



Contribution to the Theme Section 'The ecology of temperate reefs in a changing world'

Functionally redundant herbivores: urchin and gastropod grazers respond differently to ocean warming and rising CO₂

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ABSTRACT: Future ocean CO₂ and temperatures are predicted to increase primary productivity across tropical marine habitats, potentially driving a shift towards algal-dominated systems. However, increased consumption of algae by benthic grazers could potentially counter this shift. Yet, the response of different grazer species to future conditions will be moderated by their physiologies, meaning that they may not be functional equivalents. Here, we experimentally assessed the physiological response of key grazers—the sea urchin *Heliocidaris crassispina* and 2 gastropod species, *Astraliium haematragum* and *Trochus maculatus*—to predicted CO₂ concentrations (400, 700 and 1000 ppm) and temperature conditions (ambient, +3 and +5°C). In line with metabolic theory, we found that urchin metabolic rate increased at future temperatures regardless of CO₂ conditions, with evidence of metabolic acclimation to higher temperatures. The metabolic rate of *A. haematragum* was depressed only by CO₂, whereas *T. maculatus* initially had elevated metabolic rates at moderate CO₂, which were depressed by the combination of the highest CO₂ concentration and temperatures. Taxa showed differential survival, with no urchin mortality under any future conditions but substantial mortality of both gastropods under elevated temperatures regardless of CO₂ concentration. Importantly, all species had substantially reduced algal consumption in response to elevated CO₂, though the urchins only demonstrated an energetic mismatch under combined future CO₂ and temperature. Therefore, despite sharing an ecological niche, these key grazers are likely to be differentially affected by future environmental conditions, potentially reducing the strength of ecological compensatory responses depending on the functional redundancy in this grazing community.

KEY WORDS: Ocean warming · Ocean acidification · Metabolic function · Sea urchin · Functional redundancy

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1. INTRODUCTION

It is now well established that CO₂ concentrations and temperatures of the world's oceans are rising, with many negative ecosystem-level effects being recently documented (Côté et al. 2016, Wernberg et al. 2016, Henson et al. 2017, Smale et al. 2019). There is, however, increasing recognition of the ability of species to absorb changes across trophic levels (Russell et al. 2013). For example, both increasing CO₂ availability and temperature can drive increased primary productivity of benthic algae (Connell & Rus-

sell 2010, Russell et al. 2013, Brodie et al. 2014), which can drive change in community structure to algal-dominated systems (Bruno et al. 2009, O'Brien & Scheibling 2018). Trophic compensation by grazers in response to altered conditions can, however, reduce or eliminate overgrowth and system shifts (Bennett et al. 2015, Ghedini et al. 2015a,b). Therefore, community responses are not only dependent on the strength of environmental change, but also on the plasticity of key species and their ability to respond to altered conditions (Ghedini et al. 2015a,b, Mertens et al. 2015).

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To understand the drivers which underlie system shifts due to changing environmental conditions, it is first necessary to elucidate how changes to individual organisms may stabilise the community through compensatory responses or functional redundancy (Mertens et al. 2015, Bates et al. 2017). Yet, the response of grazers to future conditions (e.g. elevated CO₂ and temperature) is likely to be species-specific, with some demonstrating acclimation while others do not, leading to eventual mortality (Kroeker et al. 2010, Garrabou et al. 2013, Leung et al. 2019). While several species may fill the same functional role, the response of the system to change will be partly determined by the differential performance and survival of these species and how functionally redundant they may be within their community (Bates et al. 2017). In the tropics, where species diversity is high, each species contributes proportionally less to ecological processes within their community, because functional diversity increases with species diversity (Stuart-Smith et al. 2013). As such, any function that is potentially diminished due to the removal of one species is likely to be compensated for by other species which share a similar ecological role (Bremner et al. 2003, Stuart-Smith et al. 2013). Thus, when contemplating the future of an ecosystem under climate change, the impacts that environmental stressors may have on a community are dependent on the functional roles of individual species within that community, and how each individual species deals with stress (Covich et al. 2004).

The concept of strengthening top-down control under potentially stressful conditions is thought to be underpinned by the metabolic theory of ecology (MTE), whereby organisms that are exposed to higher temperatures generally have elevated metabolic rates and therefore intake of energetic resources (Brown et al. 2004). In more variable environments, metabolic and feeding rates initially increase with elevated temperature, as predicted by the MTE, but as conditions become more stressful, energy acquisition through feeding can become decoupled as energy conservation strategies reduce foraging (Newell & Branch 1980). Under these conditions, mismatches between the cellular costs associated with rising temperatures and the reduced supply of energy through food consumption diminishes overall fitness (Lemoine & Burkepille 2012). These responses are, however, highly species-specific, with some species maintaining energetic intake while others lose homeostasis under stressful conditions, often leading to increased mortality (Leung et al. 2019).

Here, we tested the effect of elevated CO₂ and temperature on the ability of 3 tropical subtidal graz-

ers which occupy the same habitat to maintain their key functional role (i.e. grazing) under predicted future conditions (sea urchin *Heliocidaris crassispina* and 2 gastropod species, *Astrarium haematragum* and *Trochus maculatus*). These species are widely distributed in Southeast Asia and occupy the same functional niche in subtidal rocky reefs (Yatsuya & Nakahara 2004, Wai & Williams 2005, Lau et al. 2014, Urriago et al. 2016). *H. crassispina* is the most abundant urchin and a dominant grazer in Hong Kong, with densities ranging between ~9 and 13 m⁻², and a lack of natural predators (Urriago et al. 2016). They feed on seasonally available benthic algae, ranging from macroalgae in the winter months to filamentous and crustose coralline algae (CCA) in the summer (Yatsuya & Nakahara 2004). Trochid and turbinid gastropods are commonly collocated with *H. crassispina* and also feed on a variety of different micro- and macroalgae, including diatoms attached to rocks, and red and green turf algal species (Lambrinidis et al. 1997, Cox & Murray 2006, Maboloc & Mingoa-Licuanan 2013). While smaller in size, these gastropods are generally more numerous than urchins and so potentially form an important part of the grazing fauna of benthic habitats in Hong Kong.

The response of species to elevated CO₂ and temperature depends on the intensity and duration of exposure, whether or not acclimation time is sufficient, as well as depending heavily on life stage (Sherman 2015). Of greater interest is the way which organisms respond to these potential stressors in combination, given that they can have either positive or negative interactions depending on the species (Sheppard Brennan et al. 2010, Gianguzza et al. 2014, Uthicke et al. 2014, Suckling et al. 2015, Carey et al. 2016). For example, elevated CO₂ has been shown to reduce food consumption in gastropods, with even short exposure (7 d) to 1000 µatm reducing body condition of *Trochus* sp., whereas moderate increases in temperature have the opposite effect, increasing performance (Grilo et al. 2019). Elevated temperature can, however, reduce lipid stores by up to 50% over relatively short periods (30 d), with a negative combined effect of CO₂ and temperature substantially reducing energetic stores (Valles-Regino et al. 2015), which can lead to mortality (Leung et al. 2017).

The physiological responses to environmental change of the different taxa used here, in particular metabolism and food consumption, will either enhance or reduce their ability to provide a compensatory mechanism for environmental stressors. Therefore, though these taxa share a similar ecological niche in

this habitat, their physiological coping mechanisms for stress associated with changing environmental conditions may not be synonymous. Hence, we assessed the physiological response of these 2 groups of organisms to future conditions to determine whether they can maintain their key function (i.e. grazing) under increasingly stressful environmental conditions. Specifically, as all individuals used here were adults, we hypothesised that warming would elevate metabolic rates as an immediate response to the thermal stress over the shorter exposure times in this experiment, but the additional stress of elevated CO₂ concentrations would reduce feeding activity. We further hypothesised that, as all species are found in the same habitat and exposed to the same environmental conditions, they would have similar responses to the altered conditions.

2. MATERIALS AND METHODS

2.1. Field collections

Adult urchins *Heliocidaris crassispina* and gastropods *Astraliium haematragum* and *Trochus maculatus* were collected during summer (July–August) from rocky substrate at ~2–5 m depth at Bluff Island (Sha Tong Hau Shan), Hong Kong (22° 19' 14" N, 114° 21' 12" E), and immediately transferred to outdoor fibreglass mesocosms (60 × 69 × 90 cm, D × W × H) with natural light and flowthrough sand-filtered seawater at the Swire Institute of Marine Science. After 3 wk, 1 urchin and 1 of each gastropod species were placed together into replicate (n = 3) 12 l plastic aquaria to reproduce natural conditions (i.e. 1 *H. crassispina*, 1 *A. haematragum* and 1 *T. maculatus* per tank) in the laboratory under control conditions (28°C, Hong Kong summer average temperature for subtidal waters). Aquaria were aerated with ambient air and LED lights above the tanks maintained in 12 h:12 h day:night light conditions. Food was provided ad libitum as biofilm and algal turf growth on rocks which were transported from the collection site.

2.2. CO₂ and temperature manipulation

We tested the effects of 3 temperatures (summer temperature 28°C [control], 31°C and 33°C) and CO₂ concentrations (400, 700 and 1000 ppm; pH ~8.1, 7.8 and 7.6) in crossed combinations (3 tanks per treatment, 9 treatments, total n = 27 tanks), representing

the present day and IPCC RCP 6.0 and 8.5 scenarios for the year 2100. After the 2 wk period of acclimation to laboratory conditions, aquaria were slowly raised from control to treatment conditions over 1 wk. Each aquarium had an individual glass heater to control temperature, and aquaria were submersed in water baths to further aid in temperature stability. The CO₂ concentrations were maintained in individual tanks by mixing CO₂ and air to the treatment concentrations using gas flow meters (Masterflex gas flow meters 316SS, Cole-Palmer). The tanks were set up on a semi-flowthrough system, each with individual inflow and outflow pipes, allowing water changes every 1–2 d with sand-filtered water. Experimental water conditions were regularly monitored to ensure that target values were maintained, and adjustments made if necessary (Table S1 in the Supplement at www.int-res.com/articles/suppl/m656p239_supp.pdf). Temperature and pH were monitored twice daily using a pH probe (Seven2go, Mettler Toledo). Once weekly, water samples were taken and analysed for total alkalinity using an alkalinity titrator (T50, Mettler Toledo). Seawater carbonate parameters were calculated using CO2SYS program for Excel (Pierrot et al. 2006) with constants from (Mehrbach et al. 1973) as adjusted by (Dickson & Millero 1987) from recorded temperature, pH and total alkalinity values (Table S1).

2.3. Metabolic rate

Aerobic metabolic rate (MO₂) was determined by measuring the metabolic rate after an exposure to experimental conditions for a period of 1 mo, a period defined by the high mortality in the high-temperature treatments (see Section 3.3). Each individual urchin or gastropod was placed in sealed respirometry chambers (1 and 0.5 l, respectively) filled with filtered, autoclaved, and oxygen-saturated seawater adjusted to treatment CO₂ concentrations, ensuring the absence of any gas bubbles. The chamber was then placed into a water bath at the experimental treatment temperature (i.e. 28, 31, or 33°C). A small water pump was placed in the water bath to circulate water and keep the temperature homogeneous. The organism was then left for 30 min to settle and reduce any stress caused by the movement from the experimental tanks. Oxygen concentration was recorded every 10 min for 30 min using an internal optical oxygen spot measuring system (Fibox4, PreSens). MO₂ (mg l⁻¹ g FW⁻¹ h⁻¹) was calculated using the following equation:

$$MO_2 = \Delta O_2 V / FW \quad (1)$$

where ΔO_2 is the linear regression slope of oxygen concentration over time ($\text{mg l}^{-1} \text{h}^{-1}$), V is the volume of seawater (litres), and FW is the fresh weight of the urchin (g). Blank chambers with no animals inside were run to account for any possible biological activity in the water.

2.4. Algal consumption

Algal biofilm for feeding trials was grown on plastic settlement tiles (5 cm × 20 cm) in outdoor mesocosms under natural conditions for 1 mo. For feeding trials, all individuals were segregated within the experimental aquaria using plastic mesh. After being starved for 48 h to remove all gut content, 1 pre-weighed tile was placed with each individual and left for 24 h (urchin) or 48 h (gastropods). After this time, all tiles were removed and re-weighed to determine the remaining mass of algae. Consumption rate was then calculated as the difference in algal weight measured before and after the feeding trial. To account for the difference in size between urchin and gastropods, consumption was standardised to the weight of each individual ($\text{g h}^{-1} \text{g FW}^{-1}$).

2.5. Thermal ramps

Organisms were allowed to rest for 24 h following metabolic and algal consumption assays, following which thermal ramps were carried out on each individual to determine the temperature of the maximum metabolic rate (T_{MMR}) and thermal upper lethal limit (ULL). As with metabolic measurements, individuals were placed in sealed respirometry chambers filled with oxygen-saturated seawater (CO_2 and temperature manipulated) and placed into a water bath set at 16°C (winter seawater temperature in Hong Kong). The water baths were then increased by 2°C per hour. At each 1 h mark after the increase, temperature was held static for 30 min to record the metabolic rate (as per Section 2.3; $\text{mg l}^{-1} \text{g FW}^{-1} \text{h}^{-1}$). The chamber was refreshed with water being heated and CO_2 treated alongside the experimental bath to maintain the oxygen saturation above 70% and prevent any influence of reduced oxygen concentration. Metabolic rate was recorded using the oxygen-measuring system (Fibox4) every 5 min for gastropods and 10 min for urchins due to chamber size. The temperature was ramped up until individuals reached mortality (ULL).

2.6. Statistical analysis

Two-factor ANOVAs were used to test for the effects of CO_2 (3 levels) and temperature (3 levels) on both metabolic rate and algal consumption rate separately for each species, Bonferroni-corrected for repeated tests (2 tests, $\alpha = 0.025$), with Tukey post hoc tests used to test for differences among significant factors. All data were normally distributed. Spearman's rank (r_s) tests for non-normal data were used to test for relationships between metabolic rate and algal consumption for each species. An exponentially modified Gaussian function (EMG) model was fitted for temperature ramp data to extract the T_{MMR} , ULL, and to model the change in metabolic rate over the temperature ramp. All analyses were performed using RStudio version 1.1.463 and R version 3.5.1 (2018), and at 95% confidence intervals.

3. RESULTS

3.1. Metabolic rate

The metabolic rate of *Heliocidaris crassispina* was up to 4-fold greater when exposed to the highest temperature (33°C) compared to the control temperature, but did not increase under moderate warming (31°C; Fig. 1a, Table 1). CO_2 had no effect on urchin metabolic rate. In contrast, the metabolic rate of *Astraliium haematragum* was depressed by increasing CO_2 , with both elevated CO_2 conditions (700 and 1000 ppm) causing decreased metabolic rates compared with controls (Fig. 1b, Table 1). Temperature had no effect on *A. haematragum* metabolic rate. The metabolic rate of *Trochus maculatus* was highest in the medium CO_2 treatment (700 ppm) and then depressed the most under the highest CO_2 treatment (1000 ppm) (Fig. 1c, Table 1). CO_2 and temperature also had a partial interactive effect on *T. maculatus*; only in the highest CO_2 treatment did temperature cause a decrease in the metabolic rate (Fig. 1c).

3.2. Algal consumption rate

Temperature and CO_2 both altered the consumption of algae by *H. crassispina*. At ambient (control) CO_2 concentrations, elevated temperature increased algal consumption, but the higher CO_2 treatments caused consumption rates to decrease by up to 90% (Fig. 2a, Table 2; significant $\text{CO}_2 \times$ temperature inter-

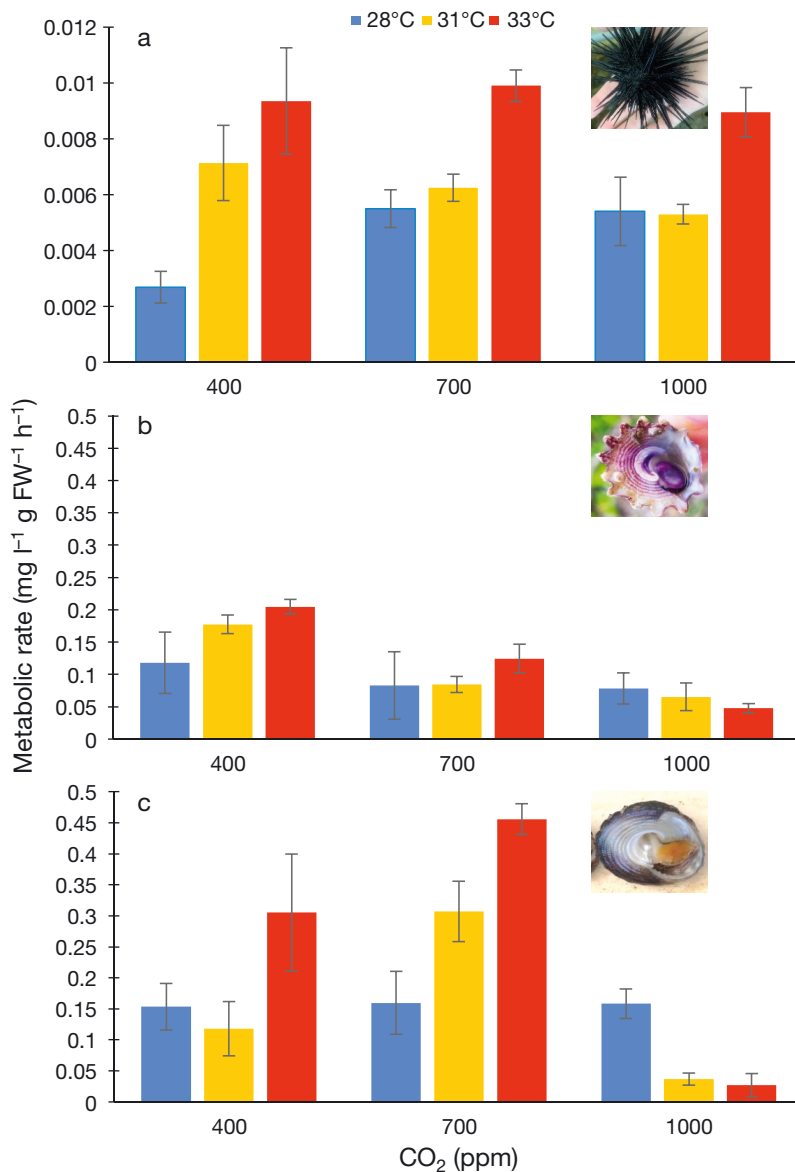


Fig. 1. Metabolic rate (mean \pm SE) of (a) *Heliocidaris crassispina*, (b) *Astralium haematragum*, and (c) *Trochus maculatus* after exposure to elevated temperature and CO₂. Bonferroni-corrected for repeated tests (2 tests, $\alpha = 0.025$). FW: fresh weight

action). This decrease created a mismatch whereby consumption of algae was reduced (Fig. 2a) when metabolic rate was elevated (Fig. 1a) under elevated CO₂ but not under elevated temperature alone. A similar response was found for *A. haematragum* and *T. maculatus*, with elevated CO₂ reducing the consumption rate substantially for both gastropods (Fig. 2b,c, Table 2). The physiological responses (Fig. 3) of the 3 species did, however, differ in that there was a positive correlation between metabolic rates and algal consumption for *A. haematragum* ($r_s = 0.46$, $p < 0.05$, Fig. 3b) but not for *H. crassispina*

or *T. maculatus* ($r_s = 0.15$, $p = 0.46$; $r_s = 0.34$, $p = 0.16$, respectively; Fig. 3a,c). For *H. crassispina*, this energetic mismatch was not apparent when exposed to higher temperatures alone but was driven by exposure to elevated CO₂ (Fig. 3a).

3.3. Thermal ramps, critical limits and mortality

By the end of the 4 wk exposure period, there was no mortality of *H. crassispina* exposed to any combination of temperature and CO₂ treatments. There was also no mortality for the gastropods under control CO₂ and temperature. In contrast, there was 100% mortality for both gastropods under moderate warming (31°C) at ambient CO₂. Under the highest temperature treatment (33°C), mortality rate for both gastropods was ~66% at ambient CO₂, which declined as CO₂ increased for *A. haematragum* but increased with CO₂ concentration for *T. maculatus* (Fig. 4).

Metabolic rates of sea urchins in thermal ramps was well described by the EMG function, demonstrating a positive relationship with temperature up until the T_{MMR}, followed by a sharp decline to mortality (ULL; Fig. S1 in the Supplement). T_{MMR} increased with warming treatments, from 31.4°C (control) to 32.2 and 34.3°C (+3 and +5°C treatments, respectively), demonstrating at least partial physiological acclimation to the elevated temperature treatments (Fig. S1, Table 3). A

similar temperature–metabolic relationship was found across all CO₂ treatments. The ULL of urchins also increased in response to the warming treatments, but with the highest ULL generally found in individuals exposed to 31°C (+3°C treatment) (Fig. S1, Table 3). Due to high mortality rates of both gastropod species in the elevated-temperature treatments, only individuals at control temperatures (28°C) had survival of enough individuals for temperature ramps; therefore, only the effect of CO₂ concentration on metabolic rates was tested for both gastropod species. T_{MMR} was lowest in the 700 ppm

Table 1. (a) Two-way ANOVA for the effects of CO₂ (400, 700 and 1000 ppm) and temperature (Temp; 28, 31 and 33°C) on metabolic rates of sea urchin *Heliocidaris crassispina* and the gastropods *Astrarium haematragum* and *Trochus maculatus*; and (b) post hoc Tukey's HSD for pairwise differences among significant factors. Significant p-values in **bold**, Bonferroni-corrected for repeated tests (2 tests, $\alpha = 0.025$)

| (a) ANOVA | Factor(s) | df | F | p |
|-----------------------|------------------------|----|-------|-----------------------|
| <i>H. crassispina</i> | Temp | 2 | 17.99 | <0.001 |
| | CO ₂ | 2 | 0.56 | 0.578 |
| | CO ₂ × Temp | 4 | 1.95 | 0.144 |
| <i>A. haematragum</i> | Temp | 2 | 1.02 | 0.382 |
| | CO ₂ | 2 | 10.56 | <0.001 |
| | CO ₂ × Temp | 4 | 1.24 | 0.328 |
| <i>T. maculatus</i> | Temp | 2 | 5.49 | 0.014 |
| | CO ₂ | 2 | 19.54 | <0.001 |
| | CO ₂ × Temp | 4 | 6.12 | 0.003 |
| (b) Tukey's HSD | Treatments | | | P _{adjusted} |
| <i>H. crassispina</i> | 33 > 28°C | | | <0.001 |
| | 33 > 31°C | | | 0.003 |
| <i>A. haematragum</i> | 400 > 700 ppm | | | 0.019 |
| | 400 > 1000 ppm | | | <0.001 |
| <i>T. maculatus</i> | 33 > 28°C | | | 0.03 |
| | 33 > 31°C | | | 0.02 |
| | 700 > 400 ppm | | | 0.02 |
| | 700 > 1000 ppm | | | <0.001 |
| | 400 > 1000 ppm | | | 0.01 |

treatment, whereas the ULL was highest in the 700 ppm treatment for both gastropods. The highest T_{MMR} was found in the highest CO₂ treatment (1000 ppm), whereas the ULL was lowest in the 1000 ppm treatment for both gastropods (Fig. S2 in the Supplement, Table 3).

4. DISCUSSION

We show that, despite sharing a similar ecological role, the response of the gastropods and urchins to predicted future temperature and CO₂ are disparate. We suggest that their physiological responses to these stressors may reflect different coping mechanisms for stressful environmental change. For the urchin, temperature drove metabolic rates, as expected in line with the MTE, but CO₂ had no discernible effect on metabolism. Elevated CO₂ did cause a potentially ecologically significant effect, however, driving a reduction in algal consumption. While the gastropods also reduced food consumption in response to altered conditions, the physiological

Table 2. (a) Two-way ANOVA for the effects of CO₂ (400, 700 and 1000 ppm) and temperature (Temp; 28, 31 and 33°C) on algal consumption rates of sea urchin *Heliocidaris crassispina* and the gastropods *Astrarium haematragum* and *Trochus maculatus*; and (b) post hoc Tukey's HSD for pairwise differences among significant factors. Significant p-values in **bold**, Bonferroni-corrected for repeated tests (2 tests, $\alpha = 0.025$)

| (a) ANOVA | Factor(s) | df | F | p |
|-----------------------|------------------------|----|-------|-----------------------|
| <i>H. crassispina</i> | Temp | 2 | 7.36 | 0.005 |
| | CO ₂ | 2 | 12.76 | 0.000 |
| | CO ₂ × Temp | 4 | 5.24 | 0.006 |
| <i>A. haematragum</i> | Temp | 2 | 7.27 | 0.006 |
| | CO ₂ | 2 | 20.11 | <0.001 |
| | CO ₂ × Temp | 4 | 6.56 | 0.003 |
| <i>T. maculatus</i> | Temp | 2 | 7.18 | 0.010 |
| | CO ₂ | 2 | 9.48 | 0.004 |
| | CO ₂ × Temp | 4 | 6.75 | 0.008 |
| (b) Tukey's HSD | Treatments | | | P _{adjusted} |
| <i>H. crassispina</i> | 31 > 28°C | | | 0.006 |
| | 33 > 28°C | | | 0.002 |
| | 400 > 1000 ppm | | | 0.001 |
| <i>A. haematragum</i> | 31 > 28°C | | | 0.006 |
| | 33 > 28°C | | | 0.045 |
| | 400 > 700 ppm | | | <0.001 |
| | 400 > 1000 ppm | | | <0.001 |
| <i>T. maculatus</i> | 33 > 28°C | | | 0.009 |
| | 33 > 31°C | | | 0.021 |
| | 400 > 1000 ppm | | | 0.004 |

responses underlying this response were disparate; *Astrarium haematragum* suppressed metabolic rates in response to elevated CO₂ and not temperature, whereas the metabolic rate in *Trochus maculatus* initially increased with the CO₂ increase, but then decreased when CO₂ was elevated further. Irrespective of these physiological differences, however, there was an overall reduction of algal consumption under the novel conditions, which could lead to a reduction in compensatory mechanisms in response to future conditions (Ghedini et al. 2015a). Temperature has a notable impact on invertebrates because it drives the rate of most biological processes (Parker et al. 2010, Byrne et al. 2011, Dupont et al. 2013, Côté et al. 2016, Zhang et al. 2017). Yet, climate change-driven temperature and CO₂ rise are inherently linked and so may not act in isolation. While interactive effects of temperature and CO₂ have been demonstrated for some urchin species (e.g. *Echinometra* sp.; Uthicke et al. 2014), whether these 2 stressors are additive, antagonistic, or have no interaction can depend on life stage and species-specific sensitivity

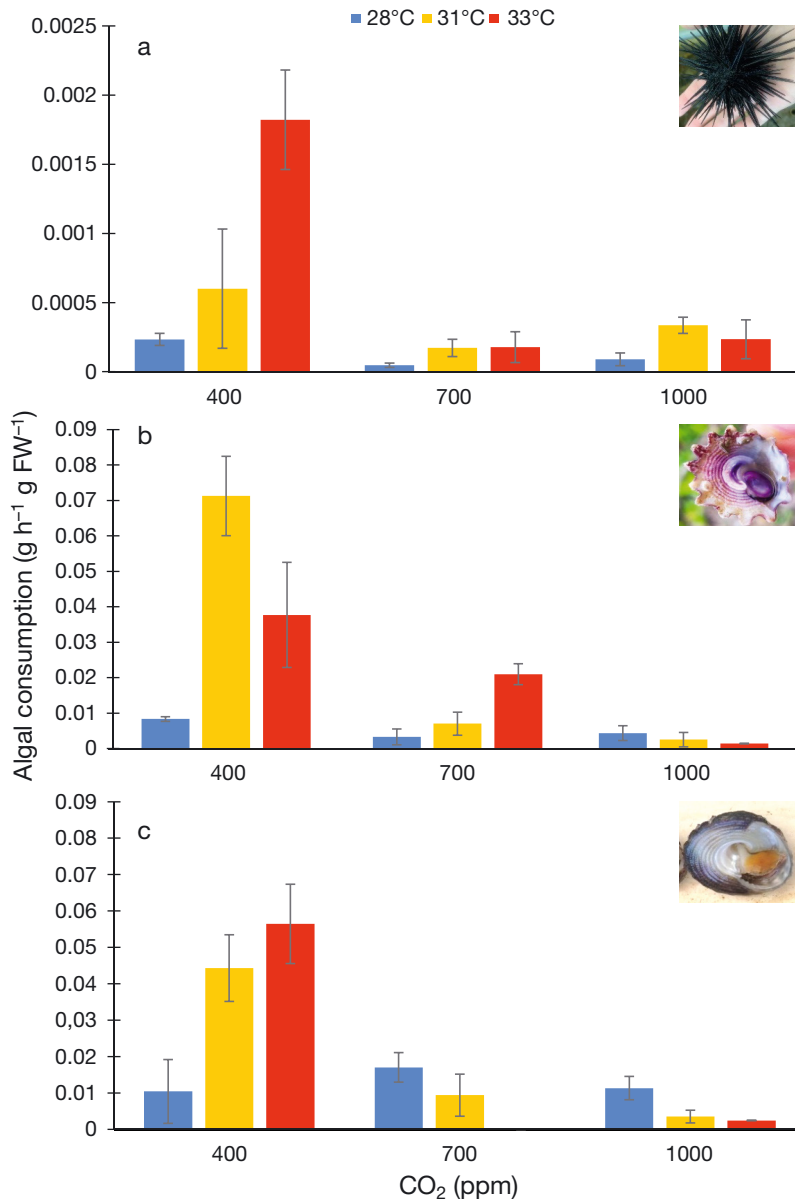


Fig. 2. Algal consumption rate (mean \pm SE) of (a) *Heliocidaris crassispina*, (b) *Astralium haematragum*, and (c) *Trochus maculatus* after exposure to elevated temperature and CO₂. Bonferroni-corrected for repeated tests (2 tests, $\alpha = 0.025$). FW: fresh weight

to different stressors (Dupont et al. 2010, Byrne & Przeslawski 2013). Here, we found that for the adult *Heliocidaris crassispina*, temperature was the primary driver of metabolism, with no effect of CO₂. Indeed, gradual warming, as with our temperature scenarios, can be the main driver in the physiological function of urchins, with metabolic depression exhibited during extreme high-temperature stress, followed by increased mortality (Harianto et al. 2018). In contrast, we found that metabolic rates increased with temperature, suggesting that predicted future

warming did not push this species beyond its temperature thresholds, above which metabolic depression would occur (Leung et al. 2017).

Despite a plethora of experimental research demonstrating the biological changes associated with increasing temperature, some field-based studies have found that sea urchin populations are not always adversely affected by acute heating events, either through direct physiological changes or through decline in food supply (e.g. the Western Australian heatwave of 2011, Smale & Wernberg 2014). This suggests that some urchin species or populations may possess physiological coping mechanisms to withstand higher temperatures (Martin et al. 2011, Foo et al. 2012, Hughes et al. 2012, Karelitz et al. 2019). Notably, we found that when exposed to predicted near-future temperatures, *H. crassispina* increased both T_{MMR} (by ~2–3°C) and ULL (by ~1–2°C). Increases in the T_{MMR} of individuals exposed to warmer temperatures have generally been interpreted as physiological acclimation to higher temperatures (Schulte et al. 2011, Schulte 2015). Conversely, complete physiological acclimation should allow for thermal compensation and the maintenance of similar metabolic rates at higher temperatures than non-acclimated animals (Seebacher et al. 2014), which was not seen in our urchins. Therefore, it is likely that *H. crassispina* exhibited partial metabolic acclimation to higher temperatures. Consequently, as under warming alone, feeding was maintained, and the

urchins in our experiment did not suffer high mortality rates, it is likely that this species will be able to maintain populations and, therefore, its ecosystem role under predicted near-future temperatures. Although there was partial metabolic acclimation to higher temperatures, there was no discernible effect of CO₂ on urchin physiology, despite high CO₂ commonly causing metabolic depression, or ‘hypometabolism’ responses in other invertebrates (Kroeker et al. 2010, Harvey & Moore 2017). While some species of mollusc have the capacity to maintain metabolic

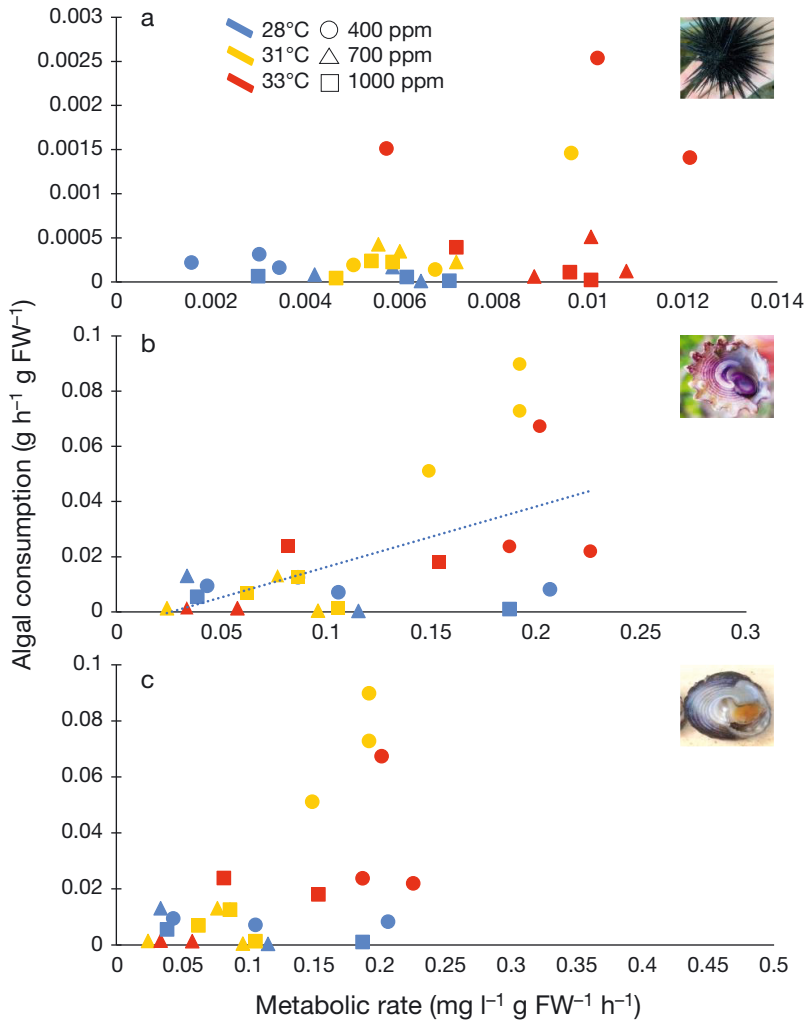


Fig. 3. Metabolic rate versus algal consumption for (a) *Heliocidaris crassispina*, (b) *Astralium haematragum*, and (c) *Trochus maculatus* after exposure to elevated temperature and CO₂. Dashed line in (b) shows significant correlation ($r_s = 0.46$, $p < 0.05$). FW: fresh weight

and feeding rates under acute exposure to hypercapnic conditions (e.g. the intertidal limpet *Patella vulgata*; Marchant et al. 2010), severe reductions in metabolism under combined hypercapnia and warming can lead to suppressed feeding and increased mortality (e.g. green abalone *Haliotis fulgens*, Tripp-Valdez et al. 2017; both gastropods in the present study). Therefore, it is likely that the negative physiological effects of depleted energy resources may have contributed to the >90% mortality seen in both gastropod species in our study and highlights the potential indirect consequences of elevated CO₂ and temperature on marine communities (Pörtner et al. 2004).

Consumption of algae was substantially reduced under elevated CO₂ for both taxa. Coupling the

physiological responses with changes to feeding habits will likely bring about different consequences for the long-term fitness and survival of the gastropods compared with the urchins. As the gastropods had depressed metabolic rates at high CO₂, a concurrent reduction in consumption is expected; less metabolic energy is required from aerobic respiration to meet these new lower energy demands (Leung et al. 2017). In contrast, although urchin metabolic rates remained high under elevated CO₂, like the gastropods, algal consumption by urchins was substantially reduced. This reduced energy intake but high energy demand results in an energetic imbalance, as there is a lack of compensatory feeding to fulfil the higher energy requirements (Lannig et al. 2010, Leung et al. 2017). Under such conditions, metabolic depression is an adaptive strategy for hypercapnic conditions seen across all animal phyla and particularly across non-cryptobiotic animals such as molluscs (Guppy & Withers 1999). In urchins, however, feeding rates seem less plastic, with other *Heliocidaris* spp. also demonstrating metabolic mismatch in response to environmental stress (Carey et al. 2016). Such energetic mismatches are a time-limited strategy causing deleterious impacts on energy homeostasis and the ensuing biological functions (Lannig et al. 2010). For

example, brittle stars *Ophiura ophiura* have a reduced rate of arm regeneration due to an energy deficit under ocean acidification (Wood et al. 2010); multiple species of gastropod have slower growth or increased mortality under acidification or temperature stress (Zhang et al. 2015, Leung et al. 2017). This diversity of morphological or physiological outcomes reflects the time-limited nature of the metabolic depression (Lannig et al. 2010), and highlights that mortality may be imminent under continued stress, which was not captured due to the duration of the present study.

While individual species may be susceptible to changes in environmental conditions, ecosystems may resist such changes where there is functional redundancy in the species which fill key roles in

Fig. 4. Cumulative mortality of gastropods (a) *Astraliium haematragum* and (b) *Trochus maculatus* after 1 mo exposure to combinations of temperature and CO₂

system function (Bremner et al. 2003, Covich et al. 2004, Stuart-Smith et al. 2013). Indeed, it is necessary to understand whether ‘functionally equivalent’ species respond in similar or different ways to changing environmental conditions in order to predict how an ecosystem may be impacted by environmental change (Aguilera 2011, Xu & Xu 2017). For example, the abundance of sea urchins is reduced under elevated CO₂ concentrations at natural analogues for future conditions (CO₂ seeps), from which a reduction in herbivory and proliferation of algae may be predicted; however, systems can maintain stasis where herbivory is not reduced when other herbivores, such as herbivorous fish, concurrently increase in abundance to fill the functional role (Baggini et al. 2015). In the present study, we demonstrate divergent biological responses between urchins and gastropods which nominally fill the same functional role. Notably, by the end of the experimental period, gastropod mortality was high, but the urchin mortality was not, suggesting that

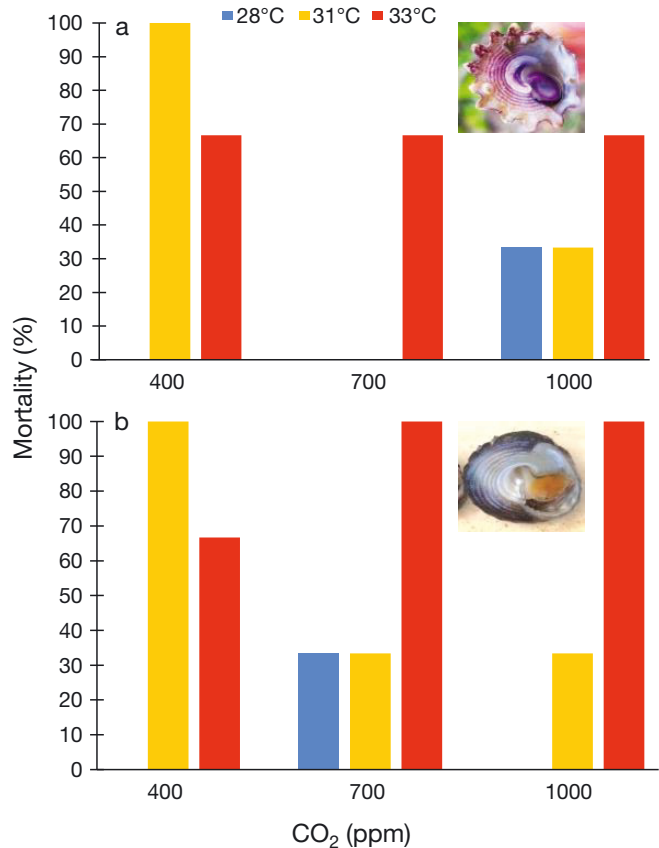


Table 3. Temperature at maximum metabolic rate (T_{MMR}) and upper lethal limit (ULL) as described by an exponentially modified Gaussian function (EMG) model for *Heliocidaris crassispina*, *Astraliium haematragum* and *Trochus maculatus* after 1 mo exposure to CO₂ (400, 700 and 1000 ppm) and temperature (28, 31 and 33°C); and difference in T_{MMR} in the elevated compared to the control treatment (400 ppm, 28°C) predicted by the EMG model. For both gastropod species (*A. haematragum* and *T. maculatus*), thermal ramps were only possible for the 28°C treatment because of the high mortality in the 31 and 33°C treatments

| Species | Exp. CO ₂ level (ppm) | Exp. temp. (°C) | T _{MMR} (°C) | Difference vs. control (°C) | ULL (°C) |
|-----------------------|----------------------------------|-----------------|-----------------------|-----------------------------|----------|
| <i>H. crassispina</i> | 400 | 28 | 31.4 | | 41.65 |
| | | 31 | 32.2 | +0.8 | 44.11 |
| | | 33 | 34.3 | +2.9 | 43.12 |
| | 700 | 28 | 33 | +1.6 | 42.64 |
| | | 31 | 40 | +8.6 | 53.66 |
| | | 33 | 33.3 | +1.9 | 43.95 |
| | 1000 | 28 | 32.7 | +1.3 | 41.85 |
| | | 31 | 33.7 | +2.3 | 42.08 |
| | | 33 | 34.8 | +3.4 | 42.49 |
| <i>A. haematragum</i> | 400 | 28 | 29.7 | | 38.10 |
| | 700 | 28 | 28.7 | +1 | 38.88 |
| | 1000 | 28 | 33.5 | +3.8 | 36.54 |
| <i>T. maculatus</i> | 400 | 28 | 30.3 | | 40.48 |
| | 700 | 28 | 26.5 | -3.8 | 42.57 |
| | 1000 | 28 | 35.4 | +5.1 | 35.89 |

the urchins ultimately succeeded in avoiding mortality due to the environmental change during this time period. Indeed, what may first appear to be a beneficial physiological coping mechanism exhibited by the gastropods (i.e. metabolic depression) ultimately led to high mortality rates, possibly because of the ultimate detrimental effect of reduced foraging (Guppy & Withers 1999, Lannig et al. 2010). Thus, this type of response may be advantageous for shorter-term environmental fluctuations but detrimental over longer periods (Mertens et al. 2015). While urchins appeared to have better survivability to these stressors, especially in isolation (e.g. warming alone), the energetic imbalance between demand and acquisition under combined stressors suggests subsequent trade-offs and eventual mortality, which may have potential negative implications for successful population maintenance under future change.

The limitations associated with shorter-term studies are that it is difficult to predict the type of trade-offs that may occur, how the organism's physiology will be impacted over a longer period and whether this would be a detriment to survival, particularly regarding more sensitive life-stages, which will govern population maintenance. One aspect of the longer-term impact of high CO₂ that is not observed in the present study is the potential for shell or test erosion. Decreasing calcification rates have been demonstrated for many marine taxa resulting from decreasing CaCO₃ (calcium carbonate) saturation (Feely et al. 2004, Kroeker et al. 2010). Echinoderms primarily produce a calcite skeleton (high-Mg calcite), and as such, increased CO₂ can alter growth rates and the pattern of development due to lower saturation rates. Near-future CO₂ has been shown to have a greater impact on spine dissolution rate than on deposition, therefore having less impact on growth for some species and more impact on erosion rates for both urchins and gastropods (Chen & Shu-lun 1997, Nienhuis et al. 2010, Wolfe et al. 2013). The effect of CaCO₃ deposition and dissolution rates differs across species; for example, elevated CO₂ impairs the growth to larval stage in *Heliocidaris tuberculata*, but not in *H. erythrogramma* (Hardy & Byrne 2014). However, concurrent warming may offer a buffering mechanism, having been demonstrated to increase the size and growth rate of urchin larvae (Sheppard Brennan et al. 2010, Wolfe et al. 2013) acting antagonistically and significantly reducing the negative impacts of elevated CO₂ (Byrne et al. 2013). Similarly, gastropods which have shells composed of mainly calcite have demonstrated elevated dissolution rates as a result of increased CO₂ (~1600 ppm) (Nienhuis et al. 2010). In comparison to the shell structure of urchins, however, most gastropods have a shell composed of aragonite, which is a less stable polymorph of CaCO₃, in addition to calcite, and are therefore potentially more at risk from dissolution due to changing ocean chemistry, including the species used in the present study (Chunhabundit et al. 2001, Nudelman et al. 2006, Chatzinikolaou et al. 2017).

In combination with reduced food acquisition due to metabolic depression, the differences between shell structure of the urchins and gastropods may therefore have contributed to the severity of the response to CO₂ and higher mortality in the gastropods. A short-term (7 d) exposure to elevated temperature and CO₂ (+4°C, ~1000 ppm) on *Trochus histrio* caused reduced feeding capacity and performance due to CO₂, though this was countered by a positive response to temperature increases (Grilo et

al. 2019), contrary to our findings which found an interactive effect of these 2 stressors. However, the longer exposure time used in our study and diminished energy reserves due to reduced consumption may have resulted in the time-limited response and concurrent mortality experienced by gastropods in the higher temperature treatments, which highlights the limitation of the short nature of this study, and differences that can occur with varying lengths of exposure.

Over a longer period of exposure, *H. crassispina* has been shown to recover and acclimate from disrupted metabolic rates caused by elevated CO₂, though longer-term impacts may include morphological damage such as wearing out of feeding apparatus (Wang et al. 2013), with effects shown to be largely regulated by exposure time for different invertebrates. For example, reduced feeding capacity over a longer period may result in reduced slower growth rates (Yatsuya & Nakahara 2004) and smaller urchins have been linked to higher population densities and therefore reduced food availability (Urriago et al. 2016). Similarly, longer-term exposure to increased CO₂ and temperature in gastropods (5 mo) when compared to shorter exposure (5 wk) shows that an initial decrease in feeding rates due to the combined effect of both these stressors was reversed over the longer time frame (Russell et al. 2013). Whether top-down control on algal biomass and habitat maintenance in subtidal rocky reefs can withstand environmental change is therefore likely to be dependent on grazer diversity (Blake & Duffy 2010, Baggini et al. 2015) and their different physiological responses to stressors, capacity to resist change, and ability to continue to fulfil their ecological role. Thus, these key species are likely to be differentially affected by future environmental change, which could potentially reduce the strength of ecological compensatory responses within this grazing community.

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