Ecological Informatics 25 (2015) 43–48

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

A biologically relevant rapid quantification of physical and biological stress profiles on rocky shores

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A R T I C L E I N F O

Article history:
Received 13 July 2014
Received in revised form 25 November 2014
Accepted 25 November 2014
Available online 3 December 2014

Keywords:
Rocky shore
Limpet
Cellana
Hong Kong
Environmental stress
Climate change

A B S T R A C T

Different combinations and intensities of physical (e.g. thermal) and biological (e.g. competition or predation) stress operate on organisms in different locations. Variation in these stresses can occur over small to medium spatial scales (cm to 10s of metres) in heterogeneous environments such as rocky shores, due to differences in sun and wave exposure, shore topography and/or recruitment. In this study we demonstrate how simple measurements can be taken that represent physical and biological stresses (stress profiles) in a given location. Using a bootstrapped principal component analysis, we identified significantly different stress profiles at four sites separated by only 10s to 100s of metres on the Shek O peninsula in Hong Kong. We then measured response to thermal stress, as determined by detachment temperature, in the limpet *Cellana grata* (which is known to be a sensitive indicator species to thermal stress) from each location. Significant differences in stress profile between locations were also seen in thermal stress tolerance of limpets from those locations. At locations where the major stresses are likely to be more physical or less biological in nature (e.g. southerly facing aspect or lower density of grazers), the mean detachment temperature was higher, whereas detachment temperature was lower at sites with more biological or less physical stress. This method is, therefore, able to determine biologically meaningful differences in stress profiles over small to medium spatial scales, and demonstrates that localised adaptation (i.e. post planktonic settlement) or acclimation of species may occur in response to these different stress profiles. The technique can be adapted to different environments and smaller or larger spatial scales as long as the stress experienced by the study species is relevant to these scales.

1. Introduction

On rocky shores few organisms live at environmentally optimal conditions, and are often forced towards the edges of their fundamental niche by biological factors such as predation and competition (Lubchenco, 1980; Somero, 2010; Underwood and Denley, 1984). Examples of these realised niches are common in the rocky shore literature, where shore height (and hence relative immersion:emersion time) provides a simple and localised environmental gradient (Colman, 1933; Harley and Helmuth, 2003). For example, transplants of algae to lower shore levels in the absence of grazers and other competitive species typically result in much higher growth rates of algae than at the shore height they normally occur (Hawkins and Hartnoll, 1985; Norton, 1985), indicating that these species usually occur outside their optimal environmental conditions.

Typically, for hard substrate marine communities there is considerable competition for space (reviewed by Paine, 1984), and as a result, many organisms will be forced towards the edges of their fundamental niches (Braunisch et al., 2008; Costantini et al., 2009). To contend with this, organisms on rocky shores must either tolerate less favourable environmental conditions such as longer periods of desiccation or thermal stress, or have the ability to be able to cope with higher levels of competition, grazing or predation (van Straalen and Roelofs, 2012).

In the rocky intertidal zone, different physical locations (shores or sites within shores) present very different sets of biological and physical challenges for a given species, and these differences can change over a range of spatial scales (see examples in Harley and Helmuth, 2003). For example, at headlands and peninsulas both wave exposure and direct sunlight (and hence temperature and desiccation levels) can vary dramatically over 10s of metres (for example, between north and south facing shores). The impact of predators, competitors and facilitators can also vary over these spatial scales (Menge et al., 1994), often as a result of differential physical factors (Benedetti-Cecchi, 2001). Such distances are normally greater than a typical organism will displace in its adult lifetime, especially when the rocky substratum is not continuous (i.e. separated by sand patches).

The classic theoretical models of Menge and Sutherland (1976, 1987) propose that the roles of physical and biological factors such as disturbance, competition and predation, differ with environmental

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http://dx.doi.org/10.1016/j.ecoinf.2014.11.006
1574-9541/

stress. Since physical stress differs at a local scale of 10s of metres (due to aspect or wave exposure), this infers that biological stresses should also vary at these scales (Benedetti-Cecchi, 2001; Harley and Helmuth, 2003), as do patterns of community structure (e.g. Hutchinson and Williams, 2001).

Adaptations to these combinations of stress (herein 'stress profiles') are likely to occur to maximise survival and reproduction (and hence fitness). Such adaptations could occur through natural selection, however, given that most rocky shore organisms have a planktonic dispersal phase (Pechenik, 1999), localised adaptations (over distances measured in 10s or 100s of metres) are likely to be acclimation responses rather than evolutionary responses (Allcock et al., 1997; Hoskin, 1997; Somero, 2010; but see Krueger-Hadfield et al., 2013).

In this study, we characterise small sections of shore separated by short distances (10s–100s of metres) in relation to a number of physical and biological parameters, to determine the combinations of physical and biological factors that influence the stress profile of organisms. Using a bootstrapped PCA approach (modified from Catlin-Groves et al., 2009; Stafford et al., 2012), we test for significant differences in types of stress acting on limpets (*Cellana grata*) on four sections of shores (each 10 m long, but all separated by <500 m) on the Shek O peninsula on Hong Kong Island. We collected limpets from these sections and tested their response to thermal stress by investigating detachment temperatures. We hypothesise that, where stress profiles differ between sections of shore, those sections where physical parameters are more important (i.e. a lower density of grazers, or a southerly aspect), will have limpets with higher detachment temperatures (i.e. animals are more resistant to temperature extremes). Equally, where stress profiles are more associated with biological stress and less with physical stresses (e.g. higher grazer density meaning more competition, northerly aspect), limpets will have lower detachment temperatures. Support for these hypotheses would indicate that the calculation of stress profiles is biologically meaningful and a useful tool to investigate differences in stress profiles over small spatial scales.

2. Methods

Four sites (continuous sections of rocky shore of 10 m in length) were selected on the Shek O peninsula on Hong Kong Island (Fig. 1) in late May 2013. Sites were selected based on initial inspection of community structure, and knowledge of the direction they faced as well as predominant wave conditions to ensure a variety of potential physical and biological stresses were captured. A 10-m line transect was placed at the height on the section of shore with the highest density of *C. grata* (this shore height differed between sites, but was recorded by measuring the vertical distance from the sea using a cross staff, see Baker and Crothers, 1987 for details). The GPS position (accuracy ± 3 m) was noted at each site, and a number of parameters measured. Grazer density (for *C. grata* and combined for all other grazers) was obtained from five haphazardly placed 50×50 cm double strung quadrats along each 10 m transect. Crevice and rockpool percentage cover and barnacle and mussel percentage cover were also recorded from these five quadrats using the point intercept technique (as described in Bohnsack, 1979). Five recordings of shore slope were taken, using a clinometer placed in the centre of each quadrat (one recording per quadrat). This sampling covered 50% of the area being considered, which has been shown to be sufficient to capture details of even the most patchily distributed organisms or shore characteristics (Stafford, 2002). Photographs of the site, in direct sunlight with a white sheet of paper in the field of view were also taken to determine rock colour (see below).

Simple computer-based analysis followed the field-based data collection. Sites were scored on an ordinal scale for exposure to sun (north facing = 1, east = 2, west = 3, south = 4) and wave exposure (west = 1, north = 2, south = 3, east = 4). Wave exposure was

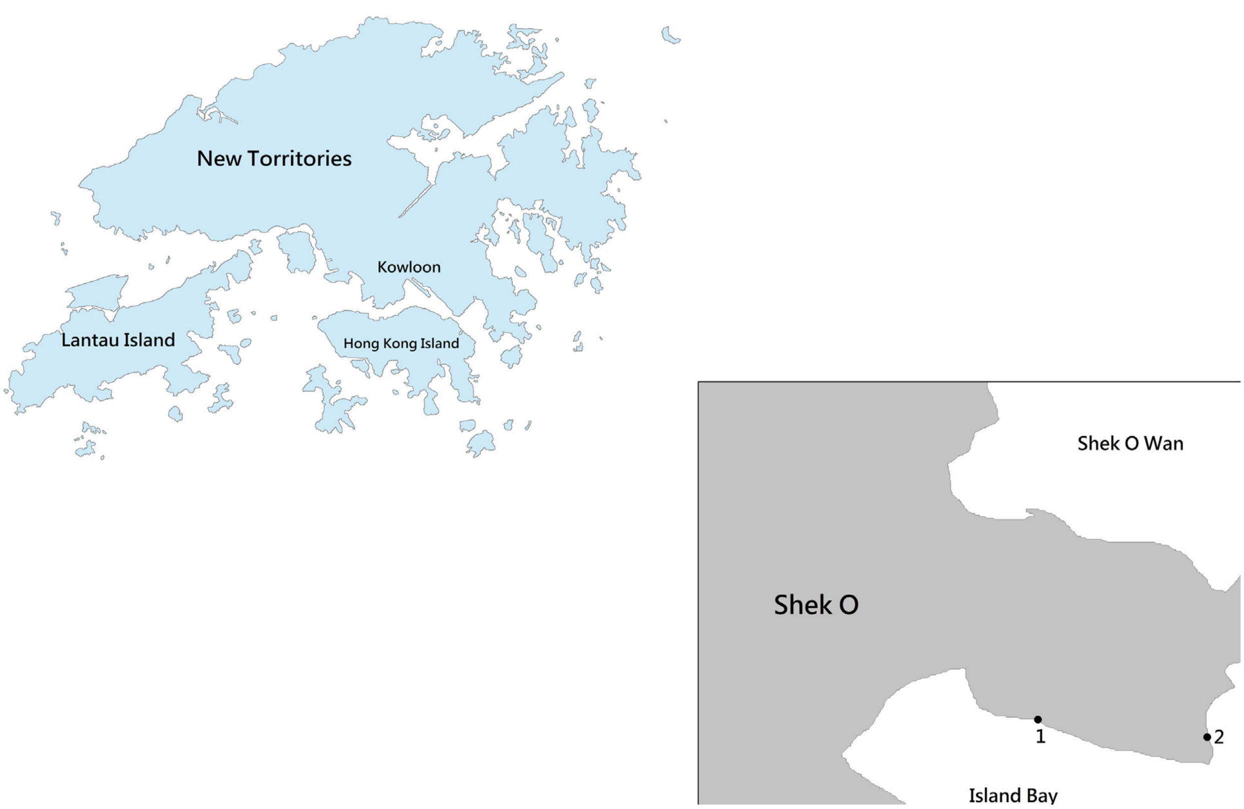

Fig. 1. Locations of the four sites on the Shek O peninsula on Hong Kong Island.