Received: 27 June 2017 | Accepted: 14 July 2017

DOI: 10.1111/gcb.13849

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Ocean acidification alters zooplankton communities and increases top-down pressure of a cubozoan predator

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Funding information
Centre for Environmental Sustainability, Grant/Award Number: CENS 0143; USU Ecology Center travel; NSW Environmental Trust; NSERC Discovery Program; FRQ-NT Programme Établissement de Nouveaux Chercheurs Universitaires

Abstract

The composition of local ecological communities is determined by the members of the regional community that are able to survive the abiotic and biotic conditions of a local ecosystem. Anthropogenic activities since the industrial revolution have increased atmospheric CO_2 concentrations, which have in turn decreased ocean pH and altered carbonate ion concentrations: so called ocean acidification (OA). Single-species experiments have shown how OA can dramatically affect zooplankton development, physiology and skeletal mineralization status, potentially reducing their defensive function and altering their predatory and antipredatory behaviors. This means that increased OA may indirectly alter the biotic conditions by modifying trophic interactions. We investigated how OA affects the impact of a cubozoan predator on their zooplankton prey, predominantly Copepoda, Pleocyemata, Dendrobranchiata, and Amphipoda. Experimental conditions were set at either current ($p\mathrm{CO_2}$ 370 μatm) or end-of-the-century OA ($p\mathrm{CO_2}$ 1,100 μatm) scenarios, crossed in an orthogonal experimental design with the presence/absence of the cubozoan predator *Carybdea rastoni*. The combined effects of exposure to OA and predation by *C. rastoni* caused greater shifts in community structure, and greater reductions in the abundance of key taxa than would be predicted from combining the effect of each stressor in isolation. Specifically, we show that in the combined presence of OA and a cubozoan predator, populations of the most abundant member of the zooplankton community (calanoid copepods) were reduced 27% more than it would be predicted based on the effects of these stressors in isolation, suggesting that OA increases the susceptibility of plankton to predation. Our results indicate that the ecological consequences of OA may be greater than predicted from single-species experiments, and highlight the need to understand future marine global change from a community perspective.

KEYWORDS
community ecology, copepods, cubozoans, gelatinous predator, jellyfish, Ocean Acidification, predator–prey, zooplankton

1 | INTRODUCTION

The composition of ecological communities is determined by the members of the regional species pool that are able to pass through a series of ecological filters (Lawton, 2000). Initially, to become part of a community, species from the regional pool have to overcome the "dispersal filter", i.e. they need to physically enter the local community. Having arrived, the species then has to pass through the "abiotic filter", i.e. it has to be physiologically capable of tolerating the abiotic conditions present in the local area. After clearing the dispersal and abiotic filters, a species must finally clear the "biotic filter". To pass through the biotic filter a species must be able to coexist with the other members of the regional species pool, species who themselves have already been able to pass through both the dispersal and abiotic filters. Co-existing with these other community members means a species must not be competitively excluded, or exploited to extinction by predators. It is impossible for a species to exert competitive or consumptive pressure (i.e. become part of the biotic filter) if it cannot pass through the dispersal or abiotic filters; thus, the filters concept is often depicted as a linear process (Figure 1, Lawton, 2000). Although the filters concept was first proposed to describe the presence or absence of species, community composition can also change through changes in species' relative abundances (Clarke, 1993; Forbes & Hammill, 2013; Roemmich & McGowan, 1995). Changes in the strength of the different filters may not necessarily lead to the exclusion of species, but community composition may still be altered through reductions in their abundance.

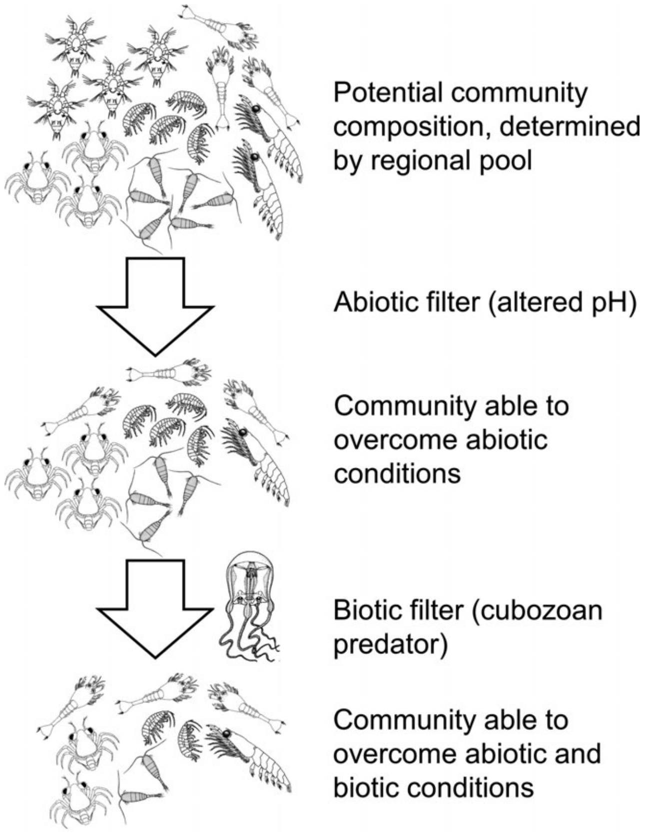

FIGURE 1 Illustration of the filters that determine the composition of a local community. The dispersal filter is not included as it did not form a part of the current experiment. The abundances of species present in the regional pool represent the potential community. The members of the regional pool that are able to cope with ocean acidification and a cubzoan predator in combination determine the final community composition. Changes in OA may alter final community composition by directly affecting the strength of the abiotic filter, or by increasing susceptibility to predation, thereby increasing the strength of the biotic filter. After Lawton (2000)

Marine zooplankton communities are often dominated by Copepoda. Of the copepods, calanoids are the most abundant and alone can constitute up to 80% of total zooplankton biomass (Beaugrand, Reid, Ibañez, Lindley, & Edwards, 2002; Lavaniegos & Ohman, 2007). The dominance of calanoid copepods, combined with the size of the world's oceans, suggests that they constitute the largest biomass of a single group of organisms on earth and play a pivotal position in the food web (Gallienne & Robins, 2001; Stibor et al., 2004; Turner, 2004). This high biomass makes marine copepods a crucial link between the ocean's primary producers and higher trophic levels (Garzke, Hansen, Ismar, & Sommer, 2016). This crucial role within pelagic marine food webs means that any reduction in copepod abundance could decrease the survival of their consumers (Cross, Beauchamp, Moss, & Myers, 2009), and have far-reaching consequences for marine communities (Frederiksen, Edwards, Richardson, Halliday, & Wanless, 2006).

The biological consequences of increased $p\mathrm{CO}_2$ levels (ocean acidification—OA) in the marine environment appear detrimental for many species (Byrne et al., 2011; Fabry, Seibel, Feely, & Orr, 2008; Kroeker et al., 2013; Przeslawski, Byrne, & Mellin, 2015). Laboratory experiments and in situ observations at high $p\mathrm{CO}_2$ sites (e.g. CO_2 vents) have revealed that for calcifying organisms such as echinoderms, molluscs, corals, and crustaceans, OA can broadly lead to reduced survival and developmental success (Gaylord et al., 2011; Hall-Spencer et al., 2008; Kroeker, Micheli, Gambi, & Martz, 2011; Sheppard Brennand, Soars, Dworjanyn, Davis, & Byrne, 2010) and alter shell mineralization (Byrne, Lamare, Winter, Dworjanyn, & Uthicke, 2013; Taylor, Gilleard, Allen, & Deheyn, 2015; Wolfe, Dworjanyn, & Byrne, 2013). However, some of the most abundant and ecologically important species (e.g. copepods) in pelagic environments possess chitinous exoskeletons that will not be as impacted by the dissolution status of sea water compared to calcifying organisms (Kroeker et al., 2013). Nevertheless, OA has been associated with reduced adult and juvenile survival (Cripps, Lindeque, & Flynn, 2014; Lewis, Brown, Edwards, Cooper, & Findlay, 2013), altered reproductive rates (Fitzer et al., 2012; Thor & Dupont, 2015), and reduced growth (Fitzer et al., 2012) in copepods. These changes may be due to changes in copepod metabolism in response to OA (Thor & Dupont, 2015), which then lead to the reallocation of resources away from reproduction. These detrimental effects of OA on chitinous species suggest that although these taxa may not suffer the same impacts on shell morphology, they are not immune to the negative effects of OA.

The total effects of OA on individual taxa may also be magnified through indirect interspecific interactions, as shown in experiments using pairs of grazers and herbivores (Poore et al., 2013), or predators and prey (Nagelkerken & Munday, 2016). Across a range of different biomes, changes in pairwise consumer-resource interactions have been shown to scale up to the community level, leading to changes in overall composition (Estes & Palmisano, 1974; Hammill, Atwood, & Srivastava, 2015a; Osman & Whitlatch, 2004). Within marine ecosystems cubozoa ("box jellyfish"), are zooplanktivorous predators that consume large volumes of zooplankton, including copepods (Buskey, 2003). Previous investigations into the effects of OA on cubozoa have shown that they are capable of surviving and asexually reproducing at pH levels as low as 7.6, although rates of asexual propagation through budding are reduced (Klein, Pitt, Rathjen, & Seymour, 2014). The ability of cubozoans to survive and reproduce (albeit at a reduced rate) under OA conditions suggests an ability to tolerate potential future ocean conditions. What is not clear is whether OA reduces the ability of cubozoans to capture prey, therefore reducing the effect of predation, or whether the physiological effects of OA on their zooplankton prey makes escape harder, therefore increasing the effect of predation. In terms of the ecological filters proposed by Lawton (Lawton, 2000), potential changes in predation strength may lead to OA having indirect effects on the strength of the biotic filter, potentially increasing the impact of OA on community structure (Figure 1).

Here, we investigate whether future OA conditions will alter plankton communities by changing the strength of the abiotic filter, or by also increasing predation risk, thereby indirectly increasing the strength of the biotic filter (Lawton, 2000). Using marine zooplankton communities and a natural predator, a cubozoan jellyfish, we conducted a microcosm experiment in which the presence of predators and OA was crossed in a 2 × 2 factorial design: $p\text{CO}_2$ 370 or 1,100 μatm crossed with predator presence/absence. We predicted that in isolation, OA conditions or the presence of cubozoan predators would alter the composition of zooplankton communities by reducing the abundances of multiple taxa, including dominant copepods. However, we also predicted that when OA and predators were present simultaneously, their combined impacts on community structure, driven by changes in copepod abundances would be greater than would be predicted from combining their isolated effects, as OA is likely to increase susceptibility to predation.

2 | MATERIALS AND METHODS

2.1 | Organism collections

Zooplankton were collected from Chowder Bay in Sydney Harbour, Australia (−33°50′59.6394″, 151°15′0.36″) using a 250 μm plankton net. Many zooplankton taxa swarm in the presence of light, a behavioral tactic that has been exploited by cubozoans (Buskey, 2003). Plankton were therefore collected at night by illuminating the water surface using 200 lumen lamps (Icon© Headlamp, Black Diamond Equipment LTD, Salt Lake City, UT, USA), then towing the plankton net 20 times through the illuminated water. After each tow the contents of the net were emptied into a 20 L white plastic bucket. The net was emptied carefully after each tow to minimize damage to organisms. While illumination can alter the relative abundances of zooplankton, a previous investigation in temperate waters showed that the use of illumination led to the exclusion of only one out of 43 taxa, as opposed to excluding nine out of 43 taxa in the absence of illumination (McConnell, Routledge, & Connors, 2010). We therefore opted to use illumination as it facilitated rapid collection of large numbers of the most abundant taxa, due to the positive phototaxis characteristic of many zooplankton (Buskey, 2003; Martynova & Gordeeva, 2010; Porter, Eckert, Byron, & Fisher, 2008). This method also substantially reduced the handling time needed to obtain sufficient populations for the experiment. Following collection, fresh sea water was added to the bucket to make the volume up to 15 L. The contents of the bucket were then thoroughly mixed through gentle stirring for 30 s, and divided into 75 subsamples each of 200 ml. Twelve plankton kreisels were then inoculated with four of the 200 ml subsamples, selected at random. We did not identify the organisms introduced into each kreisel prior to the start of the experiment to avoid stress associated with microscopic identification. To assess the initial composition of the plankton, we collected a second zooplankton sample that was handled in an identical manner (e.g. collection, 75 × 200 ml subsamples), where the subsamples were immediately fixed in 75% ethanol for later identification. These preserved subsamples were identified to ascertain initial composition and to quantify the likelihood that significant differences existed among the experimental replicates at the start of the experiment. After the zooplankton communities within these subsamples were quantified, we performed numerical simulations in which every possible combination of subsamples were randomly assigned to the different experimental kreisels, and looked for significant differences among treatments. This simulation exercise revealed that there was a <5% chance that significant differences existed among the treatments at the start of the experiment (Supplementary Materials).

The cubozoan *Carybdea rastoni* naturally occurs in and around Sydney Harbour (The Australian Museum, 2016). *Carybdea rastoni* have a broad diet consisting of zooplankton and small fish (Larson, 1976). Due to its ease of identification and capture, we used this species as the gelatinous predator in the experiment. Because of their delicate body structure, *C. rastoni* were individually collected from the water using a 2 L bucket rather than a plankton net. For the treatments containing predators, a single individual *C. rastoni* was placed in each experimental kreisel at the start of the experiment. All *C. rastoni* used in the experiment measured between 20 and 25 mm across the widest part of the bell, and we found no differences in size among treatments ($t_{(4)} = 0.35$, $p = .74$). We were able to capture sufficient *C. rastoni* for the experiment in less than 1 hr, suggesting they were relatively abundant in Chowder Bay at the time of collection.

2.2 | Experimental vessels

Custom-built plankton kreisels (Greve, 1968) were used as the experimental vessels ($n = 12$). Plankton kreisels allow pelagic zooplankton to be cultured in flow-through systems, while preventing individuals adhering to solid surfaces. Each kreisel consisted of a tank measuring 260 mm × 400 mm × 73 mm, with the circular component being a 73 mm-wide section of PVC tubing with a diameter of 210 mm (Fig. S1). Placing the circular component within the tank generates a circular current, preventing adhesion of zooplankton. A "slip" was inserted immediately adjacent to the inflow to create a more laminar flow. An outflow tube was installed in the circular component and covered with 100 μm mesh to prevent any organisms escaping. We used three kreisels in each of the four experimental treatments, and the experiment was ran for 10 day. Throughout the experiment, 150 μl of Instant Algae (Shellfish Diet 1800©, Reed Mariculture, Campbell, CA, USA) was added to each kreisel daily. As the water was only filtered to 20 μm, the flow through system also supplied phytoplankton as an additional source of food (Byrne, pers. obs.).

2.3 | Experimental conditions

The kreisels were supplied with filtered sea water (FSW; 20 μm filtered) from four 60 L header tanks. Manipulating pCO_2 within these four header tanks allowed them to supply different OA treatments to the experimental kreisels. Two header tanks were assigned as containing ambient sea water (pCO_2 370 μatm), and two contained elevated pCO_2 sea water (pCO_2 1,100 μatm, see Table 1). Each header tank consisted of a 60 L plastic tub with a tight fitting lid. Filtered sea water entered each of the header tanks at a rate of 1 L/min. The OA treatment was achieved by bubbling CO_2–enriched air vigorously through sea water using 20 cm ceramic diffusers. In the two header tanks supplying current conditions, ambient air was bubbled through the diffusers. To achieve target pCO_2 for the OA treatments, ambient air was scrubbed of CO_2 and then mixed with industrial-grade CO_2 (BOC, Sydney, Australia) through a VSO® thermally compensated low flow controller valve (Parker Hannifin, USA). A software-controlled, proportional–integral–derivative (PID) device ensured pCO_2 concentration in the gas mix at the level predicted for the year 2050 (CSIRO and Bureau of Meteorology 2016). Header tank temperatures were maintained using software-controlled solenoid valves that mixed warm and cold water to achieve a constant temperature of 21°C, representing ambient temperature at the time of collection of the plankton. Each header tank then supplied three of the experimental kreisels, via gravity, at a rate of 300 ml/min. Excess water within the header tank drained out via an overflow.

Treatment stability was monitored every second day using a handheld multimeter (Multi 3430 Set G, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Oberbayern, Germany) equipped with a temperature/pH sensor (SenTix 940, Wissenschaftlich-Technische

TABLE 1 Physico-chemical parameters of kreisels used to assign ocean acidification (OA) treatments (mean ± *SE*): temperature (°C), pH (NIST scale), salinity, total alkalinity (TA μEq/kg), dissolved inorganic carbon (DIC μmol/kg), carbon dioxide partial pressure (pCO_2 μatm), bicarbonate concentration (HCO_3^- μmol/kg), carbonate concentration (CO_3^{2-} μmol/kg), calcite (Ω_{cal}) and aragonite saturation (Ω_{ara})

	Ambient treatment						OA treatment					
Header tank	1			2			3			4		
Predator present	Yes	No	No	Yes	No	Yes	Yes	Yes	No	No	No	Yes
Kreisel number	1	2	3	4	5	6	7	8	9	10	11	12
Temperature (°C)	21.11	21.09	21.08	21.11	21.06	21.14	21.08	21.1	21.09	21.1	21.11	21.12
(±*SE*)	0.1	0.07	0.09	0.05	0.05	0.1	0.07	0.08	0.08	0.06	0.06	0.07
Salinity	34.62	34.68	34.65	34.66	34.64	34.68	34.65	34.67	34.65	34.64	34.65	34.63
(±*SE*)	0.04	0.06	0.05	0.03	0.05	0.05	0.05	0.06	0.06	0.07	0.06	0.07
pH_{NIST}	8.20	8.23	8.22	8.19	8.20	8.19	7.79	7.79	7.8	7.77	7.77	7.77
(±*SE*)	0.02	0.04	0.02	0.03	0.02	0.03	0.02	0.03	0.03	0.05	0.05	0.05
TA (μEq/kg)	2294.96	2295.64	2293.39	2298.66	2295.11	2297.55	2290.43	2298.74	2293.47	2290.37	2296.11	2294.16
(±*SE*)	10.35	10.18	5.19	7.53	4.57	6.78	9.5	5.43	6.7	9.65	14.55	7.97
pCO_2 (μatm)	367.81	356.1	353.6	379.16	367.76	364.2	1096.82	1090.78	1079.88	1161.53	1157.7	1157.56
(±*SE*)	22.49	22.5	16.28	27.02	23.38	37.95	56.38	87.37	88.44	90.2	83.84	84.17
DIC (μmol/kg)	2013.82	2001.72	2004.79	2012.6	2014.08	2013.4	2195.45	2192.62	2195.62	2204.28	2207.86	2205.92
(±*SE*)	17.01	16.37	9.89	17.03	11.98	18.84	12.92	15.45	15.21	13.85	16.12	12.54
HCO_3^- (μmol/kg)	1801.97	1782.39	1788.72	1803.57	1802.33	1805.46	2072.23	2069.02	2071.3	2083.24	2082.01	2084.14
(±*SE*)	22.81	23.24	15.37	24.45	19.41	29.37	14.01	18.38	17.97	15.4	16.9	14.41
CO_3^{2-} (μmol/kg)	200.29	208.46	204.97	197.13	200.19	195.89	88.76	89.36	90.39	84.27	85.51	85.47
(±*SE*)	7.74	8.98	6.59	8.92	8.51	12.21	3.73	5.82	5.92	5.22	5.13	5.26
Ω_{cal}	4.81	5	4.92	4.83	4.81	4.8	2.13	2.15	2.17	2.02	2.05	2.05
(±*SE*)	0.19	0.22	0.16	0.21	0.21	0.29	0.09	0.14	0.14	0.13	0.12	0.13
Ω_{ara}	3.13	3.16	3.21	3.08	3.13	3.06	1.39	1.4	1.41	1.35	1.34	1.34
(±*SE*)	0.12	0.14	0.1	0.14	0.13	0.19	0.06	0.09	0.09	0.08	0.08	0.08

Header tanks 1 and 2 supplied sea water at current oceanic conditions, header tanks 3 and 4 represent OA conditions. All ionic concentrations were calculated in CO2SYS (Pierrot et al., 2006), using CO_2 disassociation constants K_1 and K_2 from Mehrbach et al. (1973) refit by Dickson and Millero (1987), and KSO_4 from Dickson, Sabine, and Christian (2007).

Werkstätten GmbH). On each monitoring occasion, pH measurements were taken from each of the three experimental kreisels. The pH electrode was calibrated prior to use with high precision NIST buffers pH 4, 7 and 10 (ProSciTech, Townsville, QLD, Australia). Total alkalinity (TA) was determined from water samples collected every second day through potentiometric titration (907 Titrando, Metrohm) using certified reference standards (Dickson et al., 2007). Full physico-chemical parameters including bicarbonate and carbonate ion concentration ($[HCO_3^-]$ and $[CO_3^{2-}]$ and calcite and aragonite saturation states (Ω_{cal} and Ω_{ara}) were subsequently calculated using CO_2SYS (Pierrot, Lewis, & Wallace, 2006), using CO_2 disassociation constants K_1 and K_2 from Mehrbach, Culberson, Hawley, and Pytkowicz (1973) refit by Dickson and Millero (1987), and KSO_4 from Dickson et al. (2007). Values are provided in Table 1. Within each of the OA treatments, predators were randomly allocated to the three kreisels being fed by each of the header tanks. As each OA treatment was fed by two header tanks, each of which supplied water to three kreisels, one header tank would supply two predator replicates, and the other would supply one. A coin toss was used to establish which of the header tanks in each OA treatment would supply two predator replicates. Following this initial allocation, the individual kreisels that would house communities containing predators were identified using a random number generator. This process was undertaken to produce a random allocation of predators across header tanks, while also ensuring one header tank in each OA treatment did not also supply all predator treatments.

2.4 | Data collection, visualization, and statistical analyses

At the termination of the experiment, all zooplankton were collected from each of the experimental kreisels and preserved in 75% ethanol. Zooplankton abundances were calculated by identifying each individual using a Leica EZ4 stereo dissecting microscope. Differences in zooplankton community composition between treatments were visualized using multidimensional scaling (MDS) plots, a method that implements ordination methods to illustrate differences in multidimensional data. Abundance of each zooplankton taxon was used in the MDS plots, and visualized in 2-dimensions. Within this 2-dimensional space, communities that have compositions similar to each other are clustered together, whereas communities with different compositions are spaced further apart. Formal analysis of differences in the zooplankton community composition data required a simultaneous analysis of multiple response variables (abundances of each zooplankton taxa) using two explanatory variables (OA and predator presence). We therefore quantified differences in overall community composition using PERMANOVA within the vegan package, using the R statistical programming language (R Foundation for Statistical Computing, 2015). PERMANOVA analyses incorporate distance matrices, and are considered a robust metric to analyze differences in community composition (Forbes & Hammill, 2013; Hammill et al., 2015a). As our data had two independent descriptive variables (OA and presence/absence of a cubozoan predator), we performed a 2-way PERMANOVA including an interaction term. The contributions of different taxa to community level differences were calculated using SIMPER (Warton, Wright, & Wang, 2012).

While PERMANOVA indicates differences in multivariate data, it does not describe how communities differ, or demonstrate if a significant interaction represents an antagonistic or synergistic effect. To better understand how community composition is altered due to OA and predator presence, we performed 2-way ANOVAs on each zooplankton taxon to analyze differences in abundance. Within each of the ANOVA tests, we included an OA × predator interaction term. To understand whether a significant interaction term indicated an antagonist or synergistic interaction between OA and predators, we generated multiplicative risk models (Atwood, Hammill, Srivastava, & Richardson, 2014; Soluk & Collins, 1988), then compared the result of these null models to our observed data. The general form of the multiplicative risk null model (MRNM) is described by the following equation:

$$\mathrm{MRNM} = (E_{\mathrm{OA}} + E_{\mathrm{predators}}) - (E_{\mathrm{OA}} \times E_{\mathrm{predators}}) \tag{1}$$

where MRNM is the predicted effect of the combined stressors (i.e. the “null model” or the abundance we would expect if predators and OA acted independently of each other), as a proportional change in the metric of interest (e.g. the abundance of each zooplankton). E_{OA} and $E_{\mathrm{predators}}$ represent the respective observed proportional changes due to OA and the presence of a cubozoan predator. These multiplicative null models are useful as they never predict reductions in abundances greater than 100%. Should our observed reductions in zooplankton abundance due to both OA and the presence of predators be greater than predicted by the null model, this would indicate these two factors act synergistically. If reductions in abundance are less than predicted by a null model, this indicates an antagonistic interaction. We also performed numerical simulations for the taxa where a significant OA × predator interaction was found to compare predator consumption rates under ambient and elevated $p\mathrm{CO}_2$ conditions (Supplementary Materials).

Within the PERMANOVA and ANOVA tests, “header tank ID” was included as a blocking term. In all analyses, we found no significant effect of header tank ID, and no significant interactions with either predator presence/absence or OA condition (all $p > .05$). We therefore removed all terms involving header tank ID and reran the analyses.

3 | RESULTS

3.1 | Plankton community

At the end of the experimental trials, all members of the zooplankton community belonged to the subphylum Crustacea. This dominance of Crustacea is consistent with the analysis of the initial community composition, and all taxa appeared to survive well in the kreisels during the experiment (Supplementary Materials). Adult copepods were the most abundant members of the community, accounting for 91.8% of the total number of individuals. Of these copepods, the vast majority (99.6%) were members of the order

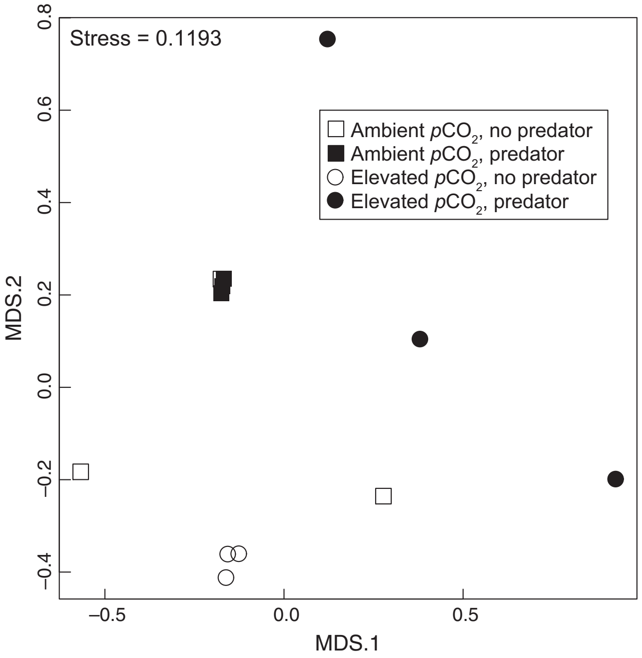

FIGURE 2 Multidimensional scaling plot illustrating how OA and the presence/absence of predators alters community composition. Each point represents the community contained within a single plankton kreisel at the end of the experiment. Distances between points are proportional to similarities in community composition, meaning nearby points represent similar communities

Calanoida, with the remainder being members of the order Cyclopoida. After adult copepods, the second most abundant members of the community were copepod nauplii (3.1%). The remainder of the community consisted of members of the orders Amphipoda (2.5%), Pleocymata (1.7%), Dendrobranchiata (0.6%), and Mysida (0.4%).

3.2 | Community-level effects of experimental stressors

We found that community-level changes in the presence of both drivers were different from what would be expected given the results of these stressors in isolation, as indicated by the presence of a significant OA × predator interaction ($F_{(1,8)} = 28.99$, $p < .001$, PERMANOVA, Figure 2). In isolation, OA was associated with significant changes in community composition ($F_{(1,8)} = 59.81$, $p < .001$, Figure 2). The addition of a cubozoan predator in isolation also led to significant changes in the zooplankton community ($F_{(1,8)} = 27.34$, $p < .001$, PERMANOVA, Figure 2). Within the zooplankton community, calanoid copepods were the greatest contributor to differences between treatments, accounting for 88.52% ± 2.30% of the differences between treatments (SIMPER).

3.3 | Effects of experimental drivers on individual zooplankton taxa

Reductions in calanoid abundances due to a combination of cubozoan predation and OA were 27.00% ± 1.50% greater than would be expected based on the results of these drivers in isolation (OA × predator interaction, $F_{(1,8)} = 45.61$, $p < .001$, ANOVA, Figure 3a). Predation rates appeared to increase under OA conditions, with cubozoan predators consuming 36.7% (95% CI: 23.02%–50.08%) of available calanoids at ambient pCO_2, and 82.7% (95% CI: 62.50%–97.98%) under elevated pCO_2 (Supplementary Materials). Abundances of pleocyematids were also reduced by 61.34% ± 7.80% more through a combination of cubozoan predators and OA than would be predicted by the effect of these stressors in isolation, demonstrated by a significant interaction term and comparison against the multiplicative null model ($F_{(1,8)} = 6.25$, $p = .033$, Figure 3b). Cubozoan predators consumed 0% (95% CI: −28.60% to 28.60%) of pleocyematids at ambient pCO_2, but the rate of consumption increased to 71.5% (95% CI: 42.09%–100.1%) under elevated pCO_2 (Supplementary Materials). These results indicate that predation rates on calanoids and pleocyematids increased under OA conditions.

In addition to the significant OA × predator interactions, abundances of certain zooplankton taxa were also reduced by each of our experimental drivers when applied in isolation. Abundances of calanoids were 59.4% ± 8.6% lower under OA conditions compared to controls ($F_{(1,8)} = 251.65$, $p < .001$, ANOVA Figure 3a). In addition, copepod nauplii were completely absent under OA conditions ($F_{(1,8)} = 110.09$, $p < .001$, Figure 3c). Under current ambient conditions, the presence of a cubozoan predator led to a 36.6% ± 9.5% reduction in the abundance of calanoids ($F_{(1,8)} = 127.46$, $p < .001$, ANOVA Figure 3a). Dendrobranchids were also entirely absent in the presence of cubozoan predators, in both ambient and OA conditions ($F_{(1,9)} = 12.00$, $p = .007$, Figure 3d).

For all other zooplankton orders and suborders (Cyclopoida, Amphipoda, and Mysida), we found no significant changes in abundance following exposure to OA conditions, the presence of cubozoan predators, or an interaction between the two (all $p > .05$, Figure 3e–g). All cubozoan predators survived, and were observed to be freely moving around the kreisels at the termination of the experiment.

4 | DISCUSSION

Our data revealed that ocean acidification (OA) can lead to substantial changes in the composition of zooplankton communities through direct and indirect mechanisms. Crucially, when compared to multiplicative null models, the changes in abundance we observed for multiple taxa under a combination of OA and predators were greater than would be expected based on the effects of these stressors in isolation. This synergistic effect indicates that OA will not only directly affect community composition by changing the strength of the abiotic filter, but also by altering the strength of the biotic filter through increasing predation risk (Lawton, 2000).

In isolation, OA and the presence of cubozoan predators were associated with significant changes in community composition, driven by reductions in calanoid copepods and copepod nauplii. These

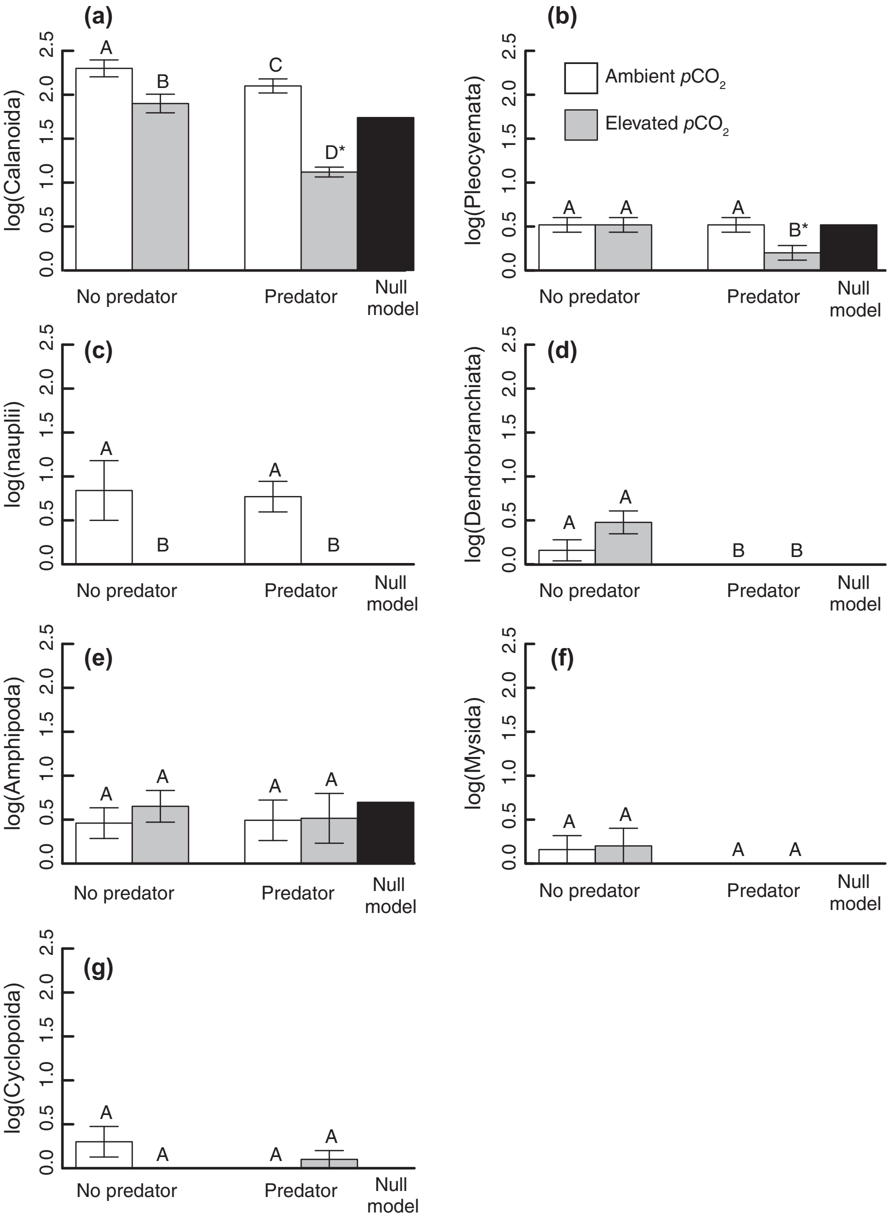

FIGURE 3 Consequences of (ocean acidification) OA and predator presence/absence on the Log$_{10}$ abundances (±1 *SE*) of zooplankton within the community. (a) Calanoida copepods, (b) Pleocyemata, (c) Nauplii of all copepods, (d) Dendrobranchiata, (e) Amphipoda, (f) Mysida, (g) Cyclopoida copepods. Different letters above bars indicate treatments that are significantly different from each other. In each panel, the black "null model" bar represents the predicted additive effects of OA and scyphozoan predators if these two factors acted independently, and asterisks indicate synergistic interaction

changes in copepod abundance indicate that OA can alter the strength of the abiotic filter to such a degree that it can detrimentally affect the most abundant member of the zooplankton community. As predicted, under current conditions, exposure to cubozoan predators also altered the composition of the zooplankton community, through reductions in abundances of Calanoida and Dendrobranchiata. These predator-mediated changes in overall community composition indicate that cubozoan predators represent a current and important component of the biotic filter.

Although the exoskeletons of chitinous organisms are less affected by OA than calcified taxa (Byrne et al., 2011; Chan, Grunbaum, & O'Donnell, 2011; Cohen, McCorkle, de Putron, Gaetani, & Rose, 2009; Gaylord et al., 2011), previous investigations show that copepods can be affected through changes in metabolic rates (Thor & Dupont, 2015), which can be compensated for by increased grazing rates (Li & Gao, 2012). These metabolic changes have been associated with reallocation of energetic resources, and may lead to a reduction in the amount of energy available for escape. Calanoid copepods have been shown to escape gelatinous predators by initiating multiple escape jumps, which can lead to less than 1% of predator encounters resulting in capture (Suchman, 2000). Because of this reliance on an energetically expensive escape strategy, any abiotic change that reduces energy available for escape could increase predation on copepods. We specifically provided an over-abundance of food to increase the chances that individuals had sufficient resources for growth and reproduction. However, we cannot rule out that under OA conditions, changes to resource requirements (Li & Gao, 2012), and metabolism (Thor & Dupont, 2015) limited the ability of zooplankton to survive in the presence of a predator. Although untested here, this may represent a series of additional physiological mechanisms by which OA affects copepod susceptibility to predation and represents an important area for future investigations.

To our knowledge, no studies have been conducted on the foraging mode of *C. rastoni*. However, similar species of cubozoan jellyfish are considered to be largely "semipassive hunters" (although see Courtney, Sachlikidis, Jones, and Seymour (2015)), using low resolution vision to seek out habitats with high prey densities and then passively collecting prey on their extended tentacles as they swim (Buskey, 2003; Garm, Oskarsson, & Nilsson, 2011). This type of foraging mode most resembles filter feeding, which is characterized as having a Type I functional response (Møller & Riisgård, 2007; Titelman & Hansson, 2006). Within a Type I functional response, predators should consume a constant proportion of their prey regardless of prey density. However, in the current study, cubozoan predators consumed a greater proportion of the available copepods under OA conditions compared with ambient (Supplementary Materials), suggesting OA increased the proportion of food available for capture. Conversely, OA may increase the food requirements of cubozoans, causing them to dedicate more effort to prey collection. This increase in prey collection effort could mean that copepods and other taxa need not become more susceptible to predation under OA conditions. The increased susceptibility of prey to predation and increased food requirements of predators may not be mutually exclusive, meaning that the observed reduction in copepods may be a byproduct of their additive effect. We therefore cannot conclusively determine whether the increased predation rates observed under OA conditions were the result of increased prey susceptibility, or increased predation effort. Future analyses into how OA alters the metabolism and behavior of both predators and prey may aid in teasing apart the individual-level or physiological-level mechanisms at the base of our results, and provide insight into whether it is OA-mediated changes in predators, prey, or both that are driving the patterns we observe here. Nonetheless, our results do demonstrate that OA increases the top-down pressure exerted on zooplankton communities by individual cubozoan predators, highlighting the importance of considering predator-dependent mortalities when considering the full impacts of OA.

All *C. rastoni* survived until the experiment was terminated after 10 days, and were observed freely moving around the kreisels. This 100% survival rate implies that *C. rastoni* are relatively tolerant of OA conditions, at least in terms of survival over a relatively short time period. Physiological investigations into the effects of OA on cubozoans have indicated that they are able to cope with near future OA conditions, showing no significant changes in survival, and maintaining asexual reproduction (although at a lower rate; Klein et al., 2014). The reduced reproduction rates observed under OA for cubozoans in previous experiments (Klein et al., 2014) may mean that although each individual cubozoan exerts more top-down pressure, there are fewer cubozoans in the ecosystem. The total net effect of the cubozoan population on their prey will therefore depend on whether the decrease in reproduction is greater than, equal to, or less than the increase in predation rates. Short-term predator–prey experiments such as ours provide insights into the factors that alter interaction strength, such as the relationships between biodiversity and strength of trophic links (Kratina, Vos, & Anholt, 2007). However, complementary longer term (>2 predator generations) experiments are necessary to understand if these short-term experiments translate to changes in overall community dynamics, rather than composition at a single time point (compare Kratina et al., 2007 to Hammill, Kratina, Vos, Petchey, & Anholt, 2015b). As the experiment we present here was conducted over a relatively short time frame (<1 predator generation), we do not know if these changes in the strength of trophic interactions translate into long-term alterations in the relative abundances of predators and prey.

At the population level, several studies have reported OA affecting life history parameters that influence population growth rates (Albright, Mason, Miller, & Langdon, 2010; Fitzer et al., 2012). Given the rapid generation time of copepods (Gillooly, 2000), nauplii introduced at the start of our experiment could have reached the adult stages by the end of the experiment. However, it is unlikely that our reduced copepod nauplii abundances were caused by an increase in the number of individuals transitioning to the adult stages, as OA was also associated with a reduction in the number of adult copepods. Furthermore, predation alone did not decrease copepod nauplii. Our observation of reduced nauplii abundances under OA conditions is therefore best explained by previously reported factors such as reduced reproduction (Fitzer et al., 2012; Thor & Dupont, 2015), reduced hatching success (Mayor, Matthews, Cook, Zuur, & Hay, 2007), or increased nauplii mortality (Pedersen, Våge, Olsen, Hammer, & Altin, 2014). Given the substantial reduction in nauplii and adult copepods we observed, OA could have significant consequences for the population trajectory of copepods, and their roles within ecosystems. We observed no nauplii under elevated $p\mathrm{CO}_2$, suggesting that copepod reproduction was dramatically reduced, potentially causing their populations to crash. Copepods are a dominant member of zooplankton communities (Beaugrand et al., 2002; Lavaniegos & Ohman, 2007) and exert significant grazing pressure on primary producers (Sommer & Sommer, 2006). A reduction in top-down control associated with an OA-mediated drop in copepod populations, coupled with the ability of phytoplankton to capitalize on the increased $p\mathrm{CO}_2$ associated with OA (Schippers, Lürling, & Scheffer, 2004), may lead to an increase in magnitude of phytoplankton blooms under future ocean conditions.

The challenges that OA poses for the production and maintenance of heavily calcified skeletons means that much previous research has focused on organisms possessing these structures (Coleman, Byrne, & Davis, 2014; Gaylord et al., 2011). While the chitinous skeletons of copepods and other planktonic crustaceans may make this group less susceptible physiologically to OA (Poore et al., 2013), the large decrease in copepod nauplii production we observed could lead to substantial reductions in copepod populations. Copepods have been proposed to account for the highest biomass of a single group of organisms on earth (Gallienne & Robins, 2001; Turner, 2004), and also form the important link between pelagic primary producers and economically important fisheries (Frederiksen et al., 2006). Reductions in copepod numbers have also been associated with declines in members of higher trophic levels such as salmon (Cross et al., 2009), highlighting that OA-mediated changes low in the food chain could influence many species in marine food webs. Understanding how OA affects lower trophic levels in a community-wide context is therefore critical to elucidating the total effects of changing oceanic conditions.

While our experiment indicates that zooplankton communities are altered through a combination of OA and predators, it was designed and conducted as a proof of concept. As our study was conducted in a single geographic location, and at only one point in time, we are cautious about generalizing our results to a wider geographic area. We can, however, speculate about how the geographic location affected our experiment, and how we may expect the results to differ in other areas. Previous studies indicate that species experiencing fluctuating conditions have been shown to be more tolerant to changes in abiotic conditions than species that experience greater stability (Lewis et al., 2013; Maas, Wishner, & Seibel, 2012). The temperate nature of Chowder Bay is associated with annual fluctuations in mean temperatures between 17 and 25°C (http://www.seatemperature.org/). While data on pH fluctuations in Chowder Bay are not available, the near shore, temperate nature of the region would suggest that pH levels are variable (Hofmann et al., 2011). These fluctuations in pH may provide a buffering effect on zooplankton communities, we therefore need to understand the interplay between magnitudes of OA and the susceptibility of different communities to determine the full community-level consequences of OA on marine communities.

We have demonstrated that OA may directly increase the strength of the abiotic filter, and indirectly increase the strength of the biotic filter in a marine plankton community. As a consequence of the indirect increase in the strength of the biotic filter, OA may not need to cause mortality in isolation to substantially change the composition of pelagic communities. Our results highlight the need to consider direct and indirect effects if we are to understand the total impacts of OA on marine communities in the coming decades (Gaylord et al., 2015; Kroeker et al., 2013; Poore et al., 2013).

ACKNOWLEDGEMENTS

The authors thank the Sydney Institute of Marine Sciences (SIMS) and particularly Josh Aldridge for assistance and access to the experimental facility. This research was supported by a Centre for Environmental Sustainability grant (CENS 0143) and a USU Ecology Center travel grant awarded to EH and a NSW Environmental Trust grant awarded to MB. PC is supported by an NSERC Discovery Program grant and a FRQ-NT Programme Établissement de Nouveaux Chercheurs Universitaires grant. This paper is contribution number 211 from the Sydney Institute of Marine Sciences.

CONFLICT OF INTEREST

No vertebrates were used in this research, data are not published or submitted elsewhere. The authors have no conflicts of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Hammill E, Johnson E, Atwood TB, et al. Ocean acidification alters zooplankton communities and increases top-down pressure of a cubozoan predator. *Glob Change Biol*. 2018;24:e128–e138. https://doi.org/10.1111/gcb.13849