Ocean warming reduces gastropod survival despite maintenance of feeding and oxygen consumption rates

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Scientific Significance Statement

Human activities are generating novel environmental conditions globally. We need to understand how organisms will respond to environmental change to better manage them and the associated ecosystems. One way to assess such changes is by measuring short-term, sublethal physiological processes. However, these physiological processes may not reflect longer-term higher-order responses such as survival. By exposing gastropods to warming and measuring both longer-term responses (i.e., survival) and short-term processes (i.e., feeding, oxygen consumption), we identified that the longer-term responses were negatively affected, despite maintenance of the short-term processes. That is, survival was reduced although feeding and oxygen consumption were unchanged. Together, these results indicate that consideration of short-term physiological processes alone may not provide an adequate indication of longer-term survival responses to change.

Abstract

Short-term, sublethal response variables are increasingly used to provide rapid indications of whole organism responses to future climate conditions. Accumulating evidence suggests, however, that these response variables may not consistently reflect whole organism responses which manifest over longer time scales. Here, we consider the effect of moderate warming on longer-term whole organism fitness, as reflected by survival, as well as two shorter-term response variables, feeding rate and oxygen consumption, for two tropical gastropod species. We found a significant reduction in survival under warming, despite no significant effect of warming on feeding or oxygen consumption rates. This result demonstrates that the maintenance of physiological rates alone is not sufficient to sustain organism survival under elevated temperatures; rather an increase in physiological process rates is likely required. Consequently, isolated short-term physiological processes may not adequately reflect longer-term whole organism responses to altered climate. For improved understanding, both short- and long-term responses need to be considered.
In an increasingly human-modified world, a diverse range of approaches is being developed to understand organism and ecosystem responses to abiotic change (Chapman 2002; Fidder et al. 2016). A relatively simple and efficient way to understand organism responses may be through the quantification of short-term response variables (measures of short-term organism responses, e.g., metabolic rates, enzyme activity, and mitochondrial dysfunction). These response variables could provide early indications of sublethal responses that will eventually influence higher levels of organization (Fidder et al. 2016). That is, environmentally induced changes in feeding or oxygen consumption can provide insights to sublethal effects that impact longer-term and higher-order processes, and related response variables such as survival, reproduction, or growth (Fidder et al. 2016; Goodchild et al. 2018). These individual-level changes can then translate to altered population dynamics and ecosystem structure. For example, in response to a fungicide, freshwater snails display changes in energetic responses reflecting acquisition (i.e., feeding) and allocation (i.e., egg macronutrient content) that could provide early indication of changes in responses related to reproductive success (i.e., hatching success, time to hatch) (Fidder et al. 2016). However, the degree to which these short-term response variables reflect whole organism health is not yet fully understood.

Temperature is a key environmental trait that can influence organism physiology and therefore whole organism performance. Global temperature is currently increasing due to human activities, and warming will continue in the future (Stocker et al. 2013). Basic metabolic theory predicts, and experimental results indicate, moderate warming will increase organism metabolic activity until an optimal level is reached, beyond which metabolizable energy intake and performance will decrease (Angilletta et al. 2002; Mertens et al. 2015). Organisms that are more metabolically active will also have greater energetic demands, and should therefore increase their feeding rates (Mertens et al. 2015). Without such changes in these energetic processes under moderate warming, organisms are likely to experience reduced fitness and survival.

While temperature has a strong impact on organism physiology globally, the effects of future warming are likely to be particularly influential in tropical regions. Tropical organisms are anticipated to be more susceptible to warming because they are more likely to live closer to their upper thermal limits than their temperate counterparts (Chapponer and Seuront 2011; Marshall et al. 2015), inhabiting stable, nonseasonal environments that confer limited physiological acclimation abilities and narrower thermal windows (Compton et al. 2007; Tewksbury et al. 2008). In coastal systems, gastropod grazers are of particular significance because of their role in shaping ecosystem structure by modifying the occurrence of substrate-occupying algae and supporting higher trophic levels (Falkenberg et al. 2013; Lorda et al. 2016). However, the capacity of gastropods to fill these roles in the future could be modified as ectotherms can be strongly influenced by external temperature changes (Ghedini et al. 2015; Mertens et al. 2015; Leung et al. 2017) (but also see Poore et al. 2016, Leung et al. 2018). Moreover, while we can draw general predictions about the responses of particular types of organisms, increasingly we are recognizing differences between functionally similar species. Consequently, there is a particular need to consider and compare the responses of distinct tropical species to environmental change.

Here, we examined the responses of two gastropod species found in the tropics to moderate, extended warming. Responses were considered in terms of longer-term survival as well as two key short-term response variables: feeding rate and oxygen consumption. This work contributes to developing a broader understanding of how organisms will respond to altered conditions at multiple scales of organization (i.e., whole-organism and sublethal physiological processes). If all responses were affected similarly by temperature, such a result could indicate the possibility of using short-term response variables to provide early indications of longer-term organism responses to anticipated climate change. Alternatively, contrasting responses would indicate the need to continue measuring multiple response variables, especially those which manifest over longer time periods, to comprehensively understand organism responses. Identifying which outcome manifests will provide a better fundamental understanding of organism responses to abiotic conditions, as well as having implications for the methods selected to assess the effects of a changing climate on natural systems.

**Materials and methods**

**Experimental design and setup**

To determine the effects of warming on tropical gastropods, we quantified the response of two species (*Chlorostoma argyrostoma*, *Lunella granulata*) to experimentally manipulated temperatures in a laboratory-based tank experiment. We considered adults of these species (maximum shell diameter *C. argyrostoma* 22.2 ± 0.4 mm, *L. granulata* 24.3 ± 0.5 mm; mean ± SE), with individuals belonging to these genera typically living to be between 5 and 10 yr of age, although they can live for 30 yr (Walsby 1977; Cooper and Shanks 2011). We exposed experimental tanks to current or future temperatures for 6 weeks from July to August 2019. The “current” temperature (25.5°C) was based on long-term measurements of the collection site in the summer experimental period (25.4 ± 0.2°C was the average temperature over the experimental months, i.e., July–August, for the last 10 yr of data published, i.e., 2009–2018, at the site nearest our collection location, i.e., Eastern Buffer station EM2; Hong Kong Environmental Protection Department - https://cd.epic.epd.gov.hk/EPICRIVER/marine/ , last accessed 30 May 2021), while the “future” temperature (+2.5°C) simulates ocean temperature anticipated between the years 2081 and 2100 (Stocker et al. 2013). We used six replicate tanks for each treatment, with replicate specimens of each gastropod species in each tank (*n* = 3 of each species per tank).
Collection of gastropods and holding conditions
We collected adult gastropods (C. argyrostroma, L. granulata) and algae (Gelidium spp.) in early July at Joss House Bay in Tai Miu Wan, Hong Kong (22.27°S, 114.29°E). We then brought experimental organisms back to the Simon F.S. Li Marine Science Laboratory, Hong Kong, and cleaned all gastropod shells of epibiotic organisms.

To allow for acclimation, prior to the experimental period we kept all gastropods and algae in separate holding tanks (19 L seawater; n = 10 individuals per tank) filled with natural seawater under current conditions (temperature = 26.1°C, salinity = 35, pH = 8.03, 12 : 12 h light : dark regime) for 7 d. During this period, we provided gastropods algae collected from the field to graze upon.

Experimental treatments
Following acclimation, we transferred individual gastropods into experimental tanks (n = 3 gastropods of each species, six total individuals per tank) where each were held isolated from the others in a cage, with the same conditions as in the holding tanks described above. We provided each gastropod a piece of algae for food, which was replenished weekly throughout the experimental period. Half of the tanks we maintained at current temperatures (n = 6), while gradually increasing temperature of the other half to the future treatment (n = 6). The water temperature in the “future” treatment tanks was warmed at a rate of 0.5°C per hour to be 2.5°C hotter than the “current” treatment tanks on the day before the experimental period. This rate was used to minimize the chance of mortality to result from initial heat shock (the first gastropod mortality was recorded 9 d after establishment of treatment conditions). Bar heaters were used inside of the tanks to establish and maintain experimental temperatures. iButtons monitored temperature in each tank, where they took recordings every 10 min (Thermochron iButton logger, Embedded Data Systems). Mean water temperature was significantly different between the current and future tanks (mean ± SE, current 25.7 ± 0.1°C, future 28.2 ± 0.1°C, F1,10 = 98.22, p ≤ 0.0001). We maintained water quality by removing fecal matter and renewing one-third weekly with fresh marine water.

Experimental responses
Responses of gastropods to experimental treatments were quantified at the end of the experiment in terms of survival, algal consumption (feeding), and oxygen consumption. We measured survival on the 39th and 40th days of the experiments (at the same time as survival was fed on for 7 d with the feeding trial started on the 31st day of the experiment and concluded on the 38th day. We quantified the change in algal mass (final – initial measurement) by gently patting the algae dry and then weighing to the nearest 0.0001 g at the beginning and end of the feeding period. The gastropods were provided sufficient algae that they were able to feed to satiation (0.1992 ± 0.0082 g; mean ± SE). For each tank, we also had control cages in which algal pieces were added without grazers; these cages indicated change driven by algal rather than grazer responses and were used to correct for any growth or tissue loss not due to the herbivores. We calculated consumed algae as: initial mass × correction factor – final mass of the piece of algae. The correction factor was: the final mass/initial mass for each control algal unit, which we then averaged to provide a single value per tank (following Renaud et al. 1990).

We measured oxygen consumption rates on the 39th and 40th days of the experiments (at the same time as survival was considered) by transferring each gastropod to an airtight chamber (55 mL falcon tubes) filled with seawater from the treatment conditions, ensuring the absence of any gas bubbles. The chamber was kept within the tank to maintain treatment temperature. We also filled chambers without gastropods with water; measurements from these were used to account for any possible biological activity in the water. Each chamber had a precalibrated oxygen spot attached to the inner wall (Fibox4 trace, PreSens). Using these spots and a fiber optic oxygen sensor, we measured oxygen concentration twice in rapid succession every minute for a 10-min period. We subtracted the background levels of oxygen consumption measured in the paired control (i.e., chamber without gastropod) from the levels of oxygen consumption measured in the experimental chamber (i.e., chamber with a gastropod) before statistical analysis.

Statistical analysis
We used PERMANOVAs (permutational analysis of variance) with Euclidian distance matrices to examine the effects of temperature and species on survival, feeding rates, and oxygen consumption. We corrected rates of oxygen consumption and feeding for controls (as described in each section above) and gastropod mass. To correct for gastropod size effects, we divided the oxygen and algal consumption rates measured for each gastropod by the gastropod wet mass. In all analyses, we treated temperature and species as orthogonal and fixed, with two levels (current and future or C. argyrostroma and L. granulata, respectively), and tank used as replicates. The PERMANOVAs were done using the PERMANOVA+ routines that are an “add-in” to the PRIMER 6 software (Clarke and Gorley 2006; Anderson et al. 2008). To evaluate the chances of committing type II errors, we used dissimilarity-based
multivariate standard error (MultSE) to assess the effect of increased sample size on the precision of our parameter estimates using the SSP package in R (Anderson and Santana-Garcon 2015; R Core Team 2020; Guerra-Castro et al. 2021).

**Results**

The survival of both gastropod species (*C. argyrostoma*, *L. granulata*) was significantly affected by temperature treatment, with reduced survival under future temperatures (pseudo-\( p = 0.02 \); Fig. 1a; Table 1, part a; Table S1a). The feeding and oxygen consumption rates of both gastropod species were not significantly affected by temperature treatment (pseudo-\( p = 0.91 \) and 0.99, respectively; Fig. 1b,c; Table 1, part b and c; Table S1b,c). For those response variables where we detected nonsignificant effects of temperature (i.e., feeding and oxygen consumption), the optimal level of precision would have been achieved through using slightly increased replication (i.e., number of tanks per treatment; used \( n = 6 \), suboptimal \( n = 6 \), optimal \( n = 8 \); Fig. S1). Thus, the number of replicates we used resulted in high precision in all groups and the lack of a significant effect of temperature we found using PERMANOVA is thus unlikely to be a type II error. Consequently, these experiments yielded detectable effects for the longer-term response variable (i.e., survival) but not those that manifest over shorter timescales (i.e., feeding and oxygen consumption). Moreover, our results show that while the responses in terms of feeding and oxygen consumption can be weak and rank variably (i.e., *Chlorostoma* has lower means for feeding and oxygen consumption under elevated temperatures).

**Table 1.** Results of the PERMANOVAs to examine the effects of temperature (current vs. future) and species (*Chlorostoma argyrostoma* vs. *Lunella granulata*) on (a) survival, (b) feeding, and (c) oxygen consumption.

| Source of variation | df | pseudo-f | pseudo-\( p \) |
|---------------------|----|----------|----------------|
| **a) Survival**     |    |          |                |
| Temperature         | 1  | 6.0000   | 0.02          |
| Species             | 1  | 2.6667   | 0.12          |
| Temperature × Species | 1 | 0.6667   | 0.44          |
| Residual            | 20 |          |                |
| **b) Feeding**      |    |          |                |
| Temperature         | 1  | 0.0009   | 0.91          |
| Species             | 1  | 0.0072   | 0.95          |
| Temperature × Species | 1 | 0.0237   | 0.88          |
| Residual            | 20 |          |                |
| **c) Oxygen consumption** | |          |                |
| Temperature         | 1  | 0.0001   | 0.99          |
| Species             | 1  | 2.4109   | 0.15          |
| Temperature × Species | 1 | 0.0793   | 0.79          |
| Residual            | 20 |          |                |

*Fig. 1.* The (a) survival, (b) feeding, and (c) oxygen consumption of gastropods (*Chlorostoma argyrostoma*, *Lunella granulata*) exposed to current or future temperature.
temperatures, while the opposite is observed in Lunella), the decline in survival with temperature is consistent in both species (Fig. 1). In addition, temperature explained a large proportion of the experimental variance in survival (Table 1a).

**Discussion**

Here, we found that warming was associated with a reduction in gastropod survival, despite no significant effect on short-term feeding or oxygen consumption rates. Together, these responses indicate that warming may negatively affect longer-term and higher-order measures, specifically whole organism fitness as reflected by survival, while key short-term energetic processes, such as feeding and oxygen consumption, may remain unchanged. Consequently, while it is proposed that sublethal, energetic-based processes could indicate whole organism responses to altered environments, our results indicate this may not always be the case. Rather, our results show there is a need to consider both short-term physiological processes and longer-term whole organism responses simultaneously.

The key response we observed was a reduction in survival under sustained, moderately elevated temperatures for both gastropod species. Such reductions in survival under warming have previously been found for gastropods (Leung et al. 2017, 2018). These responses likely result from cellular and structural damage the organisms sustained when exposed to warmer temperature (Pörtner 2002; Somero 2002). Under such circumstances, survival would require additional energy given the physiological damage sustained; while organisms may be able to adjust the rates of processes under elevations of temperature, the increased acquisition of energy was either not achieved or not maintained under this sustained elevation as both feeding and oxygen consumption rates under warmer temperatures were not significantly different from the control group after a multweek exposure. Although the warming gastropods experienced here was moderate (2.5°C), this was added to a current treatment level that represents the mean average summer temperature which could, therefore, be close to the highest that the species are able to survive. It is worth noting that using this mean average summer temperature as our “current” treatment meant that the majority of snails survived with relatively little variation when considered in comparison to the “future” treatment, particularly for Lunella. This may have contributed to the strong effect of temperature identified on survival. However, it is likely that these gastropods are sensitive to temperature. That is, as this experiment was conducted in a tropical region, where organisms are understood to generally live close to their thermal tolerance limits (Chapperon and Seuront 2011; Marshall et al. 2015), have limited physiological acclimation abilities, and narrower thermal windows (Compton et al. 2007; Tewksbury et al. 2008), such responses could be found in other tropical species when they are exposed to future environmental conditions.

In contrast to the negative effect of warming on survival, temperature had no effect on the feeding rates of the gastropods. Such a result was largely unanticipated since basic metabolic theory suggests that at moderately warmer temperatures the rate of metabolic processes would increase, meaning energy gain by enhanced feeding would be promoted (Sanford 2002; Brown et al. 2004). While unanticipated, we do not believe this result to be due to type II error. After assessing the impact of sample size on the precision of our parameter estimates, we did find that slight increases in sampling at the level of replication (tanks) would have resulted in optimal precision. However, given that the pseudo-\( p \) values for temperature effects were considerably large for both response variables (pseudo-\( p = 0.91 \) and 0.99 for feeding and oxygen consumption, respectively; Fig. 1b,c; Table 1, part b and c; Figure S1 a, b), we doubt that such increases in replication would have led to the detection of a significant effect of temperature. We instead propose that there is a biological explanation for our observations. The failure of herbivores to increase feeding rates at warmer temperatures is increasingly recognized as a common response. That is, while some herbivores exposed to warming do increase feeding (Ghedini et al. 2015; Mertens et al. 2015), they have also been observed to show no response (Poore et al. 2016; Leung et al. 2018), and even decrease (Mertens et al. 2015; Leung et al. 2017). Such seemingly contrasting responses can manifest because feeding is a hump-shaped function of temperature, which increases to a critical temperature beyond which point it is negatively influenced (Englund et al. 2011; Uiterwaal and DeLong 2020). Where herbivores do not respond to warming with increased feeding, the response may be attributed to sublethal thermal stress that modifies the rate of associated processes (e.g., aerobic metabolism) (Leung et al. 2017, 2018).

We also observed a lack of change in oxygen consumption rates under warming. This is an indication of an unchanged aerobic metabolism, potentially resulting from impacts of warming on the oxygen delivery capacity and mitochondrial function of gastropods (Peck et al. 2002; Sokolova et al. 2012; Ern et al. 2015). Alternatively, such lack of change may reflect physiological limits to the rates of these processes, or alteration to their occurrence. For example, some organisms are able to change their type of metabolism past certain thresholds (Sokolva and Pörtner 2003; Falfushynska et al. 2016), meaning that oxygen consumption is no longer a useful metric of metabolism.

The unchanged feeding and oxygen consumption rates under warming likely contributed to the observed reduction in gastropod survival. That is, because organisms can experience greater cellular and structural damage at elevated temperatures, individuals likely need to modify their energy allocation to somatic maintenance in order to survive (Pörtner 2002; Somero 2002; Leung et al. 2018). Where feeding and oxygen consumption rates are not increased, additional energy will not be available, and maintenance or upregulation of key processes may not be
possible (Pörtner 2002; Brown et al. 2004; Sokolova et al. 2012). Key processes that may be limited in such a scenario are the production and maintenance of molecular defense mechanisms, specifically heat shock proteins and antioxidative enzymes, both of which require substantial energy allocation (Pörtner 2002; Somero 2002; Tomanek 2010). More specifically, heat shock proteins have been linked with enhanced thermotolerance in a range of organisms (Haslbeck et al. 2005) by preventing proteins folding improperly or misassembling when refolding after stress as well as stabilizing proteins that are denaturing (Miller et al. 2009; Tomanek 2010). Similarly, antioxidative enzymes can influence the efficiency of molecular protection (Pörtner 2002, Somero 2002, Tomanek 2010). Where additional energy is not available, the processes associated with heat shock proteins and antioxidative enzymes cannot be enhanced to counter damage associated with warming. This ultimately limits the rates of key processes and is associated with compromised growth and body condition, potentially leading to reduced survival and therefore population persistence (Pörtner 2002; Leung et al. 2017, 2018).

Our results provide an initial indication of the potential differences in response variables that reflect short-term physiological processes and longer-term whole organism responses. We propose that additional research is required to identify the contexts where such extrapolations between different response variables would be possible, and to recognize the nature and commonality of observed responses. Considering responses at different time periods following exposure will be important; that is, here we considered the response after a relatively short, 6 week exposure period which means we may not have measured either immediate shock responses (i.e., those that occur after hours or days) and/or longer-term adjustments (i.e., those that occur after months or years). Response variables that should be considered in future studies include those considered here, as well as others that could provide more effective indications of whole organism responses (e.g., metabolic rates, enzyme activity, mitochondrial dysfunction). Measuring these responses could provide additional insight as to why the survival of organisms was affected, and also as to why feeding and oxygen consumption rates remained unchanged. That is, the reduced survival may reflect a trade-off with some other (here unmeasured) fitness component; for example, an increase in reproduction relative to maintenance. If this was the case, the survival response observed may be adaptive. In addition, future experiments should also consider the potential for behavioral responses, as it is possible that herbivores will respond to warming by modifying their behaviors in ways that allow for maintained survival, but were not possible in the experimental setting considered here. The results obtained here highlight that there can be larger variability in some response variables (e.g., feeding and oxygen consumption rates) compared with others (e.g., survival), and as such greater replication would provide more power to detect any differences that do manifest. It will also be important to consider relationships between processes in other life-history stages; we only considered adult organisms that had developed in the field in terms of one fitness component (i.e., survival) and it is possible that other life stages (e.g., early life history stages) or fitness components (e.g., reproduction) may be more or less susceptible, leading to the identification of different patterns. Finally, while we considered two temperature scenarios (current vs. future) to identify if these gastropods would be able to function under an anticipated climate change scenario, considering additional temperatures will be important to understand more fully the responses that are typically nonlinear.

While short-term physiological responses (feeding, oxygen consumption) have been proposed as early indicators of the effect of altered environmental conditions on longer-term whole organism responses, our results highlight the potential differences in responses of these different response variables. Further, by interpreting short-term responses as indicators of longer-term organism condition may infer organisms are more tolerant to environmental change than they are. Currently, however, we propose that direct measurements of longer-term processes of interest (such as survival, growth, and reproductive success) are required to predict whole-organism responses to warming.

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