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Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place

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Abstract To explore how climate may affect the structure of natural communities, we quantified the role of thermal stress in setting the high intertidal borders of the acorn barnacle, *Semibalanus balanoides*. At sites north and south of Cape Cod, a major faunal and thermal boundary on the east coast of North America, we examined the interacting effects of thermal stress and recruit density on individual survivorship. At hotter southern sites, particularly in bays, high intertidal barnacle survivorship was enhanced by experimental shading or by neighbors which ameliorate heat and desiccation stresses. In contrast, at cooler northern bay and coastal sites, neither shading nor group benefits increased barnacle survival, and mortality patterns were driven primarily by predators with largely boreal distributions. Our field results, like recent laboratory microcosm studies, suggest that predicting even simple community responses to climate change may be more complex than is currently appreciated.

Key words Rocky intertidal · Experimental ecology · Facilitation · Thermal stress · Climate

Introduction

That species interactions are sensitive to variation in environmental factors such as heat and desiccation has

long been a major theme of studies of the organization of natural communities. The early laboratory work of Gause (1934) and Park (1954) emphasized the role of temperature in dictating the outcome of competitive species interactions. On rocky shores, where there has been considerable work on the organization of natural communities, temperature and desiccation stresses are also known to be critical community-structuring forces (for reviews see Lewis 1964; Connell 1972; Little and Kitching 1996; Raffaelli and Hawkins 1996).

Most of the focus on the influence of physical factors on species interactions has been on how the strength of competitive interactions varies with physical stresses (Menge and Sutherland 1976, 1987); however, the very nature of species interactions can change in response to physical factors (Dunson and Travis 1991; Bertness and Callaway 1994). In particular, positive species interactions, where neighboring organisms benefit one another by buffering potentially limiting physical stresses, may be characteristic of physically harsh environments, and the importance of these types of interactions could increase with stresses accompanying global warming. An association between the occurrence and impact of positive, habitat-ameliorating interactions and physically stressful conditions has been widely noted (Connell and Slayter 1977; Bertness 1989; Goldberg and Barton 1992; Tilman and Downing 1994) and it has been suggested that interactions among sessile organisms may generally shift from negative, competitive interactions under physically benign conditions to positive, habitat-ameliorating interactions with increased physical stress (Bertness and Callaway 1994; Bertness and Leonard 1997; Callaway and Walker 1997). If this is generally true, variation in physical stresses may have much more marked effects on communities than simply changing the intensity of interactions.

Rocky intertidal communities are an attractive system in which to explore the role of physical stresses in mediating species interactions because spatial variation in physical stresses is very predictable and the sessile organisms that dominate these systems are amenable to

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experimental examination (Little and Kitching 1996; Raffaelli and Hawkins 1996; Bertness 1999). Most work in these systems, however, has focused on how variation in tidal height affects interactions. Little work has examined how the equally predictable variation in physical stress regionally (between bays and coastal habitats) and biogeographically (with latitude) affects species interactions and communities (see Vermeij 1978 for discussion). This is surprising, since examining these issues at larger spatial scales may be the best means available for understanding and predicting how natural systems will respond to climate change (Kareiva et al. 1993).

To investigate the idea that benthic populations in rocky intertidal habitats are sensitive to climatic variation, we examined the density-dependent dynamics of the northern acorn barnacle, *Semibalanus balanoides*, at regional (bay vs coast) and biogeographic (latitude) spatial scales. *Semibalanus* is ideal for this work. It is one of the most studied and best understood sessile shoreline organisms (Southward 1987; Anderson 1993). Moreover, while high barnacle densities enhance individual survivorship at high tidal heights due to the thermal buffering effects of neighbors (Lively and Raimondi 1987; Bertness 1989), they also lead to intense consumer pressure, intraspecific competition, and heavy mortality under physically benign conditions (Barnes and Powell 1950; Roughgarden et al. 1985).

We used Cape Cod on the east coast of North America as a biogeographical barrier. Cape Cod has long been known as a strong thermal barrier and biogeographic discontinuity in the distribution of shoreline organisms (Allee 1923; Vermeij 1978). High summer temperatures south of Cape Cod influence the distribution of high intertidal organisms, including barnacles (Wetthey 1983) and carnivorous snails (Etter 1988).

Materials and methods

To examine the hypothesis that regional and latitudinal variation in thermal stress predictably influence the nature of interactions among shoreline organisms, we manipulated densities of *Semibalanus* and quantified their survivorship when exposed to ambient climatic conditions and under experimental shades that reduced exposure to thermal stress. Both north and south of Cape Cod, rock cobbles (exposed surface areas ranging from 150 to 250 cm²) with recently metamorphosed juvenile barnacles (<1 month old) were collected at common sites in each biogeographic province and transplanted to two coastal and two bay sites. South of Cape Cod, coastal sites were Little Compton and Newport, Rhode Island, and bay sites were Mt Hope and Portsmouth, Rhode Island (see Sanford et al. 1994 and Bertness et al. 1996 for descriptions). North of Cape Cod, coastal sites were Chamberlain and Pemequid Points, Maine (see Menge 1976) and bay sites were Lower Narrows and Plummer Point on the Damariscotta River, Maine (see Leonard et al. 1998). At each site, cobbles with either high (5–10 recruits/cm²) or low (<1 recruit/cm²) initial barnacle recruit densities were transplanted to the high intertidal border of *Semibalanus* and either shaded or left exposed to ambient solar radiation. Cobbles were embedded in cement on horizontal rock benches to thermally insulate them from artificially high temperatures (Bertness 1989; Sanford et al. 1994). Shades were plastic mesh roofs that cut incoming solar radiation by ~50% and reduced rock surface temperature by 6–9°C (Bertness and Leonard 1997). At each site,

treatments were replicated ten times (total = 40 replicates/site). The experiment was set up in April–May 1996 and experimental cobbles were photographed monthly until the following September. Recruit survivorship was calculated from the photographs.

To compare thermal conditions among sites we used daily maximum air temperature data from weather stations near the sites. Our attempts to continuously measure rock surface temperatures at the sites were vandalized. For Maine we used data from the Pemquid Lighthouse and the Darling Marine Center for open-coast and protected-bay weather conditions, respectively. In Rhode Island, open-coast conditions were obtained from the Newport, Rhode Island Weather Station, and bay conditions were obtained from the weather station at the National Estuarine Research Reserve on Prudence Island. To examine temperature differences among habitats, we calculated the deviation of mean daily temperatures between habitat types. This allowed us to graphically examine subtle, but consistent differences in air temperatures between coastal and bay habitats in Rhode Island and Maine, and to compare similar habitats between Rhode Island and Maine.

Recruit survivorship data from sites north and south of Cape Cod were arcsine transformed to meet the assumptions of parametric statistics and analyzed separately with a four-factor nested

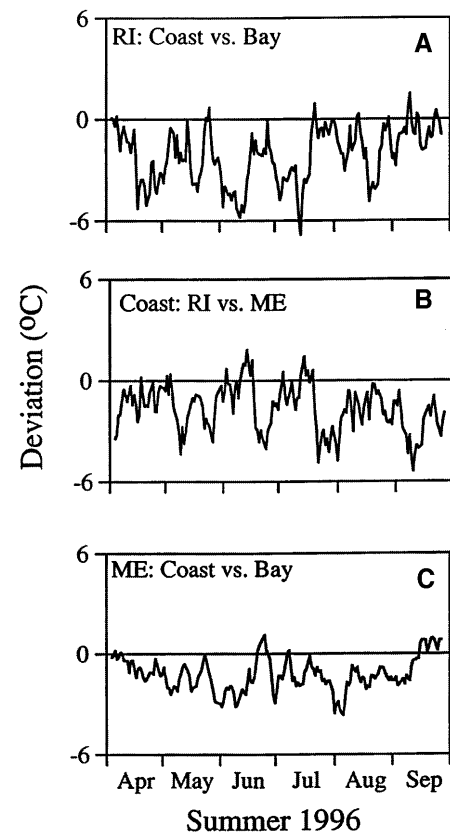


Fig. 1 Comparisons of maximum daily air temperatures during the summer of 1996 (1 April 1996–1 October 1996) between coastal and bay habitats at sites north and south of Cape Cod. Data were obtained from the Northeast Regional Climate Center. Temperatures were recorded at weather stations located within 10 km of the study sites. Graphs show the 7-day running means of the daily temperature deviations (anomalies) between relatively cooler and relatively hotter habitats. Comparison of: coastal and bay habitats in Rhode Island (A), coastal habitats between Maine and Rhode Island (B), coastal and bay habitats in Maine (C). The overall average daily deviations calculated from the 183 individual deviations were -2.03°C , -1.69°C , and -1.20°C for the three comparisons, respectively

ANOVA. Comparisons of recruit survivorship between sites north and south of Cape Cod were made qualitatively.

Results and discussion

Air temperatures during the experiment (Fig. 1) from weather stations near the sites showed that both north and south of Cape Cod, bays were hotter than open coast habitats, and that for both coastal and protected bay habitats, summer temperatures were consistently 2–3°C higher south of Cape Cod. Rock temperature differences were even greater, likely reflecting regional differences in cloud cover, fog, and water temperature. In Narragansett Bay, south of Cape Cod, summer rock temperatures are often 40–50°C (Bertness 1989), whereas north of Cape Cod in Maine where our experiments were undertaken, rock temperatures above 40°C are uncommon (Leonard et al. 1998).

Patterns of barnacle survivorship varied markedly north and south of Cape Cod (Fig. 2). South of the Cape, the survivorship of solitary barnacles, particularly those in bays, was markedly increased by shading (Fig. 2, Table 1). At bay sites, shading increased the survivorship of solitary barnacles by a factor of ten, while it more than doubled the survivorship of barnacles at coastal sites. Crowding also increased the survivorship of unshaded barnacles in bays south of Cape Cod over three times that of solitary barnacles. Shading eliminated the group benefits of neighbors in southern

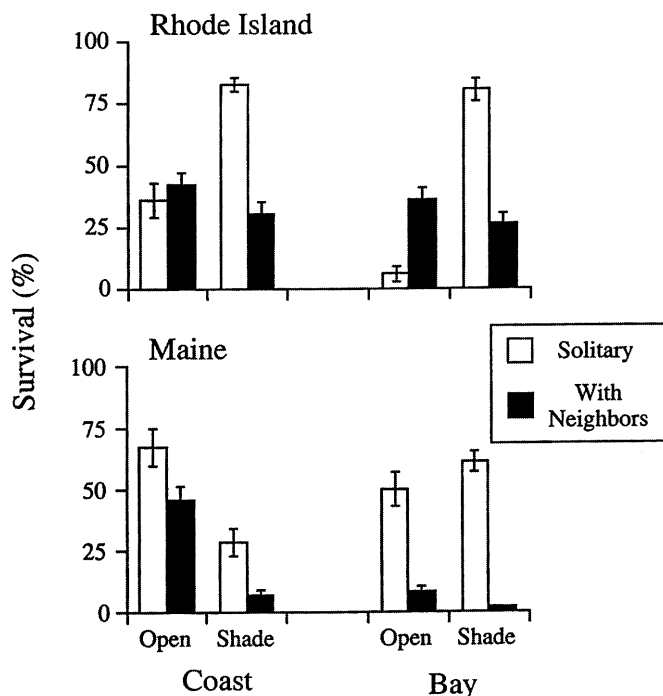


Fig. 2 Barnacle survival (%) as a function of habitat type (coastal vs bay), experimental shading (open vs shaded), and barnacle density (solitary vs with neighbors) at sites from Rhode Island and Maine. Data are untransformed means \pm 1 SE. See text for explanation of experimental design and Table 1 for statistical analysis

bays, indicating that thermal buffering was responsible for these positive group effects (Bertness 1989; Bertness and Leonard 1997). At coastal sites south of Cape Cod, neighboring barnacles did not significantly enhance individual survivorship.

North of Cape Cod (Fig. 2, Table 1) shading did not increase the survivorship of solitary or crowded barnacles in either bay or coastal habitats, suggesting that thermal stress was not as important a community structuring force at northern sites. Moreover, at northern sites with reduced thermal stress, there was no evidence of high barnacle densities enhancing survivorship at high tidal heights. In contrast to southern sites, at both northern bay and coastal sites, high recruit densities suffered higher mortality than did low-density recruits due to density-dependent predation from a boreal suite of predators largely absent at the southern sites. In northern bays, high densities of shaded and unshaded juvenile barnacles were eaten by the green crab *Carcinus maenas*, which is relatively rare south of Cape Cod (Gosner 1978) and absent from our Rhode Island sites. This was confirmed by laboratory and field experiments which showed that green crabs preferentially consumed

Table 1 Summary of the four-factor, nested analysis of variance on barnacle survival. Fixed factors were habitat, shading, and density, and the random factor was site nested within habitat. The dependent variable was percent survival calculated from photographs of each experimental cobble. Data were arcsine (square root) transformed before analysis. Separate analyses were run for sites from Rhode Island (south of Cape Cod) and Maine (north of Cape Cod). Error terms (MS for the denominator of the *F*-ratio) are indicated in the righthand column [*a* Site(Habitat), *b* Residual, *c* Shading \times Site(Habitat), *d* Density \times Site(Habitat), *e* Shading \times Density \times Site(Habitat)]. Significant *P*-values (<0.05) are italicized

| Source of variation | <i>df</i> | MS | <i>F</i> | <i>P</i> | |
|---|-----------|-------|----------|----------|----------|
| Rhode Island | | | | | |
| Habitat | 1 | 0.37 | 3.66 | 0.196 | <i>a</i> |
| Shading | 1 | 2.01 | 53.00 | <0.001 | <i>b</i> |
| Density | 1 | 1.04 | 27.53 | <0.001 | <i>b</i> |
| Site(Habitat) | 2 | 0.10 | 2.69 | 0.072 | <i>b</i> |
| Habitat \times Shading | 1 | 0.20 | 7.15 | 0.116 | <i>c</i> |
| Habitat \times Density | 1 | 0.09 | 1.20 | 0.388 | <i>d</i> |
| Shading \times Density | 1 | 4.26 | 772.78 | 0.001 | <i>e</i> |
| Shading \times Site(Habitat) | 2 | 0.03 | 0.72 | 0.488 | <i>b</i> |
| Density \times Site(Habitat) | 2 | 0.08 | 2.02 | 0.137 | <i>b</i> |
| Habitat \times Shading \times Density | 1 | 0.13 | 22.76 | 0.041 | <i>e</i> |
| Shading \times Density \times Site(Habitat) | 2 | 0.01 | 0.15 | 0.865 | <i>b</i> |
| Residual | 121 | 0.04 | | | |
| Maine | | | | | |
| Habitat | 1 | 0.21 | 0.43 | 0.581 | <i>a</i> |
| Shading | 1 | 1.17 | 51.74 | <0.001 | <i>b</i> |
| Density | 1 | 4.61 | 203.30 | <0.001 | <i>b</i> |
| Site(Habitat) | 2 | 0.49 | 21.75 | <0.001 | <i>b</i> |
| Habitat \times Shading | 1 | 1.65 | 46.14 | 0.021 | <i>c</i> |
| Habitat \times Density | 1 | 0.57 | 1.03 | 0.417 | <i>d</i> |
| Shading \times Density | 1 | 0.03 | 0.28 | 0.650 | <i>e</i> |
| Shading \times Site(Habitat) | 2 | 0.04 | 1.58 | 0.211 | <i>b</i> |
| Density \times Site(Habitat) | 2 | 0.55 | 24.27 | <0.001 | <i>b</i> |
| Habitat \times Shading \times Density | 1 | 0.16 | 1.42 | 0.356 | <i>e</i> |
| Shading \times Density \times Site(Habitat) | 2 | 0.11 | 4.87 | 0.009 | <i>b</i> |
| Residual | 120 | 0.023 | | | |

and eliminated dense aggregations of barnacle recruits (Leonard et al. 1999). At northern coastal sites, crabs were uncommon, but high barnacle densities were preferentially consumed by the carnivorous whelk, *Nucella lapillus* (see Dunkin and Hughes 1984 and Roughgarden et al. 1985 for other examples of density-dependent foraging by slow-moving shoreline predators). Snail consumer effects were particularly pronounced under shades. At the high tidal heights where our experiments were performed, whelks were uncommon, except under shades which provided them with a thermal refuge (Menge 1976; Leonard et al. 1998). Like green crab predation, *Nucella* predation effects were not seen at southern sites because this snail is also largely a boreal species whose distribution does not extend south of Cape Cod (Glude 1955; Gosner 1978).

While our results must be interpreted with caution since they come from a single experiment done in a single year, they suggest that the relatively small 2–5°C increases in average temperature predicted over the next century by most global climate models (Kareiva et al. 1993) may trigger larger changes in communities than is generally appreciated. Like recent laboratory studies (Davis et al. 1998), however, our data also caution that the resulting community changes in response to climate change may be complex and often difficult to predict even for simple systems. The thermal gradient across the Cape Cod biogeographic boundary appears to lead to substantial shifts in rocky shore community patterns and processes. Thermal stress and habitat-ameliorating group benefits play an important role in setting the high intertidal border of barnacles south but not north of the Cape. This is a predictable consequence of increased thermal stress south of Cape Cod. North of Cape Cod, however, summer thermal stress gives way to consumer pressure as the leading determinant of mortality patterns. Moreover, although group benefits were important for barnacle survival south of the Cape, high barnacle densities were more susceptible to consumer mortality north of the Cape. Thus, increased thermal stress from global warming may lead to habitat-ameliorating group benefits playing a larger role in these northern communities, but only if the distributions of barnacle consumers respond similarly to climate change. Predicting community responses to climate change is a difficult challenge for ecology, but should be possible in well-understood systems such as rocky intertidal habitats.

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