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Beyond spatial and temporal averages: ecological responses to extreme events may be exacerbated by local disturbances

Giulia Ghedini¹, Bayden D. Russell^{1,2}, Laura J. Falkenberg^{1,3} and Sean D. Connell^{1*}

Abstract

Background: The ecological consequences of climate change will be driven by a combination of both gradual and abrupt changes in climatic conditions. Despite growing evidence that abrupt abiotic change of extreme events may profoundly alter ecological processes, it remains unclear how such events may combine with longer-term global and local disturbances. Here, we focused on a key process of herbivory and tested how its strength would change in response to forecasted global (CO₂ enrichment) and local disturbances (nutrient enrichment) under abrupt (heat wave) or gradual (future temperature) changes in temperature, using an herbivorous gastropod and turf algae interaction within kelp forests as a model system.

Results: The heat wave caused the greatest magnitude of change in consumption across all treatment combinations. The positive effect of nutrient enrichment on consumption was magnified by increasing temperature, but caused surprisingly intense herbivory when combined with the heat wave. Carbon and nutrient enrichments individually increased consumption with nitrogen overriding the positive effects of CO₂.

Conclusions: These results not only reveal that the strength of ecological responses to extreme events may substantially exceed those manifested under 'average' future conditions, but also that the effects of extremes may be exacerbated by local disturbances. If disproportionate ecological change occurs where extreme events overlap with local disturbances, scientists and managers will need to recognize spatial and temporal heterogeneities of environmental change to think beyond averages.

Keywords: Climate, Temperature, Ocean acidification, Eutrophication, Heat wave, Disturbance, Herbivory

Background

Climate change is driven by both the consequences of gradual changes in climatic conditions (i.e. 'trends') and also their increased variability (i.e. 'events') [1, 2]. There is growing consensus on the importance of understanding ecological responses to 'events' rather than 'trends' as climate extremes may drive profound ecological changes over short-time scales [3–5]. Extreme events represent discrete, pulse disturbances that cause abrupt changes to the abiotic environment relative to the life cycle of most organisms or ecological processes [2]. Hence, such short-term extreme variation in climatic

conditions can be biologically more significant than longer-term trends of change to which organisms have greater probability of acclimation, adaptation and, ultimately, evolution [2, 6, 7].

Evidence of the importance of climate extremes as drivers of ecosystem dynamics, structure and function is increasing through field observations and experimental studies [8–13], although the severity of the impacts of extreme events remains variable [9]. Despite the potential ecological importance of extremes, most climate change research, particularly in the marine environment, remains focused on average trends of change (but see [5, 12, 13]). Hence, our understanding of ecological responses to extreme and abrupt changes in abiotic conditions remains poorly developed [14]. Since extreme events are becoming increasingly common and intense [15, 16] and their ecological effects on communities can

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be significant [9, 12], we need to move beyond trend-based studies to include studies of 'events'.

Changes in climate are, however, not occurring in isolation from other human-driven disturbances. Notably, extreme events will interact with longer-term local and global stressors to drive change [14, 17, 18]. As ecological responses are often driven by small-scale variability in environmental conditions, efforts to manage and conserve natural communities in the face of increasing abiotic change require consideration of how global and local stressors may combine to drive ecological change [14, 19]. Hence, establishing the nature of interactions between multiple stressors acting at different spatial and temporal scales is critical to build a more accurate framework to predict the ecological consequences of an increasingly variable environment [20, 21]. Whilst the importance of studying stressors in combination, rather than their individual effects, has long been recognized and research has been moving towards studies of multiple stressors [22–24], the combined effects of climate extremes with other disturbances remain very much unexplored [25].

Coastal areas are particularly vulnerable to such interactions as they often experience combinations of changes in climatic conditions (e.g. temperature, CO₂ enrichment) and local stressors (e.g. nutrient enrichment) [23, 26, 27]. Moreover, shallow coastal areas are not only exposed to gradual changes in temperature due to warming but also more frequently experience abrupt changes during heat waves [12, 15]. Whilst the effects of warming on individual organisms and trophic interactions are relatively well understood [28–30], such predictions may be complicated in a multi-stressor context. In particular, anticipations of the ecological effects of changing climate may be complicated if the effects of abrupt (i.e. heat waves) or gradual changes in temperature (i.e. long-term predictions) are differentially modulated by co-occurring stressors [31, 32].

Herbivory is an ecological process that rapidly responds to abiotic changes driven by global (e.g. temperature, CO₂) and local stressors (e.g. nutrients) in terrestrial [33, 34] and aquatic systems [35–37]. As temperature is one of the main determinants of metabolism, predicted changes in temperature are expected to be a focal factor in determining strength of herbivory [28–38]. Whilst long-term warming may increase herbivory mainly by directly enhancing consumer metabolism [29], such effects on consumption can be reduced or even reversed with further increases in temperature [38]. For example, herbivores may reduce consumption rates when temperature increases to values that approach their physiological limits [39]. To complicate predictions, however, is the consideration that rates of herbivory are not only determined by direct effects of abiotic changes, but also by indirect effects mediated by changes in food quality and palatability

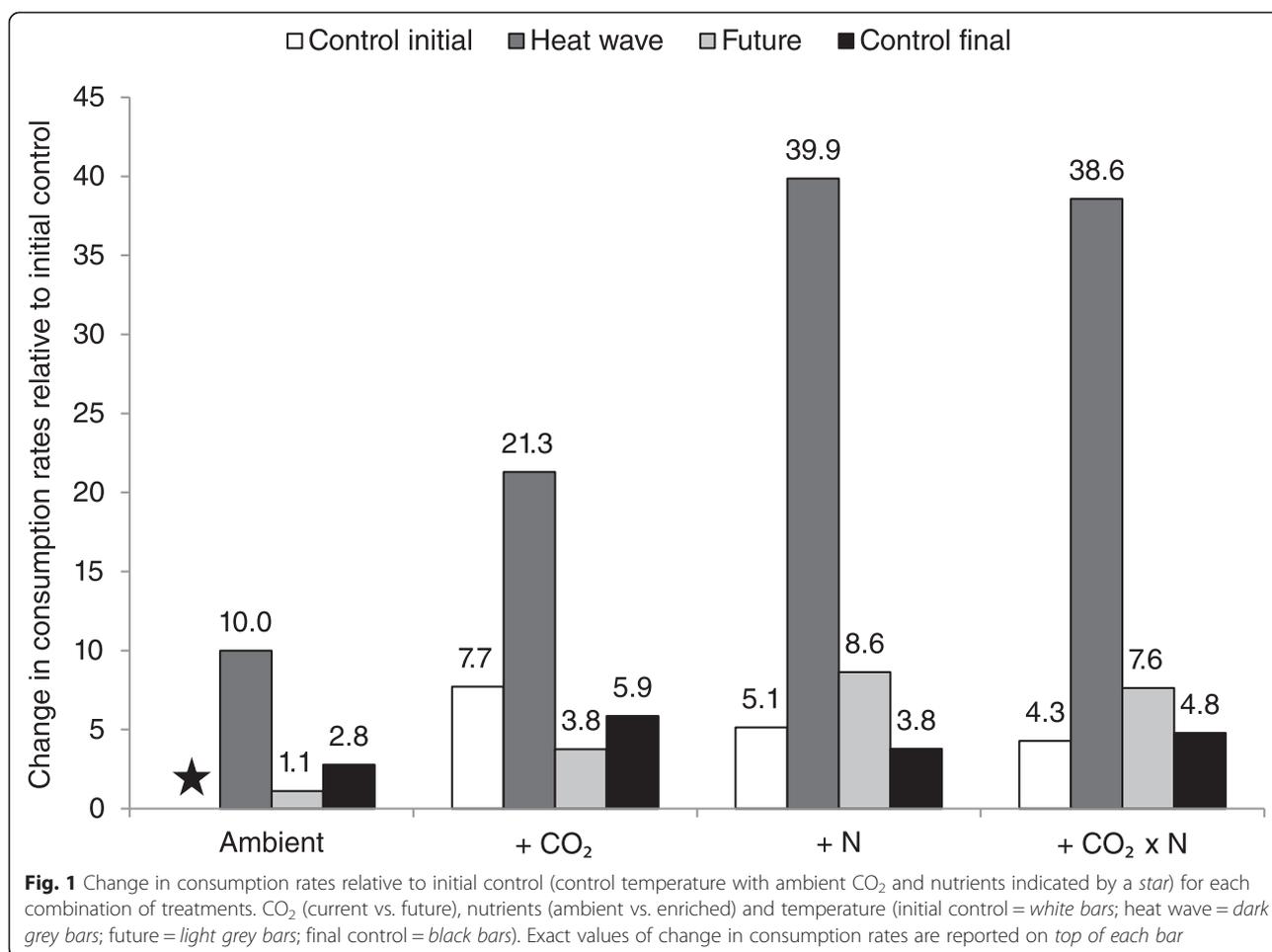
[33, 40, 41]. Hence, the effects of temperature on herbivory may be mediated by co-occurring changes in the abiotic environment [41]. For instance, changes in the availability of carbon and nitrogen indirectly modify consumer pressure by altering plant (or algal) composition and nutritional quality, often increasing consumption rates as nitrogen content increases [33, 40, 42]. Therefore, strength of herbivory will ultimately not only be determined by the changes in temperature experienced by consumers (i.e. abrupt vs. gradual) but also by carbon and nitrogen availability in the environment. To date, however, there has been no assessment of how abrupt changes in temperature (i.e. heat waves) may interact with carbon and nitrogen enrichment to alter consumption rates relative to gradual warming scenarios. Therefore, despite the increasing occurrence of heat waves, we are unable to predict the direction and magnitude of changes in herbivory during such events.

Here, we provide an experimental assessment of how abrupt (heat wave) and gradual changes in temperature (predicted future temperature) may differentially interact with long-term global (CO₂ enrichment) and local stressors (nutrient enrichment) to alter herbivore pressure. Our experimental assessment focuses on a model herbivore-plant interaction between an herbivorous gastropod and turf-forming algae within kelp forests. We predict that changes in herbivory observed under future temperatures will not only differ from those observed during an extreme event, but also that their effects will be differentially mediated by co-occurring global and local disturbances.

Results

Changes in consumption rates were driven by an interaction between temperature and nutrient treatments as well as by an interaction between CO₂ and nutrients (Fig. 1, Table 1, Additional file 1).

Notably, the heat wave event caused the greatest magnitude of change in consumption rates across all treatment combinations (Fig. 1, Table 1). Specifically, under ambient nutrient conditions, the heat wave increased consumption rates between 10 and 20 times relative to the initial control temperature (Fig. 1). The effects of the heat wave were magnified by nutrient enrichment, so that consumption increased up to 40 times relative to initial control rates (Fig. 1). Conversely, the effects of future temperature on consumption were not distinguishable from those of control temperatures (Fig. 1); the Student-Newman-Keuls test, indeed, did not identify any significant change in consumption rates between future and control temperatures (either initial or final control) under either ambient or enriched nutrients (Table 1, Additional file 1).



Whilst nutrient enrichment did not alter consumption rates at control temperature (either initial or final control), nutrients significantly increased consumption rates at future temperature and this effect was exacerbated by the heat wave (Table 1, Additional file 1). Consumption rates were not different between ambient and enriched nutrients at both the initial and final control temperatures set at 16 °C (i.e. the two controls behaved in the same way), but nutrients elevated consumption within future and heat wave treatments (Table 1). The lack of detectable differences between controls of 16 °C at the beginning and end of the experiment indicated not only that the responses were due to the treatments per se but also that elevated temperatures did not have long-lasting effects on herbivory.

As mentioned above, consumption rates were also altered by an interaction between carbon and nitrogen treatments (Table 1). Whilst carbon enrichment significantly increased consumption rates at ambient nutrient conditions, this effect was not visible in the presence of nutrient enrichment (Fig. 1, Table 1).

Nutrient enrichment significantly increased consumption rates with a stronger effect at ambient rather than enriched CO₂ conditions (Fig. 1, Table 1).

Discussion

Since frequency and intensity of extreme events increase with climate variability [16], abrupt changes in abiotic conditions might become stronger ecological drivers than gradual changes [2, 14]. Here, we show that the ecological effects of an extreme event (i.e. heat wave) substantially exceeded those of long-term global (i.e. future temperature, CO₂ enrichment) and local abiotic changes (i.e. nutrient enrichment). Indeed, the magnitude of change in consumption rates of herbivores caused by the heat wave over a short-time scale (hours) was significantly greater than that elicited by all other experimental conditions (up to 40 times greater than control conditions).

As temperature is a main determinant of consumer metabolism [28, 30], we anticipated that both the heat wave and future temperature treatments would enhance

Table 1 ANOVA on *per capita* consumption rates

Source	df	MS	F	p
Temperature (T)	3	6.95	103.28	0.0000*
CO ₂	1	0.39	5.82	0.0187
N	1	2.94	43.70	0.0000*
T × CO ₂	3	0.04	0.62	0.6048
T × N	3	1.66	24.60	0.0000*
CO ₂ × N	1	0.56	8.36	0.0052*
T × CO ₂ × N	3	0.07	1.09	0.3588
Residual	64			

SNK on T × N

Ambient nutrients: H >> F = C _i = C _f	Heat wave: +N >> -N
Enriched nutrients: H >> F = C _i = C _f	Future: +N > -N
	Initial Control: +N = -N
	Final Control: +N = -N

SNK on CO₂ × N

Ambient nutrients: +CO ₂ >> -CO ₂	Ambient CO ₂ : +N >> -N
Enriched nutrients: +CO ₂ = -CO ₂	Enriched CO ₂ : +N > -N

Analyses ($n = 5$) were done for the four levels of temperature (initial control temperature: C_i; heat wave: H; future: F; final control: C_f), two levels of CO₂ (current: -CO₂ vs. future: +CO₂) and two levels of nutrients (ambient: -N vs. enriched: +N). The critical value of significance has been adjusted to $\alpha = 0.01$ (see the 'Methods' section). Data were non-transformed. The symbol * denotes terms significant at $\alpha = 0.01$

consumption. Contrary to our predictions, only the heat wave resulted in a significant increase in consumption rates. This result reinforces the notion that extreme events are likely to prompt stronger ecological responses than gradual trends of change and, therefore, deserve a greater research focus [4, 14]. Whilst gradual changes may allow time for organisms to acclimate and ultimately adapt [2, 7], abrupt changes can rapidly alter the strength of ecological processes by challenging the acclimatory capacity over short periods of time [2, 9].

The absence of significant effects of future temperatures on consumption rates suggests that even a relatively short acclimation period (3 months) may be sufficient to allow subtidal gastropod grazers to acclimate to near-future conditions and, thus, show subtle or no ecological changes to such conditions [43]. It is, however, possible that our effects of future warming were minimized by the previously experienced heat wave as grazers were exposed to future temperatures after the heat wave event. Hence, we are cautious not to overstate the absence of effects of gradual warming. Importantly, we detected that the effects of the local stressor (i.e. nutrient enrichment) were differentially mediated by changes in temperature (i.e. control vs. future temperature vs. heat wave). Progressive increases in temperature exacerbated the effects of nutrient enrichment, which caused the strongest increases in consumption rates when combined with the heat wave. These results indicate that abrupt and

gradual changes in temperature may differentially mediate ecological responses to co-occurring stressors. Hence, understanding regional and local vulnerability to environmental change requires consideration of how abrupt and gradual changes in abiotic conditions may interact with other stressors acting at different spatial and temporal scales [21, 23, 44].

Importantly, the combined effect of the heat wave and the local stressor caused surprisingly intense herbivory, with a magnitude of change substantially greater than that caused by any other stressor or combination of stressors. If the ecological effects of extreme events are exacerbated by local change (e.g. nutrient pollution), then our ability to anticipate and mitigate the consequences of climate change may be substantially challenged if such interactions are not recognized. In locations with intensive terrestrial-based human activities (e.g. cities or agriculture), in particular those likely to experience more intense and frequent rainfall events, nutrient enrichment from land runoff may accelerate change, particularly when in combination with warmer temperatures [27, 45, 46]. This awareness, however, also empowers local managers as mitigation of the effects of climate extremes may be possible through management of local stressors [21, 27, 47, 48].

Nutrient enrichment is frequently associated with the decrease in water quality along coastal areas [23, 49], where it often interacts in non-additive ways with co-occurring stressors to drive ecological change [23, 27]. Accordingly, we found that nutrient enrichment not only increased consumption with increasing temperature but also interacted with carbon enrichment to alter consumption rates. Variations in carbon and nitrogen availability in the environment are well-known factors in driving changes in consumer pressure by altering the palatability and composition of primary producers [34, 40] as well as through direct effects on consumers [50, 51]. As increases in the nutrient content of algae often drive increases in consumption [40], it is possible that changes in herbivory rates are more strongly influenced by changes in nutrient rather than carbon availability. Similarly, we found that the effects of nutrients on consumption overrode those of carbon enrichment. In contrast, warming often stimulates herbivory by directly increasing the energetic demand of consumers [29, 39]. Although we do not exclude possible indirect effects mediated by algae, the strong increases in consumption that we observed during the heat wave are more likely a consequence of increased consumer metabolism rather than indirect effects. Changes in the composition or nutritional quality of algae, indeed, would seem unlikely given the short duration of the extreme event (i.e. hours).

The intensification of abiotic change due to human activities is expected to increase variation in strength of

herbivory across regions [29]. Such variation might be driven not only by the combination of stressors locally experienced but also by the rapidity and magnitude of abiotic change. Here, for example, we show that abrupt and gradual abiotic changes may differentially interact with local stressors to alter rates of herbivory in substantially different ways. Changes in top-down pressure can have profound effects on community structure [52], but the community-level implications of such changes are strongly context-dependent and require consideration of both the response of herbivores to specific stressors and the effects of these stressors on primary producers. Where changes in herbivory do not reflect changes in productivity, strong increases in consumption during heat waves may impact primary producers if herbivores consume over short periods of time a substantially greater amount of food than would normally be consumed [12, 53]. Conversely, where abiotic change stimulates consumption to vary in a proportional way to changes in productivity, increased herbivory can provide a stabilizing mechanism against community change [54]. For example, in the system that we consider, an increase in consumption of turf algae by gastropod grazers can counter the expansion of these weedy species promoted by increasing levels of abiotic change [54]. However, when abiotic change (e.g. temperature) exceeds the physiological tolerance of herbivores, these can become inactive [39, 55] meaning that such compensatory effect may fail as herbivory is strongly suppressed.

Despite the recognized importance of interactions among local and global stressors [22, 56] and of extreme events in driving ecological change [4], we lack a framework to predict the combined effects of climate variability and long-term abiotic change [14, 25]. Hence, forecasting ecological responses to extreme events and how these responses vary depending on interactions with co-occurring stressors remains a major challenge [5, 56]. The results here presented not only emphasize how interactions among multiple stressors drive variability in ecological responses, but also demonstrate that the ecological effects of extreme events can be profoundly different (and stronger) than the effects of gradual abiotic change. This result is a timely reminder given that much of our understanding of the effects of environmental change remains based on studies of one or two environmental parameters that focus on average change [14].

In conclusion, it is particularly insightful that local change can exacerbate the effects of extreme events. Despite growing recognition that extreme events shape ecological communities [2, 4, 12, 13], their ecological effects remain variable and difficult to anticipate [9]. If disproportionate ecological change occurs where extreme events overlap with local disturbances, scientists and managers will need to recognize spatial and

temporal heterogeneity of environmental change to think beyond averages.

Methods

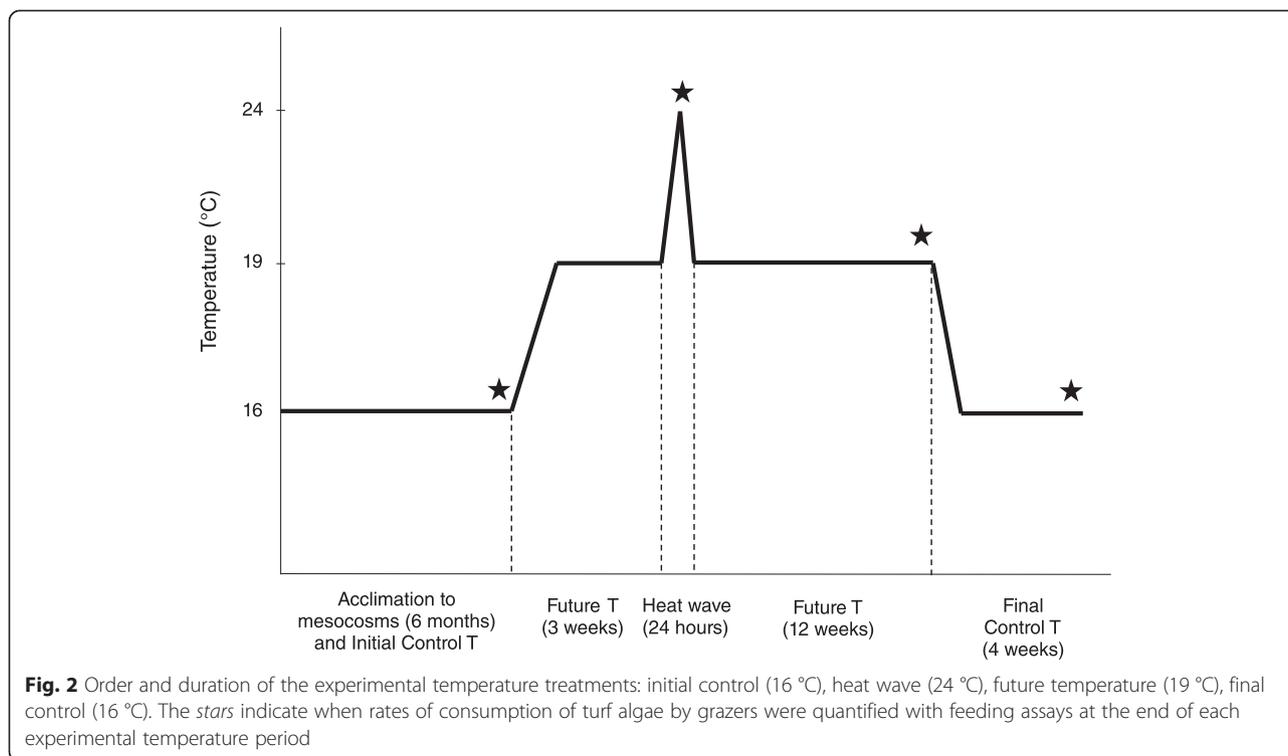
Experimental protocol

Gastropod grazers (*Turbo undulatus*) were collected on a shallow subtidal rocky reef within a kelp forest (O'Sullivan Beach, South Australia, Australia) and, then, acclimated in aquaria at seasonal ambient temperature (16 °C) and experimental levels of CO₂ and nutrients (see below for details) for 6 months prior to experiments at the University of Adelaide, South Australia. We had five replicate aquaria (L 40 × W 30 × H 20 cm, 15 L) for treatment combination of CO₂ (current vs. future) and nutrients (ambient vs. enriched), each aquaria with one grazer ($n = 5$). The aquaria were exposed to full sunlight and its natural daylight cycle. Following acclimation, consumption rates of grazers were measured at different temperature scenarios to which the same grazers were exposed over time (see the 'Temperature treatments' section below, Fig. 2), whilst maintaining constant CO₂ and nutrient treatments. During the entire period of acclimation and experiments, grazers were kept in cages (10 × 10 cm, $n = 1$ grazer per cage per aquaria) and were fed with turf algae (defined as in [57]) grown on panels (10 × 10 cm) in the same experimental conditions that the grazers were exposed to.

CO₂ and nutrient treatments

During the entire duration of the experiment, including the initial 6-month acclimation period, levels of CO₂ and nutrients were maintained constant for each treatment. The target partial pressure of CO₂ ($p\text{CO}_2$) was based on the current ambient (current, 400 ppm of CO₂) and the prediction under the RCP6.0 scenario for the year 2100 for atmospheric CO₂ (future, 950 ppm) [15] (Additional file 2). Elevated CO₂ concentrations were maintained by bubbling air with enriched CO₂ into the appropriate mesocosms using a Pegas gas mass flow controller (Columbus Instruments, CO, USA), whilst ambient CO₂ treatments were maintained by bubbling ambient air. Water pH_{NBS} was measured daily, and titration was performed during each trial to determine alkalinity using an automated titrator (888 Titrand, Metrohm, USA). Partial pressure of CO₂ was calculated from measured pH_{NBS}, alkalinity, temperature and salinity using the CO2SYS program for Excel [58] with constants from Mehrbach et al. [59] as adjusted by Dickson and Millero [60] (Additional file 2).

Nutrients were enhanced using Osmocote Plus® (Scotts) controlled release fertilizer (6 months release: 15 % N, 5 % P, 10 % K), which was placed in nylon mesh bags (1-mm mesh size) and attached to the bottom of mesocosm assigned to enriched nutrient treatments (5 g



per mesocosm). These nutrient additions were used to achieve elevated nutrient concentrations which reproduced those of dissolved inorganic nitrogen (DIN) in urban catchments under moderate to heavy rainfall events (DIN 0.55 ± 0.13 mg/L; enriched nutrients) in contrast to ambient nutrient conditions (DIN 0.09 ± 0.02 mg/L; ambient nutrients) [41], as used in previous experiments [42].

Temperature treatments

Following the initial 6-month acclimation period at control temperature conditions (16 °C as average spring/autumn water temperature of South Australia), consumption rates were measured with feeding assays (see the 'Response variables and Analyses' section below) to establish a baseline of consumption rates among the treatments at control temperature (i.e. 16 °C) at the start (initial control) and end of the experiment (final control) (See Fig. 2 for experimental design; Additional file 2 for experimental conditions). The analytical inclusion of consumption rates measured at the initial and final control temperatures enabled the identification of treatment effects during the intervening times (i.e. heat wave and future temperature).

After the initial control, all grazers were gradually acclimated to predicted future average temperature ('future temperature', 19 °C) for 3 weeks, representing a three degree increase on top of the control temperature as predicted by global warming trajectories [15]. At the end of

this 3-week period, temperature was increased by 4 over a 24-h period (from 19 to 23 °C), simulating a heat wave event during which consumption rates were quantified to assess the effects of abrupt abiotic change. The magnitude of change in temperature was comparable to the heat wave described by Wernberg et al. 2013 [12], which was up to 4° (24 °C) above the high summer temperatures (20 °C) for Western Australia.

Subsequently, temperature was reduced back to the future temperature treatment (19 °C) which was maintained for three consecutive months over summer. Consumption rates were quantified again at the end of this period to assess the effects of long-term warming. Finally, temperature was gradually reduced over a week to the control temperature level (16 °C) at which grazers were maintained for three more weeks prior to quantifying consumption rates to establish a final control.

Response variables and analyses

Feeding assays were run at the end of each temperature exposure period (initial control, heat wave, future temperature, final control; see Fig. 2) to measure the rate at which grazers consumed turf algae. Each grazer was provided with a fresh panel (10 × 10 cm) of turf algae at the start of each feeding assay. Turf cover on the panel was measured at the start and at the end of the feeding assay. *Per capita* consumption rates were then determined as the percentage cover of turf algae consumed per grazer per hour in each treatment combination of

temperature, CO₂ and nutrients. The duration of feeding essays was of 24 h for the heat wave (and initial control) and 96 h for future temperature (and final control). Percentage cover of algae was measured using a quadrat the same dimensions as the panel, divided into 25 sub-quadrats and assigning between 1 and 4 points in percentage cover to each of the 25 sub-quadrats according to the cover of turf present, so that the total sum would be 100 in a panel completely covered by turfs (as used in [54]). We agree that separating the direct and indirect causes of change in herbivory offers useful insights into the drivers of change, but this analysis would not improve our interpretation as to whether herbivory is modified by extreme events and their interactions with long-term trends and local disturbances.

Feeding rates were compared among temperature, nutrients and CO₂ treatments using univariate analyses of variance ($n = 5$). The three factors were treated as fixed and orthogonal with four levels for temperature (initial control, heat wave, future, final control), two for CO₂ (current vs. future) and two for nutrients (ambient vs. enriched). These feeding rates were derived from the same individuals within the same temperature treatments that were adjusted through time but crossed with independent combinations of enriched CO₂ and nutrients. Hence, our measures of feeding rates are not independent of temperature; this non-independency might have increased the probability of type I error rates because variation between grazers within a treatment is likely to be smaller within temperature treatments than when estimated from independent individuals. To reduce the probability of type I error, therefore, we revised the critical level of alpha from 0.05 to 0.01 [61].

Additional files

Additional file 1: Consumption rates. (DOCX 22.8 kb)

Additional file 2: Experimental conditions. (DOCX 23.3 kb)

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

GG, SDC, BDR conceived and designed experiments. GG performed the experiments, analysed the data and wrote the manuscript. SDC, BDR and LJF assisted with interpretation of results and manuscript feedback. All authors read and approved the final manuscript.

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