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Not all space is created equal: Distribution of free space and its influence on heat-stress and the limpet *Patelloida latistrigata*

Justin A. Lathlean [a,b,*]

[a] School of Biological Sciences, University of Wollongong, New South Wales 2522, Australia
[b] Department of Zoology and Entomology, Rhodes University, Grahamstown 6139, South Africa

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ABSTRACT

For most marine benthic communities unoccupied primary substrata, or free space, is considered the principle limiting resource. Substratum temperatures, desiccation rates and hydrodynamic characteristics of free space, however, may vary depending on patch size and isolation and therefore potentially influence biotic processes. This paper investigates the relationship between small-scale changes in the availability and configuration of free space, heat stress and abundance of the small rocky intertidal gastropod *Patelloida latistrigata* within southeastern Australia. Using infrared thermography I show that heat stress of rocky intertidal communities increased linearly with increasing amounts of free space on three neighbouring shores during four separate sampling intervals from October 2009 to January 2010. Abundances of *P. latistrigata* generally declined with increasing availability of free space and the associated increases in heat stress. An experimental manipulation that altered the configuration but not the availability of free space demonstrated that both heat stress and *P. latistrigata* abundance are not affected by small-scale changes in the configuration of free space. The small-scale distribution of *P. latistrigata*, however, was significantly influenced by differences in the configuration of free space with limpets displaying bimodal distributions within areas characterised by unevenly distributed free space. Since the distribution of *Patelloida* varies depending on the configuration of free space but thermal properties at the scale of individual limpets do not then we might expect *Patelloida* to be responding to changes in other abiotic factors, such as hydrodynamic forces and desiccation rates, which may change with the configuration of free space. This study highlights the dynamic and usually unexamined relationship between abiotic stress and the availability and acquisition of resources by marine benthic invertebrates.

1. Introduction

As global temperatures continue to rise biological interactions that ameliorate harsh abiotic conditions and buffer the impact of future climate change may become increasingly important (Bruno et al., 2003; Crain and Bertness, 2006; Keppel and Wardell-Johnson, 2012; Silliman et al., 2011). The role of positive interactions are particularly important amongst rocky intertidal communities that experience considerable hydrodynamic forces and extreme heat stress during periods of aerial exposure (Bertness and Callaway, 1994; Bertness and Leonard, 1997; Connell, 1972; Connolly and Roughgarden, 1999). For example, canopies of intertidal macroalgae reduce thermal stress of underlying substrata and invertebrates by lowering temperatures, evaporative water loss and solar radiation (Bertness and Grosholz, 1985; Bertness et al., 1999b). Such species are usually referred to as ecosystem engineers (Jones et al., 1994, 1997). As many intertidal organisms have been shown to live at or close to their thermal limits, amelioration by microhabitats is predicted to play a vital role in mitigating the potentially negative impacts of climate change (Bruno et al., 2003; Denny and Harley, 2006; Somero, 2010).

For most hard bottom marine benthic communities, unoccupied primary substrata, or free space, is considered the principle limiting resource (Dayton, 1971; Gaines and Roughgarden, 1985; Minchinton and Scheibling, 1993). Free space is usually created by physical disturbances or biotic processes such as predation and senescence and is reduced by recruitment and growth of sessile organisms (Elahi and Sebens, 2012; Sousa, 1984). The amount of free space has been shown to be a leading factor governing rates of larval settlement, recruitment and food supply within marine benthic habitats (Bertness, 1989; Gaines and Roughgarden, 1985; Minchinton, 1997; Minchinton and Scheibling, 1993). Abiotic characteristics of free space, however, may vary depending on

* Correspondence address: School of Biological Sciences, University of Wollongong, New South Wales 2522, Australia.
E-mail address: jlathlean@gmail.com

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patch size and isolation, which in turn may influence biological processes. For example, Lathlean et al., (2012) demonstrated that during aerial exposure substratum temperatures on a rocky intertidal shore decreased with increasing percent cover of the barnacle *Tesseropora rosea*. Lathlean et al. (2013) also showed that bare rock immediately adjacent to adult barnacle tests was cooler than isolated bare rock just a few centimetres away from nearest the barnacle. Consequently, barnacles that settled close to adult tests displayed greater early post-settlement growth and survival (Lathlean et al., 2013).

Intertidal barnacles have been shown to mitigate thermal stress for a wide variety of taxa (Barnes, 2000; Cartwright and Williams, 2012; Harley, 2006; Lathlean et al., 2012; Thompson et al., 1996). For example, during winter on tropical rocky shores in Hong Kong the gastropods *Echinolittorina malaccana* and *E. vidua* are predominantly found on open rock surfaces, whilst in summer they migrate to areas dominated by the barnacle *Tetraclita japonica* (Cartwright and Williams, 2012). Here, the interstitial spaces between barnacle tests (i.e. free space) represent a relatively benign microhabitat for these gastropods potentially providing shelter from hydrodynamic forces and reduced desiccation and heat stress. Given the proposed ameliorating effects of barnacles, mussels and oysters on thermal stress, a negative relationship between cover of these organisms and environmental temperatures would be expected. However, the thermal benefits of increased densities might be outweighed by increased competition (i.e. for both space and food). Furthermore, the utilisation and abiotic characteristics of biogenic habitats may vary depending on the configuration, not just the availability, of free space. For example, the ability of organisms to acquire food may differ depending on whether resources are uniformly distributed.

On rocky shores of southeast Australia, the small limpet *Patelloida latistrigata* is found almost exclusively amongst aggregations of the barnacle *Tesseropora rosea* (Creese, 1982). The underlying processes responsible for this association remain largely unknown but may be driven by a combination of factors including (i) reduced heat/desiccation and or hydrodynamic stresses, and (ii) reduced competition with the larger intertidal limpet *Cellana tramoserica* (Creese, 1982; Klein et al., 2011; Underwood et al., 1983). The physical characteristics produced by biogenic habitats are susceptible to modification over relatively short periods of time (in comparison to non-living structures) and associated organisms such as *P. latistrigata* must be capable of responding to these changes. *P. latistrigata* is therefore a suitable organism to investigate how changes in the configuration and availability of free space may alter the physical properties (i.e. heat stress) and subsequent utilisation of biogenic habitats.

The aim of this paper is to investigate the effects of small-scale changes in the availability and configuration of free space on the heat stress and abundance of the rocky intertidal gastropod *P. latistrigata*. Using infrared thermography (IRT) I specifically test (i) whether abundances of *P. latistrigata* vary with changes in the availability of free space and substratum temperatures, and (ii) whether modifying the distribution of free space alters heat stress, abundance and small-scale distribution of *P. latistrigata*.

2. Materials and methods

2.1. Study sites

The study was undertaken on three exposed rocky shores located along the southeast coast of Australia: Garie Beach (34°10′38″S, 151°03′58″E), Wollongong (34°25′22″S, 150°54′31″E), and Kiama (34°39′54″S 150°51′19″E) (Fig. 1). Each rocky shore was composed of grey or brown siltstone, had a northeast to southerly aspect and an overall slight to moderate inclination (7–15°). The topographic landscape of each rocky platform is moderately complex producing a number of differing microhabitats including, most notably, horizontally sloping rocky substrata that becomes fully emerged during low tide. Primary substrata within the mid-shore region at each site is dominated by the surf barnacles *Tesseropora rosea* (approx. 30–50% cover) and *Catomerus polymerus* (less than 5% cover) (J.A. Lathlean, unpublished data). Consequently, in the absence of algae, the combined percent cover of these two barnacles are inversely related to the availability of free space amongst these shores (Garie Beach: $r=-0.897$, $p<0.05$; Wollongong: $r=-0.832$, $p<0.05$; Kiama: $r=-0.781$, $p<0.05$).

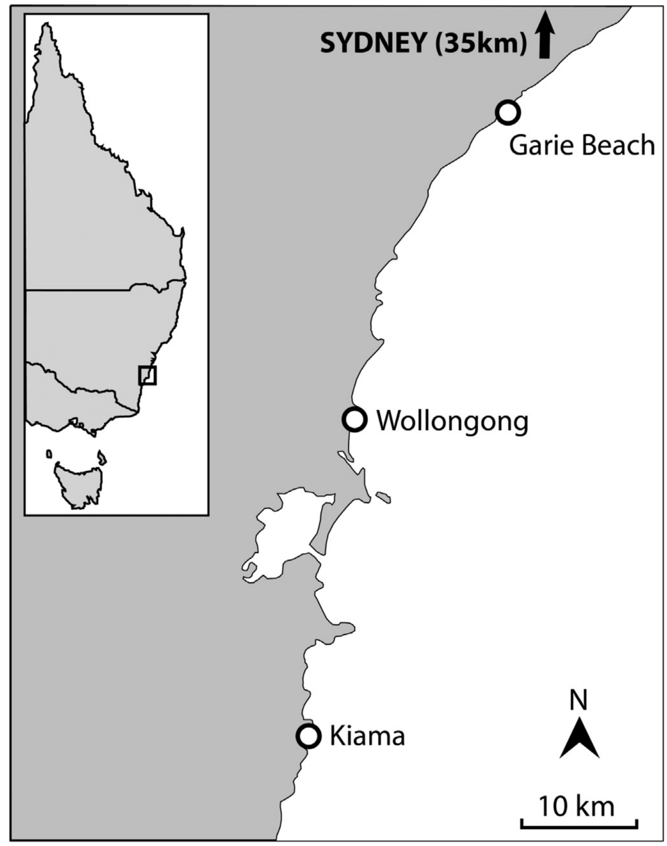

Fig. 1. Map of study region and the three study sites.

2.2. Quantifying availability of free space and *P. latistrigata* abundance

The fine-scale distribution and abundance of barnacles on rocky intertidal shores of southeast Australia have previously been shown to be highly variable (Underwood and Chapman, 1996). To test the affect this small-scale variability of free space (i.e. the inverse of barnacle cover) has on the abundance of *P. latistrigata* between 15 and 36 haphazardly placed photoquadrats (20 cm × 20 cm) were sampled within the midshore region at all three study sites during low tides that fell between 11:00 and 14:00 during the following four sampling intervals: (i) 29 October–1 November 2009, (ii) 12–14 November 2009, (iii) 28–November 2009, and (iv) 9–11 January 2010. These photoquadrats were not fixed but varied in their relative positions along the shore during each of the four sampling intervals. Photoquadrats were placed in areas that were dominated by the presence of barnacles without ephemeral or encrusting macroalgae. Sampling periods were chosen in an attempt to target periods of high heat-stress. Pairs of TidbiT® v2 Temp data loggers (Onset Stowaway logger, model