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Short Communication

Functional changes in reef systems in warmer seas: Asymmetrical effects of altered grazing by a widespread crustacean mesograzer

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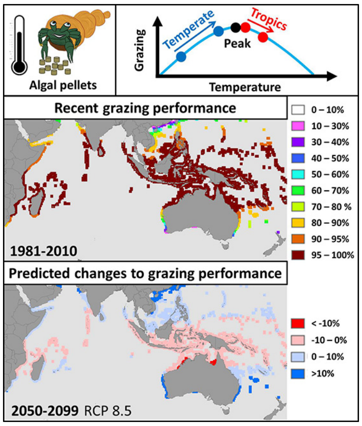
HIGHLIGHTS

- Warmer seas may alter species interactions and ecological functions (e.g. grazing).
- We measured grazing response in the lab and modelled changes under future climates.
- Grazing changes unimodally with temperature and may increase in Indo-Pacific.
- Small decreases in tropics offset by big increases at higher latitudes in the future.
- Similar responses in other grazers suggest possible broad effects as seas warm.

GRAPHICAL ABSTRACT



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ABSTRACT

Grazing is a pivotal function in many marine systems, conferring resilience to coral reefs by limiting algal overgrowth, but triggering phase shifts on temperate reefs. Thus, changes to consumption rates of grazing species in response to higher future temperatures may have broad ecological consequences. We measured how the consumption rates of a widespread mesograzer (the hermit crab *Clibanarius virescens*) responded to changing temperatures in the laboratory and applied these findings to model the spatial footprint on grazing animals throughout the Indo-Pacific region under climate change scenarios. We show that mean grazing capacity may increase in shallow coastal areas in the second half of the century. The effects are, however, asymmetrical, with tropical reefs predicted to experience slightly diminished grazing whilst reefs at higher latitudes will be grazed substantially more. Our findings suggest that assessments of the effects of climate change on reef ecosystems should consider how warming affects grazing performance when predicting wider ecological impacts.

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1. Introduction

Marine ecosystems are increasingly affected by a suite of stressors (Boyd et al., 2015; Hoegh-Guldberg et al., 2007) which may interfere with important ecological processes that contribute to ecosystem resilience (Bellwood et al., 2003; Hoegh-Guldberg and Bruno, 2010; Mumby et al., 2007). Surplus nutrients can lead to excessive algal growth and cause some ecosystems (e.g. coral reefs) to undergo phase shifts to alternative states, upsetting trophic structure and reducing biodiversity (Hempson et al., 2018). However, the functional roles of certain consumer groups can help ecosystems resist such changes (Goldenberg et al., 2018). Grazers, for example, exert strong top-down control on the abundance of primary producers in all benthic marine habitats (Poore et al., 2012), which can mitigate the effect of algal blooms (e.g. in coral reefs (Hughes et al., 2007) and rocky shores (Worm and Lotze, 2006)), in effect increasing ecosystem resilience via resistance to phase shifts (e.g. from coral to algal dominated systems (Mumby et al., 2007)). The effect of grazers on primary producer abundance is strong globally, with both macrograzers and mesograzers (which are generally less recognised as ecosystem engineers) exerting strong control over algal biomass across most marine habitats (Poore et al., 2012). In temperate reefs, which are generally algae dominated, high grazing capacity may have the opposite effect and actually trigger phase shifts (Bennett et al., 2015), sometimes rapidly in response to even short term temperature changes (Wernberg et al., 2016). However, the process of grazing may also be affected by disturbance itself.

Various stressors (e.g. acidification, eutrophication, temperature rise) are known to alter grazer biomass and/or consumption rates (Boyer et al., 2004; Mumby et al., 2006; Wernberg et al., 2016) These stressors can trigger broad changes to ecological function (Hoegh-Guldberg and Bruno, 2010; Smith, 2008), with temperature especially pertinent to tropical species (Perez et al., 2016). As such, temperature plays a role in defining species distributions (Lancaster, 2016), with strong predictive capacity for identifying the latitudinal range of both tropical and temperate marine species (Poloczanska et al., 2013; Stuart-Smith et al., 2017). Changes in temperature can trigger behavioral responses within the distribution (Briffa et al., 2013; Poloczanska et al., 2013), in some cases altering the feeding and metabolic rates (Fussmann et al., 2014; Rall et al., 2010). The shape of the relationship between grazing rates and temperature within the range of a species is a pivotal variable in predicting how rising sea temperatures will impact ecological functions. The simplest model would suggest that feeding rates rise in a linear fashion with temperature (e.g. Elner, 1980; Smith, 2008), probably resulting from faster metabolism at higher temperatures (Fussmann et al., 2014, Rall et al., 2010). However, the shape of the relationship cannot be truly linear because feeding rates will plateau or decline as temperatures approach physiological tolerance limits (Newell and Branch, 1980). Thus, it is plausible, if not likely, that the functional response to rising temperature is unimodal (hump shaped).

It follows that rising sea temperatures may increase grazing performance only if the temperature change corresponds or approaches the peak behavioral response. Conversely, temperature beyond the peak behavioral response point will result in lower consumption rates. Understanding this relationship, especially where peak grazing occurs and how rapidly it declines at sub-optimal temperatures may support predictions of ecosystem responses to climate warming. Field studies can rarely manipulate temperatures sufficiently to identify end-points (for both ethical and practical reasons), whereas this is possible in the laboratory. Thus, we opted to test the effect of temperature on feeding rates under controlled laboratory conditions using a common shallow-water mesograzer, the yellow-footed hermit crab (*Clibanarius virescens* (Kraus, 1843)). This crab is widely distributed across a broad latitudinal range (approx. N37° to S37°) in low intertidal and shallow subtidal habitats throughout the tropical and warm temperate Indo-West Pacific (Dunbar, 2005; Kunze and Anderson, 1979; Morgan, 1988), and is possibly the most diffusely distributed hermit crab in the region (Lewinsohn, 1982). These crabs have shown demonstrable physiological responses to temperature changes (e.g. respiration rate increases with temperature (Dunbar, 2005)), that are consistent with the metabolic theory of ecology. This theory suggests that body size and temperature induce predictable effects on metabolic rate and resource uptake that are relatively consistent across taxa (Brown et al., 2004). Thus, if measurable changes to the grazing capacity of these widespread mesograzers are indicative of similar effects on other consumers, this could suggest concurrent wide-ranging changes to grazing in coastal ecosystems.

Here we quantify the shape of the grazing-temperature response of a widespread shallow water mesograzer (*C. virescens*), and model how climate change may affect its contribution to this important ecosystem function. We do this first by establishing the effect of temperature on the feeding and behavior of *C. virescens* in the laboratory. We then estimate the effect of climate change (temperature rise) by applying these findings to model potential changes in grazing performance throughout the present distribution of *C. virescens* under two climate change scenarios - RCP 4.5 and RCP 8.5 (Moss et al., 2010; NOAA/ESRL Physical Sciences Division, 2018) across two yearly periods: January to March (JFM); and July to September (JAS).

2. Material and methods

We measured grazing rate of the yellow-footed hermit crab in the laboratory across temperatures between 23 °C and 38 °C. Crabs were collected from shallow water at low tide at Burleigh Heads, Queensland, Australia (S 28° 5′ 21″, E 153° 27′ 18″) on multiple occasions in the months leading up to an acclimation period. They were then acclimatised to the laboratory conditions and feeding schedule for at least three months prior to inclusion in these experiments. Monthly average sea surface temperatures (SST) in the region range between 21.4 °C in August, to 27.1 °C in February (World Sea Temperature, 2018). Crabs were kept in aquaria at constant 23 °C, under a 12 h light/dark regime, and on a four day feeding cycle (i.e. crabs were fed the same algal pellets as used in these experiments once every four days). In the morning of the fourth day of each feeding cycle (and prior to feeding), a sub-set of crabs were selected at random (from a pool of approximately 200 total crabs) and placed into individual containers within larger water baths (one bath per temperature treatment). Each water bath contained 10 crabs in individual containers. Given the expectation that crab size may affect consumption rates, crab size was restricted to those with shell volumes between 500 and 1500 mm^3 to maintain similar size distributions across all treatments. Shell volume was calculated from height and width measurements and no difference in mean size was observed among levels.

Temperature was increased to one of five experimental levels (23, 26, 30, 34, 38 °C) gradually over a six hour period in an effort to mirror daily warming cycles in shallow waters. An additional level above 38 °C was attempted (target 42 °C). However, temperatures between 39 and 40 °C elicited a clear stress response, with many crabs exiting their protective shells and moving in an erratic twitching manner and this treatment was therefore abandoned.

In this experiment we simulate the effect of grazing by using algal pellets of a standard size to quantify grazing rates. Thus, after reaching the target temperature, 10 × 1 mm algal pellets were provided to each crab (New Life Spectrum AlgaeMAX 1 mm sinking pellets, containing nine types of algae). The number of pellets consumed was recorded after 1 h. Sample sizes per level ranged between 30 and 39, for a total of 177 hermit crabs. We note here that because hermit crabs exchange shells it was impracticable to identify individual crabs. Thus, we were unable to quantify any potential re-use of individual crabs throughout the experiment beyond ensuring that no crab was included more than once every four days.

The response of grazing rate to temperature was used to develop a model of grazing performance, which we then used to predict grazing