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# LATITUDINAL VARIATION IN SPECIES INTERACTIONS: A TEST IN THE NEW ENGLAND ROCKY INTERTIDAL ZONE

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Abstract. How species interactions vary as a function of habitat characteristics continues to be an important debate in ecology. Using the barnacle-seaweed assemblage common in New England rocky intertidal habitats, I tested the hypothesis that species interactions switch from negative to positive at sites across the Cape Cod faunal barrier because of latitudinal variation in thermal stress and predation intensity between these regions. I manipulated Ascophyllum nodosum canopies in the high zone of two sites from each region and then determined the consequences for underlying Semibalanus balanoides recruits and adults for two years (January 1995 through January 1997). In both years, algal canopies reduced barnacle recruitment and growth rates at all sites but greatly increased survival rates only at the southern sites. When integrated in a demographic framework, these data showed that the reproductive fitness potential of individuals was facilitated by the algal canopy at southern sites but was reduced under similar conditions at northern sites. At southern sites, this was likely the result of buffering from physical stresses in the absence of predators. At northern sites, any buffering from physical stress was likely offset by an increase in mortality in the presence of predators. Interestingly, this variability in species interactions appeared to be associated with subtle variation in climate. Facilitation was evident only during 1995, the warmest year on record since 1900. In contrast, interactions were entirely negative during 1996, a slightly cooler year. These results suggest that species interactions in the intertidal zone may be sensitive to even subtle changes in climate. Interspecific buffering of neighbors from thermal stress is likely to be common in other systems and suggests that both aquatic and terrestrial vegetation may become increasingly important to local species persistence as climates change during the next century.

Key words: Ascophyllum nodosum; direct vs. indirect effects; fitness consequences; habitat amelioration; interactions, positive and negative; latitude effects on species interactions; New England (USA) rocky intertidal zone; Nucella lapillus; predation; Semibalanus balanoides; thermal stress.

#### INTRODUCTION

Pattern and process across biogeographic spatial scales have been of interest to ecologists since the time of Darwin. Increases in diversity across latitudinal gradients and between ocean basins are well known (Fischer 1960, MacArthur 1965, 1972, Spight 1976, Wallace 1878), although the ultimate mechanism for their origin and maintenance remains unclear (Rhode 1992, Rosenzweig 1995). Biological processes have long been argued to vary across large spatial scales (Mac-Arthur 1972, Vermeij 1978), and latitudinal variation in predation, in particular, has been associated with differences in morphology in many organisms (Mayr 1963, Bakus 1969, Vermeij and Veil 1978). Although species interactions have been hypothesized to vary biogeographically (e.g., Vermeij 1978, Dethier and Duggins 1988), experimental tests of these hypotheses have been relatively rare (but see Jeanne [1979], Bertness et al. [1981], Menge and Lubchenco [1981] for exceptions). This scarcity of experimental data is at least partly due to the logistical difficulties of conducting manipulative experiments at large spatial scales.

Over the last twenty years, work within single biogeographic regions has highlighted how abiotic conditions can alter the relative importance of biological processes in governing community structure (Connell 1961, Menge 1976, Menge and Sutherland 1987). These results, largely from marine habitats, predict that as physical stress increases, predation pressure decreases and intraspecific competition increases (i.e., the consumer stress models of Menge and Olson [1990]). Work on vascular plants in terrestrial habitats has similarly suggested that the role of competition varies with stress (Grime 1973, 1977, Tilman 1988) although there is much controversy surrounding this assertion (Grime 1979, Weldon and Saulson 1986, Wilson and Keddy 1986, Moloney 1990, Grace 1991, Goldberg and Barton 1992). When physical stress becomes extreme, however, competitive interactions may be replaced by facilitative interactions (Bertness and Callaway 1994) if the "competitor" modifies the physical habitat and alleviates the stressful conditions (e. g., Bertness and

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Shumway 1993, Bertness and Hacker 1994). In these cases, a species may have higher fitness when in association with a "competitor" than when it is living alone.

While productive, this debate on the dichotomy between competition and facilitation ignores the fact that species can influence each other in ways that do not strictly involve limiting resources. One organism can influence the recruitment, survival, growth, or reproduction of another and these effects can vary in both space and time. For example, subtidal algae can alter the recruitment and growth of benthic invertebrates by altering propagule delivery and food acquisition without actually competing for resources (Duggins et al. 1990, Eckman and Duggins 1991).

The debate between competition and facilitation should be broadened further to address the many positive and negative ways in which organisms influence each other's fitness. This is critical because the overall effect of one species on another may be positive, negative, or neutral depending on the magnitude and direction of the individual effects (e. g., Underwood 1986). Demography offers an excellent framework in which to address these types of multiple effects (McPeek and Peckarsky 1998). Simultaneous variation in recruitment, survival, and fecundity as a function of the presence or absence of a species can be entered into a standard life table and the net effect evaluated as the product of these individual effects. Many of the previous studies of facilitation, however, have focused only on survival (e. g., see review by Callaway [1995]) and few have considered these multiple effects. This is especially true of interactions that vary as a function of life-history stage. To more fully understand the role of positive and negative interactions in natural communities requires a focus on these types of multiple, interactive effects (Greenlee and Callaway 1996, Callaway and Walker 1997).

The debate must also move beyond documenting the direct effect of one species on another and begin to incorporate indirect effects. Although there are exceptions, many of the previous studies have focused on pairwise interactions (e. g., Bertness and Shumway 1993). This has unintentionally disregarded the large number of species that comprise most biological communities and the numerous indirect interactions (both positive and negative) that occur among them. Interaction modifications, where the non-trophic effects of one species alters the interaction between two other species, may be common and important indirect interactions in many communities (Wootton 1993). It is clear that a synthetic approach, which focuses on how spatial and temporal variability in the environment influences both direct and indirect interactions, will help ecologists better understand how species interactions vary in natural habitats (Callaway and Walker 1997, McPeek and Peckarsky 1998).

The marine intertidal may be an ideal system in

which to investigate spatial and temporal variation in species interactions. Most intertidal organisms are known to be sensitive to thermal and desiccation stresses, which can vary at both small and large spatial scales (Lewis 1964, Wethey 1983, 1984). Most importantly, these physical stresses can often be alleviated by the presence of other species. For example, intertidal algal canopies often keep the substrate moist at low tide and can thus reduce the physiological stress of the organisms underneath (Dayton 1971, Menge 1978, Underwood and Denley 1984 and references therein). Because of the large amount of work done in these communities (see Lewis 1964, Paine 1994, Little and Kitching 1996), there is also an ecological context in which to place experimental work done at broader scales. Experimental manipulations to understand how species interactions vary at larger scales may also be a powerful way to predict how species and communities will respond to global climate change in the future.

In this study, I hypothesized that interactions between a large, canopy-forming intertidal alga (Ascophyllum nodosum) and a sessile, filter-feeding invertebrate (Semibalanus balanoides) should vary at latitudinal spatial scales in New England, USA, because of predictable differences in environmental stress (temperature) and predation by the carnivorous whelk, Nucella lapillus. Seasonal temperature fluctuations in New England are some of the largest in the world (Menge 1976) with summer air temperatures greater than in either Great Britain or the west coast of North America (Barnes 1958a). In addition, subtle but important differences in summer air temperature have been hypothesized to influence the distribution of, and interactions among, intertidal organisms between sites to the north and south of the Cape Cod peninsula in Massachusetts (Barnes and Barnes 1959, Wethey 1983). Observations I made in 1994 at exposed intertidal habitats in Rhode Island (south of Cape Cod) indicated that the upper distribution of the Semibalanus zone was generally coincident with the top of the Ascophyllum zone but that at similar sites in Maine (north of Cape Cod) it extended beyond it (see Methods: Study sites and zonation patterns, below). The southern pattern is atypical of most intertidal habitats where barnacles generally persist above the algal zone in all but the most protected habitats (Stephenson and Stephenson 1948, Carefoot 1977, Menge 1978, Ricketts et al. 1985; personal observations). This observation is consistent with a reduction in mortality from thermal stress north but not south of Cape Cod.

Cape Cod is also a well-known faunal break (Gould 1840, cited in Allee 1923) that separates the Atlantic Boreal fauna to the north from the Atlantic Temperate fauna to the south (Gosner 1978). *Nucella lapillus* is the primary predator of barnacles in New England and also has a largely boreal distribution (Gosner 1978). These biogeographic patterns and the experimental findings of Menge (1976) in northern New England

suggest that predation pressure may be reduced south of Cape Cod. In addition, by harboring whelks and increasing their foraging efficiency (Menge 1978), the algal canopy indirectly increases barnacle mortality at those sites where whelks are present. This suggests that the direct positive effects of the algal canopy on barnacle survival (by alleviating temperature stress) may be critical to the maintenance of barnacle populations south of the Cape but that the negative, indirect effects of the canopy on predators (an interaction modification sensu Wootton 1993) may overwhelm any direct positive effects at northern sites.

To test these ideas, I experimentally manipulated algal canopies at northern and southern sites and evaluated the consequences for both barnacles and their predators. I quantified canopy effects at different barnacle life-history stages and then integrated these component effects in a demographic framework. I hypothesized that the algal canopy would decrease fecundity at all sites but that it would increase survival only at the southern sites. If the positive effects of the canopy were stronger than its negative effects, the association would result in higher fitness (defined as the product of survival and fecundity) at the southern sites. I also took advantage of the differences in climatic conditions in 1995 and 1996 to determine whether this interaction was associated with year-to-year variation in climate.

#### METHODS

#### Study sites and zonation patterns

Two sites in Rhode Island and two in Maine (New England, USA) were chosen to test this hypothesis (Fig. 1). All sites were semi-exposed, intertidal habitats consisting of gently sloping granite benches interspersed with large granitic boulders. Each site was oriented approximately south-south east. Sites were protected from the largest ocean swells by either small offshore islands or large seaward rock benches. The two southern sites, Sakonnet Point (41°27'14" N, 71°11'35" W) and Middletown (41°28'31" N, 71°14'30" W), were located on the eastern and western sides, respectively, of Narragansett Bay, Rhode Island. The two northern sites, Chamberlain (43°53'7" N, 69°28'29" W) and Pemaquid (43°50'8" N, 69°30'29" W), were located along the eastern shore of Pemaquid Neck. Although experiments in Maine were not conducted exactly where others have worked (e. g., Menge 1976, 1978), these sites have been the subject of considerable past research.

Observations made during May–September 1994 suggested that the acorn barnacle, *Semibalanus balanoides*, extended above the *Ascophyllum nodosum* zone at northern sites, but at southern sites it was present only under the algal canopy. To determine if this was due to a vertical extension of the barnacle zone rather than a contraction of the algal zone, distribution patterns were quantified at all sites using standard surveying equipment and then standardizing elevations to



FIG. 1. Map of New England (USA) showing the opencoast study sites in Rhode Island (RI) and Maine. Cape Cod is a well-recognized faunal barrier between these two regions.

mean lower-low water (MLLW). Because the tidal range differs between Rhode Island and Maine (1.4 m vs. 3.5 m above MLLW, respectively), elevations were expressed as the percentage of time that zones were exposed to aerial conditions within each region. Tidal height data were obtained from TideGuide version 1.30 (Zihua Software, Pacific Grove, California, USA). The tops of the *Ascophyllum nodosum* and *Semibalanus balanoides* zones were quantified by sampling 10 elevations per zone across approximately 20–40 m of each study site. Differences in exposure time of each zone between northern and southern sites were analyzed using nested ANOVA with site nested within region.

### Barnacle demographics and variable species interactions

Positive and negative interactions between the algal canopy and understory barnacles were examined at these four sites for two years, from January 1995 through January 1997. In November 1994 I created circular clearings in the Ascophyllum canopy (radius ~1.0 m) at its upper border in the high zone of all sites (n = 8 clearing/site). Canopy plots (n = 8 plots/site) were unmanipulated areas that, at low tide, had a 100% cover of A. nodosum. The absolute tidal height of all plots was set to keep the percentage of time exposed to aerial conditions (~60%) constant between regions. Within each canopy and cleared plot, I set up two permanent quadrats ( $25 \times 25$  cm) on the rock substrate marked at their corners with galvanized bolts. Quadrats were nestled between the A. nodosum holdfasts (in can1018

opy plots) and initially had an intermediate cover  $(\sim 50\%)$  of barnacles.

Each spring one of the two quadrats in each plot was scraped to bare rock with a putty knife (without disturbing *A. nodosum* holdfasts or canopy cover) and used to evaluate the effect of the canopy on barnacle recruitment, survival, growth, and fecundity. Because adult barnacles may generally be less susceptible to physical stress than new recruits (Foster 1969, 1971), I used the unmanipulated quadrat to evaluate the influence of the canopy on the "adult" population (defined as all individuals >1 yr old, sensu Wethey 1984). In addition, scraped quadrats (n = 8 quadrats/site) were established in the zone directly above the *Ascophyllum* canopy at all sites to evaluate regional differences in barnacle recruitment, survival, growth, and reproduction above the zone influenced by the algal canopy.

In 1996 I incorporated a predation treatment to attempt to partition the mortality of barnacle recruits into the direct effect of the algal canopy on reduced thermal stress and the indirect effect of the canopy on predation intensity (Menge 1978). At all sites I attached 20  $\times$  $20 \times 5$  cm galvanized wire mesh cages and cage controls to cleared quadrats in all canopy and cleared plots. Unfortunately, this treatment was unsuccessful at manipulating predator abundance (unpublished data) because cages were frequently damaged by waves and corrosion of the wire mesh often compromised the tight fit of the cages to the substrate. Accordingly, I analyzed only the results from the uncaged quadrats. Densities of whelks were measured three times during each summer at all sites in these uncaged quadrats and average predator abundance was analyzed using analysis of variance. Differences in predator abundance were related qualitatively to patterns of barnacle mortality among regions and years.

At the end of the settlement season (Rhode Island = end of March, Maine = beginning of May), barnacle recruitment was measured in the field in the cleared quadrats using sampling grids. Barnacles that survived through the summer were sampled using similar techniques in late October in both 1995 and 1996. Change in density of the "adults" was determined from photographs of the unmanipulated quadrats at the beginning (March 1995), middle (August 1995), and end (October 1996) of the experiment.

In both years, growth and reproductive output of recruits and adults were quantified from three individuals haphazardly selected from each of the cleared and unmanipulated quadrats (total sample size: recruits = 72 individuals per site per year, adults = 48 individuals per site per year). In New England, barnacles reproduce in early fall, fertilized eggs mature over the winter, and larvae are released only once a year in early spring (Barnes 1958b). Individuals were sampled in mid-winter (December–January) after larvae had fully matured but before they had been released. Barnacles were carefully removed from the rock using surgical scalpels, kept on ice in the field, and then frozen at  $-10^{\circ}$ C in the laboratory. Within 4 mo barnacles were thawed in seawater and then each individual was dissected into shell, somatic, and reproductive (i.e., larvae) tissue. Tissue components were dried at 35°C for 24 h before weighing on a microbalance (precision =  $\pm 0.01$  mg).

# Statistical analysis

Differences in recruit and adult barnacle survival as a function of the canopy, region, and site were tested using nested analysis of covariance (ANCOVA) on surviving barnacle density in October. Site was considered a random factor (nested within region) and canopy and region were considered fixed factors. Density the previous spring was the covariate. Because space is often the limiting resource for barnacles, mortality is frequently density dependent (i.e., greater mortality on high densities than low densities of recruits; Connell 1985). ANCOVA statistically factors out any densitydependent effects on survival by removing the influence of initial density on final density. This approach, however, has two assumptions that were verified before the analysis proceeded (Underwood 1997). First, the relationship between the dependent variable and the covariate must not vary among treatments (homogeneity of slopes). Second, the range of the covariate must be broadly similar among treatments.

Differences in the demographic parameters of barnacle recruits and adults as a function of the algal canopy, region, and site were analyzed with nested analysis of variance for both 1995 and 1996. As before, site was considered a random, nested factor. Differences in growth were evaluated using total soft tissue (somatic + reproductive tissue) as the dependent variable. Similar analyses were performed on fecundity (total larval mass) and reproductive fitness potential. Reproductive fitness potential was defined in the demographic sense as "1,m," (an individual's probability of survival multiplied by its reproductive output). Because of the broad dispersal capability and open population structure of Semibalanus, I could evaluate neither the complete life table for this species (but see Eckman [1996] for a conceptual and empirical approach) nor the contribution of individual effects to population growth rate (i.e., a sensitivity analysis of  $\lambda$ ; McPeek and Peckarsky 1998).

In addition, there were often large differences in these parameters among sites (see Table 1). These differences could have been due to a number of uncontrolled factors including (1) differences in larval supply (Raimondi 1990), (2) phytoplankton composition (Barnes and Barnes 1959), (3) increased egg size at northern sites (Crisp 1959), (4) temperature-dependent or flow-mediated plasticity in growth rates (Southward 1955, Sanford et al. 1994), or (5) genetic differentiation among sites or regions (Crisp 1964). My primary interest was not in the absolute magnitude of these parameters but rather in their variation with the algal April 2000

canopy between regions. I therefore standardized the data for differences among sites before statistical analysis by converting each datum to reflect its deviation (either larger or smaller) from its site mean. Analyses were then performed on these deviations  $(\ln (x + 1))$ transformed to meet the assumption of normality and variance heteroscedascity). Positive or negative species interactions were defined from the direction of a statistically significant "canopy" effect in the analysis of variance. In addition, regional differences in the magnitude and direction of these species interactions were identified by a significant "canopy  $\times$  region" effect in the same analyses. Because this was a nested design, the error term for the F ratio for both canopy and canopy  $\times$  region effects was the canopy  $\times$  site (region) term.

#### Abiotic conditions

Physical factors were recorded during the two years of the study to relate the biotic results to spatial and temporal variation in abiotic conditions. I tested for variation in wave exposure among sites because barnacle mortality is known to be reduced at sites of high wave splash (Lewis 1964). This was done by quantifying wave exposure at all sites approximately monthly from December 1995 through August 1996 using spring-loaded dynamometers (Denny 1983, Bell and Denny 1994). These instruments measure the maximum force imposed by breaking waves over the sampling interval. Unfortunately, these instruments do not measure the average conditions that exist at a site and it is these average conditions that may be most important to organisms that suffer daily emersion. Estimating wave exposure by eye, however, can be misleading (see Bell and Denny 1994) and dynamometers, although not flawless, are probably the best technique currently available to estimate wave splash.

Dynamometers (n = 5 instruments/site) were bolted to the rock in the center of circular plots (1-m radius) cleared of macroalgae in the same area as the canopy manipulations. Measurements of spring extension (in millimeters) were converted to maximum force (in newtons) using the equations in Bell and Denny (1994). By late May 1996, dynamometers at the Pemaquid site were being continuously vandalized because of heavy foot traffic. I therefore removed the wave meters from this site and no data were collected there throughout the rest of the summer.

To test the hypothesis that regional variation in species interactions was associated with differences in thermal stress, I quantified the overall thermal regime at all sites during the summers of 1995 and 1996. In 1995, maximum rock-surface temperatures were collected approximately every 2 wk from June through October using min/max thermometers (Taylor Scientific, model number 5458). Thermometers were placed under the Ascophyllum canopy and in cleared plots in the high zone of all sites (n = 2 thermometers per canopy treatment per site). In 1996, sample size was increased to 8 thermometers/site but temperatures were collected only in cleared plots. This design increased the power of detecting differences in thermal characteristics among sites. Both wave exposure and thermal data were analyzed using repeated-measures, nested analysis of variance with region, site and time as factors. As before, site was considered a random factor and was nested within region.

I used weather-station data to supplement these direct measures of temperature. Overall differences in climatic conditions between Maine and Rhode Island were quantified using data acquired from the Northeast Regional Climate Center. Maximum daily air temperature had been recorded for 1995 and 1996 at landbased sites in Newport, Rhode Island (41°30' N, 71°21' W), and Boothbay, Maine (43°52' N, 69°35' W), both in close proximity to the respective study sites. Daily differences in temperature from April to September between regions and years were used to quantify spatial and temporal differences in climatic conditions. Patterns in thermal regime, wave exposure, and predator abundance were compared qualitatively to the experimental results on variation in species interactions.

#### RESULTS

### Zonation patterns

The upper limit of the Ascophyllum canopy on the shore was similar between study sites in Maine and Rhode Island (Fig. 2;  $F_{1,2} = 0.90$ , P = 0.442) but the upper limit of the barnacle zone differed between regions ( $F_{1,2} = 19.85$ , P = 0.047). At southern sites, the upper limit of barnacle zone was coincident with the upper limit of the algal canopy, but at northern sites it extended beyond the algal canopy (Fig. 2, daily emersion = 62% vs. 75%, respectively).

### Variable species interactions: barnacle recruits

The algal canopy strongly influenced barnacle recruitment, survival, growth, and fecundity during the two years of this study and this had large effects on their reproductive fitness potential. Recruitment at the four study sites ranged from 4.06–24.41 individuals/ cm<sup>2</sup> in 1995 and 1996 (Table 1). The canopy decreased barnacle recruitment at all sites largely because of mechanical abrasion of the substrate (i.e., "algal whiplash"; Dayton 1971, Menge 1976, Leonard 1999*a*) and this effect did not vary between regions (Leonard 1999*b*).

In contrast, in both 1995 and 1996 the effect of the canopy on survival of barnacle recruits varied significantly between regions (Table 2). The canopy increased survival at the southern sites but not at the northern sites (Fig. 3). At the southern sites, survival was always highest under the canopy, intermediate where the canopy had been removed, and lowest above the algal zone (Fig. 3). At northern sites, survival was

TABLE 1. Recruitment, survival, growth, and fecundity of *Semibalanus balanoides* recruits and adults during 1995 and 1996 at four rocky intertidal sites in New England.

			Recruitmen	ıt‡	Survival§	
Stage	Year	Site <sup>†</sup>	(no./cm <sup>2</sup> )	n	(%)	n
Recruits	1995	Sakonnet, RI	$14.38 \pm 2.01$	22	$6.3 \pm 2.3$	22
		Middleton, RI	$14.77 \pm 2.60$	24	$9.0 \pm 3.3$	22
		Chamberlain, ME	$9.36 \pm 1.03$	23	$30.6 \pm 3.0$	23
		Pemaguid, ME	$6.22 \pm 0.96$	24	$14.1 \pm 3.5$	22
	1996	Sakonnet, RI	$24.41 \pm 2.12$	24	$10.3 \pm 2.4$	24
		Middleton, RI	$17.36 \pm 1.95$	24	$12.6 \pm 6.2$	24
		Chamberlain, ME	$7.65 \pm 1.05$	24	$46.1 \pm 6.0$	24
		Pemaquid, ME	$4.06 \pm 0.77$	24	$38.0 \pm 6.4$	21
Adults	1995	Sakonnet, RI	NA	NA	$-60.01 \pm 28.05$	14
		Middleton, RI	NA	NA	$-57.00 \pm 26.52$	16
		Chamberlain, ME	NA	NA	$-45.91 \pm 20.72$	15
		Pemaquid, ME	NA	NA	$12.15 \pm 6.27$	16
	1996	Sakonnet, RI	NA	NA	$66.90 \pm 15.56$	16
		Middleton, RI	NA	NA	$18.50 \pm 21.05$	16
		Chamberlain, ME	NA	NA	$3.90 \pm 17.41$	15
		Pemaquid, ME	NA	NA	$33.92 \pm 18.36$	15

*Notes*: For each parameter, both the site means  $\pm 1$  SE and the sample size (*n*) are given. These site means were used to generate the proportional deviations used in the ANOVAs to test for variable species interactions between regions (see *Methods: Statistical analysis* for further clarification). Reproductive fitness potential (survival × fecundity) was also calculated from these data.

 $\dagger RI = Rhode Island, USA; ME = Maine, USA.$ 

‡ Recruitment was not applicable (NA) for adult barnacles because recruitment refers only to input from the planktonic larval pool.

For adult barnacles, "survival" refers to the net change in adults (measured as no./100 cm<sup>2</sup>) between time periods. This overall measure is the sum of an increase due to recruits that survive beyond the first year (and hence, become reclassified as adults) and a decrease due to mortality of established adults.

generally similar under the canopy and in cleared plots but was always highest above the algal zone (Fig. 3). Most importantly, the strength of the positive effects of the canopy at southern sites varied among years (Fig. 3: compare 1995 to 1996 for southern sites). In 1995 at southern sites there was very low survival in cleared plots (in fact, 1 sE of the mean overlaps 0 individuals/ cm<sup>2</sup>) and 100% mortality above the algal zone. However, recruit mortality at the southern sites in 1996 was less severe, as evidenced by the considerable survival in the cleared plots and especially that above the algal zone.

Although the exclusion cages did not effectively control predator densities (see Methods: Barnacle demographics ..., above), barnacle mortality patterns in uncaged quadrats at northern sites were related to differences in predator densities in cleared, canopy, and above-canopy plots. During both years, Nucella lapillus at northern sites were in greatest abundance under the algal canopy, intermediate in cleared plots and absent above the algal canopy (Fig. 4; 1995,  $F_{1,27} = 17.88$ , P < 0.001; 1996,  $F_{1,28} = 4.551$ , P = 0.038). The low recruit survival in canopy and cleared plots was associated with the presence of predators while the high survival above the algal canopy was associated with the absence of predators (compare Figs. 3 and 4). In contrast, although N. lapillus were present at the southern sites (unpublished data) they were never observed in the high zone during the two years when this experiment was done (Fig. 4). Lower survival in the cleared plots at southern sites (Fig. 3) could not therefore be attributed to predation in these treatments.

While the canopy had regionally variable effects on recruit survival, it had universally negative effects on growth and reproduction. The canopy inhibited recruit growth in both 1995 and 1996 (Fig. 5; 1995,  $F_{1,2} = 20.23$ , P = 0.046; 1996,  $F_{1,2} = 249.20$ , P = 0.004), but this effect did not vary between regions in either year (1995,  $F_{1,2} = 2.06$ , P = 0.287; 1996,  $F_{1,2} = 0.04$ , P = 0.855). Similarly, the canopy decreased recruit fecundity in both years (Fig. 5; 1995,  $F_{1,2} = 31.42$ , P = 0.030; 1996,  $F_{1,2} = 30.22$ , P = 0.032) and this did not vary between regions (1995,  $F_{1,2} = 2.36$ , P = 0.264; 1996,  $F_{1,2} = 0.03$ , P = 0.873).

When integrated, these data indicate that the net effect of the algal canopy on recruit reproductive fitness potential varied between northern and southern sites and between years. In 1995 the canopy increased reproductive fitness potential at southern sites but decreased it at northern sites (Fig. 5,  $F_{1,2} = 4.17$ , P = 0.046). In 1996 the canopy decreased reproductive fitness potential at all sites (Fig. 5,  $F_{1,2} = 7.69$ , P = 0.008) and this effect did not vary between regions ( $F_{1,2} = 0.04$ , P 0.868).

Above the algal canopy, recruit growth, fecundity, and reproductive fitness potential were generally greater at northern sites than at southern sites (Fig. 5) although these relationships were clouded by high variability at southern sites. In 1995 no recruits survived in this zone at southern sites and fitness was therefore

TABLE 1. Extended.

	Fecundity				
п	(mg/ind.)	п			
15	$0.16 \pm 0.09$	15			
14	$0.09 \pm 0.04$	14			
24	$1.54 \pm 0.33$	24			
22	$1.21 \pm 0.23$	22			
23	$0.10 \pm 0.04$	23			
20	$0.06 \pm 0.05$	20			
24	$1.17 \pm 0.22$	24			
22	$0.74 \pm 0.13$	22			
16	$0.75 \pm 0.10$	16			
15	$0.94 \pm 0.13$	15			
15	$3.86 \pm 0.80$	15			
13	$1.59 \pm 0.41$	13			
16	$1.20 \pm 0.26$	16			
14	$1.19 \pm 0.31$	14			
16	$0.54 \pm 0.20$	16			
13	$1.59 \pm 0.41$	13			
	<i>n</i> 15 14 24 22 23 20 24 22 16 15 13 16 14 16 13	$\begin{tabular}{ c c c c c c } \hline Fecundity \\ \hline $n$ (mg/ind.) \\ \hline 15 & 0.16 \pm 0.09 \\ 14 & 0.09 \pm 0.04 \\ 24 & 1.54 \pm 0.33 \\ 22 & 1.21 \pm 0.23 \\ 23 & 0.10 \pm 0.04 \\ 20 & 0.06 \pm 0.05 \\ 24 & 1.17 \pm 0.22 \\ 22 & 0.74 \pm 0.13 \\ 16 & 0.75 \pm 0.10 \\ 15 & 0.94 \pm 0.13 \\ 15 & 3.86 \pm 0.80 \\ 13 & 1.59 \pm 0.41 \\ 16 & 1.20 \pm 0.26 \\ 14 & 1.19 \pm 0.31 \\ 16 & 0.54 \pm 0.20 \\ 13 & 1.59 \pm 0.41 \\ \hline \end{tabular}$			

zero. In 1996 neither recruit growth, fecundity, nor fitness were significantly different between northern and southern sites above the algal canopy (all  $F_{1,2} < 7.39$ , P > 0.113). This was largely due to the high variability in fecundity and reproductive fitness potential at southern sites but not at northern sites (Fig. 5).

#### Variable species interactions: adult barnacles

The strength of negative and positive interactions between the canopy and the underlying adult barnacles also differed between regions and years. During 1995, survival was elevated under the canopy at southern sites but reduced by the canopy at northern sites (Fig. 6, Table 3). The overall pattern of survival in 1996 was similar to that in 1995 (Fig. 6) but its magnitude was lower and the resulting canopy  $\times$  region interaction



FIG. 2. Zonation patterns at replicate study sites north and south of Cape Cod. Data are the percentages of days (mean  $\pm 1$  sE) that the top of the *Ascophyllum nodosum* and *Semibalanus balanoides* zones are exposed to aerial conditions at each site. Sak. = Sakonnet Point, Rhode Island; Midd. = Middleton, Rhode Island; Cham. = Chamberlain, Maine; and Pem. = Pemaquid Lighthouse, Maine.

was statistically insignificant (Table 3). This was due to the high variation in canopy effects among sites within regions (Table 3). This year-to-year variation in canopy effects on adult survival at southern sites was analogous to that seen for barnacle recruits.

As with the recruits, adult growth and fecundity were reduced in the presence of the canopy during both years (Fig. 7; Growth: 1995,  $F_{1,2} = 36.69$ , P = 0.024; 1996,  $F_{1,2} = 102.59$ , P = 0.010; Fecundity: 1995,  $F_{1,2} = 35.08$ , P = 0.027; 1996,  $F_{1,2} = 177.68$ , P = 0.006). Similarly, these effects did not vary between region (Growth: 1995,  $F_{1,2} = 4.69$ , P = 0.156; 1996,  $F_{1,2} = 6.77$ , P = 0.122; Fecundity: 1995,  $F_{1,2} = 8.02$ , P = 0.122; Fecundity: 1995,  $F_{1,2} = 8.02$ , P = 0.122; Fecundity: 1995,  $F_{1,2} = 8.02$ , P = 0.122; Fecundity: 1995,  $F_{1,2} = 8.02$ , P = 0.122; Fecundity: 1995,  $F_{1,2} = 8.02$ , P = 0.020, P = 0.020

TABLE 2. Survival of barnacle recruits as a function of region and site during 1995 and 1996, analyzed using nested analysis of covariance.

Source of variation	df	MS	F	Denominator Ms <sup>+</sup>	Р
1995					
Region	1	3.51	0.42	а	0.583
Site(Region)	2	8.32	14.02	b	< 0.001
Canopy	1	14.22	38.61	с	0.025
Canopy $\times$ Region	1	18.47	50.15	с	0.019
Canopy $\times$ Site(Region)	2	0.37	0.62	b	0.542
Recruit density	1	3.49	5.88	b	0.019
Residual	52	0.59			
1996					
Region	1	0.22	1.20	а	0.338
Site(Region)	2	0.18	1.12	b	0.336
Canopy	1	1.27	102.25	с	0.010
Canopy $\times$ Region	1	4.02	324.16	с	0.003
Canopy $\times$ Site(Region)	2	0.01	0.08	b	0.928
Recruit density	1	2.02	12.18	b	0.001
Residual	55	0.17			

*Notes*: Recruit density  $[\ln(x + 1)$ -transformed] was the covariate, and final density  $[\ln(n + 1)$ -transformed] was the dependent variable. The statistical assumption of homogeneity of slopes was satisfied in both years: 1995,  $F_{7,45} = 1.81$ , P = 0.109; 1996,  $F_{7,48} = 1.06$ , P = 0.406. In addition, the range of the covariate was broadly similar among the study sites. † Denominator Ms for the F ratios are: a = Site(Region), b = Residual, c = Canopy × Site(Region).



FIG. 3. Survival of barnacles that recruited during the spring of each study year at the end of October in 1995 and 1996 in  $25 \times 25$  cm<sup>2</sup> quadrats located under the canopy, in areas cleared of the canopy or above the zone influenced by the canopy. Data are adjusted densities (mean  $\pm 1$  sE) from the analysis of covariance using recruitment density as the covariate and final density as the dependent variable. See Table 2 for statistical analyses.



FIG. 4. Predator densities as a function of region and treatment during 1995 and 1996. Predators (*Nucella lapillus*) were sampled in the permanent quadrats three times during each summer. Densities were averaged over the summer. Values in the figures are means  $\pm 1$  SE. Although present in the low zone (data not shown), *N. lapillus* were never found in the high zone at southern sites or above the canopy at northern and southern sites.



FIG. 5. Demographic parameters of barnacle recruits during 1995 and 1996. Parameters measured were growth, fecundity, and reproductive fitness potential (survival  $\times$  fecundity). Values are the deviation (mean  $\pm 1$  sE) of each parameter from its site mean. NA indicates that no individuals survived and that growth and fecundity could therefore not be measured.

0.105) except in 1996 when fecundity was reduced more under the canopy in northern sites than in southern sites ( $F_{1,2} = 31.05$ , P = 0.031).

Like those for recruits, these data for adults show that canopy effects on adult reproductive fitness varied between regions and between years. In 1995 adult reproductive fitness potential was facilitated by the canopy at southern sites but was reduced by the canopy at northern sites (Fig. 7,  $F_{1,2} = 23.15$ , P = 0.041). In 1996 the canopy had a consistently negative effect on reproductive fitness potential at both northern and southern sites (Fig. 7,  $F_{1,2} = 24.87$ , P = 0.038). These results for adults were strikingly similar to those obtained for barnacle recruits.

#### Abiotic conditions

Measurements of physical factors suggested that thermal regime but not wave exposure differed between Maine and Rhode Island. There was no evidence that northern and southern sites were of different wave exposure (Fig. 8) as maximum wave force did not vary between regions from December 1995 through May 1996 (Table 4). From May through September there FIG. 6. Survival of adult barnacles (non-recruits) during 1995 and 1996. Values are the net change (mean  $\pm 1$  sE) in the number of adults/100 cm<sup>2</sup> from November 1994 to November 1995 (1995) and from November 1995 to November 1996 (1996). See Table 3 for statistical analyses.



was also no overall difference among regions in maximum wave force, but exposure did vary among regions over time during this latter half of the summer (Fig. 8, Table 4). When tropical storm Daniel impacted New England in July 1996, there were large waves at Chamberlain (and likely Pemaquid, although not measured there) but not at Middletown or Sakonnet (*personal observation*). Other than this single time period, wave exposure differed very little between any of the study sites.

In contrast, there were subtle but potentially biologically important differences in thermal regime between northern and southern sites (Fig. 9). This was evidenced by both rock surface temperatures (Fig. 9) and weather station data (Fig. 10). In summer 1995, overall rock-surface temperatures did not differ between regions but did vary between regions over time (Table 5). The algal canopy reduced rock surface temperatures by ~6.6°C at both northern and southern sites (Fig. 9, Table 5). Contrary to expectations, however, temperatures in the open plots of the northern sites in early summer were higher than those of the southern sites (Fig. 9). By the beginning of August this pattern had reversed and southern sites were slightly but consistently warmer than northern sites until October.

In summer 1996, rock temperatures were nearly significantly different between regions (i. e., P = 0.094; Table 4). Overall, rock temperatures at southern sites were 1.5°C warmer than at the northern sites (Fig. 9). Like 1995, temperatures also varied significantly between regions over time (Table 5). In early summer there was little difference in rock temperature between regions, but by the end of July temperatures at southern sites were consistently several degrees higher than those at sites in Maine (Fig. 9).

Land-based weather-station data corroborated these direct measures of temperature and indicated that Rhode Island was, on average, several degrees warmer than Maine (Fig. 10). This was true in 1995 and 1996 although the magnitude of this difference was smaller in 1996 (i.e., 1.69° vs. 2.40°C, Table 6). These data also revealed that 1995 was a warmer summer overall, especially in Rhode Island (Fig. 10). This finding is in agreement with other meteorological records that show 1995 was the hottest summer on record since 1900 (Easterling et al. 1997).

# DISCUSSION

My results contribute to the continuing debate on the influence of site "quality" on species interactions and suggest that the intensity and direction of interactions can change with physical stress and predation intensity at large spatial scales. In this study, subtle differences in temperature north and south of Cape Cod and regional differences in predator abundance were associated with differences in negative vs. positive interactions between the algal canopy and the underlying barnacles. In addition, year-to-year variation in the net

TABLE 3. Results of nested ANOVAs on adult barnacle survival (measured as yearly changes in adult barnacle density (no./ 100 cm<sup>2</sup>) during 1995 and 1996.

			1995		1996				
Source of variation	df	MS	F	Denom- inator мs	Р	MS	F	Denom- inator MS	Р
Region	1	24 644.8	1.73	a	0.320	7517.3	0.57	а	0.528
Site(Region)	2	14 284.7	3.96	b	0.025	13 110.3	2.99	b	0.059
Canopy	1	49 104.5	11.69	с	0.076	4290.1	0.28	с	0.650
$Canopy \times Region$	1	165.730.5	39.45	с	0.024	26 164.3	1.71	с	0.322
$Canopy \times Site(Region)$	2	4200.7	1.16	b	0.320	15 340.4	3.50	b	0.037
Residual	54	3611.9				4386.9			

*Notes:* Analysis of covariance was not used (as in Table 2) because the covariate (initial adult density) was not broadly similar among the study sites. The denominator MS for the F ratios were: a = Site(Region), b = Residual,  $c = Canopy \times Site(Region)$ .



FIG. 7. Demographic parameters for adult barnacles during 1995 and 1996. Data and presentation are analogous to those in Fig. 5.

effect of the algal canopy on reproductive fitness potential occurred because of variation in barnacle survival rather than reproductive output. These results suggest that the local persistence of species in some intertidal habitats may be dependent on the presence of other species that can modify the increasingly severe environment predicted under global warming scenarios.

# Constituent effects of the algal canopy on barnacles

The individual effects of the Ascophyllum nodosum canopy on barnacles (i.e., recruitment, growth, and fe-



FIG. 8. Wave exposure at northern and southern sites collected from December 1995 through October 1996 using spring-loaded dynamometers. Data are maximum force (means  $\pm 1$  sE) estimated from spring displacement measured at approximately monthly intervals.

cundity) were largely consistent with work done in intertidal systems in the past. The canopy inhibited barnacle recruitment at all study sites in both years via mechanical "whiplashing" of the substrate (Leonard 1999*a*). This effect has often been found on wavebeaten shores (Dayton 1971, Menge 1976, Grant 1977, Hawkins 1983) and appears to be a common feature of large, canopy-forming algal assemblages.

Similarly, barnacle growth and fecundity were significantly lower under algal canopies than in cleared plots. This common observation (Lewis 1964, Wethey 1985) was similar at both northern and southern sites and did not vary between years. Interestingly, growth rates (and fecundity) were not enhanced under algal canopies compared to open plots at southern sites, where higher temperatures were hypothesized to impose severe physiological stress on metabolic and reproductive processes (cf. Barnes and Barnes 1959, Cossins and Bowler 1987). Artificially shading barnacles has been shown to alleviate these stresses and result in higher growth rates (Bertness 1989, Bertness and Gaines 1993). However, the physical structure provided by algal canopies also alters patterns of water flow

TABLE 4. Results of repeated-measures nested ANOVAs on wave-exposure data.

						June–September 1996				
Source of variation	df	MS	F	Denom- inator MS	- P	df	MS	F	Denom inator MS	I- Р
Region	1	58.83	1.40	a	0.359	1	204.80	0.66	а	0.566
Site(Region)	2	42.14	0.15	b	0.861	- 1	310.08	1.81	b	0.203
Instrument(Site)	16	278.67				12	171.36			
Time	3	121.13	6.66	с	0.001	5	2267.87	38.24	с	< 0.001
Time × Region	3	224.98	1.23	d	0.379	5	984.25	8.57	d	0.017
Time $\times$ Site(Region)	6	183.57	10.10	с	< 0.001	5	114.90	1.65	с	0.218
Time $\times$ Instrument(Site)	48	18.18				60	69.77			

*Notes*: Analyses were done separately for the period December 1995–May 1996 and June 1996–September 1996 because instruments were vandalized at Pemaquid (Maine, USA) during the summer of 1996, and data could not be collected there. The dependent variable was maximum force (in newtons) calculated from the spring-loaded dynamometers. The denominator Ms for the F ratios were: a = Site(Region), b = Instrument(Site),  $c = Time \times Instrument(Site)$ ,  $d = Time \times Site(Region)$ .



FIG. 9. Thermal characteristics at northern and southern sites collected during the summers of 1995 and 1996 with min/max thermometers. Values are the maximum temperature (mean  $\pm 1$  sE) recorded during each preceding interval. In 1995, data were collected in cleared plots and under the canopy (n = 2 plots per treatment per site). In 1996, data were collected less frequently and only in cleared plots but with higher replication within sites (n = 8 plots per site).

(Eckman et al. 1989) and can modify feeding behavior by interfering with deployment of the feeding structure (Palmer et al. 1982). In my study, positive effects of the algal canopy on organism growth (through alleviation of physiological stress) were apparently outweighed by negative effects on food acquisition.

In contrast to these negative effects, the algal canopy had a large positive impact on organism survival, but this was evident only at the southern sites. In both years, barnacle survival in Rhode Island was highest under the canopy, intermediate in cleared plots, and lowest in the zone above the algal canopy. Gastropod predators were rare at these sites and mortality rates were consistent with those 'expected from variation in thermal stress alone. This contrasts sharply with northern sites, where survival was generally similar under the canopy and in cleared plots but was always highest above the algal zone. The abundance of the carnivorous gastropod Nucella lapillus at these northern sites was high under the canopy, intermediate in cleared plots, and low at higher tidal heights. These predators often seek refuge under the algal canopy and are well known to feed on *Semibalanus balanoides* (Menge 1983). Any direct reduction in mortality under the canopy because of lower thermal stress at northern sites was apparently offset by an indirect increase in mortality from predators mediated by the canopy (Menge 1978, Minchinton and Scheibling 1993).

Counter to my original hypothesis, results for the adults were similar to those of the recruits for both years. Adults, like recruits, were sensitive to the experimental removal of the canopy and to the ensuing changes in environmental conditions and predator abundance. The similarity in response of recruits and adults to canopy manipulation suggests recruits in these habitats are unlikely to escape thermal conditions over time by growing in size (Foster 1971).

# Abiotic conditions associated with variation in barnacle survival

Variation in survival rates was not associated with differences in wave exposure (Fig. 8) but may have



FIG. 10. Temperature anomalies (deviations in  $^{\circ}$ C) between weather stations located near the open coast in the north (Maine) and south (Rhode Island). Data are 7-d running averages of the differences in daily maximum air temperature collected from 1 April through 1 October. Top panel: Difference between northern and southern sites during 1995. Middle panel: Similar comparison for 1996. Bottom panel: Difference between 1995 and 1996 at the southern sites. Negative differences (in the middle and top panels) indicate that the north was cooler than the south. Positive differences (in the bottom panel) indicate that 1995 was warmer than 1996. Summary statistics are shown in Table 6.

· ·				Denominato	r
Source of variation	df	MS	F	MS	Р
Summer 1995					
Region	1	0.48	0.01	а	0.935
Site(Region)	2	56.50	2.76	b	0.123
Canopy	1	1935.55	324.30	с	0.003
$Canopy \times Region$	1	0.54	0.09	с	0.793
$Canopy \times Site(Region)$	2	5.97	0.29	b	0.755
Thermometer(Canopy $\times$ Site)	8	20.47			
Time	10	92.64	20.47	d	< 0.001
Time $\times$ Region	10	60.50	11.05	e	< 0.001
Time $\times$ Site(Region)	20	5.47	1.21	d	0.326
Time $\times$ Canopy	10	6.27	1.34	f	0.277
Time $\times$ Canopy $\times$ Region	10	3.28	0.70	g	0.715
Time $\times$ Canopy $\times$ Site(Region)	20	4.69	1.04	ď	0.430
Time $\times$ Thermometer(Canopy $\times$ Site)	80	4.53			
Summer 1996					
Region	1	119.31	9.12	а	0.094
Site(Region)	2	13.09	0.58	h	0.566
Thermometer(Site)	28	22.52			< 0.001
Time	6	69.36	23.22	i	0.019
Time $\times$ Region	6	43.21	4.02	е	0.001
Time $\times$ Site(Region)	12	10.76	3.60	i	
Time × Thermometer(Site)	168	2.99			

TABLE 5. Results of repeated-measures nested ANOVAs on substrate temperature ( $^{\circ}C$ ) as a function of region, site, canopy, and time.

*Notes*: The dependent variable was maximum temperature of the rock substrate over 2-wk periods during the summers of 1995 and 1996. In 1996 the canopy treatment was eliminated, and within-site replication was increased from 2 to 8 thermometers/site. Denominator Ms for the F ratio were: a = Site(Region),  $b = Thermometer(Canopy \times Site)$ ,  $c = Canopy \times Site(Region)$ ,  $d = Time \times Thermometer(Canopy \times Site)$ ,  $e = Time \times Site(Region)$ ,  $f = Canopy \times Site(Region)$ ,  $g = Time \times Canopy \times Site(Region)$ , h = Thermometer(Site), and  $i = Time \times Thermometer(Site)$ .

been related to subtle differences in climatic conditions in 1995 and 1996 in the absence of predators. Weatherstation data from Rhode Island and Maine indicated that 1995 was a warmer summer than 1996 (Fig. 10), in agreement with global climate data showing 1995 was the warmest year since 1900 (Easterling et al. 1997). The correspondence between my experimental results and these yearly climatic conditions suggests that these species interactions may be sensitive to subtle overall differences in temperature in regions where the influence of predators is minimal. Differences in air temperature of only a few degrees have also been hypothesized by Wethey (1983) to affect the distribution and abundance of intertidal organisms. Although tissue temperatures were not measured, both maximum

TABLE 6. Summary statistics of daily temperature anomalies (difference between Maine and Rhode Island) in maximum temperature collected at weather stations near the study sites during the summers of 1995 and 1996.

Statistic	1995	1996
Negative anomalies (%)	70	65
Mean daily temperature diff. (°C)	-2.40	-1.69
1 SD of mean daily temp. diff. (°C)	4.29	4.15
1 SE of mean daily temp. diff. (°C)	0.32	0.31
Minimum daily difference (°C)	-15.11	-10.30
Maximum daily difference (°C)	7.83	8.54
n	183	183

*Note:* Fig. 10 (top and middle panels) graphically presents the 7-d running average of the original 183 daily anomalies.

air and rock temperatures at southern sites commonly approached the thermal limits of *Semibalanus balanoides* (i.e., 40°C; Southward 1958, Foster 1969, 1971), further suggesting a causal link between yearly variation in thermal stress and variation in species interactions.

These conclusions, however, should be taken cautiously because the direct measures of rock temperature did not closely match the indirect measures of local conditions made using weather-station data. For example, weather-station data indicated that Maine was cooler than Rhode Island during June–July in 1996 but direct measurements of substrate temperature showed no difference among the regions at this time. This may partly be because overall weather patterns may not accurately predict physical conditions at specific study sites (see Helmuth 1998, 1999) as well as due to differences in sampling frequency between thermometers and weather-station data.

Differences in instrument replication also make comparisons among years difficult. For example, during 1995 when species interactions varied between regions, low thermometer replication and low statistical power made it difficult to detect differences in substrate temperature between northern and southern sites. Average differences in temperature of only  $1-3^{\circ}$ C, however, may be biologically important but difficult to detect using min/max thermometers. Instead of thermometers, Leonard et al. (1999) used computer-controlled thermApril 2000

istors to readily detect differences in substrate temperature  $<2.5^{\circ}$ C among New England intertidal habitats that had significant effects on the mortality of *Semibalanus balanoides*. Although expensive, these thermistors may be the best means to detect subtle differences in physical conditions among sites. In lieu of these instruments, weather-station data may be useful in relating experimental results to broad-scale climatic conditions (Hargrove and Pickering 1992).

Finally, it should be noted that my study was done at only two sites in each region over two years. This experimental design resulted in low statistical power to detect differences among regions and cautions that my findings may not apply generally to all New England intertidal habitats. Despite these limitations, my data are the first to document the previously inferred difference in physical conditions across the Cape Cod peninsula that has been argued to be important in the distribution and ecology of rocky-shore organisms (Wethey 1983).

# Direct and indirect interactions and the net effect on organism fitness

Although examples of positive interactions are becoming increasingly common in the literature (e. g., Carlsson and Callaghan 1991, Bertness and Shumway 1993, Agular and Sala 1994, Berkowitz et al. 1995, Callaway 1995), few studies have taken a demographic approach to evaluate the nature of species interactions. For example, although Carlsson and Callaghan (1991) showed that a sedge growing with a shrub in the Arctic tundra had a higher growth rate than when growing alone, there was no attempt to determine effects of the shrub on seed supply, germination success, or mortality, all of which directly contribute to fitness. Integrating these effects as "l<sub>x</sub>m<sub>x</sub>" (survival probability × reproductive output) is critical in determining if a net interaction is positive or negative.

In my study, integrating component parts revealed that the overall interaction between the algal canopy and barnacles switched from negative to positive between regions to the north and south of Cape Cod. Moreover, this interaction differed between the two years of the study. Because of an overwhelmingly large direct effect on survival in 1995 at the southern sites, the algal canopy facilitated the reproductive fitness potential of barnacle recruits there. On the other hand, the net interaction with the canopy was consistently negative at northern sites, evidently due to canopymediated indirect effects on predation pressure combined with lower reproductive output under the canopy. In 1996, when the canopy-mediated effect on survival was weaker at southern sites, fitness did not vary between regions.

From these data, I conclude that net species interactions switched from positive at southern sites (because of few predators and elevated temperatures) to negative at northern sites (because of a suite of boreal predators in a region of reduced temperatures). My results support the hypothesis that small differences in physical factors can be important in governing species interactions over 100s of kilometers and that the combination of direct and indirect effects that vary across the life history determine the magnitude and direction of overall species interactions. Long-term experiments at a series of sites along the New England coastline (which would increase statistical power) will be necessary to evaluate the validity and generality of these conclusions.

# The changing nature of species interactions during global climate change

Few scientists question that humans have significantly altered global carbon and nitrogen cycles and have had profound effects on climate (Vitousek et al. 1997). Greenhouse gases are expected to increase at least into the 21st Century, resulting in a 1.5–4.5°C warming trend and an increase in the temporal and spatial variability of many aspects of the global climate (Gates 1993). Temperature-sensitive species and those with whom they interact are likely to be influenced by these changing conditions.

As climate continues to warm, algal canopies in the high intertidal zone of sites in southern New England may buffer species from local changes in distribution. The upper limit of barnacles may largely be set by the presence of algal canopies in the future, while in areas without canopies the vertical limit may be much lower.

Species persistence at sites to the north is harder to predict because of the indirect effect of the canopy on barnacle predators. As in the south, barnacles may come to rely on the buffering capacity of these common species of algae, especially if the predators shift their distribution more than that of the barnacles. Alternatively, as climate warms, the refuge from predators above the algal canopy at northern sites (Menge 1976) may vanish and predator-prey interactions under the canopy may intensify. This could result in local extinction of either predator, prey, or both. The outcome will depend on the relative susceptibility of predator and prey to regional changes in climate (Menge and Olson 1990) and their interactions with organisms that can modify the local conditions. Variable species interactions, such as those documented here, are likely to be evident in other habitats as well, where a single species or suite of species strongly moderates physical conditions. Further work in these and other habitats would contribute substantially to our understanding of how ecological and evolutionary dynamics in natural communities might change over the next century.

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