Organismal homeostasis buffers the effects of abiotic change on community dynamics

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Abstract. The problem of linking fine-scale processes to broad-scale patterns remains a central challenge of ecology. As rates of abiotic change intensify, there is a critical need to understand how individual responses aggregate to generate compensatory dynamics that stabilize community processes. Notably, while local and global resource enhancement (e.g., nutrient and CO_2 release) can reverse dominance relationship between key species (e.g., shifts from naturally kelp-dominated to turf-dominated systems), herbivores can counter these shifts by consuming the additional productivity of competing species (e.g., turfs). Here, we test whether consumer plasticity in energy intake to maintain growth in varying environments can underpin changes in consumption that buffer varying levels of productivity. In response to carbon and nutrient enrichment, herbivores increased consumption of higher-quality food, which acted as a buffer against enhanced production, while maintaining organismal processes across varying abiotic conditions (i.e., growth). These results not only suggest plasticity in feeding behavior, but also in energy acquisition and utilization to maintain organismal processes. Such plasticity may not only underpin organismal homeostasis, but also compensatory dynamics that emerge from the aggregate of these responses to buffer change in community processes.

Key words: abiotic change; compensation; homeostasis; resistance; stability; trophic interactions.

INTRODUCTION

The assessment of links between fine-scale processes and broad-scale patterns remains a central challenge of ecology and relies heavily on the interfacing of phenomena that occur across scales of biological organization (Wootton 2001). By elucidating the mechanisms that influence processes across scales, we may not only understand the emergence of patterns, but also anticipate how communities may resist environmental change (Levin 1992). Key to this ability is the understanding of how individual responses to environmental variation can stabilize aggregate community processes, such as productivity and biomass. Attempts to account for such stabilizing effects center on theories of compensatory dynamics (see Gonzalez and Loreau [2009] for a review), which describe how an individual's response to environmental change may underpin the dynamics that buffer variation in population (Reed et al. 2013) and community processes (Hoover et al. 2014, Ghedini et al. 2015).

Compensatory dynamics may not only stabilize ecosystem properties where species are lost to environmental disturbance (Ernest and Brown 2001, Ruesink and Srivastava 2001), but also where abiotic change directly modifies ecosystem processes, e.g., productivity (Ghedini et al. 2015). A general consequence of human modification of the abiotic environment is to enhance resource availability (e.g., carbon and nutrient enrichment), which

has been repeatedly linked to change in community structure through alteration of bottom-up dynamics (Smith and Schindler 2009, Isbell et al. 2013). Community change may occur where resource enhancement alters competitive interactions by increasing productivity of opportunistic or subordinate species, which may over time replace normally dominant species (Bertness et al. 2002, Connell et al. 2013, Yan et al. 2014). For example, kelp forests can shift to turf-dominated states where intensifying abiotic change (e.g., nutrient pollution, carbon enrichment) progressively favors the expansion of subordinate weedy species (i.e., turf algae) at the expenses of dominant kelp (Connell et al. 2008, Strain et al. 2014). Critically, changes in per capita consumption by herbivores may buffer enhanced productivity, not only in response to nutrient enrichment (McAllister et al. 1972, Sarnelle 1992, Russell and Connell 2005), but also to other resource disturbances (Ghedini et al. 2015, McSkimming et al. 2015). By keeping turf abundance in check and maintaining turf-free space, herbivores facilitate kelp recruitment and persistence (Gorman and Connell 2009). The aggregate of such changes in consumption can generate a mechanism of trophic compensation that stabilizes community productivity in varying environments (Connell and Ghedini 2015). While changes in strength of herbivory have been documented in response to both direct (e.g., environmental stress; O'Connor 2009) and indirect effects of abiotic change (e.g., food quality; Stiling and Cornelissen 2007), it remains unclear whether it is possible to identify an underlying mechanism that can account for the

emergence of trophic compensation as a stabilizing mechanism to a range of abiotic disturbances.

Where abiotic change influences the input and transfer of energy in a system (e.g., by enhancing productivity), the mechanisms underpinning compensatory dynamics may be assessed in the context of an individual's need to maintain organismal homeostasis in varying environments (e.g., by modifying consumption). Since flows of energy and nutrients link levels of biological organization in a community (Nisbet et al. 2000, Enquist et al. 2003), changes in the requirement and utilization of energy by individual organisms influence community dynamics (Brown et al. 2004, Sousa et al. 2008). There is extensive recognition that abiotic change can alter the energetic balance of consumers directly, through alterations of their physiological homeostasis (e.g., ocean acidification, temperature; Poertner and Farrell 2008, Queirós et al. 2014), or indirectly, through alteration of the quality of their resources (e.g., carbon or nutrient enrichment; Stiling and Cornelissen 2007, Falkenberg et al. 2013a). Therefore, consumers often modify the quality and quantity of food consumed to adjust their energy intake in response to varying environments (Tylianakis et al. 2008, Kordas et al. 2011). Such individual-level changes in the acquisition of energy and its utilization to maintain organismal homeostasis could underpin compensatory dynamics that stabilize community processes. Indeed, the aggregate effects of minor changes to individual interactions can exert significant effects on community structure (Tylianakis et al. 2008).

Consumers can modify their feeding behavior in response to variation in abiotic conditions, resource availability and quality (Kaspari et al. 2012). Plasticity in feeding behavior is common because many taxa experience variable environments and are limited in their ability to move to patches of habitat with better quality resources or lower levels of environmental stress (e.g., limited mobility, physical barriers, homogeneous environments). Such plasticity can be observed in the form of compensatory feeding where consumers, and herbivores in particular, increase food consumption to compensate for low quality resources (Berner et al. 2005, Suzuki-Ohno et al. 2012) or stressful environments (Duarte et al. 2015, Jager et al. 2016). In addition, feeding plasticity is also observed where consumers tend to maximize consumption of high-quality resources (Jacobsen and Sandjensen 1994, Falkenberg et al. 2013a), thus enhancing their fitness as suggested by classical ecological theory (Optimal Foraging Theory; Pyke 1984). By adjusting consumption, therefore, consumers can meet their energetic requirements and maintain nutritional homeostasis and optimal growth in varying environments, while also fully exploiting available resources (Kaspari et al. 2012, Flores et al. 2014).

The wide range of feeding responses requires consumers to exert a certain control over their metabolism and implies an ability to modify to some extent their energy budget in response to environmental variation (Sousa et al. 2010, Kooijman 2013). The evolutionary advantage of a flexible energy budget would be to allow for some adaptation to short-term environmental changes (Stumpp et al. 2012, Jager et al. 2016) and to maximize utilization of variable resources (Kooijman 2013). If such plasticity underpins the individual's need to maintain homeostasis, then the aggregate responses to abiotic variation may generate dynamics that buffer change in community processes.

Here, we use a model consumer–resource interaction to investigate the idea that trophic compensation and its stabilizing effects on primary productivity are a consequence of plasticity in energy intake (by adjusting consumption) to maintain organismal processes (i.e., growth) in varying environments. Our assessment centers on the interaction between marine herbivorous gastropods and turf algae (see Connell et al. [2014] for definition of turf algae) that is key to the persistence of kelp forests. Combinations of abiotic modification from local (nutrient enrichment) through to global scales (CO_2 enrichment) increase the probability of loss of kelp forests by favoring the expansion of subordinate, turf algal species at the expenses of dominant kelp (Connell et al. 2008, Falkenberg et al. 2013b). Resistance to this shift occurs by a strengthening in per capita consumption of turf algae by herbivorous gastropods that might prevent the expansion of these opportunistic species (Ghedini et al. 2015). We hypothesize that the ability of individual consumers to modify consumption (energy intake) in response to changing environments not only underpins their individual tendency to maintain organismal processes (growth), but may also underpin a compensatory dynamic that absorbs increased productivity.

Materials and Methods

Experimental setup

To test whether individual consumers were able to adjust to abiotic change to maintain growth while concomitantly providing a counterbalancing mechanisms to increased productivity (i.e., increased per capita consumption), we exposed herbivorous gastropods and turf algae to the individual and combined effects of CO_2 (current vs. future) and nutrient enrichment (ambient vs. elevated) for nine consecutive months (270 d) at seasonal ambient temperature (see Appendix S1: Table S1). Treatments of CO_2 and nutrients were fully crossed in an orthogonal design, with five replicates per treatment ($n = 5$ turf algae exposed to individual consumers and $n = 5$ control turf algae). Experiments were done in aquaria (40 cm long × 30 cm wide × 20 cm high, 20 L) filled with seawater and exposed to full sunlight and its natural day–night cycle at The University of Adelaide, South Australia. Within each aquarium, algal turfs and grazers were placed in cages (10 × 10 cm) to quantify rates of primary production and its consumption. On fiberboard panels of the same dimensions (10 × 10 cm) algal

turfs were initially recruited in the field and developed in aquaria. These panels were then randomly assigned to either cages with a grazer (i.e., to test the enrichments effects in the presence of herbivory) or to cages without grazers (i.e., to test the same effects in the absence of herbivory). The experimental density of grazers equates to natural densities, so that one individual grazer per cage (one individual in 10×10 cm cage) approximated their natural densities observed decades ago (~113.9 individuals/m^2; Clarkson and Shepherd 1985) and more recently (~110 individuals/m^2; Russell and Connell 2005). These grazers are continuously present on rocky coasts across seasons in similar densities (Russell and Connell 2012). In each aquarium, one-third of the water volume was replaced with fresh seawater twice weekly to maintain water quality.

The target partial pressure of CO_2 levels (pCO_2) was based on the current ambient levels (current, ~400 ppm of CO_2) and the prediction under the IS92a scenario for the year 2100 for atmospheric CO_2 (future, ~850 ppm; IPCC 2013; see Appendix S1: Table S2). Elevated CO_2 concentrations in future CO_2 aquaria were maintained with air enriched with CO_2 controlled by a Pegas gas mass flow controller (Columbus Instruments, Columbus, Ohio, USA), while ambient air was used for ambient CO_2 aquaria. Water pH_{NBS} was measured daily and titration was performed monthly to determine total alkalinity (T_A) using an automated titrator (888 Titrando; Metrohm, Riverview, Florida, USA). Partial pressure of CO_2 was calculated from measured pH_{NBS}, T_A, temperature, and salinity using the CO2SYS program for Excel (Pierrot et al. 2006) with constants from Mehrbach et al. (1973) as adjusted by Dickson and Millero (1987).

Nutrients were enhanced using Osmocote Plus (Scotts Australia, Bella Vista, NSW, Australia) controlled-release fertilizer (6-month release: 15% N, 5% P, 10% K), which was placed in nylon mesh bags (1 mm mesh size) and attached to the bottom of aquaria assigned to enriched nutrient treatments and replaced monthly. Nutrient concentrations (5 g of fertilizer per aquarium) were chosen to reproduce the concentrations of dissolved nitrogen that occur in urban catchments as a consequence of continuous nutrient input (i.e., 3 km of wastewater plume; Fernandes et al. 2012) or as pulsed events of moderate to heavy rainfall from storm water runoff (Gorman et al. 2009); our target value of ~0.50 mg/L fell within the range of field observations, i.e., 0.3–0.8 mg/L (see Appendix S1: Table S2). Ambient nutrient conditions were reproduced by using seawater from urban catchments unaffected by wastewater or storm water events (<0.1 mg/L; Gorman et al. 2009; see Appendix S1: Table S2). Concentrations of supplied nutrients were quantified on three occasions ($n = 3$) by collecting water samples using 25-mL sterile syringes, filtered with a 0.45-μm glass fiber filter, and frozen before being analysed on a Lachat Quickchem 8200 Flow Injection Analyzer (Hach Company, Loveland, Colorado, USA) for ammonia, nitrite + nitrate (NO_x), and phosphate.

Herbivores and algae

Consumers used for the experiment were herbivorous gastropods (*Turbo undulatus*) that were collected on a shallow rocky reef among kelp forests (O'Sullivan, South Australia, Australia) in April 2013. Herbivores were acclimated in aquaria at ambient conditions for one month prior to exposing them to the experimental treatments ($n = 5$). Herbivores were then randomly assigned to experimental units (one individual per cage per aquaria) and continuously maintained in the relevant treatments for nine consecutive months until February 2014. During the entire experimental period, consumers were continuously fed with turf algae grown on panels (10×10 cm) in the same treatment conditions (one panel per herbivore replaced weekly) and initially recruited from turf algae collected in the field. Control panels of turf algae were placed within empty cages to quantify productivity ($n = 5$) across all experimental treatments.

Response variables

At the start of the experiment, herbivorous gastropods were chosen to be of similar sizes such that their shell length and body mass did not differ among treatments (see *Results* and Appendix S4: Table S2). The length of the shell and the body mass of each consumer were measured again at the end of the experiment to calculate individual growth rates, which were quantified as changes in length (mm) and mass (g) per month under each experimental condition ($n = 5$). We then calculated the ratio of individual growth rates to consumption to test for changes in the efficiency of converting energy (consumption or nitrogen content of food) into biomass (growth; i.e., changes in length or mass) under carbon, nutrient enrichment, and their combination ($n = 5$).

To test whether changes in consumption occurred proportionally to changes in productivity, productivity and consumption were measured on three separate trials, each of the duration of one week and spaced across three seasons (winter, spring, and summer). The effects of carbon and nutrient enrichment on changes in productivity, consumption, and on their ratio (i.e., productivity to consumption) were analysed by averaging the results of the three trials ($n = 5$). Productivity was measured as increase in percentage cover of turf algae per hour by quantifying initial and final turf cover on control panels (i.e., not exposed to herbivores) and dividing total increase in productivity for the number of hours. Consumption rates were measured as percentage cover of turf algae consumed per herbivore per hour, including differential turf growth rates among treatments as measured on control panels. At the end of each trial we measured turf percentage cover in the presence and absence of grazers to assess whether herbivory was effective in keeping turf expansion in check under carbon and nutrient enhancement.

At the end of the experiment, turf algae were collected from panels from each treatment and analysed for carbon (% C), nitrogen (% N), and energetic content (Joules per gram). Turf algae were collected by carefully scraping algae off from each panel using a razor blade. Following collection, the samples were preserved by freezing them at −20 °C. At the time of analyses, samples were defrosted, rinsed with Milli-Q water, and dried for 48 h in an oven at 60°C. Each sample was then ground to a fine powder using a mortar and pestle. A subsample of the powder (~3 mg; $n = 3$ per treatment) was analysed for carbon and nitrogen content (% N and % C) using an isotope ratio mass spectrometer (Hydra 2020 ANCA-GSL Version 4.0; Sercon, Crewe, Cheshire, UK). Another subsample of the powder (~0.2 g; $n = 3$ per treatment) was used to form a tablet and combusted to determine the energetic content of the algae (Joules per gram) using an IKA C2000 calorimeter with an IKA KV500 digital cooling system (IKA® Works (Asia) Sdn Bhd, Selangor, Malaysia).

Statistical analyses

Two-way analyses of variance (ANOVAs) were used to test the effects of treatments of enrichment (i.e., nitrogen, carbon and their combination) on productivity, consumption, drivers of consumption (i.e., carbon [% C], nitrogen content [% N], and energetic content of food) and herbivore body size. In all analyses, the factors of CO_2 and nutrients were treated as fixed and orthogonal, with two levels in each factor (CO_2, current vs. future; nutrients, ambient vs. elevated). Significance was set at $\alpha < 0.05$ and, where significant treatment effects were detected, Student-Newman-Keuls (SNK) post hoc comparison of means was used to determine which factors differed. Pearson's correlations related increasing rates of consumption with productivity and with concentrations of nitrogen in food; correlations were also used to relate variation in herbivore growth rates with rates of consumption and nitrogen content of their food across treatments.

To quantify the treatment effect on changes in energy intake vs. changes in consumer growth rates, we calculated the average effect size of each treatment relative to ambient conditions; to do so, we used consumption and nitrogen content of algae as a measure of energy, and changes in mass and shell length as a measure of growth. For each of the four variables (consumption, N content, mass, and shell length), effect sizes were calculated as the mean absolute change within each treatment relative to ambient conditions. Mean and standard error were calculated from the values estimated by randomly pairing the five replicates per treatment with the five ambient replicates. The results here presented were randomly chosen among those calculated from 10 possible combinations.

Results

While carbon and nutrient enrichment enhanced turf growth (ANOVA; nutrients, $F_{1,16} = 14.72$, $P = 0.002$;
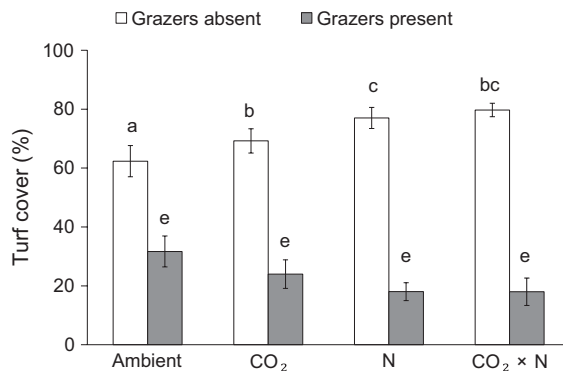

FIG. 1. Relative to ambient conditions in which herbivores were present, turf cover did not significantly differ among treatments in the presence of grazers (gray bars, $n = 5$ replicates); this indicates that herbivory countered the otherwise positive effects of carbon, nutrient enrichment, and their combination on turf productivity in the absence of grazers (white bars, $n = 5$ replicates). Bars sharing a letter do not differ significantly in SNK tests. Values are mean ± SE.

CO_2, $F_{1,16} = 9.86$, $P = 0.006$), these conditions concomitantly stimulated proportional increases in consumption (nutrients, $F_{1,16} = 16.57$, $P = 0.001$; CO_2, $F_{1,16} = 15.99$, $P = 0.001$), such that the ratio of productivity to consumption remained similar across treatments (nutrients, $F_{1,16} = 1.92$, $P = 0.19$; CO_2, $F_{1,16} = 0.73$, $P = 0.41$; $CO_2 \times N$, $F_{1,16} = 0.02$, $P = 0.89$; see Appendix S2: Table S1). By increasing consumption on more productive algae, per capita changes in feeding rates by herbivores generated a compensatory dynamic that countered the positive effects of carbon, nutrient enrichment, and their combination on turf production. Indeed, relative to ambient conditions, turf cover did not significantly differ among treatments in the presence of grazers (ANOVA; nutrients, $F_{1,16} = 3.18$, $P = 0.1$; CO_2, $F_{1,16} = 0.79$, $P = 0.4$; $CO_2 \times N$, $F_{1,16} = 0.45$, $P = 0.5$), but significantly increased under nutrient ($F_{1,16} = 43.36$, $P = 0.000$) and carbon (ANOVA; $F_{1,16} = 5.99$, $P = 0.026$) enrichment in the absence of grazers (Fig. 1; see Appendix S2: Table S2).

Increases in consumption rates were positively correlated not only to turf productivity (linear regression; $P < 0.05$, $R^2 = 0.39$, $N = 20$), but also to the nitrogen content of these algae (linear regression; $P < 0.05$, $R^2 = 0.51$, $N = 20$), which progressively increased under carbon enrichment, nutrient enrichment, and their combination (Fig. 2). Indeed, algae exposed to intensifying abiotic change were of greater nutritional quality having greater % N (i.e., lower C:N ratio) and energetic value relative to ambient treatments (see Appendix S3: Fig. S1, Table S1); with % N correlating significantly to energy content ($P < 0.001$, $R^2 = 0.79$, N = 12; see Appendix S3: Fig. S2). Therefore, in response to carbon and nutrient enrichment, consumers substantially increased their energy intake not only by increasing consumption rates (by 36% under CO_2, 37% under N, and 47% under $CO_2 \times N$ relative to ambient), but also by consuming resources of greater quality (nitrogen content increased
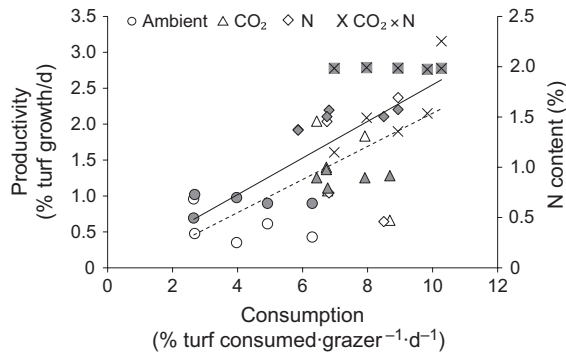
Fig. 2. Rates of consumption across treatments ($N = 20$) were correlated with increases in productivity ($P < 0.05$, $R^2 = 0.39$; white, dashed line) and nitrogen content of algae ($P < 0.05$, $R^2 = 0.51$; gray, solid line). Symbols ($n = 5$ replicates) are circles, ambient conditions; triangles, CO_2 enrichment; diamonds, N enrichment; crosses, CO_2 and N enrichment.

by 28% under CO_2, 57% under N, and 68% under $CO_2 \times N$ relative to ambient).

Despite increases in energy intake (i.e., increased consumption of higher-quality resources), consumer growth rates displayed less variation than concomitant changes in consumption and nitrogen content of food across treatments (Fig. 3). Overall, there was a positive effect of nitrogen enrichment on growth rates, particularly for changes in mass (see Appendix S4: Table S1), such that consumers exposed to nutrient enrichment had a greater final mass, but not shell length, relative to other treatments (see Appendix S4: Table S2). Nonetheless, growth efficiency tended to decrease in grazers exposed to abiotic change, indicating a lower efficiency of converting energy intake (consumption or nitrogen content) into biomass (mass or shell length) (see Appendix S4: Fig. S1). Specifically, for both mass and length, growth efficiency relative to consumption decreased significantly under CO_2 enrichment (see Appendix S4: Table S3) and growth efficiency relative to nitrogen content of algae decreased significantly under both CO_2 and nutrient enrichment (see Appendix S4: Table S4). Hence, increases in energy intake were not fully reflected in changes in growth rates, such that variation among individual herbivores was not significantly explained by changes in consumption (mass, $P = 0.68$, $R^2 = 0.01$; length, $P = 0.40$, $R^2 = 0.04$, $N = 20$; Fig. 4) or nitrogen content of their food across treatments (mass, $P = 0.17$, $R^2 = 0.01$; length, $P = 0.25$, $R^2 = 0.07$; $N = 20$; see Appendix S4: Fig. S2).

Discussion

Our study examines how individual-driven responses to abiotic change (consumption) can generate dynamics that stabilize community processes (productivity). We found that herbivores responded to carbon and nutrient enrichment by increasing per capita consumption of higher-quality resources, thus, negating the effects of

abiotic change on turf productivity. This change in feeding behavior may be accounted for by the Optimal Foraging Theory, which explains that consumption is driven by an organism's tendency to maximize its fitness by feeding on resources that are more energetically profitable (Pyke 1984). Nonetheless, the specific mechanism underlying changes in consumption differs between carbon and nitrogen enrichment, reflecting the plasticity of consumers in response to varying abiotic conditions.

Enriched CO_2 conditions likely stimulated compensatory feeding (Berner et al. 2005, Suzuki-Ohno et al. 2012), that is an increase in consumption on the more nitrogen-rich food to compensate for the energetic costs of decreased pH conditions (Queirós et al. 2014). The increase in nitrogen content under CO_2 enrichment likely reflects the stronger limitation of C than N in turfs, which is why nitrogen uptake in turfs occurs at a greater rate once the C limitation is decreased or eliminated by CO_2 enrichment (Falkenberg et al. 2013b). This increase in energetic value of food has the potential to offset the increase in maintenance costs of calcification processes (Kroeker et al. 2010, Queirós et al. 2014) and acid-base regulation in calcifying herbivores experiencing acidification (Stumpp et al. 2012). Indeed, while CO_2 enrichment can increase maintenance costs (Wittmann and Portner 2013), these can partly be met by increasing feeding (Duarte et al. 2015) and reducing maintenance costs (Stumpp et al. 2012, Jager et al. 2016). Differently, enriched nutrient conditions may have stimulated feeding mainly by increasing the quality of resources (i.e., nitrogen content and energetic value) of which herbivores maximized consumption. While consumers would have to consume less of the nitrogen-rich food to meet their
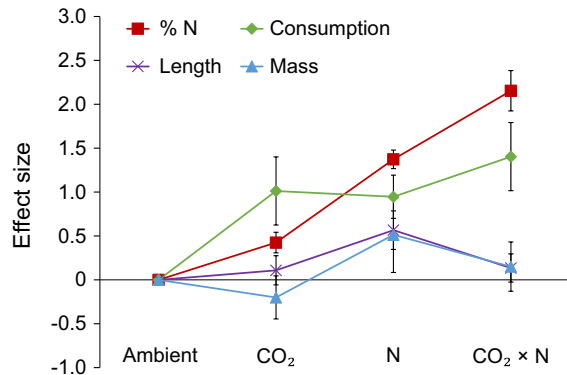

Fig. 3. Growth rates of consumers (changes in mass and shell length) exhibited less variation than concomitant changes in the quantity (consumption) and quality (nitrogen content of algae) of food consumed across treatments. The graph shows the mean effect size calculated as the mean absolute change within each treatment relative to ambient conditions for each variable. Mean and SE were calculated from the values estimated by randomly pairing the five replicates per treatment with the five ambient replicates. The results here presented were randomly chosen among those calculated from 10 possible combinations. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]
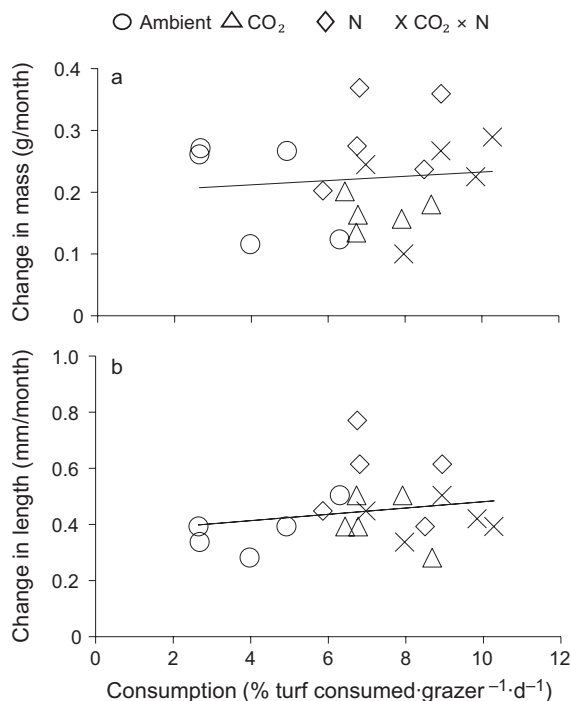
Fig. 4. Variation in (a) mass and (b) shell length of herbivores ($N = 20$) was not significantly explained by changes in consumption across treatments (mass, $P = 0.68$, $R^2 = 0.01$; length, $P = 0.40$, $R^2 = 0.04$). Symbols ($n = 5$ replicates) are circles, ambient conditions; triangles, CO_2 enrichment; diamonds, N enrichment; crosses, CO_2 and N enrichment.

energetic requirements, this behavior is common (Jacobsen and Sandjensen 1994, Falkenberg et al. 2013a) and may be evolutionarily advantageous to maximize fitness in response to blooming or sparse resources (Kooijman 2013).

Notably, regardless of the specific mechanism underlying changes in consumption in response to carbon and nutrient enrichment, consumer growth rates showed less variation across treatments than concomitant changes in the quantity and quality of food consumed. This result indicates that herbivores were not only able to compensate for the increased energetic costs of CO_2 enrichment (Duarte et al. 2015, Jager et al. 2016), but also to divert the extra energy intake under nutrient enrichment to processes other than growth (e.g., reproduction). Indeed, while we did find positive effects of nutrient enrichment on changes in consumer mass, we also found a decrease in growth efficiency. If the extra energy intake gained through consumption of higher-quality food was not entirely directed toward growth, it is possible that part of this energy was diverted toward better quality storage, reproduction (Nisbet et al. 2000), or partly dissipated through increased maintenance costs (Jager et al. 2016). While this idea is speculative, recent developments of the Dynamic Energy Budget theory suggest that the amount of energy directed toward maintenance might be more flexible than previously considered (Kooijman

2013, Jager et al. 2016). While seemingly counterintuitive, the evolution of a certain degree of plasticity in energy intake and allocation is plausible if consumers are to maximize fitness by exploiting blooming or sparse high-quality resources (Kooijman 2013) and also sustain organismal processes (i.e., maintenance, growth and reproduction) when resources are scarce or in stressful environments (Stumpp et al. 2012, Duarte et al. 2015). Flexibility in energy budget can, thus, be ecologically and evolutionary important at the organismal level to maintain nutritional homeostasis and optimal growth in varying environments (Sousa et al. 2010). Importantly, such plasticity may not only underpin the ability of individual organisms to adjust to environmental variation, but also the capacity of communities to resist such variation without continuous re-structuring.

Where individual organisms modify physiological processes to maintain homeostasis in changing environments (Rapport et al. 1985, Hoover et al. 2014), the aggregate of these responses may reduce the effects of abiotic change at more complex levels of ecological organization (e.g., populations, communities; Lenton 1998). Adjustments to environmental change by individual organisms may underpin mechanisms that buffer change on aggregate community processes via compensatory dynamics. Such plasticity might be common as consumers often experience environments with varying abiotic conditions and resources (Kaspari et al. 2012, Flores et al. 2014). For example, we found that consumers exposed to carbon, nitrogen enrichment, and their combination responded to these varying conditions by modifying consumption to different extents while maintaining similar growth. Importantly, while rates of productivity increased under resource enhancement, these effects were countered by increases in consumption, which occurred proportionally to changes in productivity such that the relative strength of the two processes remained similar under each treatment. Hence, while consumer responses to abiotic variation may reflect the need of individuals to maintain organismal processes in varying environments, collectively these responses may represent a mechanism that reduces the size of change in community processes.

While plasticity in energy budget might underpin stabilizing mechanisms to abiotic change, this buffering capacity can be lost due to the existence of trade-offs between costs for basal maintenance in changing environments and costs for fitness-related processes (e.g., reproduction; Sokolova et al. 2012). For example, if the energetic costs of carbon enrichment cannot be entirely met, a reduction in individual fitness might lead to a decrease in size of consumer populations over time (Queirós et al. 2014), thus potentially lowering consumer control over primary productivity. Conversely, if individuals benefit from abiotic change (e.g., nutrient enrichment) and increase their fitness, these changes may result in growth of the size of consumer populations. Such demographic responses can act to compensate for

enhanced productivity over broader spatial or temporal scales (Gil et al. 2015). Nevertheless, in some systems, population increases might lead to an overconsumption of primary production causing shifts in regime (Silliman et al. 2013). Hence, the assessment of how fine-scale responses influence broader-scale patterns may not only offer insights on the mechanisms that absorb change, but also on how positive feedbacks can maintain shifted regimes (e.g., Bennett et al. 2015).

A contemporary challenge for ecology is to anticipate change or stasis in community structure and functioning in response to environmental change. Key to this prediction is the understanding of mechanisms through which individual responses to abiotic modification underpin compensatory dynamics that counter change in community processes (Gonzalez and Loreau 2009). While processes that occur at the level of individual organisms cannot be directly scaled up across levels of ecological complexity, large-scale patterns can be understood as emerging from the collective behaviors of assemblies of smaller units (Levin 1992, Wootton 2001). We suggest that organismal homeostasis acts as a basis for compensatory dynamics that buffer the effects of abiotic change. While behavioral and physiological plasticity is well known to be a key mechanism through which individual organisms adapt to changing environments and modify ecological processes (Charmantier et al. 2008, Bolnick et al. 2011), there is less recognition for its consequences on community stability (Free and Barton 2007, Violle et al. 2012). It is possible that fine-scale processes might generate large-scale patterns of stability where organismal responses that work toward homeostasis collectively buffer change in community dynamics.

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