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Shore level differences in barnacle (*Chthamalus dalli*) recruitment relative to rock surface topography

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ABSTRACT

Local recruitment of marine invertebrates is often variable and can be an important determinant of population structure and dynamics. Here, we examined recruitment of barnacles relative to rock surface topography (cracks) over 4 years at 5 sites in Hokkaido, Japan. We used recruitment over multiple years to test for differences in barnacle response to rock surface topography among shore levels under natural conditions and varying recruit densities. Our results showed that barnacles exhibit different recruitment patterns in relation to surface topography over small spatial scales (50 cm) with barnacles in upper intertidal associating more with cracks ($p<0.0001$). In general, we found that barnacles tend to recruit more frequently within cracks in the upper shore and this result was not a function of barnacle density or available crack sites.

1. Introduction

In open populations, such as marine sessile organisms, local recruitment is an important determinant of population structure and dynamics (Roughgarden et al., 1988; Hughes, 1990; Menge, 2000). These populations often show high spatial and temporal variability (Roughgarden et al., 1988; Raimondi, 1990; Menconi et al., 1999) that can be related to variations in success and magnitude of settlement and to post-settlement mitigating influences (Menge, 2000; Hixon et al., 2002). Settlement strategies often demonstrate habitat selectivity that reflects avoidance of post-settlement mortality factors. For example, tunicates are known to settle on the shaded underside of structures, a behaviour that protects the delicate adult tunic from damage by UV light (Bingham and Reyns, 1999) and coral larvae settle most frequently on surfaces that pose the lowest risk of overgrowth and smothering (Harrington et al., 2004).

Barnacle settlers may also express habitat selectivity, allowing increased post-settlement survival via settlement to surfaces with favourable rugosity characteristics (Wethey, 1986; Walters and Wethey, 1996). Recent attention has been paid to the influence of surface heterogeneity on settlement and recruitment of barnacles (Herbert and Hawkins, 2006). Early evidence showed strong settlement preference for ridged surfaces (Pomerat and Weiss, 1946; Gregg, 1948) and many studies have shown barnacle settlement preference for rough surfaces (Crisp, 1974; LeTourneux and Bourget, 1988; Mullineaux and Butman, 1991; Skinner and Coutinho, 2005) and cracks or pits (Crisp and Barnes, 1954; Wethey, 1984, 1986; Raimondi, 1990). Crisp and Barnes (1954) termed the association of settled barnacles with cracks in rocks “rugophilic” behaviour.

Rocky intertidal habitats are characterized by tidal gradients, or sharp vertical changes in environmental conditions on a scale of tens of centimetres (e.g., Connell, 1972). Previous studies demonstrate that shore level can alter community structure, population dynamics, and process determining them (Doty, 1946; Jenik and Lawson, 1967; Bertness, 1981; Raffaelli and Hawkins, 1996; Menconi et al., 1999; Miron et al., 1999) and likewise may affect the degree of association of barnacles to cracks. To our knowledge, however, this hypothesis has not been tested. We expect that barnacles may show differential settlement and/or survival in relation to surface topography over small vertical spatial scales where physical factors, such as desiccation stress, vary (Connell, 1972).

The goal of this study was to compare the proportion of barnacles recruiting to cracks among shore levels under varying conditions of barnacle density and crack availability.

2. Materials and methods

2.1. Field census

A rocky intertidal area in Akkeshi Bay, located in north-eastern Hokkaido, Japan (43°2′59″N, 144°46′41.5″E) was used to study barnacle recruitment (Fig. 1). Five plots were located on semi-exposed, roughly vertical (slopes varied from 58° to 87°) metamorphic rocky shore that faced roughly north. Maximum tidal amplitude at this location is roughly 160 cm. Plots were separated by approximately 25 m each and were permanently marked using screws drilled into the rock face. Each

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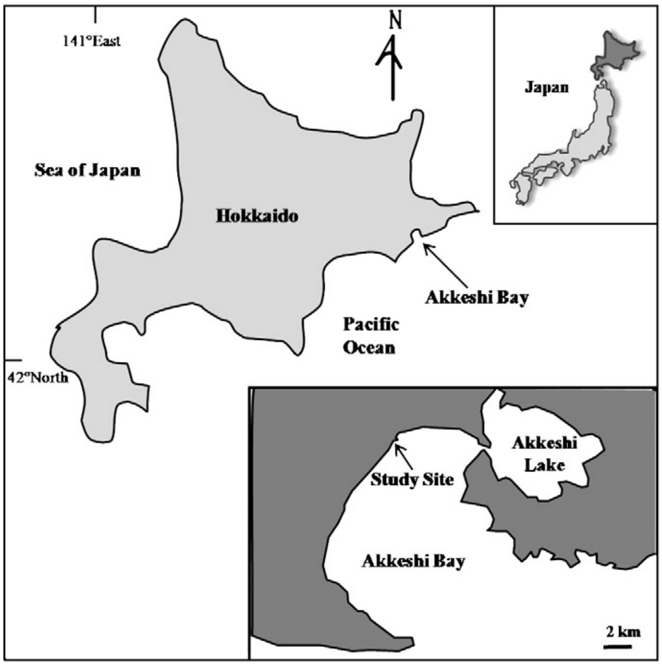

Fig. 1. Location of study area. Top right inset shows location of Hokkaido (shown in dark shading) within Japan. Main map shows location of Akkeshi Bay within Hokkaido. Lower right inset shows location of study area within Akkeshi Bay.

spring, beginning in 2004 and continuing through 2007, at each of the five plots, an area 30 cm horizontally and 100 cm vertically centered on mid-tide was cleared of all surface organisms in April, by burning with gas torches and physical clearing with wire brushes during low tide (following Barnes and Powell, 1950). This vertical range covered the habitat occupied by the barnacle population at these plots. Each plot was divided vertically into 3 shore levels; upper, middle and lower intertidal (Fig. 2). Detailed description of the study site and biogeographical features of the area can be found in Okuda et al. (2004) and Nakaoka et al. (2006).

After clearing each spring, plots were not disturbed further and natural recruitment of barnacles (*Chthamalus dalli*) progressed (in this region this species settles during summer (Kado, 2003)). Ten photographs of quadrats (5 × 5 cm) were taken within each shore level at each plot 125 days after clearing using a Canon IXY Digital 320 camera (macro setting, 180 dpi, taken 10 cm from the rock surface, 18 pixels/mm). Two photographs from each tide level and each plot were randomly selected to be used for analysis. Some photographs were unusable due to fog on the camera lens or low density of barnacles (<20 individuals per photo were not used), resulting in a total of 24 photographs from the upper shore and 30 each from the middle and lower shores.

2.2. Analysis

Each photograph was used to map locations of barnacle recruits and locations of cracks in the rock surface (using XYit Digitizer software, Geomatix Ltd. UK). In this study we considered cracks to be small and steep indentations in the rock surface and on the order of 2 mm wide and 1 mm deep and recruits were all barnacles that settled and survived between the time of rock clearance and photographing. Photographs used in analysis ranged in barnacle density between 23 and 513 barnacles per 25 cm^2 (mean = 201 ± 27 95% C.I.). Distance from each mapped barnacle recruit to the nearest crack and total length of cracks in each map was measured using a program written in R (R Development Core Team, 2007; Baddeley and Turner, 2005). All photographs were also visually analysed and each barnacle was assigned a status of "on" or "off" cracks based on whether it was attached within (on) or outside (off) a crack. Influence of shore level on proportion of barnacles on cracks was analysed using logistic regression with total length of crack and barnacle density as covariates (barnacle density and crack length were normalized using square root transformation). These covariates were used because total crack length and density of barnacles varied among maps and both are important determinants of association with cracks. Differences in total length of crack represents differential opportunity to settle on a crack and increased density may mean early settlers occupy crack space so subsequent settlers cannot (pre-emptive competition).

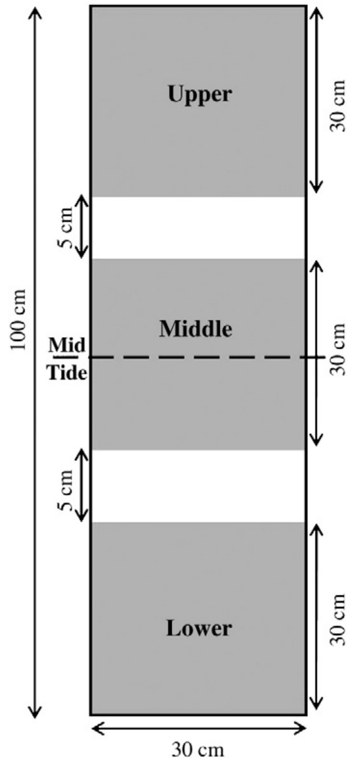

Fig. 2. Layout of all 5 study plots. Permanent anchors were drilled into rock to ensure repeated annual use of the same plots. Grey shading shows areas that were used for comparison among shore levels. White areas were not used and acted as a boundary between shore levels.

2.3. Model simulation

To test observed locations of barnacles relative to cracks, another program was written in R (R Development Core Team, 2007; Baddeley and Turner, 2005) to generate maps containing randomly located barnacles and cracks. Randomly generated cracks and barnacle populations had the same density as those observed from photographs based on summary statistics (mean, median, maximum, minimum and standard deviation) from empirical observations within each shore level over all plots and dates. The randomization was run 1000 times for each shore level, and proportion of barnacles on and off cracks was recorded.

3. Results

Barnacle recruits in upper intertidal plots showed a greater affinity to cracks and more barnacles were observed within 1 mm of a crack (on or within approximately one body length of crack) in upper versus middle and lower intertidal (Fig. 3). In the upper shore, a significantly greater proportion of barnacles were on cracks than in the lower intertidal ($p < 0.0001$, Fig. 4 and Table 1). There was no significant difference between proportion of barnacles on cracks in

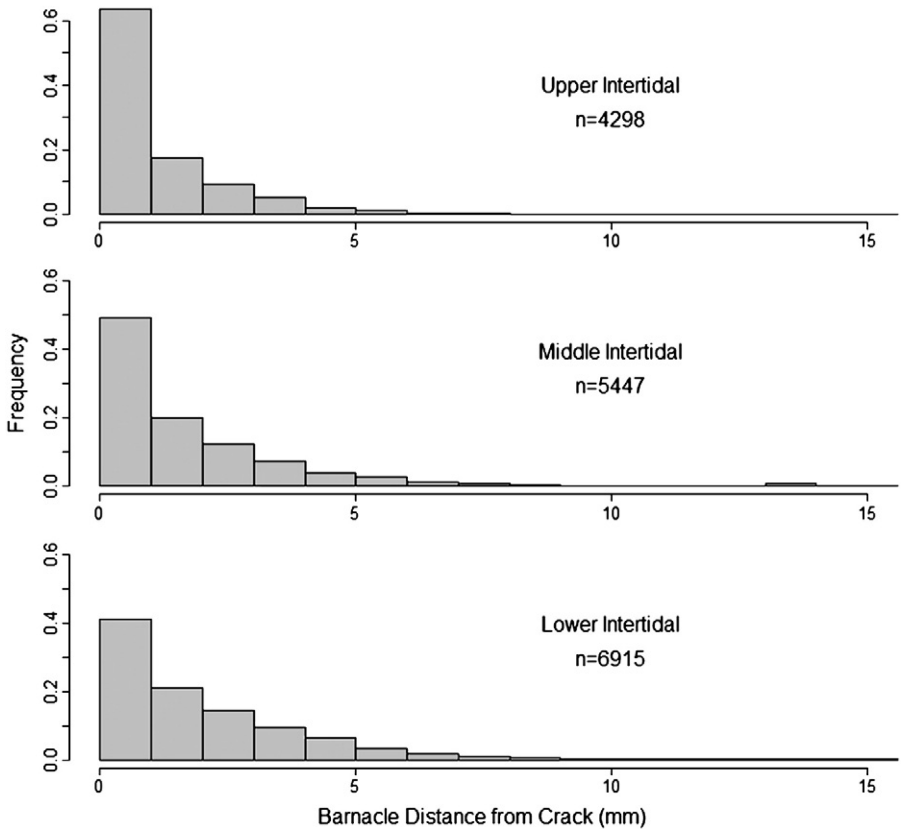

Fig. 3. Histogram of distance between barnacles to the nearest crack as measured from maps (all years and all plots combined for each tide level).

middle and lower intertidal. The covariates were also significant predictors of proportion of barnacles on a crack with total crack length showing a positive effect and barnacle density showing a negative effect (Table 1, $p<0.00001$; $p=0.017$ respectively). Random simulation of barnacle and crack locations showed approximately 25%, 27% and 28% of barnacles on a crack in the upper, middle and lower intertidal respectively (Fig. 4, hatched bars).

4. Discussion

Sharp environmental and biological gradients dominate rocky intertidal habitats and can be characterized as strong desiccation stress, higher temperatures and increased solar radiation in the upper shore with higher predation and competitive influences in the lower shore (Connell, 1972). Here, we observed a change in the frequency of use of cracks as recruitment habitat for barnacles (*C. dalli*) with shore level. Crisp and Barnes (1954) introduced the term “rugophilic” to describe the preference for cracks demonstrated by settling barnacles and here we show an increased association between recruits and cracks that may result from an increased rugophilic tendency of barnacles in the upper shore compared to the middle and lower shores. Alternatively, this pattern may result from higher post-settlement mortality outside of cracks in the upper shore.

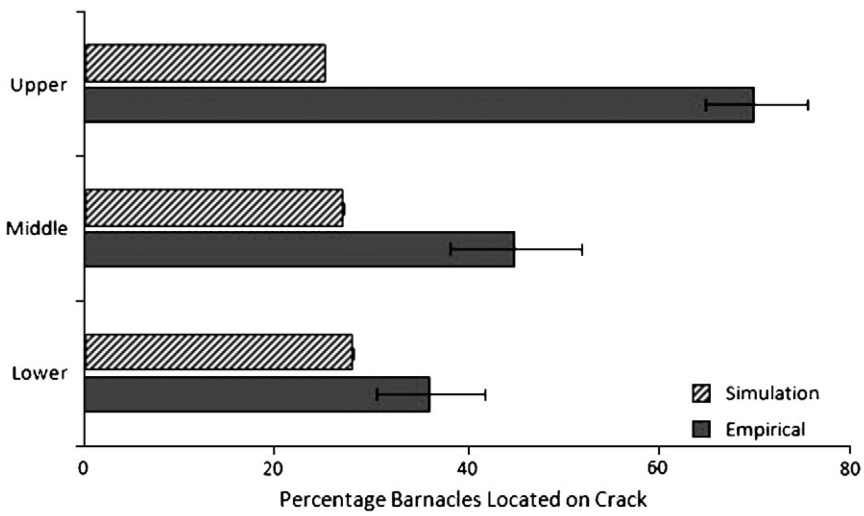

Fig. 4. Proportion of barnacles located on cracks by shore level. Error bars show 95% confidence intervals (confidence intervals for simulated values are too small to be visible on this plot). Hatched bars show the proportion of barnacles on cracks based on random simulation of locations. Total *n* for empirical bars are upper = 4298, middle = 5447, lower = 6915.

Table 1
Results of logistic regression for effect of shore level on proportion of barnacles recruited to cracks with barnacle density and total crack length per photo as covariates. Barnacle density and crack length were normalized using square root transformations.

	Regression coefficient	DF	Deviance	*p*
Shore level	2.3 (low vs. mid) 3.4 (low vs. up)	2	91.3	<0.0001
Density	−0.0073	1	5.7	0.017
Total crack length	0.21	1	33.8	<0.0001
Density × shore level	−0.089 (low vs. mid) −0.18 (low vs. up)	2	0.26	0.88
Total crack length × shore level	−0.14 (low vs. mid) −0.11 (low vs. up)	2	1.3	0.52
Density × total crack length	−0.004	1	0.009	0.93
Density × crack length × shore level	0.006 (low vs. mid) 0.009 (low vs. up)	2	0.4	0.82

Recruitment to cracks and depressions offers the advantage of protection from the increased environmental threats of the upper shore such as desiccation (Raimondi, 1990), insolation (Wethey, 1984; Chiang et al., 2003), and high temperatures. Cracks can also offer protection from threats encountered in the lower shore, such as predation or incidental mortality due to bulldozing organisms (Keough and Downes, 1982). Here we observed that at all shore levels, the proportion of barnacles on cracks was higher than that expected from random simulations and thus barnacles could be settling in a selective way within cracks at all shore levels. Alternatively, because recruitment (as measured here) represents integration of settlement and subsequent survival, this pattern may represent higher survival within cracks at all shore levels. We observed that a higher proportion of barnacles occurred close to cracks in the upper compared to middle and lower shore locations. This indicates that settlement and/or post-settlement survival was higher in cracks in the upper shore.

Barnacles associated with cracks may benefit from increased survival due to mitigation of mortality factors within cracks. Contradictory evidence can be found in previous studies examining settlement in cracks and differential survival. Wethey (1984) saw 10 times higher settlement rate in cracks versus outside cracks, yet did not observe an increase in barnacle survival when settled in cracks. Alternatively, Chabot and Bourget (1988) identified a strong decrease in mortality due to ice scour for barnacles that settle within cracks. In an examination of intertidal settlement cues, Miron et al. (1999) observed greater survival of early barnacle recruits in the lower shore compared to the upper shore. If this is also true for the sites examined here, decreased upper shore survival may create greater pressure for rugophilic settlement within this shore level. Survival was not directly measured in this study and thus cannot be tested.

Other authors have demonstrated variation in barnacle response to cracks or surface roughness based on barnacle density and available crack sites (Wethey, 1984; Raimondi, 1990; Hills and Thomason, 1996; Prendergast et al., 2009). During daily analysis of settlement patterns of *Semibalanus balanoides*, Wethey (1984) observed up to 30% of recruits settling in cracks when crack availability was high, but only 2–5% of settlers settling within cracks when crack availability was lower. Raimondi (1990) demonstrated that as settlement densities of *Chthamalus anisopoma* in pits increased, their preference for settling within pits decreased. In the examination of settlement patterns of *S. balanoides*, Prendergast et al. (2009) showed that once a threshold of settlement density was reached, surface texture was no longer an important factor in cyprid settlement. In this study we were able to use multiple years and a range of densities and crack lengths to test association of barnacles with cracks over shore level within these varying conditions. The proportion of barnacles on cracks showed a negative relationship with density which agreed with previous reports (Wethey, 1984; Raimondi, 1990). Likewise, a positive association observed between total crack length and proportion of recruits on cracks agreed with previous studies (Wethey, 1984). Here, the influence of shore level on proportion of recruits to cracks was maintained over various densities and crack lengths with no significant interactions, indicating that the shore level change in association with cracks is not confounded with differences in density or habitat availability. To further elucidate the underlying factors of greatest importance to this pattern this experiment should be replicated at more sites with differing exposure, thermal regimes, and rock types. In addition, experiments designed to test possible mechanisms determining this pattern (settlement preference, differential survival etc) should be carried out.

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