hardyhead)	10	24 ± 5 mm
Crustaceans	*Palaemon spp.* (caridean shrimp)	10	10 – 30 mm
Gastropods	*Bulla quoyii*	10	400 ± 42 mg
	Thalotia conica	12	385 ± 218 mg
	Phasianella australis	20	252 ± 770 mg
	Cantharidus spp	10	150 ± 89 mg
	miscellaneous species	4	275 ± 223 mg

Table S8: Community composition at the end of the experimental period. Average biomass and abundance were taken across all 12 mesocosms, which explains the larger standard deviations for the taxa with a strong climate treatment effect. Consumers were measured as wet mass and primary producer as dry mass. Consumer taxa that were not identified to species level but comprised clearly distinct morphotypes are given with 'likely several spp.'. The classification of primary consumers into feeding guilds is based on their stable isotope signatures and the literature.

approx. trophic level	Functional group	Taxa	Biomass ± SD (g)	Abundance ± SD
Secondary consumers	Fishes	6 spp. of teleost fishes	8.68 ± 2.07	19.5 ± 2.9
	Predatory invertebrates	shrimps, crabs, sea stars and predatory gastropods, likely several spp. each	5.38 ± 2.00	10.7 ± 3.1
Primary consumers	Ascidians *(filter feeders)*	likely several spp.	5.06 ± 4.17	5.3 ± 3.4
	Sponges *(filter feeders)*	likely several spp.	5.04 ± 5.24	4.6 ± 3.0
	Detritivores	polychaetes, oligochaetes and brittle stars, likely several spp. each	3.06 ± 1.64	61.5 ± 24.0
	Non-cryptic molluscs *(herbivores)*	7 spp. of larger gastropods	122.03 ± 66.59	30.8 ± 18.2
	Copepods *(herbivores)*	benthic, likely several spp.	0.53 ± 0.27	158993.4 ± 62811.5
	Cryptic molluscs *(herbivores)*	chitons, limpets and small gastropods, likely several spp. each	7.93 ± 3.53	32.8 ± 13.5
	Macro-crustaceans *(herbivores)*	tanaids and amphipods, likely several spp. each	1.15 ± 0.71	6871.5 ± 4172.7
Primary producers	Macrophytes	20+ spp. of brown, red and green algae	49.63 ± 21.12	-
	Turf algae	likely many spp.	105.61 ± 81.17	-
	Cyanobacteria	likely several spp.	10.50 ± 16.28	-
	Benthic microalgae	likely many spp.	0.44 ± 0.15	-
	Phytoplankton	likely many spp.	0.21 ± 0.04	-

Table S9: ANOVAs to test the effects of ocean acidification, warming and their interaction on the physical condition (Fulton's K) of the fish individuals. First, mixed models with Mesocosm (n=3) as random effect were fitted. The effect of Mesocosm was highly insignificant for all taxa following likelihood ratio tests [16]. Thus, Mesocosm was removed for the final test statistics. All response variables were log10-transformed. To improve data properties due to low and variable abundances, the ecologically and morphologically very similar species little weed whiting and blue weedy whiting were pooled.

Taxon	Source of variation	df	MS	F-ratio	P-value	Mesocosm effect
Longfin goby	OA	1	<0.0001	0.004	0.951	L=0.263, df=1, p=0.608
	T	1	<0.0001	0.004	0.953	
	OA × T	1	0.0002	0.050	0.823	
	Residuals	73	0.0045			
Whiting	OA	1	0.0335	1.447	0.236	L=0.096, df=1, p=0.757
	T	1	0.0327	1.412	0.242	
	OA × T	1	0.0462	1.998	0.165	
	Residuals	40	0.0232			
Zebrafish	OA	1	0.0002	0.014	0.905	L=0.246, df=1, p=0.620
	T	1	0.0053	0.472	0.496	
	OA × T	1	0.0034	0.306	0.584	
	Residuals	38	0.0112			
Leather jacket	OA	1	<0.0001	0.015	0.905	L<0.001, df=1, p=0.986
	T	1	<0.0001	0.008	0.929	
	OA × T	1	<0.0001	<0.001	0.998	
	Residuals	15	0.0027			
Hardy head	OA	1	0.0093	2.407	0.129	L<0.001, df=1, p=0.999
	T	1	0.0108	2.798	0.102	
	OA × T	1	0.0125	3.238	0.080	
	Residuals	39	0.0039			

df = degrees of freedom; MS = mean squares; L = log likelihood ratio statistic

Seawater Parameters

For each mesocosm, temperature and pH were measured daily at around midday (Mettler Toledo SevenGo™ SG2, calibrated daily) and salinity (SR6 refractometer, Vital Sine) and total alkalinity (total of n = 8 per mesocosm; Gran titration; 888 Titrando, Metrohm, Switzerland) fortnightly. Alkalinity measures were accurate within 1% of certified standards (reference material from A. Dickson, Scripps Institution of Oceanography). pCO_2, bicarbonate, carbonate and the saturation states of calcite and aragonite were calculated using CO2SYS for Excel [11] with constants from Mehrbach et al. [12] refit by Dickson and Millero [13]. An overview of seawater properties is provided in Table S10, a trajectory of pH and temperature throughout the entire study period in Figure S8, and the diurnal variability in pH produced by community metabolism by Figure S9.

Table S10: Average seawater properties over the 4.5 months of climate manipulation. Standard deviations indicate the variability between mesocosms.

Parameter	Control	elevated CO_2	elevated T	elevated CO_2+T
Temperature (°C)	21.0 ± 0.14	20.9 ± 0.04	23.7 ± 0.19	23.7 ± 0.08
pH_{NBS}	8.14 ± 0.004	7.89 ± 0.009	8.12 ± 0.002	7.89 ± 0.009
Salinity (ppt)	36.3 ± 0	36.3 ± 0	36.3 ± 0	36.3 ± 0
Total Alkalinity (μmol kg^{-1})	2482 ± 4	2485 ± 5	2486 ± 6	2493 ± 3
pCO_2 (μatm)	465 ± 5	905 ± 6	500 ± 8	915 ± 25
HCO_3 (μmol kg^{-1})	1995 ± 6	2186 ± 3	1985 ± 2	2166 ± 9
CO_3 (μmol kg^{-1})	200 ± 2	123 ± 1	206 ± 2	135 ± 3
Ω Calcite	4.74 ± 0.05	2.91 ± 0.02	4.90 ± 0.05	3.20 ± 0.07
Ω Aragonite	3.09 ± 0.04	1.90 ± 0.01	3.22 ± 0.03	2.10 ± 0.05

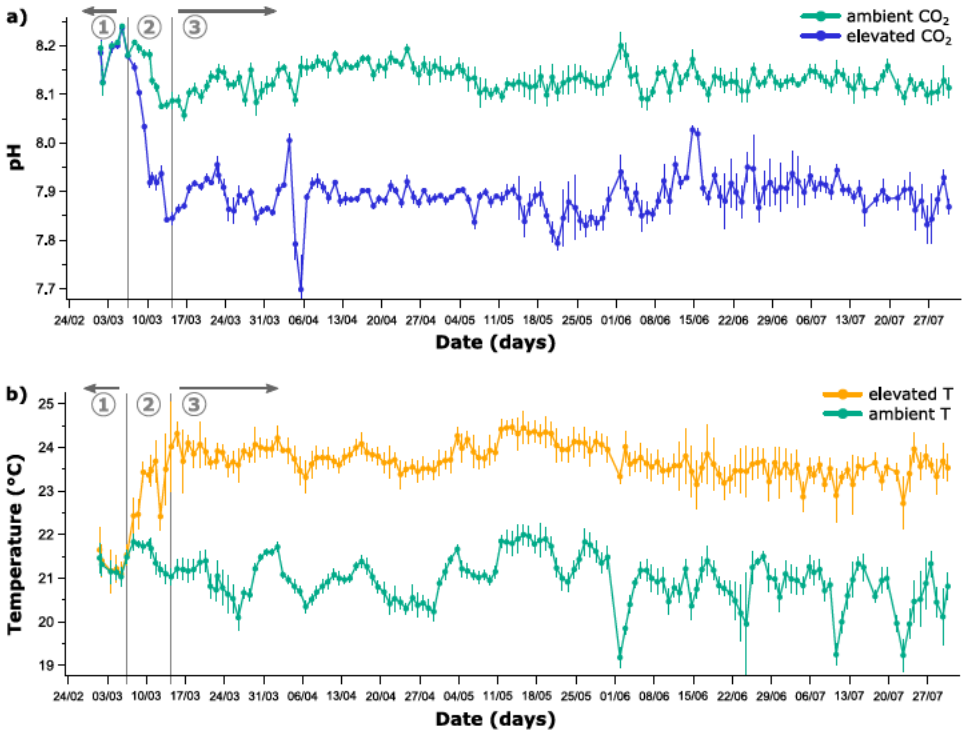

Figure S8: Acidification **(a)** and warming **(b)** throughout the experiment, including the last week of acclimatization to captivity **(1)**, the progressive elevation to treatment levels **(2)**, and the 4.5 months at treatment levels **(3)**. Mean ± SD are based on the daily measurements of the n = 6 mesocosms at ambient or elevated levels.

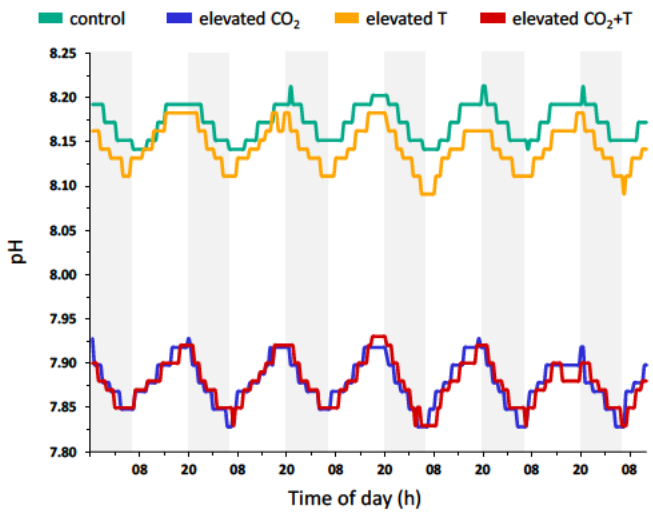

Figure S9: Diurnal fluctuations in pH over a 5 day period. Measures were only taken for one mesocosm per treatment combination to serve as example. For these 4 mesocosms in parallel, pH was recorded in 30 min intervals with a pH logger. Grey bands mark night-time and white bands day-time hours.

Biomass Sampling

The specific methods used to sample the different types of organisms are listed below. The biomass of all organisms was extrapolated to the scale of the mesocosm for the later data analysis. In case organisms were sampled in multiple habitats separately, biomass estimates were combined according to the relative area of each habitat.

1) All fishes, shrimps and larger gastropods were caught at the mesocosm scale across habitats.

2) All crabs, chitons, limpets, small gastropods, annelids, brittle stars and amphipods were collected via picking and sieving (1 mm mesh) after taking apart each rocky reef patch (n = 4 rocky reef patches per mesocosm).

3) Copepods in the rocky reef were sampled through artificial habitat units made of aquarium filter sponges (L x H x W = 60 x 25 x 40 mm, pore size 2-5 mm, Fig. S7b) that had been incubated for 1 month (n = 2 subsamples per mesocosm). Numbers were counted under a stereo microscope and a random subset of individuals photographed and measured to estimate biomass using average biovolume.

4) Tanaids, annelids and copepods in the seagrass and open sand habitats were sampled through sediment cores (65 mm diameter, 15 mm depth). Individuals were extracted by floatation with Ludox TM colloidal solution with a specific gravity of 1.18 and collected on a 45 μm sieve (n = 4 subsamples per mesocosm). While the tanaids were weighed directly, the mass of the much smaller annelids and copepods was calculated as in (2) by combining counts under the stereo microscope and biovolume estimates.

5) All macrophytes were scraped from the rocky reef (n = 4 rocky reef patches per mesocosm).

6) Turf algae were scraped from the rocky reef, tank wall and seagrass leaves (n = 13 subsamples per mesocosm).

7) Benthic microalgae were assessed from the top layer of the open sand habitat. Chlorophyll *a* was extracted from the sand with 90 % acetone, measured spectrophotometrically (6405 UV/Vis, Jenway) and its concentration calculated [14] (n = 8 subsamples per meso). Chlorophyll *a* mass was extrapolated to organic carbon mass (×40) and total dry mass (×1.53, redfield ratio for diatoms).

8.) Cyanobacteria could form visible 'carpets' on the horizontal surfaces in the mesocosms, where they intermixed with the turf algae on the rocky reefs and other microalgae on the sand. To obtain separate biomass estimates, the percent cover of turf algae versus cyanobacteria on the rocky reefs (n = 4 rocky reef patches) and microalgae versus cyanobacteria on the sand (n = 2 subsample areas) was assessed before disturbing the habitat using the software Coral Point Count with Excel extensions[15]. This percent cover data

was then used to correct the estimates for turf algae (6) and microalgae (7) and to obtain an estimate for the mass of the cyanobacteria.

9.) Phytoplankton was estimated through the filtration of 4 litres of mesocosm water using Whatman GF/C glass fibre filters and subsequent Chlorophyll *a* measures as in (7) (n = 2 subsamples per mesocosm). Chlorophyll *a* mass was extrapolated to organic carbon mass (×40) and total dry mass (×1.2, redfield ratio).

Stable Isotope Analysis

The material for isotope analysis for sediment organic matter, particulate organic matter, and cyanobacteria was collected separately from the biomass sampling. Sediment organic matter was collected from the surface 1 mm of sand of an undisturbed area to maximize the contribution of microalgae. Particulate organic matter was collected by filtering ~500 l of mesocosm water through a 32 µm screen, thus comprising a mixture of phytoplankton, zooplankton and detritus. Cyanobacteria layers were picked with tweezers from the horizontal habitat surfaces.

Figure S10: Codes for taxa included in Figure 1 that can be interpreted using Table S11. Colours represent trophic levels: green = primary producers, orange = primary consumers, and red = secondary consumers. The unreadable aggregation of taxa in the control plot includes Asc, Spo, Pol, Bri, G1, G2, G3 and G5.

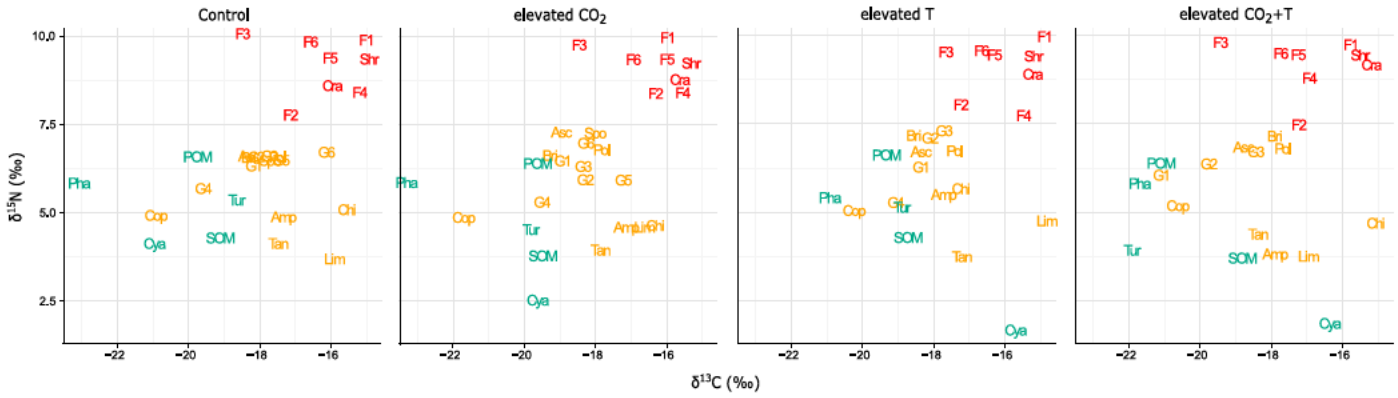

Table S11: Taxonomic groups included in the stable isotope analysis. The sample sizes for each climate treatment are the total across the 3 replicate mesocosms.

approx. Trophic level	Functional group	Taxon	Code	# samples				# individuals per each sample
				Control	CO_2 elevated	T elevated	CO_2+T elevated	
Secondary consumer	Fishes	*Favonigobius lateralis*	F1	9	9	9	9	1
		Acanthaluteres vittiger	F2	3	7	4	6	1
		Girella zebra	F3	8	9	9	9	1
		Neoodax balteatus	F4	8	7	2	6	1
		Haletta semifasciata	F5	4	7	7	5	1
		Atherinosoma microstoma	F6	9	8	9	9	1
	Predatory invertebrates	*Palaemon spp.* (shrimps)	Shr	9	14	14	13	1
		Brachyura (crabs)	Cra	5	4	5	5	1
			Total	*55*	*65*	*59*	*62*	
Primary consumer	Filter feeders	Ascidiacea	Asc	5	6	6	4	1
		Porifera (Sponges)	Spo	6	5	x	x	1
	Detritivores	Ophiuroidea (Brittle stars)	Bri	3	3	3	3	2-3
		Annelida (mainly Polychaeta)	Pol	12	12	12	12	~8
	Non-cryptic molluscs (≙ larger gastropods)	*Bulla quoyii*	G1	9	9	9	5	1
		Phasianella australis	G2	9	9	8	3	1
		Thalotia conica	G3	9	9	6	5	1
		Turbo spp.	G4	2	3	3	x	1
		Stomatella impertusa	G5	3	3	x	x	1
		Cantharidus spp.	G6	3	3	x	x	1
	Copepods	Copepoda	Cop	6	6	6	6	~100
	Cryptic molluscs	Chitons (Polyplacophora)	Chi	6	6	4	6	3
		Limpets (Patellidae)	Lim	5	6	6	5	1
	Macro-crustaceans	Amphipoda	Amp	5	6	5	5	4
		Tanaidacea	Tan	6	6	6	6	~18
			Total	*89*	*92*	*74*	*60*	
Primary producer	Macrophytes	Phaeophyceae (Brown algae)	Pha	6	6	6	6	4
	Turf algae	Turf algae	Tur	6	6	6	6	bulk
	Cyanobacteria	Cyanobacteria	Cya	6	6	6	6	bulk
	Benthic microalgae	Sediment organic matter	SOM	6	6	6	6	bulk
	NA	Particulate organic matter	POM	6	6	6	6	bulk
		(30+ µm)	*Total*	*30*	*30*	*30*	*30*	

x = taxa either absent or at insufficient biomass/abundance for analysis, i.e. ecologically extinct;
bulk = larger amount of material used without counting the 'individuals' due to their small size

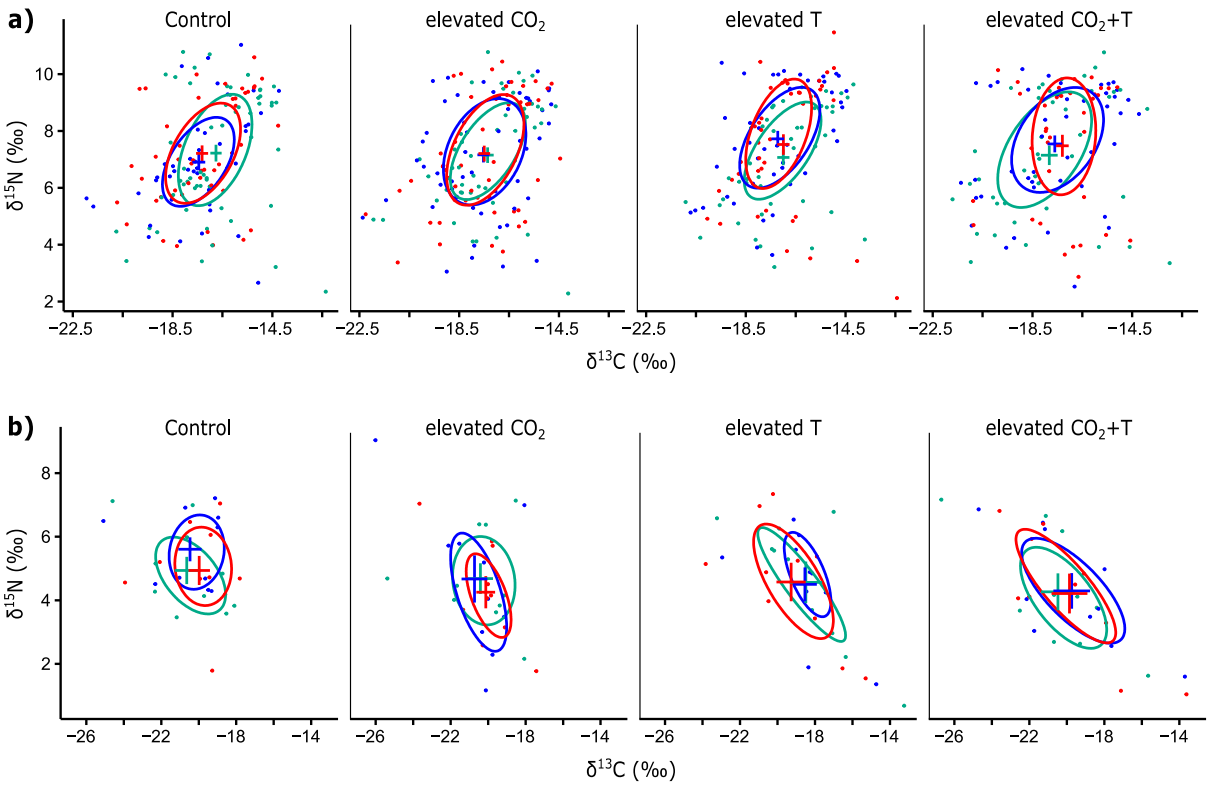

Figure S11: Trophic niches of individual mesocosm food webs to check for a potential difference between mesocosms of the same climate treatment. **a)** Includes all consumers and **b)** all basal resources. Each colour represents one of n = 3 mesocosms with individual stable isotope samples (small points), standard ellipses, and centroids with standard errors (crosses).

Table S12: Testing for possible differences in stable isotope signatures between mesocosms of the same climate treatment for **a)** all consumers and **b)** all basal resources. The linear model including CO_2, Temperature and their interaction as fixed effects, Mesocosm as random effect, and individual stable isotope samples as replicates was compared to the same model but excluding Mesocosm (restricted maximum likelihood fit [16]). Likelihood ratio tests show that Mesocosm as random effect does not significantly improve the model fit in all cases.

	Response variable	Model	AIC	log-Lik	L-Ratio	P-value
a)	Consumer $\delta^{15}N$	with Mesocosm	2384.3	-1186.2	4.52E-07	0.9995
		without Mesocosm	2382.3	-1186.2		
	Consumer $\delta^{13}C$	with Mesocosm	2206.8	-1097.4	5.18E-07	0.9994
		without Mesocosm	2204.8	-1097.4		
b)	Basal resources $\delta^{15}N$	with Mesocosm	478.5	-233.3	6.75E-08	0.9998
		without Mesocosm	476.5	-233.3		
	Basal resources $\delta^{13}C$	with Mesocosm	548.9	-268.5	6.61E-08	0.9998
		without Mesocosm	546.9	-268.5		

AIC = Akaike information criterion; log-Lik = log-likelihood

Table S13: Testing for possible differences in stable isotope signatures between mesocosms of the same climate treatment at the taxon level. The linear model including CO_2, Temperature and their interaction as fixed effects, Mesocosm as random effect, and stable isotope samples as replicates was compared to the same model but excluding Mesocosm (restricted maximum likelihood fit [16]). This analysis was only conducted for taxa that were perfectly balanced in terms of replication at all levels (treatment, mesocosm and sample) and that had at least 2 isotope samples per mesocosm. Mesocosm as random effect is only significant in 1 out of 18 cases, which is a ratio close to what would be expected purely due to chance.

Taxon	Isotope ratio	Model	AIC	log-Lik	L-Ratio	P-value
Longfin goby	$\delta^{15}N$	with Mesocosm without Mesocosm	75.0 73.2	-31.5 -31.6	0.234	0.628
	$\delta^{13}C$	with Mesocosm without Mesocosm	83.8 82.4	-35.9 -36.2	0.585	0.445
Annelida	$\delta^{15}N$	with Mesocosm without Mesocosm	121.5 120.0	-54.7 -55.0	0.519	0.471
	$\delta^{13}C$	with Mesocosm without Mesocosm	147.2 145.2	-67.6 -67.6	<0.001	1.000
Copepoda	$\delta^{15}N$	with Mesocosm without Mesocosm	59.7 57.8	-23.9 -23.9	0.053	0.818
	$\delta^{13}C$	with Mesocosm without Mesocosm	48.7 48.2	-18.3 -19.1	1.494	0.222
Tanaidacea	$\delta^{15}N$	with Mesocosm without Mesocosm	41.8 40.1	-14.9 -15.0	0.254	0.614
	$\delta^{13}C$	with Mesocosm without Mesocosm	63.4 63.3	-25.7 -26.7	1.907	0.167
Macrophytes	$\delta^{15}N$	with Mesocosm without Mesocosm	89.6 87.6	-38.8 -38.8	<0.001	1.000
	$\delta^{13}C$	with Mesocosm without Mesocosm	114.6 112.6	-51.3 -51.3	<0.001	1.000
Turf algae	$\delta^{15}N$	with Mesocosm without Mesocosm	79.0 77.0	-33.5 -33.5	<0.001	1.000
	$\delta^{13}C$	with Mesocosm without Mesocosm	63.8 62.5	-25.9 -26.2	0.702	0.402
Cyanobacteria	$\delta^{15}N$	with Mesocosm without Mesocosm	72.2 70.2	-30.1 -30.1	<0.001	1.000
	$\delta^{13}C$	with Mesocosm without Mesocosm	101.5 99.5	-44.8 -44.8	<0.001	1.000
Sediment organic matter	$\delta^{15}N$	with Mesocosm without Mesocosm	53.6 51.8	-20.8 -20.9	0.264	0.607
	$\delta^{13}C$	with Mesocosm without Mesocosm	64.8 67.5	-26.4 -28.7	4.602	**0.032**
Particulate organic matter	$\delta^{15}N$	with Mesocosm without Mesocosm	50.6 48.6	-19.3 -19.3	0.037	0.848
	$\delta^{13}C$	with Mesocosm without Mesocosm	77.8 75.8	-32.9 -32.9	<0.001	1.000

AIC = Akaike information criterion; log-Lik = log-likelihood

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CHAPTER V

GENERAL DISCUSSION

KEY FINDINGS

My PhD research advances our understanding of the ecological impacts of future climate by connecting the responses of individuals to the dynamics of species communities. An overview of the key findings is provided in Table 1. They reveal how direct effects of abiotic change can be countered or accelerated by ecological processes that collectively reinforce stability or change.

Table 1: Key findings of my PhD research showing how individual-level effects to ocean acidification (OA) and warming (T) scale-up to the community level.

Individual responses		Community dynamics
Impaired behaviour of motile consumers under OA in ecologically simple situations	⇨	Buffered through ecological complexity so that consumers are able to fulfil ecological roles, i.e. prey population control and transfer of energy to higher order predators
Increased food demand of consumers under T due to accelerated physiology	⇨	I) Stronger top-down forcing by predators causing over-consumption of prey populations, II) consumption unable to meet energy demand (ingestion inefficiency) in 2° producer causing disruption of trophic flows, and III) riskier behaviour in prey to meet energy demands which increases mortality through predation
Boosted 1° production under OA via CO_2-enrichment and T via accelerated physiology	⇨	OA: Enhanced bottom-up forcing propagates to higher trophic levels increasing food web productivity T: Inefficient or disrupted energy flows lead to bottom-heavy food webs
Sensitivity to T is associated with functional traits: I) expansion of 'weedy' 1° producers, II) ability to resist in larger motile omnivores and predators, III) poor performance by herbivores, detritivores and filter feeders	⇨	Shift in functional composition and trophic pyramid structure (i.e. no density substitution), with expansion at top and bottom and contraction in centre of food web and likely collapse into bottom-heavy food web in the long run
T limits the potential for adaptive trophic behaviour	⇨	Food web architecture remains stable and thus unable to compensate for loss of sensitive and proliferation of benefiting taxa, i.e. no trophic compensation and functional redundancy

Communities coped well with ocean acidification due to various compensatory processes at simple and complex levels of biological organisation. Consequently, an overall increased productivity and standing biomass throughout the food web emerged as the dominant effect of ocean acidification, i.e. acidification primarily acted as a resource through CO_2-enrichment. Even some taxa which are considered vulnerable to ocean acidification based on two decades of laboratory research showed no signs of decline at the community level. As such, fishes – which can show strong impairment in key behaviours [1-3] – were able to fulfil ecological roles of prey population control and energy transfer to higher trophic level.

Likewise, calcifying species including gastropods, chitons and calcareous algae sustained their populations despite the increased energetic cost of calcification [4-6]. While surprising, these findings from the mesocosm are not the exception as my meta-analysis identified similar population dynamics at natural CO_2 vents [7-9].

In contrast, ocean warming drove community degradation by shifting the balance in key ecological processes. Dynamics with the potential to compensate for the uneven sensitivities between taxa and functions failed to engage – given the fundamental influence of temperature on physiology [10-12] – which allowed impacts to cascade through the community unrestrained. A novel community structure emerged that would likely undermine ecosystem stability and services. The stress through warming also reversed the significance of acidification for the community. Whilst not affecting communities negatively in isolation, acidification reinforced community degradation in combination with warming. This indicates a limited capacity of communities to resist acidification that depends on co-occurring stressors.

CHAPTER INTEGRATION

The chapters complemented each other to provide a predictive understanding of the overall outcome of the mesocosm experiment; that is, why acidification acted as a resource and warming as a stressor. In chapter II, my PhD thesis started by identifying alterations to production and consumption under future climate. Several underlying mechanisms could be revealed through clever manipulations since chapter II was restricted to a single compartment of the mesocosm community that comprised three clearly structured trophic levels. However, responses to future climate vary between species and systems as demonstrated through the meta-analysis in chapter III. To represent better the complexity found in nature, I expanded my investigations to the entire mesocosm community with chapter IV, which include a large variety of habitats, species and functions.

An understanding of the complex community of chapter IV was aided by the insights on trophic processes gained during chapter II. For example, community wide primary production increased under acidification in chapter IV, measured as gross O_2 production. The faster growth of micro-phytobenthos in the absence of herbivores in chapter II suggests that this indeed indicated a positive direct effect on primary producers (i.e. CO_2-enrichment), and not an indirect effect through changes in herbivory that led to higher standing biomass. Moreover, various consumers groups with different characteristics (e.g. fish, crustaceans and molluscs) increased in standing biomass under acidification alone in chapter IV. According to chapter II, this is likely a result of the successful propagation of excess primary production up the food web. Instead, warming lead to considerably lower standing biomass in different primary consumer groups (i.e. grazers, detritivores, filter-feeders) in chapter IV. Here,

chapter II offers two explanations that possible acted in combination. Chapter II suggests, on the one hand, an inefficient trophic transfer from primary to secondary producers and, on the other hand, the overconsumption of prey by predators facing elevated metabolic demand.

The changes in standing biomass of trophic levels in chapter IV were generally less clear-cut compared to chapter II. This was expected given that chapter IV integrated over many more species and trophic interactions, each varying in their response to future climate. Notably, predatory invertebrates increased in standing biomass under the combined effect of acidification and warming but fishes did not. Consequently, under the stressor combination, an overall increase in tertiary producers is shown in chapter IV (predatory invertebrates and fishes), while tertiary producer biomass remains unchanged in chapter II (one species of fish). Why predatory invertebrates but not the fishes benefited from warming is unclear.

Chapter III studied the performance of consumers more closely and thereby laid the foundation for the food web processes investigated in chapter II and IV. The transfer of energy up the food web would be reduced wherever consumers are significantly impaired in their ability to find prey, as may be the case under ocean acidification [1,3]. This direct effect of ocean acidification would confound any indirect effects such as changes to bottom-up or top-down forcing. However, chapter III suggests that the direct effects of ocean acidification were likely compensated at the organism level in our mesocosms. This explains why the excess primary production under acidification transferred efficiently to higher trophic levels, as observed in the other two chapters. In contrary, under warming, chapter III showed that consumers became more constrained in their foraging to meet higher metabolic demands. This direct effect of warming may have contributed to the inflexibility of consumers to adjust to the changing landscape of resources, as demonstrate with the stable isotope analysis in chapter IV.

LIMITATIONS

The mesocosm approach was chosen for my PhD research as it allowed to study both individual and community level response to ocean acidification and warming and associated ecological processes. However, this trade-off between realism and environmental control involved several limitations that are typical for mesocosm studies [13].

At the individual level, physiological or behavioural effects needed to be tested amongst the mosaic of habitats and the species community, both of which developed a specific character in each mesocosm over the duration of the project. This not only made it more difficult to detect the effects due to background variation but also increased the risk of potential confounding factors. Here, a simple aquaria study would certainly have provided more

precise measurements and allowed to conduct a considerably larger number of truly independent replicates.

At the community level, while great effort was made to design the mesocosms as closely as possible to the natural world, they nevertheless represented an artificial and simplified ecosystem. Most notably, the spatial scale of 1,800 L was considerably smaller than the home ranges of many species, the biological diversity did not equal the diversity of natural communities and excluded higher-order predators, and the time scale of 4.5 months was too short to integrate seasonal variation especially in temperature. Due to the limitations of the mesocosms in respect to space and time, genetic adaptation [14-16] and the substitution of sensitive taxa with functional equivalents from warmer waters [17,18], though of great significance, were not tested for. Still, the mesocosms allowed for several generations in smaller-bodied taxa and offered a diversity of species with varying thermal niches from which to select. Ultimately, changes that are inherent to specific functions – e.g. the increase in primary production, cost of calcification or food demand in consumers – will occur even in case of rapid and complete genetic and taxonomic adaptation of communities.

The meta-analysis on the buffering effect of ecological complexity under ocean acidification aimed to mitigate some of these limitations by combining studies from both simple and complex settings. Yet, whilst the inclusion of studies on different species and systems benefited the generalisation of the main finding, it raised further questions about the nature of the underlying mechanisms. Unfortunately, the number of experiments is currently insufficient, especially at higher levels of complexity, to understand which aspects of complexity (i.e. space, time, learning, social environment, etc.) and which organismal traits (i.e. sensory functioning, mobility, reproduction, etc.) are responsible for the buffering. A larger sample size that would allow answering these questions may be reached in the future through an expansion of the meta-analysis to other taxonomic groups (besides fishes and decapod crustaceans) and human stressors (besides acidification).

FUTURE DIRECTIONS

Other approaches in the field of ocean acidification and warming have their specific set of strengths and limitations, too. Therefore, a complementary thinking, where the insights from various approaches are integrated, is critical to gain a predictive understanding of future ocean ecosystems. Yet, the research effort over the past two decades has been dominated by laboratory studies testing single species in isolation [19]. Whilst providing invaluable knowledge on direct physiological and behavioural responses of many taxa, such studies cannot directly be extrapolated to the ecosystem level [1,20]. To guaranty a rapid advancement in the field, this existing knowledge base now needs to be complemented by studies on the ecological effects of future climate; that is, the field has to move beyond a

simple science [21]. Larger-scale mesocosms in the laboratory or in situ, like the one presented here or elsewhere [5,22-24], are needed from around the world not only to study further ecological processes but also to identify which responses are universal and which vary among local systems. More focus should also be placed on natural analogues such as latitudinal temperature gradients [25,26] and CO_2 vents [8,27,28], as their higher level of complexity offers a critical stepping stone from mesocosms to real ecosystems [13]. My PhD included research at a CO_2 vent which is however not yet compiled into a manuscript.

While such studies in the laboratory or field have indeed become increasingly popular in recent years, even they may not be realistic enough for a holistic view of the future interaction between humans and ocean ecosystems. As such, todays mesocosms are still too restricted in space and time, as discussed above, and natural analogues lack adequate replication, independency from control areas, and do not allow for stressor combinations. The importance of the latter is also demonstrated by my PhD research, where the impact of one global stressor (i.e. acidification) is radically altered in the presence of another (i.e. warming) in an unpredictable way.

In my opinion, a next generation of mesocosms that combines the strengths of natural analogues and today's mesocosms has the potential to become the final stepping stone in realism towards natural ecosystems. These future mesocosms could enclose a larger section of natural habitat *in situ*, such as a reef or a seagrass meadow, and simulate acidification and warming over years to decades. Due to their size, environmental impact and financial costs, such projects would require an entirely different approach to science. Based on my mesocosm experience, the design, construction and maintenance of such a project would be the most costly and challenging part and should thus be organized from the top down by collaborating governments. Then, scientists from around the world and from all disciplines could test their hypotheses within the established mesocosms through specific sampling and smaller scale experiments. Clearly, this would allow individual research groups to ask the big questions that had been beyond their budget. More importantly perhaps, it would be an unprecedented opportunity to integrate knowledge across disciplines and to gain a holistic understanding of future ocean ecosystems. Such projects could also become hubs for science-education where young and old can connect with our ocean and experience firsthand how ecosystems may change if we do not act. They may even become a symbol for reason and international collaboration towards a brighter future of humanity in harmony with nature.

IMPLICATIONS

The implications of my research for science and society are far-reaching. I advanced our knowledge in both the basic and applied sciences, through the study of fundamental ecological dynamics including trophic cascades and ecological compensation in the context of two pervasive human stressors. By demonstrating that species communities can be limited in their capacity to resist the predicted warming, my findings highlight the urgency for actions against causes and consequences of human CO_2 emissions.

Slowing the rate of change is evidently the first and most critical step [31-33]. Successful reductions in CO_2 emissions require strict government regulations including carbon tax and greater investments into renewable energies and a scientific education of the people that puts individual life-style choices into the bigger picture [34]. In a second step, ecosystems need to be liberated from the pressures of local stressors [32,35,36] as these will almost certainly accelerate the impacts of future climate. Most notably, the collapse into short and bottom-heavy food webs that is predicted by my findings would likely be reinforced through nutrient enrichment via enhanced bottom-up forcing [37-40] and overfishing via trophic simplification [41-44].

My research also identifies ecological functions that are vulnerable under ocean warming but essential for the maintenance of ecosystem integrity. In this respect, habitat forming primary producers [21,22,45] larger invertebrate herbivores and top predators [46,47] should receive special attention by management. Inevitably, ecosystems will reorganize to some degree and alter their services. I reveal the potential for increased food web productivity through CO_2-enrichment in ecosystems less impacted by warming, which may also benefit fisheries. In contrast, a collapse in food webs through ocean warming, mediated by an architecture that is unable to adapt, may endanger the productivity and diversity of fisheries.

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