RECRUITMENT VS. POSTRECRUITMENT PROCESSES AS DETERMINANTS OF BARNACLE POPULATION ABUNDANCE

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Abstract. Determining the relative contributions of recruitment vs. postrecruitment processes to adult populations is an unresolved issue. The ''recruit–adult'' hypothesis suggests that the density of recruits is a good predictor of adult density when low but not when high. That is, the relative importance of recruitment vs. postrecruitment factors varies inversely with increasing density of recruits. In a rocky intertidal habitat at two Oregon coastal sites, a field experiment was done using two barnacle species to test this hypothesis. The relative impacts of these factors on adult barnacle abundance was determined using a reciprocal transplant design to manipulate both the density of barnacles established by recruitment and the postrecruitment conditions (tidal height, wave exposure) in which they lived.

The relative contribution of recruitment to adult densities was strongly context dependent and species specific. While density of recruits clearly influenced density of adults for both species in most combinations of site, zone, and exposure, the effects of physical and biotic factors ranged from strong to weak. For *Chthamalus,* recruitment generally had a stronger impact on density of adults than did postrecruitment processes, while for *Balanus,* postrecruitment factors tended to have stronger effects than did recruitment. These differences were an apparent consequence of differential susceptibilities to postrecruitment processes. *Chthamalus* was more tolerant of both biotic and abiotic forces than was *Balanus* and usually had high survival during periods of high *Balanus* mortality.

Heat and desiccation were identified as the primary postrecruitment mortality factors in the high zone, whereas biotic interactions (competition and predation) were the most likely postrecruitment mortality processes in the mid-zone. Mortality was generally density dependent at the site with the strongest effects of postrecruitment processes, and generally density independent at the site with the strongest effects of recruitment. To determine whether trends were more consistent with the recruit–adult hypothesis at larger scales, data for each species were pooled across exposures (zone scale) and across exposures and zones (site scale) and also were compared to literature data from sites around the world (global scale). Each analysis led to the conclusion that recruitment can be a strong determinant of density of adults, but that the magnitude of this relationship depends on context, varies with species, and can be strongly modified by postrecruitment processes. Even when density of recruits is low, postrecruitment factors can be important in determining density of adults. Thus recruitment is a necessary but sometimes insufficient determinant of adult population density. These results support earlier suggestions that predictive models must incorporate both recruitment and postrecruitment factors and will thus depend on understanding the coupling between benthic and pelagic processes.

Key words: Balanus glandula; Chthamalus dalli; competition; density dependence or independence; Oregon (USA); physical stress; predation; recruit–adult relationships; recruitment; rocky intertidal; transplant experiment; wave exposure.

INTRODUCTION

Appreciation of the potential importance of recruitment or propagule establishment on population and community structure has a long history in ecology (e.g., Thorson 1950, Harper 1977, Young 1990, Grosberg and Levitan 1992). In terrestrial habitats, for instance, ecologists have recognized the potential importance of variation in density of recruits to community development and structure (e.g., Marks 1974, Connell and Slatyer 1977, McAuliffe 1988, DeSante 1990, Schupp 1990, Augspurger and Kitajima 1992, Callaway 1992, Keeley 1992). In marine environments, evaluating the role of recruitment in determining population and community variation has been particularly vexing because most populations are open to the departure and entry of propagules (Thorson 1950). This fact, and the difficulty of direct observation, has made investigation of the link between recruits and adults in pelagic environments particularly difficult. For these and other reasons, the relationship between recruitment and adult pelagic fish

populations, for example, remains elusive despite the decades-long attention of fisheries research (e.g., Bakun 1996).

In nearshore benthic environments, recruitment to adult populations is more easily quantified. Despite this greater approachability in benthic environments, however, concentration on recruit–adult relationships is relatively recent. In the 1980s, interest was stimulated by three studies in particular. First, in a review, Underwood and Denley (1984) criticized marine ecologists because most had not evaluated the influence of recruitment in their studies of community regulation. Second, in studies of barnacle recruitment in central California, Gaines and Roughgarden (1985) concluded that population structure and dynamics varied with density of recruits. Specifically, they suggested that with high recruitment, barnacle abundance fluctuated in time and space, while with low recruitment, barnacle populations fluctuated less. These authors suggested that greater predation intensity in high recruitment populations accounted for the sharp decreases observed in variable populations. Later, Roughgarden et al. (1988) extended this local-scale hypothesis to a coastal scale, suggesting that, with decreasing latitude along the west coast of North America, density of recruits decreased and had a larger relative effect on intertidal populations. For brevity, I will call this idea the recruit–adult hypothesis.

In the hope that sharper insights may arise from studies in which recruitment is more readily quantified, benthic ecologists have focused strongly on recruit–adult relationships. Three general questions have been asked (review in Caley et al. [1996]). First, what factors affect recruitment variation in space and time? Second, do temporal and spatial variation in recruitment underlie variation in adult populations? Third, what is the relative importance of recruitment vs. postrecruitment processes in determining population density, and ultimately, community structure? That is, to what extent do patterns of abundance and distribution in natural communities depend on recruitment, a process that *establishes* pattern, in comparison to factors such as competition, predation, facilitation, or disturbance, processes that *modify* pattern? To date, most research has focused on the causes of variation in recruitment, and the influence of recruitment variation on adult abundance. This is perhaps due in part to the great interest in understanding the causes of seemingly inexplicable extreme variation in recruitment of managed fisheries, and the regular, dramatic collapse of populations exploited by humans for food (Botsford et al. 1997).

These issues are clearly important (e.g., Caffey 1985, Raimondi 1990, Sutherland 1990, Farrell et al. 1991, Carr 1994) and are the subject of much ongoing research (Caley et al. 1996). Understanding the influence of recruit–adult relationships on community structure, however, will ultimately depend on studies that investigate simultaneously both population establishment and postestablishment factors (e.g., Gaines and Roughgarden 1985, Menge and Sutherland 1987). Several investigations have addressed this issue for a variety of organisms (e.g., barnacles [Connell 1985, Fairweather 1988, Sutherland 1990, Menge 1991, Minchinton and Scheibling 1991, 1993, Berlow and Navarrete 1997] mussels [Robles et al. 1995, Robles 1997] gorgonians [Gotelli 1988], fishes [Hixon and Beets 1993, Levin 1994, Carr and Hixon 1995, Pfister 1996, Hixon and Carr 1997], crabs [Eggleston and Armstrong 1995]). Few, however, have incorporated manipulations of density of recruits in relation to postrecruitment processes (for exceptions, see Fairweather [1988], Robles et al. [1995], and Hixon and Carr [1997]).

The experiment reported here tested both recruitment and postrecruitment effects on adult densities of two intertidal barnacles, *Balanus glandula* and *Chthamalus dalli* (hereafter termed *Balanus* and *Chthamalus*). Density of recruits was manipulated by placing settlement plates in areas differing in regimes of recruitment, species interactions, and physical conditions. Reciprocal transplants of plates allowed tests of the relative effects of these factors on adult barnacle abundance. One goal was to test the prediction that, when low, density of recruits per se is the primary determinant of density of adults (e.g., Gaines and Roughgarden 1985; see Prediction 1 below). Within a cohort, this prediction is a truism (Holm 1990). At least in the short term, low recruitment must invariably produce low adult density; low recruitment cannot produce high density. This fact underlies the primary difficulty with observational tests of this prediction (i.e., observing adult densities in habitats with known low recruitment rates). Environments with low rates of recruitment will necessarily support low adult abundances, but without high recruitment in such environments, it is not possible to determine if high recruitment leads to high or low adult abundance. This was a major motivation for doing the transplant experiment reported here.

Below I report the results of experiments done simultaneously at two sites, Boiler Bay and Strawberry Hill, differing in both biotic and physical conditions (e.g., Menge et al. 1997a). The experiment was designed to test four predictions of the recruit–adult hypothesis:

Prediction 1. When recruitment is low, recruit density is a strong predictor of, and explains a high proportion of, the variance in adult barnacle density.

Prediction 2. When recruitment is high, recruit density is a weak predictor of, and explains a low proportion of, the variance in adult barnacle density.

Prediction 3. Recruitment and postrecruitment processes have similar effects across species (*Balanus* and *Chthamalus*), tidal heights (mid-zone and high zone), and wave exposures (exposed and protected).

Prediction 4. The recruit–adult hypothesis applies across all spatial scales, ranging from local to geographic.

Methods

Organisms and community

The research was done in a well-studied rocky intertidal community on the Oregon coast (see Farrell 1991, Menge 1992, Menge et al. 1994, Navarrete 1996, Navarrete and Menge 1996, Berlow 1997, Menge et al. 1997*a, b*). Both *Balanus* and *Chthamalus* are important components of upper shore rocky intertidal communities along the temperate west coast of North America (e.g., Paine 1966, 1974, 1981, Dayton 1971, Gaines and Roughgarden 1985, Farrell 1991, Connolly and Roughgarden 1998). These barnacles have planktonic larvae whose settling stages (cyprids) and early recruits (metamorphosed juveniles) are readily visible to the naked eye (e.g., Barnes 1953, Connell 1961*a, b,* 1970, Crisp 1961). In California, *Chthamalus fissus,* a congener of *C. dalli,* matures in ~two months, or at 2 mm basal diameter, and *Balanus glandula* matures at ~six months, or 5 mm basal diameter (Hines 1978). Further, Connell (1970) estimated that in the San Juan Islands, *Balanus* were mature at one year when they were ~7 mm in basal diameter. Although growth rates vary with site, field observations in Oregon suggest similar time periods to maturation for *Chthamalus* and *Balanus.* Barnacles settling as late as November probably reached adulthood well before summer.

Study sites

The study was done from July 1989 to September 1990 at Boiler Bay (44°50′ N, 124°03′ W; hereafter BB) and Strawberry Hill (44°15′ N, 124°07′ W; hereafter SH), ~80 km apart on the central coast of Oregon, USA. BB and SH have been described in detail elsewhere (D'Antonio 1985, Gaines 1985, Turner 1985, Marsh 1986, Farrell 1988, Menge 1992, Menge et al. 1994, 1997*a, b*). Briefly, both are broad, solid rocky benches with striking gradients of exposure to waves, ranging from areas beaten by heavy surf to areas sheltered from strong wave forces. Both have classic (Ricketts et al. 1985) patterns of zonation, with high intertidal barnacle/fucoid-dominated zones, mid-intertidal mussel-dominated zones, and low intertidal bare/algal-dominated zones.

Environmental gradients

At the two study sites, ecological processes vary within sites with wave exposure and tidal elevation, and differ between sites in relation to phytoplankton productivity (e.g., Menge et al. 1994, 1997*a, b*). The following summary, based mostly on earlier studies, summarizes the ecological settings of the experiments described in the following section.

Physical conditions.—At BB and SH, the biota are distributed along horizontal and vertical environmental gradients (see Lewis 1964, Stephenson and Stephenson 1972). Wave forces vary most along the horizontal gradient (e.g., Lewis 1964, Menge 1976, Denny 1988, Menge et al. 1996), whereas desiccation (i.e., rate of water loss) and thermal stress (i.e., rate of heat gain or loss) vary most along the vertical gradient (e.g., Lewis 1964). Wave splash decreases towards more sheltered sites, however, and confounds these relationships. As a general consequence, the most stressful conditions (warmer, drier) occur at high zone–protected areas and the least stressful conditions (cooler, wetter) occur at midzone–exposed areas. Between sites, quantification of wave forces revealed no ecologically significant difference in regimes of wave exposure, but measurements of air temperature at low tide suggested that SH was somewhat warmer (~4°C) than BB (Menge et al. 1996, 1997*a*).

Ecological processes.—Intra- and interspecific competition and whelk predation are generally the major biotic factors affecting barnacles, but their impacts can vary both between sites, and among combinations of wave exposure and tidal height within sites. In general, growth rates of sessile invertebrates, as well as rates of biotic interactions such as predation and competition are greater at SH than at BB (Menge et al. 1994, 1996, 1997*a,* Navarrete and Menge 1996; B. Menge, *unpublished data*). Within sites, predation and competition, both intra- and interspecific, were weak in high zones and stronger in mid-zones (e.g., Farrell 1991) and are greater at exposed than at protected areas (Menge et al. 1994, 1996, 1997*a,* Navarrete and Menge 1996; B. Menge, *unpublished data*). In the mid-zone, predation is mostly attributable to whelks (Navarrete 1996, Berlow 1997; B. Menge, *unpublished data*), and mussels are the dominant space competitor (Menge et al. 1994, Navarrete 1996, Berlow 1997; see also Dayton 1971, Paine and Levin 1981, Paine 1984). *Balanus* and *Chthamalus* are important early successional species, and can temporarily dominate space in disturbed patches in the mussel bed (e.g., Paine and Levin 1981, Navarrete 1996, Berlow 1997). The rank order of competitive dominance among acorn barnacles in this community is *Semibalanus cariosus > Balanus > Chthamalus* (Dayton 1971). At SH and BB, however, most space competition occurred between *Balanus* and *Chthamalus* (Farrell 1991, Navarrete 1996, Berlow 1997).

Limpet grazing, a mortality source for recently settled barnacles (Dayton 1971, Farrell 1991), has an impact on algae at all areas (P. Halpin, *unpublished data*; B. Menge, *unpublished data*). Limpets had access to all recruit collectors, but grazing effects were not evaluated in the present study. Although waves dislodge mussels in Oregon as in Washington state (Dayton 1971, Paine and Levin 1981), disturbance from waves has little effect on barnacles attached to rock in the mid-zone, either within or between sites, unless crowding is intense.

Apart from whelks, other predators evidently have little effect on high and mid-zone barnacle populations. Gulls reduced gooseneck barnacle (*Pollicipes poly-*
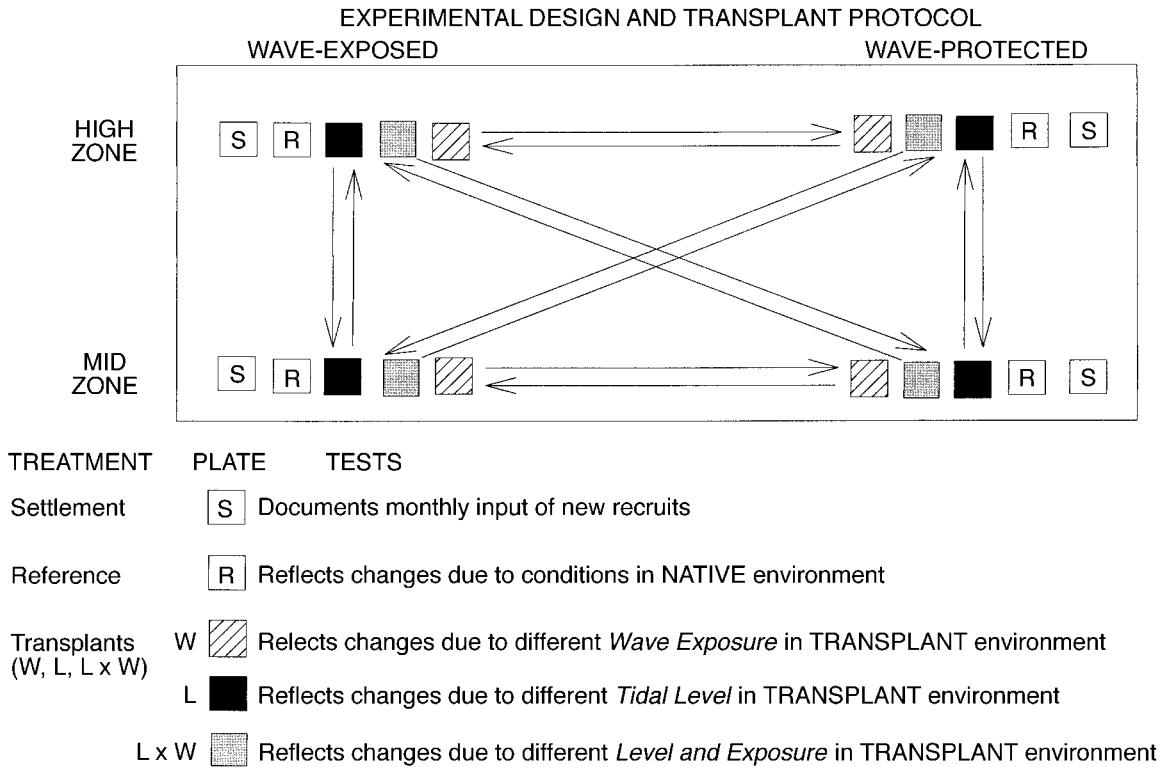
EXPERIMENTAL DESIGN AND TRANSPLANT PROTOCOL

FIG. 1. Design of transplant experiment at a site. Five replicate blocks were done at each combination of site, zone, and exposure. See *Methods: Experimental design* for additional explanation.

merus) densities in Washington state (e.g., Wootton 1992, 1993*a, b*, 1994), but neither gulls (*Larus* spp.) nor other birds (Surfbirds *Aphriza virgata,* American Black Oystercatchers *Haematopus bachmani*) influenced acorn (or gooseneck) barnacles at BB or SH (Marsh 1986; B. Menge et al., *unpublished data*). Large sea stars (*Pisaster ochraceus*), a low zone occupant (e.g., Paine 1966, 1974, Menge et al. 1994), were never observed near high or mid-zone transplants. Small sea stars (juvenile *Pisaster ochraceus, Leptasterias hexactis*), often common in mussel beds, foraged only a few centimeters into clearings within the mussel matrix, and were rarely seen near our transplants.

Experimental design

At BB and SH, the experiment was done in high and mid-zones at exposed and protected sites (Fig. 1). Recruits were transplanted after they had settled onto plexiglass settlement plates (10 cm × 10 cm × 6 mm) coated with Safety-Walk (3M, Minneapolis, Minnesota, USA), a rubbery, uniformly rough-textured surface that attracts barnacle settlers (Farrell et al. 1991). Each plate was fastened with a stainless steel screw to a rock surface, using a predrilled hole. Plates were framed with bands of marine epoxy (2 cm in width) that were flush with, and tapered away from, the plate surface to minimize edge effects due to flow disruption and to prevent spinning.

In Oregon, barnacles recruit from March to December (*unpublished data*). Both *Chthamalus* and *Balanus* may settle several times during this period, although most successful recruitment occurs from July through November. This extended recruitment season makes difficult efforts to test the relative effects on adult abundance of recruitment and postrecruitment factors. I reduced the effects of this lengthy recruit accumulation period by adjusting times of deployment and transplantation. Plates were installed in June 1989, prior to the onset of highest recruitment, and were transplanted in December 1989, when recruitment had ceased (e.g., Farrell 1991; see Fig. 2). The experiment was terminated in September 1990 when distinguishing 1989 and 1990 cohorts became difficult and loss of plates became a problem in some treatments.

Five replicates of each treatment were established in a completely randomized block design (Sokal and Rohlf 1995; see Fig. 1). One plate per block, hereafter termed the settlement plate, was replaced monthly. Monthly recruitment on open surfaces was estimated by patterns occurring on these plates. Collected plates were taken to the laboratory where cyprids and early juveniles of *Balanus* and *Chthamalus* were counted. Other barnacle species (e.g., *Semibalanus cariosus, B. nubilus*) rarely settled on plates. *Semibalanus* settles patchily in space and time and is typically a later successional species (e.g., Dayton 1971, Paine and Levin
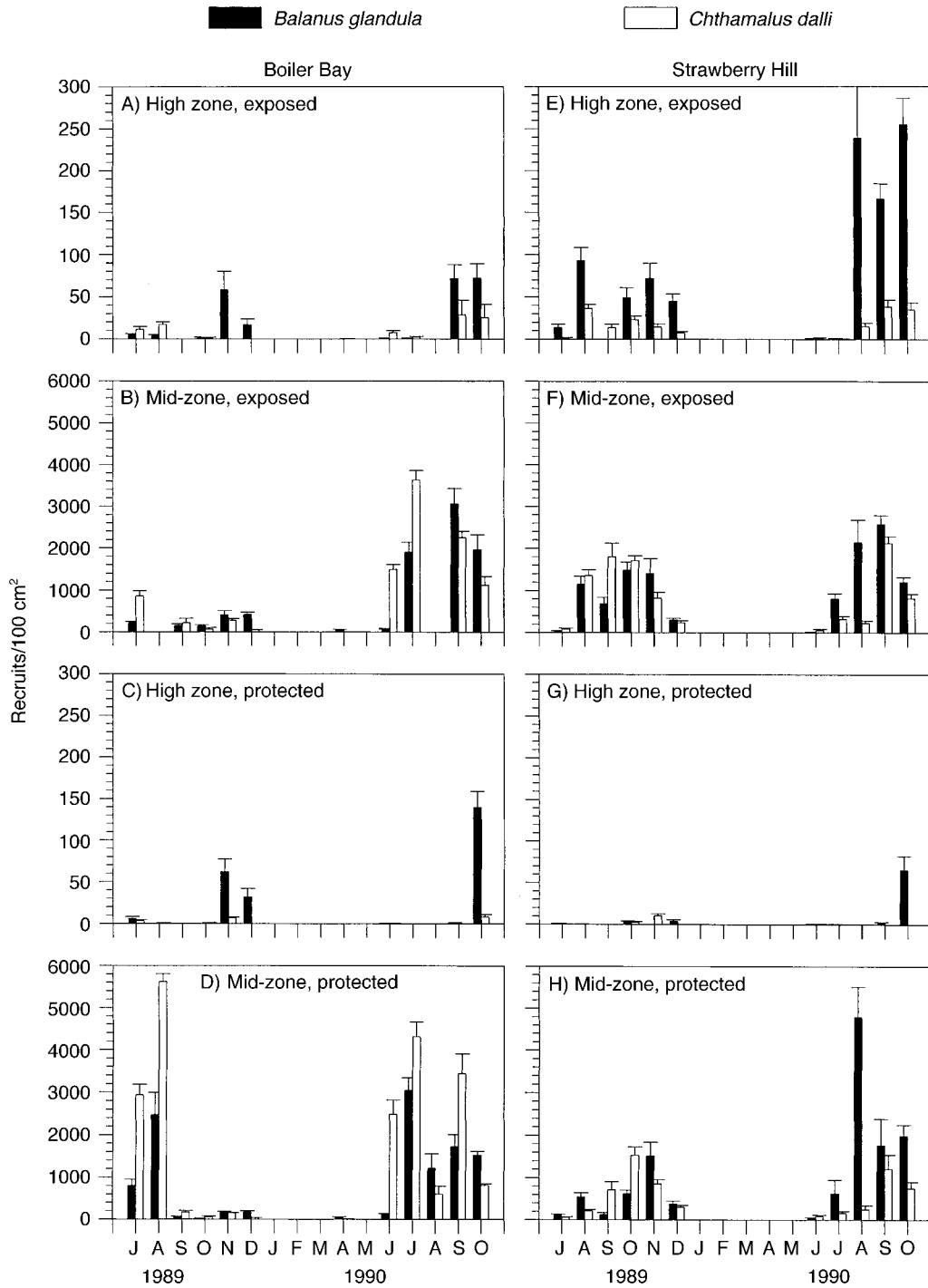
FIG. 2. Recruitment of *Balanus glandula* and *Chthamalus dalli* on settlement plates ($n = 5$) at Boiler Bay and Strawberry Hill from July 1989 to October 1990. Note that in this figure, and also in Fig. 3, scales for the *y*-axes are different because of the great between-zone difference in density of recruits. Error bars show +1 SE of the mean.

1981). *B. nubilus* is scarce and restricted to very low intertidal zone, wave-exposed areas. Although settlement densities on plates are higher than those on natural rock surfaces (*unpublished data*), recruitment always occurred simultaneously on both.

The remaining four plates of each block remained on the shore for the duration of the experiment (Fig. 1). On 12–13 December, plates were collected and randomly assigned to one of four treatments. Plates were then reattached to the rock to randomly preassigned

TABLE 1. Tidal heights of barnacle transplant experiments.

Intertidal zone	Site	Exposed			Protected		
		Range (m)	Median (m)	Mean ± 1 SE (m)	Range (m)	Median (m)	Mean ± 1 SE (m)
High	BB	2.35–2.68	2.62	2.54 ± 0.07	2.23–2.47	2.35	2.36 ± 0.04
	SH	2.32–2.50	2.41	2.42 ± 0.04	2.35–2.59	2.50	2.48 ± 0.04
Mid	BB	0.98–1.10	1.04	1.05 ± 0.02	1.01–1.13	1.07	1.07 ± 0.05
	SH	1.10–1.77	1.28	1.38 ± 0.12	1.40–1.55	1.52	1.50 ± 0.03

Notes: Statistics are based on five replicates. Heights were measured with a surveyor's level using the predicted low tide level for the date on which measurements were taken as the benchmark. Measurements were taken on calm, sunny days in midsummer.

positions within each block. Recruitment densities differed with level and exposure, so this scheme produced at each site sets of plates with a range of barnacle densities at each combination of level and exposure, often with differing relative abundances of *Balanus* and *Chthamalus.*

The transplant experiment thus shifted summer- and autumn-recruited barnacles (July to December 1989) from one environmental regime to another, where they spent their postrecruitment life during the subsequent winter, spring, and early summer (December 1989 to September 1990). Treatments (Fig. 1) were:

1) Reference plates (abbreviated REF), reflecting changes in barnacle abundance occurring in the native habitat, remained in their original zone–exposure combination in the same block. Reference plates were carried away from and then back to their place of origin to treat them similarly to transplants. Except for this brief trip, REF barnacles experienced the same environmental conditions from settlement through adulthood. No attempt was made to place them in the same orientation as when they settled because no pattern of orientation among the individuals on the plates was observed.

2) Transplants between zones (LEVEL) exposed recruits to either higher or lower intertidal zones at the same wave exposure in which they settled. Barnacles transplanted from the high zone to the mid-zone, for example, recruited in the high zone but spent most of their postrecruitment life in the mid-zone.

3) Transplants between wave exposures (WAVE) exposed recruits to either more or less wave-exposed areas in the same zone in which they settled. Barnacles transplanted from wave-exposed to wave-protected areas, for example, recruited in wave-exposed areas but spent most their postrecruitment life at wave-protected areas.

4) Transplants between zones and wave exposures (L × W) exposed recruits to conditions of zone and wave-exposure opposite to those in which they settled. Barnacles transplanted from mid-zone–exposed to high-zone–protected areas, for instance, recruited at wave-exposed, mid-zone areas but spent their postrecruitment life at wave-protected, high-zone areas. To reduce confusion when presenting results, different transplant treatments will be termed REF, LEVEL, WAVE, and L × W, as abbreviated above, and factors will be termed site, exposure, and zone.

Plates were photographed in December 1989, and February, April, June, July, August, and September 1990. Barnacle abundance was quantified from photographs both by counting individuals (per 100 cm^2) and by estimating percent cover (using clear random-dot vinyl quadrats; we counted a maximum of 100 dots). The number of dots overlying each barnacle species was a direct estimate of percent cover. Fates of individual barnacles were not followed. The 1989 cohorts were readily distinguishable by size from those that recruited after December 1989. Analysis of densities examined only changes in the 1989 cohort, allowing a focus on the recruit–adult and density–mortality relationships. To aid the evaluation of the potential influence of postrecruitment processes, including competition from subsequent recruits, the percent cover analysis included both 1989 and 1990 cohorts.

At all sites, relative tidal height (as judged from prevailing community patterns and not absolute height) guided placement of replicates in each combination of site, zone, and exposure. High-zone plates were placed in the approximate center of the barnacle/fucoid alga zone, above the highest mussels and below the upper limit of barnacles. Midzone plates were placed in areas cleared by natural disturbances in mussel beds in the approximate middle of the mussel zone. Since the absolute height of zonal boundaries varies with site and exposure (due to differences in wave spray, predation, and other factors; e.g., Lewis 1964, Menge et al. 1994), the absolute tidal height of replicates varied with site and exposure (Table 1). Variation in tidal height associated with site (percentage variance explained = 0.6%) and exposure (1.8%) was small compared to zone (93%), however (three-way ANOVA; $P \leq 0.006$, df = 1, 31). I therefore assume that within zones, the plates were all effectively at the same tidal height between sites and exposures.

Data analysis

SYSTAT statistical software (version 7.0.1) on an IBM-compatible PC was used for data analysis. The effects of the different factors on barnacle density over

time was tested using repeated-measures analysis of variance (RM-ANOVA), but the primary tools of analysis were analysis of variance (ANOVA) and least squares regression. Determination of whether or not differences among site, level, and exposure contributed to differences in cumulative recruitment densities and pretransplant recruit densities employed three-way ANOVA. Recruit–adult density relationships were analyzed using linear regression, on transformed data when appropriate. Several specific analyses were performed. The strength of the relationship between recruit (December 1989) and adult (August 1990) density for each barnacle species was analyzed at three spatial scales: within each zone–exposure combination at each site (smallest scale: 1–10 m), within each zone at each site (exposures combined; intermediate scale: 10–100 m), and within each site (zones and exposures combined; largest scale: ~80 km). In addition to allowing analysis of effects of different scales, pooling data across all four treatments by site, zone, and exposure creates a wide range of transplanted densities of recruits in areas with naturally low recruitment. Use of different combinations of site, zone, and exposure provided a range of postrecruitment conditions as well, although the range of conditions was generated by comparison and not by manipulating different postrecruitment processes. Prior to pooling, ANCOVA (analysis of covariance) was used to test for exposure and exposure $\times$ zone differences in recruit–adult relationships. No differences in recruit–adult regressions were detected in the analysis at lower spatial scales, either as a main effect or through an interaction with the covariate, recruit density ($P \geq 0.13$). Finally, discriminant analysis (Dillon and Goldstein 1984) was used to examine the relationship between recruit density and the relative importance of recruitment (as estimated by the proportion of variance explained, R^2) in determining adult density. Data were R^2 and mean recruit densities for each of the eight combinations of site, zone, and exposure. I used regression analysis to test the prediction that the relative importance of recruitment in determining adult density decreases with increasing recruit density at a global scale using available literature data from sites in Europe, North America, Central America, and Australia. Finally, to determine the influence of data from the present study on this global correlation, I examined the global recruit–adult relationship with and without data from this study.

To determine if the effect of postrecruitment processes was density dependent or density independent, I tested the hypothesis that the slopes of recruit–adult regressions equaled 1.0. On a log–log scale, a slope = 1.0 signifies constant mortality across all densities, or density independence (e.g., Caley et al. 1996, Hixon 1998). Slopes > 1.0 and < 1.0 indicate positive and negative density-dependent effects, respectively.

I examined probability plots of residuals and plots of residuals against estimated values, respectively, to determine if residuals were normally distributed and if errors were independent (Wilkinson 1997). These assumptions were met in most analyses after transformation ($\ln[x + 1]$ for densities; arcsin[square root] for percent cover and for proportional data). In cases where the assumptions were not met even with transformation, probabilities were highly significant, indicating that the analysis was likely to be reliable (e.g., Underwood 1981).

RESULTS

Barnacle recruitment

In 1989 and 1990, both *Balanus* and *Chthamalus* settled primarily from midsummer to late autumn (Fig. 2). As others have observed, both in Oregon and elsewhere (e.g., Connell 1985, Gaines and Roughgarden 1985, Farrell 1991, Farrell et al. 1991), recruitment by these barnacles sometimes varied dramatically in the short term. For example, at BB mid-zone–exposed, after dense settlement in July 1990, no recruitment occurred in August, but dense settlement occurred again in September. In contrast, in August 1990, moderate recruitment occurred at BB mid-zone–protected and SH mid-zone–exposed. At SH mid-zone–protected, *Balanus* settled very densely but *Chthamalus* did not.

Several other patterns were evident. First, overall, barnacle recruitment, on a monthly basis (Fig. 2), cumulatively from July to December 1989 (Fig. 3A, B) and as reflected by pre-transplant densities on treatment plates (Fig. 3C, D) was between one and two orders of magnitude lower in the high zone than in the mid-zone (Tables 2, 3). Site and exposure contributed to variation in density as well but to a much smaller extent (Tables 2, 3, compare R^2 values). Second, although site and exposure accounted for relatively little variance, settlement densities of each barnacle species differed with site and wave exposure as well as with zone (Figs. 2, 3, Tables 2, 3; three-way interactions were significant for both species).

Several trends also were evident in the cumulative recruitment densities. In the SH high zone and for *Chthamalus* (but not *Balanus*) at BB, densities of recruits were greater at exposed than at protected sites (Fig. 3A). At high-zone–exposed areas, densities were greater at SH than at BB (Fig. 3A). At high-zone–protected areas, densities were greater at BB for *Balanus* but similar between sites for *Chthamalus* (Fig. 3A). Overall cumulative high-zone densities of *Balanus* were greater than those of *Chthamalus* (*t* test; $t = 3.11$, $P = 0.0057$, df = 19). In the mid-zone, cumulative recruit densities of both *Balanus* and *Chthamalus* were lowest at BB exposed, and were similar among other site–exposure combinations (with the exception that the greatest density occurred for *Chthamalus* at BB protected; Fig. 3B). Overall, cumulative mid-zone densities of *Balanus* were less than those of *Chthamalus* (*t* test; $t = -3.38$, $P = 0.0032$, df = 19).
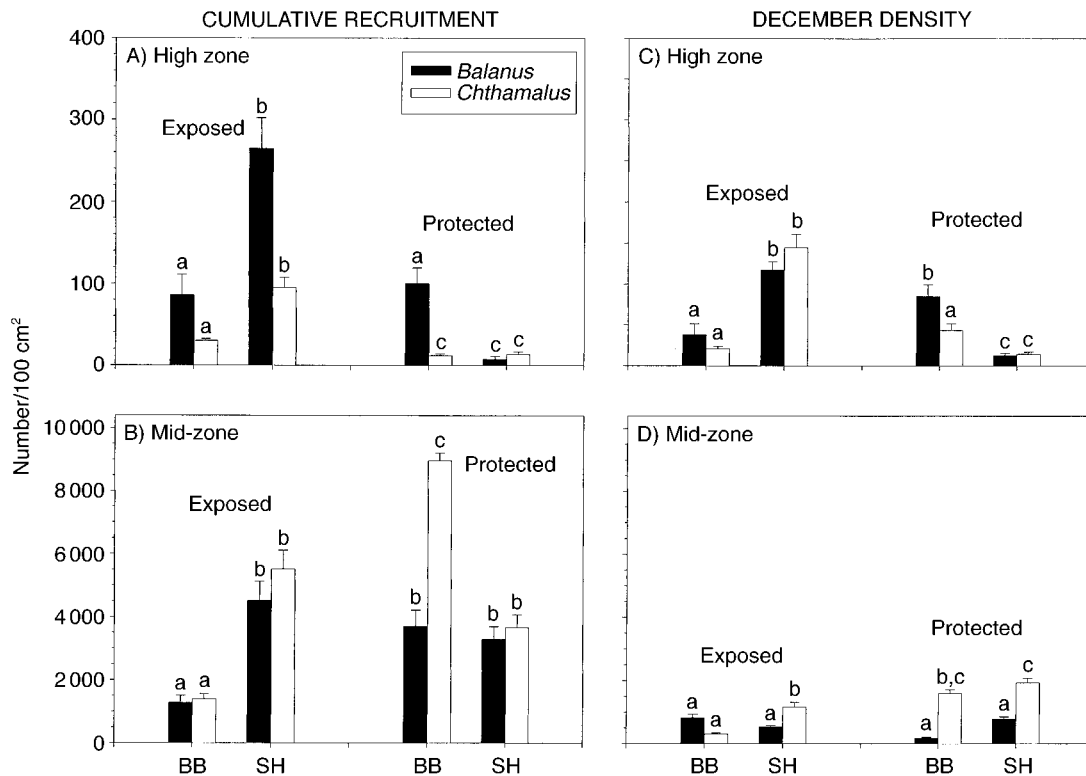
Fig. 3. The left-hand panels show cumulative recruitment during the 1989 recruitment season, July to December at Boiler Bay and Strawberry Hill in (A) the high zone and (B) the mid zone. The right-hand panels show pretransplant (December) recruit densities on treatment plates (C) in the high zone and (D) in the mid-zone. Error bars depict +1 SE of the mean. Means with different letters above the error bar are significantly different ($P < 0.05$, Bonferroni multiple comparisons test).

Densities of recruits on high-zone treatment plates in December 1989 just prior to transplantation, averaged over all treatments (REF, LEVEL, WAVE, and L × W), reflected cumulative recruit densities with the exception of SH high-zone–exposed (compare Fig. 3, panels A and C). In the mid-zone, however, pretransplant densities on treatment plates were much lower than cumulative densities of recruits (compare Fig. 3B

TABLE 2. Analysis of variance comparing cumulative recruitment from July to September 1989 of *Balanus glandula* and *Chthanialus dalli* by site (Boiler Bay and Strawberry Hill), zone (high and mid), and wave exposure (exposed and protected) on settlement plates.

Source of variation	df	Mean square	F ratio	P	R^2
A) *Balanus glandula*					
Site	1	0.0016	0.006	0.94	<0.001
Zone	1	151.09	531.39	<0.00000001	75.6
Exposure	1	4.01	14.12	0.0007	2.0
Site × zone	1	3.66	12.87	0.001	1.8
Site × exposure	1	17.56	61.76	<0.00000001	8.8
Zone × exposure	1	10.51	36.98	0.0000009	5.3
Site × zone × exposure	1	3.87	13.62	0.0008	1.9
Error	32	0.2843			
B) *Chthamalus dalli*					
Site	1	1.6432	15.45	0.0004	0.006
Zone	1	252.02	2369.7	<0.00000001	90.5
Exposure	1	1.2932	12.16	0.001	0.5
Site × zone	1	0.3107	2.92	0.10	0.001
Site × exposure	1	6.93	65.16	<0.00000001	2.5
Zone × exposure	1	11.96	112.42	<0.00000001	4.3
Site × zone × exposure	1	0.9999	9.40	0.0044	0.4
Error	32	0.106			

Notes: $N = 5$ replicate plates per site × zone × exposure combination. R^2, the coefficient of determination, indicates the proportion of variance explained by each factor.

TABLE 3. Analysis of variance comparing pretransplant (December 1989) densities of barnacle recruits (*Balanus glandula* and *Chthamalus dalli)* by site (Boiler Bay, Strawberry Hill), zone (high, mid), and wave exposure (exposed, protected) on transplant plates.

Source of variation	df	Mean square	F ratio	P	R^2
A) *Balanus glandula*					
Site	1	1.3121	2.50	0.12	0.003
Zone	1	255.0606	485.0	<0.00000001	57.6
Exposure	1	18.8811	35.91	<0.00000001	4.3
Site × zone	1	7.9413	15.10	0.0002	1.8
Site × exposure	1	6.7424	12.82	0.0005	1.5
Zone × exposure	1	0.4652	0.88	0.35	0.001
Site × zone × exposure	1	72.8909	138.6	<0.00000001	16.5
Error	152	0.5259			
B) *Chthamalus dalli*					
Site	1	16.3039	33.68	<0.00000001	2.5
Zone	1	474.0485	979.3	<0.00000001	71.5
Exposure	1	0.7391	1.53	0.22	0.001
Site × zone	1	0.8944	1.85	0.18	0.001
Site × exposure	1	44.5323	91.99	<0.00000001	6.7
Zone × exposure	1	43.9330	90.75	<0.00000001	6.6
Site × zone × exposure	1	8.7992	18.18	0.00004	1.3
Error	152	0.4841			

Note: Data from all four treatments (REF, LEVEL, WAVE, and L × W) were combined because treatments had not yet been initiated, so $N = 20$ replicate plates per site × zone × exposure combination.

to 3D), most likely due to space limitation. Settlement plates were replaced monthly and thus provided new space for settlement, but space on the nonreplaced treatment plates was increasingly limited over time as plates were filled by earlier recruits (*personal observation*). Because recruit densities were so much lower in the high zone than in the mid-zone, space was rarely limiting on high-zone plates (*personal observation*).

Transplant experiment

To evaluate Predictions 1–4, data were analyzed in several ways. Below, density changes in the 1989 barnacle cohort on reference plates are summarized, and then compared to changes on transplant plates. Then recruit–adult relationships are presented, including consideration of patterns of mortality in relation to recruit density at each combination of site, level, and exposure. Finally, evidence for density-dependent mortality is evaluated. These analyses form the basis for an examination of the recruit–adult analyses in relation to the predictions of the recruit–adult hypothesis in the *Discussion.*

Density changes.—As expected, densities always declined, but trends varied with site, level, exposure and transplant treatment (Figs. 4 and 5; RM-ANOVA, Site × Zone × Exposure × Treatment interaction was significant: for *Balanus* $F = 44.3$, df = 3, 106; for *Chthamalus* $F = 14.9$, df = 3, 104; $P < 0.000001$ in both cases; results not shown). For both species at both BB and SH, differences among replicates with the same site, zone, and exposure were not significant (RM-ANOVA: at BB, for *Balanus* $F = 0.44$, $P = 0.78$, df = 4, 63; for *Chthamalus* $F = 0.28$, $P = 0.89$, df = 4, 61;

at SH, for *Balanus* $F = 0.26$, $P = 0.90$, df = 4, 65; for *Chthamalus* $F = 0.23$, $P = 0.92$, df = 4, 65).

In the following, for simplicity, density trends are presented without reference to a formal RM-ANOVA analysis. Examination of the strength of recruit–adult relationships and their consistency with the recruit–adult hypothesis was the primary aim of this study, and I judged that little further insight would be gained by presenting a complete RM-ANOVA analysis in addition to the regression analyses.

1. *REF Patterns.*—Recruit densities were sparse on virtually all reference and transplant plates originating from the high zone (Figs. 4 and 5). By definition, these conditions persisted through August, so hereafter I focus on treatments with high initial densities.

At BB, mid-zone densities varied with exposure. *Balanus* recruited more densely than *Chthamalus* on exposed plates and less densely than *Chthamalus* on protected plates, and these relative differences persisted through August 1990 (Fig. 4B, D). Patterns of change varied by species and exposure, however. On exposed plates, barnacle densities, especially of *Balanus,* dropped sharply between December 1989 and February 1990 (Fig. 4B). On protected plates, in contrast, barnacle densities remained similar to transplant densities through August 1990, and *Chthamalus* was dominant throughout (Fig. 4D). At SH, *Chthamalus* recruited more densely than *Balanus* at both exposures (Fig. 5B, D). As at BB–exposed, SH densities fell sharply between December 1989 and February 1990 at both exposures, and low densities persisted through August 1990.
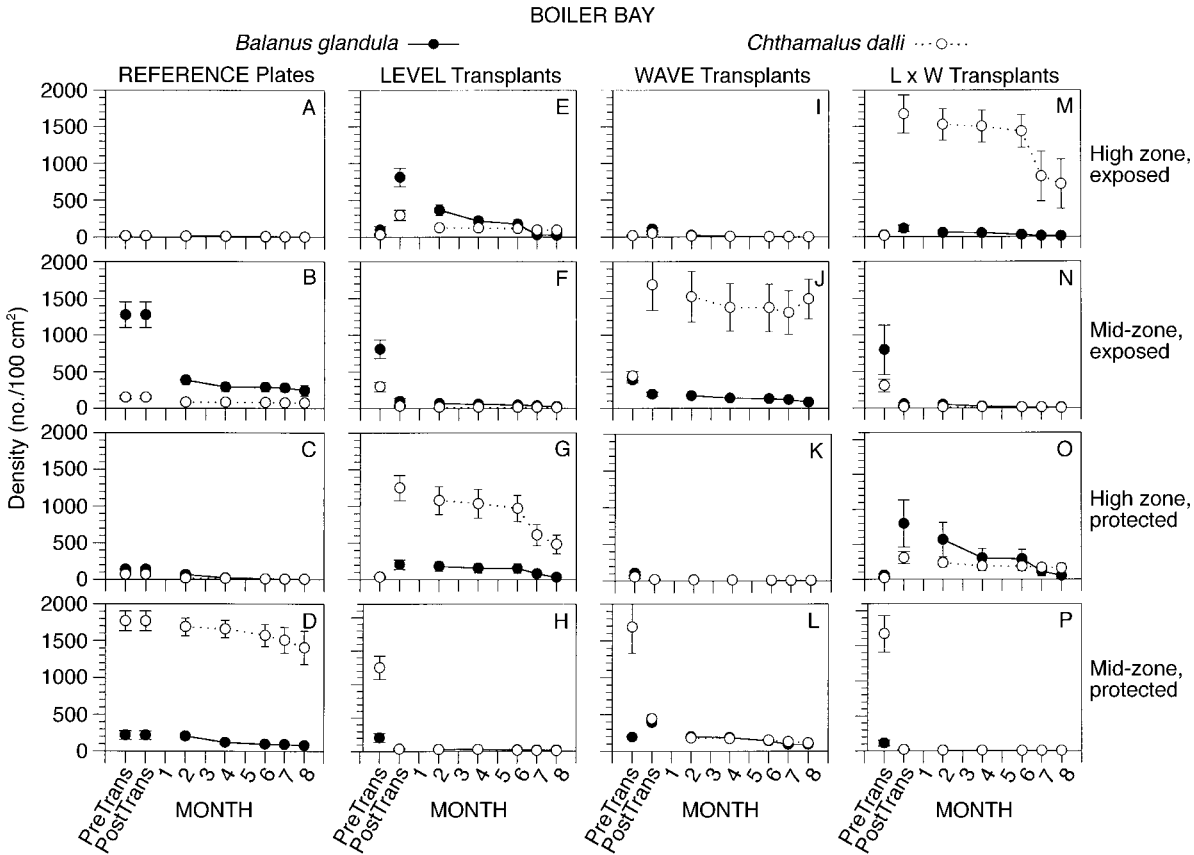
2. *Transplant Patterns.*—In LEVEL treatments at

BOILER BAY

Balanus glandula —●—   *Chthamalus dalli* ···○···

FIG. 4. Changes in densities of barnacles in Boiler Bay on REFERENCE plates (panels in column 1) and LEVEL, WAVE, and L × W transplant plates (panels in columns 2–4) at (in order from top to bottom) high-zone, exposed areas; mid-zone, exposed areas; high-zone, protected areas; and mid-zone, protected areas ($n = 5$ in each case). PreTrans refers to pretransplant recruit densities, and PostTrans refers to posttransplant recruit densities, both in December 1989. Months are shown by number: 1 = January, 8 = August. When densities of the two barnacle species are the same, or nearly so, the unfilled *Chthamalus* symbol covers the filled *Balanus* symbol. In panel J, the increase in *Chthamalus* density in August 1990 was a consequence of the loss of a replicate with low barnacle density. Error bars represent ± 1 SEM. When no error bar is visible, it is equal to, or smaller than the radius of the symbol.

both sites, transplants to the high zone made *Balanus* the numerical dominant on exposed plates and *Chthamalus* the numerical dominant on protected plates (Figs. 4 and 5; compare panels A and E, C and G). Mortality was high, however, especially for *Balanus,* and by August 1990, either *Chthamalus* was the denser barnacle (Fig. 4E, G, 5G) or all individuals were dead (Fig. 5E).

Transplant densities were less different in WAVE than in LEVEL treatments (Figs. 4I–L, 5I–L; compare pretransplant to posttransplant densities). At both sites, *Chthamalus* was more numerous on WAVE plates after transplantation (Figs. 4J, L, 5J, L). This dominance persisted longer at exposed sites, but in all cases except SH exposed, densities of both species fell steadily through August 1990.

In L × W treatments, transplant densities were relatively high for both species at both sites (Figs. 4M, O, 5M, O) with the exception of *Balanus* at BB high zone–exposed (Fig. 4M). Subsequent survival on these high-zone plates was poor for both species except for

Chthamalus at BB high-zone–exposed, and barnacles were scarce or virtually absent by August 1990 (Fig. 4M).

Recruit–adult relationships.—In contrast to the natural differences in means and ranges of density of recruits between sites, levels and exposures, similar ranges of recruitment densities were established when data were pooled across treatments (Fig. 6). Examination of trends across larger spatial scales was aided by pooling of data, first across exposures, and then across zones. In such analyses, two cautions are necessary. First, adults can never be more numerous than recruits, so by definition, all recruit–adult regressions will fall on or below the upper bound of equal numbers of each. As a consequence, recruit–adult regressions are more likely to be significant than regressions in which the data points are free to vary in either direction around the line of equality (McGuinness and Davis 1989). Second, pooling data across tidal heights, exposures, and sites combines data that are heterogeneous in the spe-
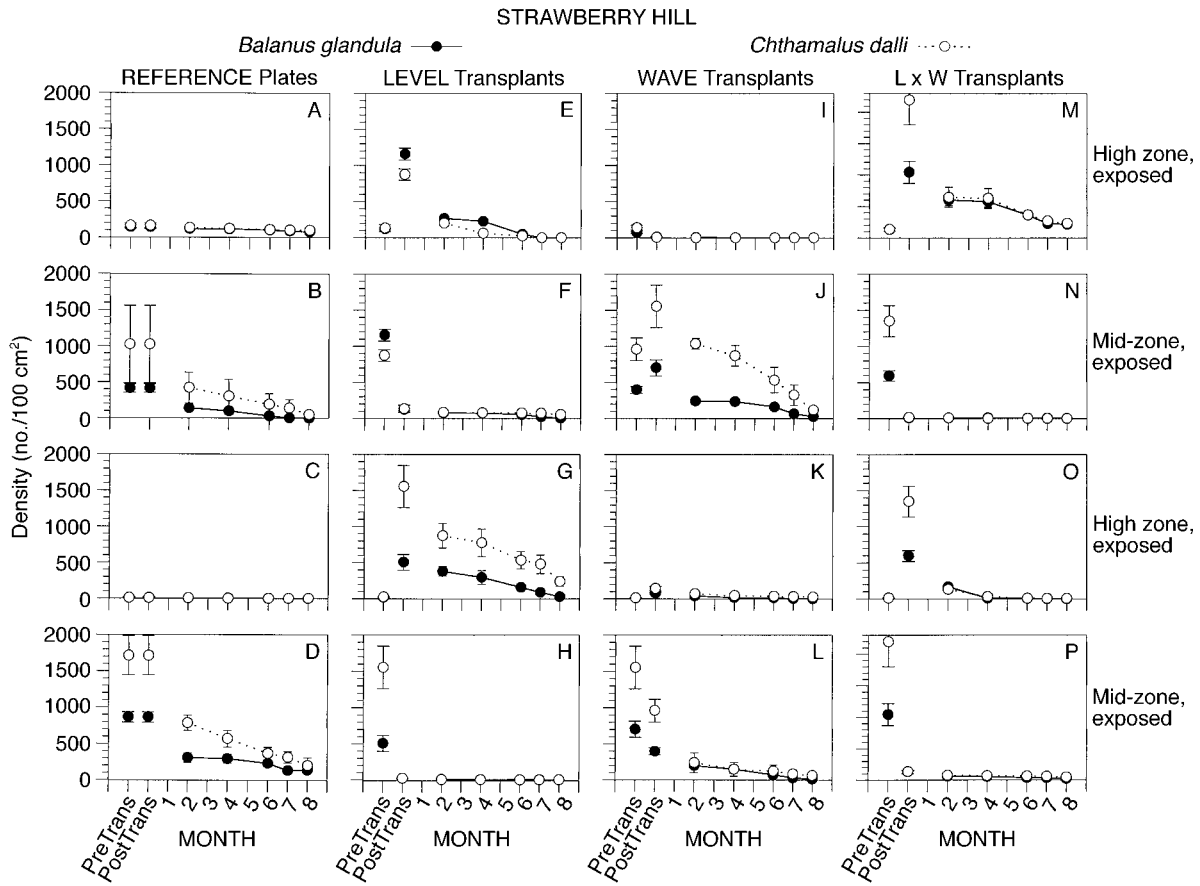
FIG. 5. Changes in densities of barnacles, at Strawberry Hill on REFERENCE plates (panels in column 1) and LEVEL, WAVE, and L × W transplant plates (panels in columns 2–4). See Fig. 4 caption for further details.

cific conditions that produced them. For example, low adult densities can be produced from high recruit densities by mortality from predation, competition, disturbance, or thermal/desiccation stress. Nonetheless, pooling allows consideration of whether or not recruit–adult relationships are density dependent or density independent at different spatial scales. Such evaluations do not require knowledge of the specific ecological processes producing the relationship. Inferences regarding the specific processes that underlie the relationship, whether density-dependent or density-independent, will be tentatively evaluated by examining changes in percentage cover of barnacles in relation to field observations during the experiment and results of other studies in the same system.

1. *Boiler Bay.*—At the smallest scale (< 10 m), density of recruits was a relatively accurate predictor of density of adults for *Chthamalus* regardless of exposure, tidal level or site (Fig. 6A–D; Table 4, $P < 0.0001$ in all cases, $R^2 \geq 0.79$). In contrast, for *Balanus,* recruitment was a poorer predictor of density of adults (Fig. 6A–D). In the high and mid-zones, recruit densities were correlated with adult densities in all cases (Table 4; $P \geq 0.017$). Midzone regressions for *Balanus,*

however, explained less variance than did those for *Chthamalus* (67 and 68% vs. 87 and 91%, at exposed and protected areas, respectively). High zone regressions explained even less of the variance in *Balanus* than in the mid-zone (28 and 36% at exposed and protected areas, respectively). Note that this variation was not related to differences in the relationship between initial density of recruits and densities 2 mo after transplantation (Fig. 7A, B; Table 4). In all combinations for both species, recruitment explained a relatively high proportion of the variance in barnacle density in February 1990 ($R^2 \geq 0.78$).

At the intermediate scale (10–100 m), similar trends were seen, and densities of recruits and adults were correlated in all cases (Fig. 8A, B). In both zones, recruitment predicted density of *Chthamalus* adults (R^2: high zone = 0.83, mid-zone = 0.89) better than it did for *Balanus* (R^2: high zone = 0.31, mid-zone = 0.61).

2. *Strawberry Hill.*—At both small and intermediate scales, recruitment was a much poorer predictor of final density of adults for both barnacle species at SH than at BB (Figs. 6E–H, 8C, D; Table 4). As at BB, at SH the relationships between adult and recruit densities of
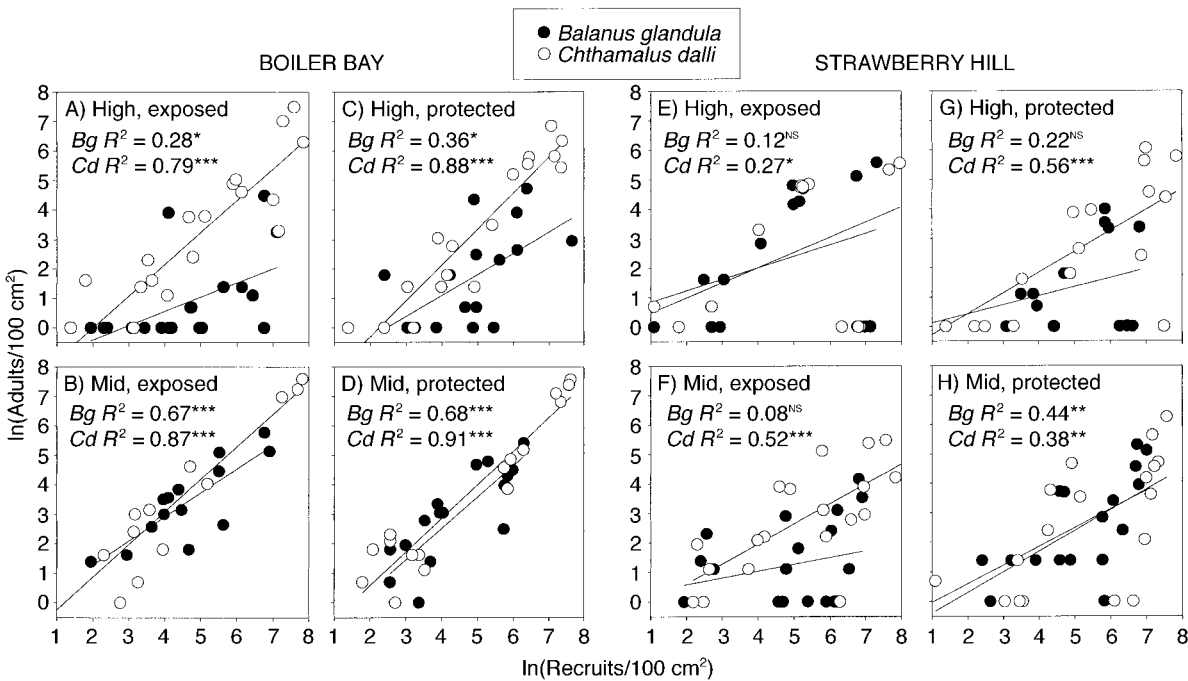
FIG. 6. Recruit (December 1989)–adult (August 1990) relationships (ln–ln) at each site × zone × exposure combination for *Chthamalus* and *Balanus* (initial $n = 20$). Coefficients of determination (R^2) are shown for each species ($Bg = Balanus$; $Cd = Chthamalus$). Lines are least-squares regressions; asterisks indicate significance levels (see Table 4 for details). NS, $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Chthamalus were generally stronger than for *Balanus* (Figs. 6E–H, 8C, D; Table 4).

At the smaller scale, density of recruits explained a greater proportion of the variance in adults for *Chthamalus* than for *Balanus* in three of four cases. Recruit density was correlated to adult density in all cases for *Chthamalus,* but only in one of four cases for *Balanus* (Table 4). At SH, there was no clear zone-dependent difference in the predictive capacity of the recruit–adult relationship (Fig. 6E–H), but except for *Chthamalus* in the mid-zone, recruit–adult correlations explained more variance at protected areas than at exposed areas (range = 1.8× to 5.5×). As at BB, in February, recruitment explained a uniformly high proportion of the variance in density of barnacles in all cases (Fig. 7C, D), again indicating that the differences among species, zone, and exposure were not dependent on trends existing shortly after transplantation.

At the intermediate scale, recruit density was correlated with adult density in all cases (Fig. 8C, D), but recruitment was a relatively poor predictor of density of adults, especially for *Balanus.* Recruitment explained twice as much of the variance for *Chthamalus* than for *Balanus,* but for each species, R^2 values were similar in each zone.

At the larger scale (~80 km), pooling across exposures and zones indicated that density of *Chthamalus* recruits explained a higher proportion of adult variance at BB than at SH ($R^2 = 0.83$ vs. 0.42). Recruit–adult correlations were weaker for *Balanus* at both sites ($R^2 = 0.27$ at BB, 0.18 at SH). Despite the low variance explained for *Balanus,* density of recruits was correlated with density of adults of both species at both sites.

Density-dependent vs. density-independent mortality.—At the smaller scale, density-dependent effects occurred in 4 of 16 possible cases (Table 4, $P_{slope} = 1.0$ column; Fig. 6). For *Balanus,* high density led to greater mortality at BB high-zone–exposed (slope = 0.484, $P = 0.011$), SH high-zone–protected (slope = 0.306, $P = 0.0003$), and SH mid-zone–exposed (slope = 0.231, $P = 0.0007$). Density-dependent mortality of *Chthamalus* evidently occurred in only one case, SH mid-zone–exposed, although the trend was only weakly significant (slope = 0.678, $P = 0.049$).

At the intermediate scale, evidence for density-dependent mortality occurred in five of eight possible cases (Fig. 8). At BB, barnacle mortality was mostly density independent (log–log slope = 1.0), with the exception of *Balanus* in the high zone, where negative density dependence occurred. At SH, all recruit–adult relationships were negatively density dependent (log–log slope < 1.0).

At the larger scale, density-dependent mortality occurred in three of four cases, with *Chthamalus* at BB as the only exception (Fig. 9A, B). Although these analyses suggest a trend toward greater density dependence when larger scales are considered, this trend may be at least partly a function of sample sizes, which

TABLE 4. Linear regression analyses of the correlations between February (posttransplant) or August (final) densities of the 1989 barnacle cohort (dependent variables), and December densities of the 1989 barnacle cohort (recruitment densities; independent variables).

Site	Habitat	Species	Month	b_0	b_1	df	MS	MSE	F	P	R^2	$P_{\text{slope}=1.0}$
Boiler Bay	high zone, exposed	*Balanus*	Feb	−0.017	0.826	1,18	30.721	0.489	62.8	<0.0001	0.777	⋯
		glandula	Aug	−1.378	0.484	1,18	10.550	1.511	6.98	0.017	0.279	0.011
		Chthamalus	Feb	−0.982	1.068	1,18	83.011	0.374	221.7	<0.0001	0.925	⋯
		dalli	Aug	−2.176	1.082	1,18	85.093	1.258	67.6	<0.0001	0.790	0.54
Boiler Bay	high zone, protected	*Balanus*	Feb	−0.425	0.986	1,15	29.772	0.194	153.3	<0.0001	0.911	⋯
		glandula	Aug	−1.761	0.715	1,15	15.655	1.882	8.32	0.011	0.357	0.27
		Chthamalus	Feb	−1.111	1.095	1,15	66.656	0.295	226.3	<0.0001	0.938	⋯
		dalli	Aug	−2.762	1.222	1,15	83.052	0.732	113.5	<0.0001	0.883	0.072
Boiler Bay	mid-zone, exposed	*Balanus*	Feb	0.933	0.732	1,18	23.002	0.138	166.9	<0.0001	0.903	⋯
		glandula	Aug	−0.348	0.812	1,12	16.177	0.667	24.2	0.0004	0.669	0.28
		Chthamalus	Feb	−0.393	1.008	1,18	75.314	0.250	301.1	<0.0001	0.944	⋯
		dalli	Aug	−1.349	1.104	1,11	69.729	0.967	72.1	<0.0001	0.868	0.44
Boiler Bay	mid-zone, protected	*Balanus*	Feb	−0.387	0.990	1,16	28.946	0.279	103.6	<0.0001	0.866	⋯
		glandula	Aug	−1.740	1.062	1,15	30.696	0.955	32.2	<0.0001	0.682	0.75
		Chthamalus	Feb	−0.643	1.043	1,16	85.149	0.269	316.0	<0.0001	0.952	⋯
		dalli	Aug	−1.696	1.136	1,14	90.841	0.670	135.5	<0.0001	0.906	0.18
Strawberry Hill	high zone, exposed	*Balanus*	Feb	−0.313	0.945	1,15	54.811	0.229	239.7	<0.0001	0.941	⋯
		glandula	Aug	0.450	0.390	1,13	8.377	4.826	1.74	0.21	0.118	0.06
		Chthamalus	Feb	−0.035	0.864	1,15	70.739	0.281	251.3	<0.0001	0.944	⋯
		dalli	Aug	−0.053	0.517	1,13	22.013	4.657	4.73	0.049	0.267	0.06
Strawberry Hill	high zone, protected	*Balanus*	Feb	−0.428	0.936	1,16	78.193	0.589	132.8	<0.0001	0.892	⋯
		glandula	Aug	−0.179	0.306	1,15	8.032	1.856	4.33	0.055	0.224	0.0003
		Chthamalus	Feb	−0.587	0.909	1,16	82.876	0.781	106.1	<0.0001	0.869	⋯
		dalli	Aug	−0.980	0.705	1,15	46.757	2.460	19.01	0.0006	0.559	0.09
Strawberry Hill	mid-zone, exposed	*Balanus*	Feb	0.734	0.712	1,18	26.502	0.154	172.1	<0.0001	0.905	⋯
		glandula	Aug	0.109	0.231	1,18	2.780	1.877	1.48	0.239	0.076	0.0007
		Chthamalus	Feb	−1.280	1.106	1,18	86.882	0.304	285.7	<0.0001	0.941	⋯
		dalli	Aug	−0.764	0.678	1,18	32.714	1.652	19.81	0.0003	0.524	0.049
Strawberry Hill	mid-zone, protected	*Balanus*	Feb	−0.351	0.907	1,17	46.054	0.157	292.5	<0.0001	0.945	⋯
		glandula	Aug	−0.660	0.629	1,16	21.263	1.663	12.78	0.0025	0.444	0.051
		Chthamalus	Feb	−1.424	1.029	1,17	72.948	0.988	73.9	<0.0001	0.813	⋯
		dalli	Aug	−1.086	0.695	1,16	30.354	3.101	9.79	0.006	0.380	0.19

Notes: The regression model was ln(February [or August] density + 1) = b_0 + b_1(ln[December density + 1]), where b_0 = intercept and b_1 = slope. In all cases initial $n = 20$; replicate loss sometimes led to final $n < 20$. For this analysis, data from all four transplant treatments (REF, LEVEL, WAVE, L × W) were combined for each level × wave-exposure combination. $P_{\text{slope}=1.0}$ is the probability for a test of the hypothesis that the slope of the regression for August = 1.0; $P < 0.05$ indicates that the slope differs significantly from 1.0.

were, at maximum, 20, 40, and 80 plates at the smaller, intermediate, and larger scales, respectively.

Relative importance of recruitment vs. postrecruitment factors.—The proportion of the variance in density of adults explained by recruitment can be a useful estimator of the relative importance of recruitment vs. postrecruitment processes in determining barnacle density, at least in the context of the experiment (e.g., Menge 1991). To evaluate the relative importance of recruitment, I treated each combination of site, zone, and exposure as an independent estimate of the recruit–adult relationship for each species. While each of these combinations had distinct physical and biotic conditions, strictly speaking, this assumption of independence may not be correct because conditions associated with zone and exposure are nested within site. Moreover, sample sizes were small. Therefore, the following analysis must be considered tentative.

Average density of recruits in December and R^2 for each of the eight regressions (i.e., each site, zone, and exposure combination) were compared separately for *Balanus* and *Chthamalus.* I used linear discriminant analysis (Dillon and Goldstein 1984) to determine the

extent to which each combination sorted with respect to these two variables. The analysis suggests that the proportion of the variance (R^2) in density of adults in August 1990 explained by recruitment differed between species by site (Fig. 10). For *Balanus,* the relative importance of recruitment did not vary systematically with recruit density, but for *Chthamalus,* importance was low when recruitment was high (SH) and high when recruitment was low (BB; Fig. 10).

DISCUSSION

In this system, both recruitment and postrecruitment processes appeared to have strong effects on adult barnacle densities. The relative impacts of each clearly varied with species, exposure, level, and site, each combination of which has its own regime of effects of physical conditions and species interactions. Since both physical and biological processes vary along the complex environmental gradients that characterize this system, I first evaluate the ecological context in which the changes in barnacle density occurred. I then return to the predictions of the recruit–adult hypothesis and evaluate the relative effects of recruitment and postrecruit-
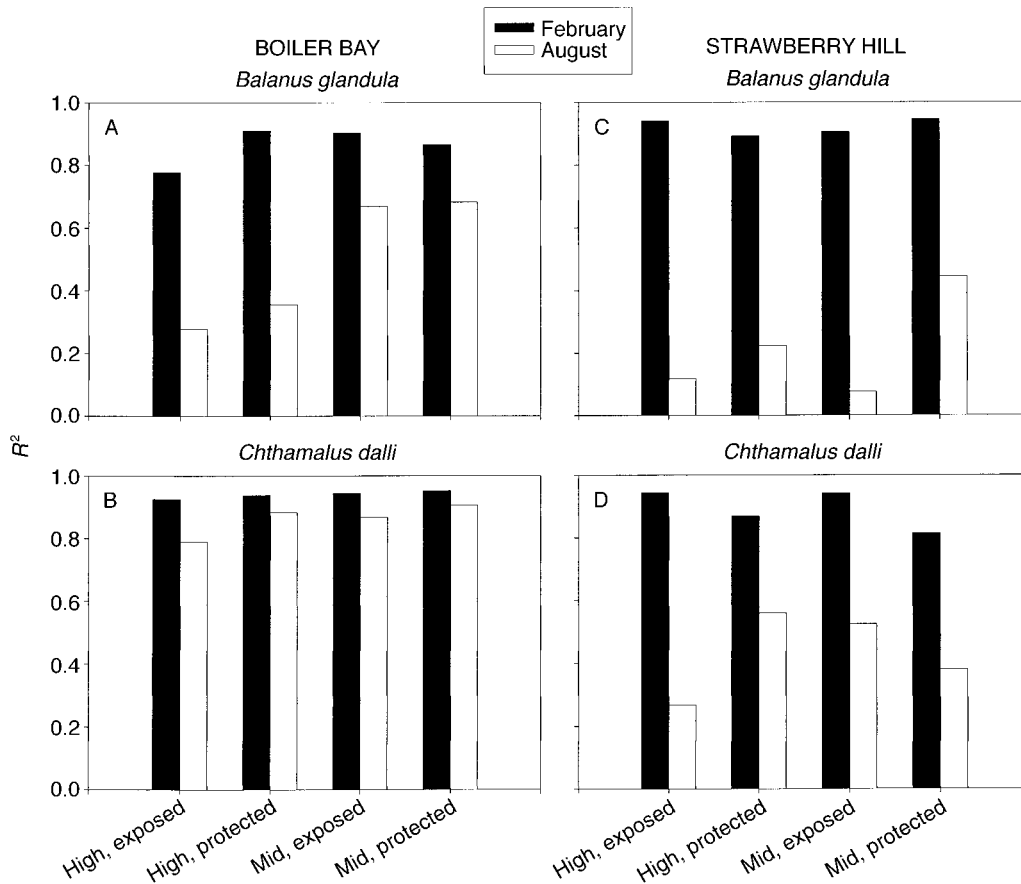
Fig. 7. Coefficients of determination (R^2) of ln–ln regressions between February 1990 barnacle densities on transplants and recruit densities (solid bars) and August 1990 transplant (adult) densities and recruit densities (open bars).

ment factors. Finally, I consider the broader relationship of this study to previous investigations, and explore issues needing further research.

Ecological context: percent cover changes

Density can be a poor metric of space usage. For instance, depending on whether barnacles are large or small, equal densities can occur with both high and low surface cover. Within a cohort, density changes can only be negative, but percent cover changes can be either negative, due to mortality, or positive, due to growth or subsequent recruitment (e.g., Petraitis 1995). Negative, mortality-induced changes in percent cover reflect postrecruitment processes such as environmental stress, physical disturbance, competition, and predation. Since space-limited competition is likely to be intense when covers approach 100%, high percent covers are suggestive of strong competition (Connell 1961a, 1970, Dayton 1971). Thus, percent cover can be a better indicator of space limitation than density. Since *Balanus* grows faster than *Chthamalus,* and reaches larger sizes (e.g., Connell 1961a, 1970), percent cover is also likely to reflect the relative dominance of each species better than density. Percent cover

changes are presented in Figs. 11 and 12, with a summary of the processes inferred to have caused these changes. These interpretations were based on observations made both directly in the field and in the photographs, and in both prior and subsequent experimentation (B. Menge et al., *unpublished data*).

Percent cover trends differed somewhat from density trends (Figs. 11 and 12). First, although low recruitment density usually resulted in low adult percent cover (compare Figs. 4 and 5 panels A, C to Figs. 11 and 12, panels A, C), an exception to this trend (REF treatment at SH high-zone–exposed, percent cover increased until summer; Fig. 12A) suggested that growth can compensate for low initial densities. In this case, *Balanus* outgrew *Chthamalus*, overcoming an initial slight numerical advantage by the latter.

When recruitment density was high, further contrasts between percent cover and density results were evident (Figs. 4, 5, 11, and 12). In general, percent cover tended to fluctuate more than did density changes. Further, percent cover changes included both increases and decreases, while by definition density of the 1989 cohort only declined. More specifically, in high-zone transplants, changes appeared governed primarily by
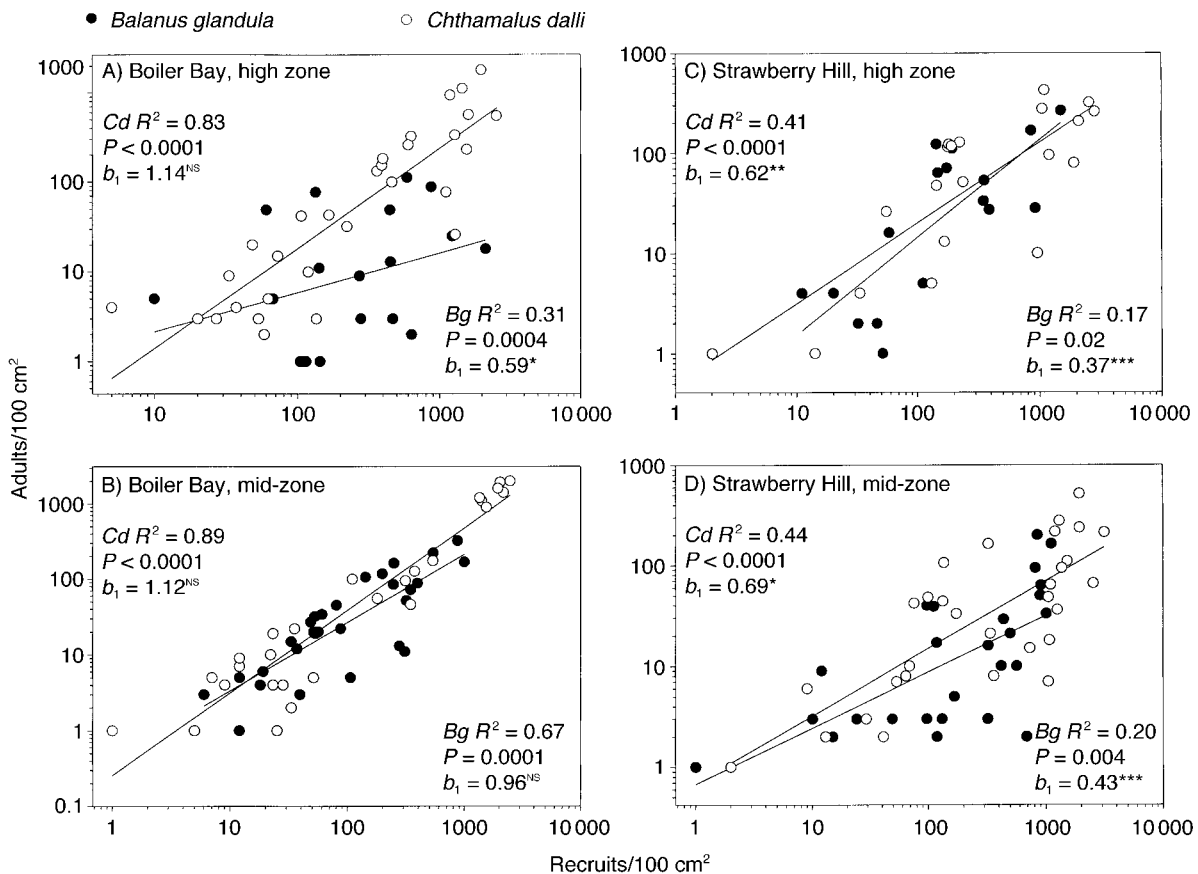
FIG. 8. Recruit–adult density correlations for each site × zone combination (combined exposures; initial $n = 40$). R^2, P values, and slopes (b_1) for each regression line are shown for each species. Significance levels indicate whether or not slopes are significantly different from 1.0: NS, $P > 0.05$; *$P < 0.05$; ***$P < 0.001$.

growth, competition (winter), and heat and desiccation stress (summer; Figs. 11E, G, M, O, 12E, G, M, O). In the mid-zone, site-related differences were evident (Figs. 11B, D, J, L, 12B, D, J, L). At BB, percent cover changes were mostly due to growth and competition between barnacle species. At SH, competition with mussels, predation, and later recruitment appeared to be the primary factors affecting barnacles.

Although prior work has shown that *Balanus* is competitively dominant to *Chthamalus* (Connell 1961*a, b,* Dayton 1971, Farrell 1991; see winter and spring changes in Fig. 12B, D, J, L), my experiments suggest that high recruitment of *Chthamalus* relative to *Balanus* can lead to a reversal of this outcome. At BB, when *Chthamalus* had an initial numerical (Fig. 4D) and percent cover advantage (Fig. 11D, J), *Balanus* was virtually eliminated. Note that these differential trends were not evident in the density analyses (Fig. 4).

Changes in percent cover indicated that predation and interspecific competition with mussels (*Mytilus trossulus*) were important components of the postrecruitment environment for barnacles at SH but not at BB. In both exposed and protected mid-zones at SH,

whelks decreased *Balanus* abundance sharply (Fig. 12B, D, J, L). On the mid-zone–exposed REF plates, mussels were another important source of *Balanus* mortality (Fig. 12B).

These changes in percent cover are thus consistent with the notion that when low, recruitment determines final abundance of both barnacle species, but when high, both recruitment and postrecruitment processes can have important effects, at least in the short term. High zones appeared stressful to both barnacle species in summer, but at other times, biotic factors such as growth and competition were important. Conditions in the high zone at BB evidently were more favorable to *Chthamalus* while conditions at SH were more favorable to *Balanus.* Mid-zones were more variable, but postrecruitment biotic processes were clearly strong when initial recruitment was high. As in the low zone (Menge et al. 1994, 1997*a,* Navarrete and Menge 1996), mid-zone biotic processes appeared more intense at SH than at BB. Changes due to growth, competition, and predation were all faster, and their effects greater, at SH than at BB. The major difference between sites in postrecruitment effects was that predation ap-
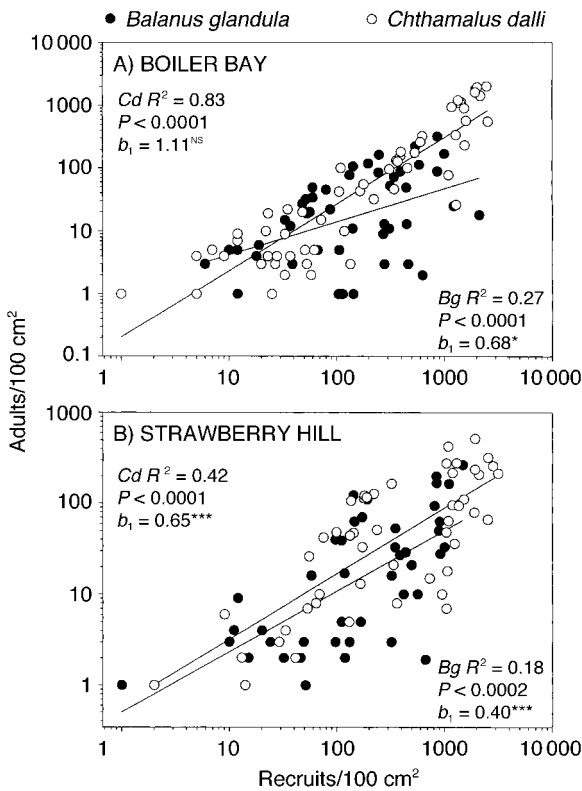
FIG. 9. Recruit–adult density correlations at each site (zones and exposures combined) for *Balanus* and *Chthamalus*. See Fig. 8 caption for further details.

peared stronger at SH (four of four cases with high recruitment in the mid-zone had changes attributable to predation; Fig. 12B, D, J, L) than at BB (zero of four cases had predation effects; Fig. 11B, D, J, L).

Recruitment impact: evaluation of predictions

Prediction 1: When low, recruitment is a strong predictor of density of adults relative to postrecruitment effects.—As noted in the *Introduction*, tests of this prediction of the recruit–adult hypothesis were facilitated by experimentally creating higher than usual recruitment densities, together with low densities, in environments where recruitment is naturally low. Transplants from mid-zones and high zones to high zones generated such a scenario. Under such conditions, the hypothesis predicts that densities of recruits and adults should be highly correlated. That is, recruit density and not postrecruitment processes should be the main determinant of adult abundance.

Results indicated that under these conditions the strength of the recruit–adult relationship varied by site and species with a suggestion of exposure effects as well (Fig. 6). Density of adults was more strongly dependent on the density of recruits at BB than at SH. The recruit–adult relationship was tighter for *Chthamalus* than for *Balanus* and tended to be stronger at protected than exposed areas, especially at SH. Hence,

creation of a wider than normal range of densities of recruits in a habitat with naturally low recruitment led to contrasting recruit–adult relationships for these species. For the small, slow-growing, weakly competitive, but relatively stress-tolerant *Chthamalus,* recruit density predicted adult density well in the high zone at BB, and somewhat less well at SH (Fig. 6). For the larger, faster growing, more competitive, but less stress- and predation-tolerant *Balanus,* recruit density predicted density of adults relatively poorly, particularly at SH (Fig. 6). Support for Prediction 1 was thus mixed.

Prediction 2: When high, recruitment is a weak predictor of adult density relative to postrecruitment processes.—Tests of this prediction of the recruit–adult hypothesis were facilitated by experimentally creating lower than usual recruitment densities, together with high densities, in environments where recruitment is naturally high. Transplants from high and mid-zones to the mid-zone generated such a scenario. Under such conditions, the hypothesis predicts that recruit–adult
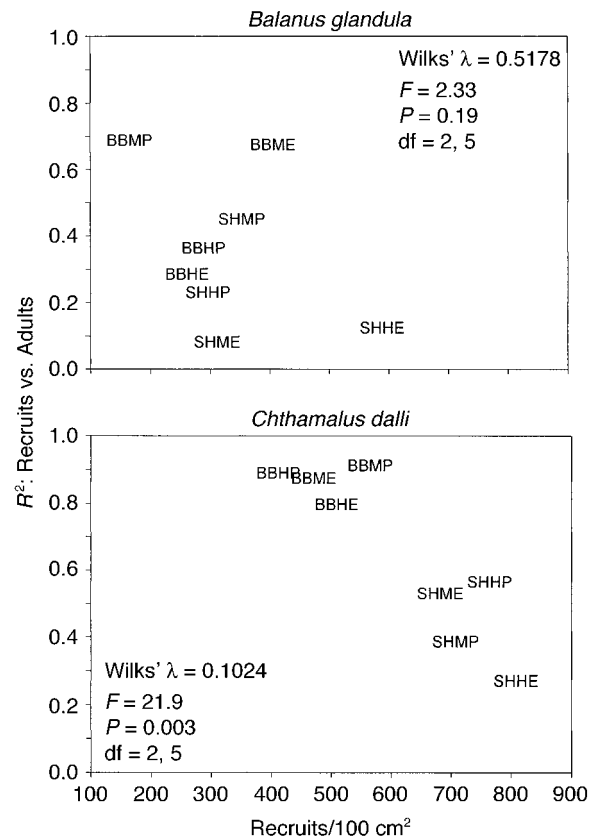

FIG. 10. Proportion of the variance in recruit–adult correlations explained by recruit density vs. recruit density for each site × zone × exposure regression. For each abbreviation in the plots, the first two letters refer to the site (BB = Boiler Bay, SH = Strawberry Hill), the third letter gives the zone (H = high, M = mid), and the last letter gives the exposure (E = exposed, P = protected). Statistics show results of linear discriminant analysis for each species.
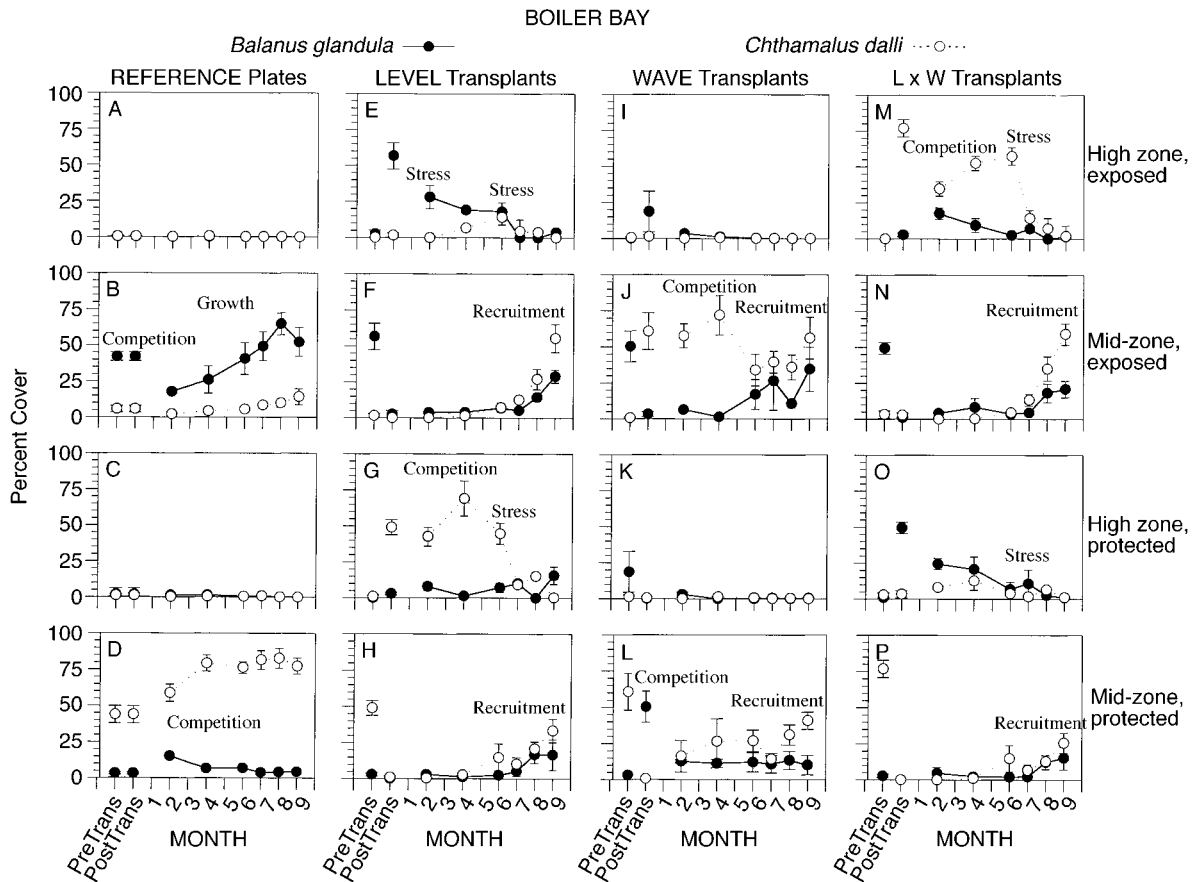
FIG. 11. Changes in percent covers of barnacles at Boiler Bay on REFERENCE plates (panels in column 1) and LEVEL, WAVE, and L × W transplant plates (panels in columns 2–4). Within the panels, "Stress," "Competition," "Growth," and "Recruitment" refer to the processes inferred to be responsible for changes occurring during the time under each term. See Fig. 4 caption for further details.

relationships should be weak. That is, postrecruitment processes should overcome recruitment in determining adult densities.

As in the low recruitment environment (high zone), recruit–adult relationships in mid-zone experiments were stronger for *Chthamalus* than for *Balanus,* were stronger at BB than at SH, and with the exception of *Chthamalus* in the mid-zone at SH, tended to be slightly (BB) to strongly (SH) higher at protected areas (Fig. 6). The underlying causes of postrecruitment processes in the mid-zone were primarily biotic interactions, and at each site and exposure, the specific processes responsible were more heterogeneous than in the high zone (Figs. 11 and 12). Hence, as in the high zone for Prediction 1, results in the high recruitment environment were both consistent and inconsistent with Prediction 2. Postrecruitment processes did indeed generate weak recruit–adult relationships, but only at SH. Moreover, recruit–adult relationships were actually similar to or tighter than those in the high zone in four of four cases at BB and two of four cases at SH. Thus, in these experiments, recruitment was consistently a

strong predictor of adult density regardless of the recruitment environment. These results suggest that, in this example at least, recruitment and postrecruitment processes are in fact decoupled. Recruitment can be an important determinant of adult abundance regardless of the postrecruitment environment, and postrecruitment processes can be an important determinant of adult abundance regardless of recruit density. The variable consistency of these results with Predictions 1 and 2 indicate that both species and habitat characteristics may be important modifiers of the recruit–adult hypothesis.

Prediction 3: Both species will respond similarly to pre- and postrecruitment processes.—It is clear that, when considered in detail, the data are not consistent with this prediction. However, when considered at a somewhat larger scale and in a community context, similarities in patterns of recruitment and in recruit–adult relationships were also evident for these barnacles. Thus, despite differential susceptibilities to physical and biotic processes, both settled more densely in mid-zones than in high zones (Figs. 2 and 3). Both had

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Balanus glandula ——●——   *Chthamalus dalli* ○   *Mytilus trossulus* ——▽ –
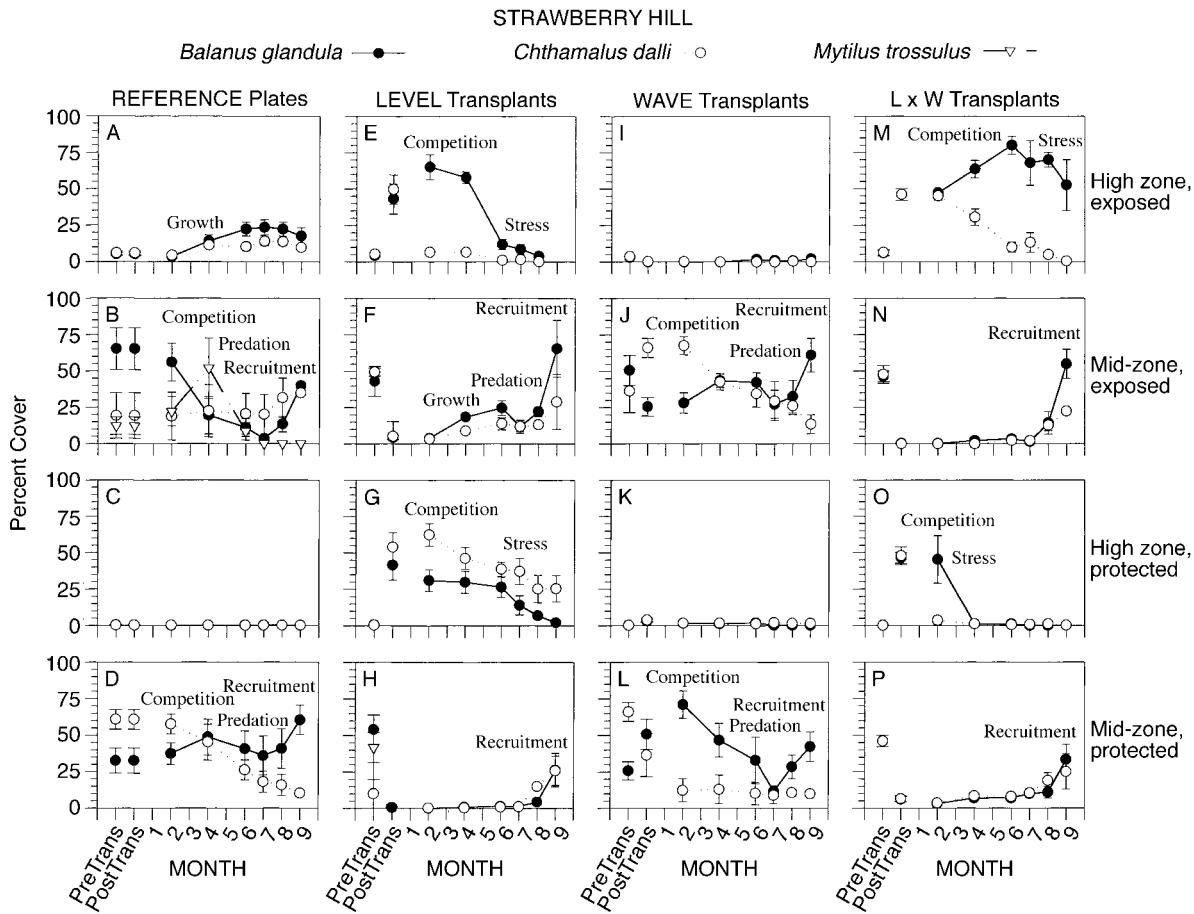

FIG. 12. Changes in percent covers of barnacles and mussels (*Mytilus trossulus*) at Strawberry Hill on REFERENCE plates (panels in column 1) and LEVEL, WAVE, and L × W transplant plates (panels in columns 2–4). Within the panels, "Stress," "Competition," "Growth," "Predation," and "Recruitment" refer to the processes inferred to be responsible for changes occurring during the time under each term. See Fig. 4 caption for further details.

tighter recruit–adult correlations at BB than at SH (Fig. 6) suggesting similar responses to site/level differences. Therefore, although the two species have indisputably ecologically distinct responses to recruitment, biotic processes, and physical conditions, when viewed in a multispecies context, they have broad ecological similarities as well.

Spatial scale and the relative importance of recruitment

Prediction 4: Recruit–adult relationships at larger spatial scales vary with recruitment.—The heterogeneity in recruit–adult relationships observed when comparing across treatments within each combination of site, zone, and exposure (e.g., Fig. 6) and the variable support for Predictions 1 and 2 may be a consequence of spatial scale as well as of differences in species-specific responses. The recruit–adult hypothesis was based on a localscale study of a single species (*Balanus glandula*; Gaines and Roughgarden 1985). Later, this hypothesis was proposed as the underlying basis for a

perceived geographic pattern in both barnacle abundance and community structure along the west coast of North America (Roughgarden et al. 1988). Recent evidence has confirmed the predicted barnacle abundance pattern in the high zone for *Balanus* (abundance is high in Oregon and low in California), but the opposite pattern was observed for *Chthamalus* (Connolly and Roughgarden 1999). Modeling by these workers suggests that the *Chthamalus* pattern may depend on the coupling of larval transport and competition for space with *Balanus*.

Compared to the smaller scale evaluation of the present study, both the present analysis (Figs. 8, 9) and these modeling results suggest that the postulated inverse relationship between density of recruits and its relative importance in determining density of adults may be stronger at larger scales. As suggested by Fig. 10, however, an inverse relationship was observed at the scale of sites combined (BB + SH) for *Chthamalus* but not for *Balanus*. Even at the scale of the ~80 km distance between the two sites, these two barnacle spe-

TABLE 5. Summary of results of studies investigating relative impact of recruitment and postrecruitment factors on species' abundance.

Community	Organism	Species†	Max. recruit. density (no./0.01 m²)	Zone	Postrecruit. mortality	Effect on adult density (% variance explained)		Reference‡
						Recruitment	Post-recruit.	
France, rocky intertidal (cold temperate)	barnacle	Sb	2 400	high–low	ND	high (69%)	ND	a
	barnacle	Cs	1 800	high–low	ND	high (62%)	ND	
Scotland, rocky intertidal (cold temperate)	barnacle	Sb	11 500	high	high	low (19%)	high	c
			6 900	mid–low	high	low (1%)	high	
			1 900		high	low (1%)	high	
Nova Scotia, rocky intertidal (cold temperate)	barnacle	Sb	0.7 ± 0.5	high (A)	low (0%)	high	low	h
			126 ± 76	mid (A)	low (18%)	high (96%)	low	
			339 ± 79	low (A)	high (68%)	low (1%)	high	
			2.5 ± 2.3	high (B)	low (7%)	high (97%)	low	
			12 ± 9	mid (B)	int. (49%)	? (NS)	?	
			50 ± 26	low (B)	high (100%)	low	high	
New England, rocky intertidal (cold temperate)	barnacle	Sb	274 ± 62 to 909 ± 96	mid–low	high	low (11%)	high (51%)	g
	barnacle		6 100	mid	high	low (8%)	high	b
	mussel	Me	120 ± 53 to 1 955 ± 648	mid–low	high	low (<1%)	high (78%)	g
San Juan I., Washington, rocky intertidal (cold temperate)	barnacle	Bg	240	high	low	high (52%)	low	c
Eastern Australia, rocky intertidal (warm temperate)	barnacle	Tr	3.3 ± 0.5 to 8 ± 2	mid	int.	int. (~33%)	int. (~43%)	d
Pacific coast, intertidal (tropical)	barnacle	Cf	~6 500	high–mid	low	high (52–94%)	low	f
Pacific coast, Panama, rocky intertidal (tropical)	barnacle	Cf	24	high	high	high (39%)	low (8%)	g
	barnacle	Bi	0.44	mid–low	high	high (68%)	low (9%)	
	oyster	Op	0.44	mid–low	high	high (61%)	low (10%)	
	oyster	Ce	1.04	low	high	high (87%)	low	
Florida limestone, subtidal (subtropical)	gorgonian	Lv	0.25	−1.5 m	low	high (52%)	low	e

Notes: ND = no data available. The "A" and "B" designations in the "Zone" column refer to two different sites at Minchinton and Scheibling's (1991) Nova Scotia study area.

† Species abbreviations: Bg, *Balanus glandula*; Bi, *Balanus inexpectatus*; Ce, *Chama echinata*; Cf, *Chthamalus fissus*; Cs, *Chthamalus stellatus*; Lv, *Leptogorgia virgulata*; Me, *Mytilus edulis*; Op, *Ostrea palmula*; Sb, *Semibalanus balanoides*; Tr, *Tesseropora rosea.*

‡ Key to reference codes: (a) Hatton (1938; cited in Connell 1985), (b) Grant (1977; cited in Connell 1985), (c) Connell (1985), (d) Fairweather (1988), (e) Gotelli (1988), (f) Sutherland (1990), (g) Menge (1991), (h) Minchinton and Scheibling (1991).

cies appear to be responding differently to recruitment and postrecruitment ecological processes. It is interesting that at the scale of Oregon plus California, patterns for *Balanus* and not for *Chthamalus* are consistent with the recruit–adult hypothesis, while at the scale of the central Oregon coast, patterns for *Chthamalus* and not *Balanus* appear consistent with the hypothesis (Fig. 10). This difference is probably at least partially explained by zone-related differences; Connolly and Roughgarden (1998) analyzed only high-zone data, while my experiments were done in both high and mid-zones.

The Oregon results may be a consequence of a relatively small range of densities of recruits, since compared to California and some other regions, all Oregon sites appear to be high-recruitment sites. On a geographic scale, densities of recruits in Oregon do appear to be high. Compared to central California, for instance, recruitment (per square centimeter) was far higher in Oregon (Table 5). Peak densities reported by Farrell et al. (1991) near Pacific Grove, California were ~0.55 individuals/cm². In 1989–1990, peak densities at the Oregon sites ranged from ~2.5 individuals/cm² in the high zone to ~58 individuals/cm² in the mid-zone.

Comparable peak densities (8.5–25.0 individuals/cm²) were observed further north in the San Juan Islands, Washington (Connell 1985). Even greater disparity occurred in comparisons to tropical sites in Panama, where recruit densities were very low (Menge 1991). Strictly speaking, these densities are not comparable due to the use of different techniques in measuring recruitment, but field observations of recruitment on natural substrata in Oregon suggest that similar magnitudes of difference would occur were all data obtained from natural rock surfaces. A recent study, using identical methods at sites ranging from central Oregon to central California, confirms the recruit density gradient implied by the above data (S. R. Connolly et al., *unpublished data*).

To examine the hypothesis at an even larger, global scale, and incorporate a broader range of recruitment densities, I examined the literature for examples of other studies in which recruit–adult correlations were available (Table 5). In general, the data are consistent with the predictions of the recruit–adult hypothesis. Studies ranging from tropical to cold temperate regions, by a variety of investigators, suggest that with increasing recruit density, recruitment explains a decreasing amount of variance in density of adults (Fig. 13A). While most studies were on acorn barnacles, a few involved bivalves and one study examined gorgonians (Table 5). Given the heterogeneity inherent in such analyses (e.g., in approach, methods, designs, sampling schemes), the statistically significant inverse correlation in Fig. 13A is intriguing. These data thus support and expand on the analysis that first documented such a pattern for barnacles (Connell 1985; data are included in Fig. 13, Table 5).

How do Oregon results compare to data from these literature studies? When summarized for each species at a scale similar to those used in Fig. 13A (site × zone), incorporation of data from the present study reduces the proportion of variance in density of adults explained by recruitment by 11%, but does not change the significance of the correlation (Fig. 13B). This reduction in relative importance of recruitment stems from the occurrence of a wide range of R^2 values over a small range of recruit densities. Data from Nova Scotia show a similar spread within a region from areas with a high importance of recruitment (high and mid-zones; NSH and NSM in Fig. 13) and low importance of recruitment (low zone; NSL in Fig. 13), but with a broader range of densities of recruits. In contrast to this high variability within a region, all data from high, mid-, and low zones in Scotland occurred in the lower right of Fig. 13, while all data from Panama fall toward the upper left. No other study considered a similar range of tidal levels, so further assessment of the factors underlying these contrasting regional patterns is not possible.

Community regulation and the recruit–adult hypothesis

The present analysis suggests that modification of the recruit–adult hypothesis is appropriate. Although low recruitment was evidently of high importance in determining density of adults, under conditions of high recruitment, recruit density had a wide range of impacts on adult density, ranging from strong to weak (Figs. 6, 8, 9, and 13). For example, in the global analysis, data toward the high end of the recruit density range span nearly the full range of R^2 (Fig. 13). My analysis suggests that the variable importance of recruitment at high densities may be a function of species and habitat characteristics. Thus, predicting densities of adults in areas of high recruitment must take into account a suite of factors, including recruit density, postrecruitment processes, and differential responses of species.

Beyond this context dependency at high recruitment rates, the present analysis also raises questions about whether or not recruit density, when low, is necessarily the primary determinant of adult abundance. As noted earlier, this prediction must be a truism, in the sense that low inputs of recruits cannot yield high adult densities. Yet, in some cases with low recruitment rates, under some circumstances, postrecruitment processes can also have a powerful influence on densities of adults, and may have at least as important an effect as recruitment (high-zone analysis; see also Connell 1985, Holm 1990, Minchinton and Scheibling 1991). For example, recruitment was low and strongly predicted the density of adult barnacles and oysters on rocky shores on the Pacific coast of Panama (e.g., Fig. 13; see Menge 1991). Yet field experiments showed that in the absence of predation, densities of barnacles and bivalves increased to exceptional densities, albeit slowly (>2.5 yr were required to reach ≥50% cover; Menge et al. 1986a). Even more strikingly, exposure of these experimental concentrations of prey to predators (fishes and invertebrates) revealed that predation intensity was extraordinarily high. Within a few days abundance of barnacles declined sharply to near zero (Menge et al. 1986b). Rock oysters (*Chama echinata*), better defended against fish predators and occurring in layers, lasted longer but survival decreased exponentially, and sharp decreases in cover occurred within a month (Menge et al. 1986b). Hence, despite low recruitment, predation was an important postrecruitment process in this community, and with low recruitment was responsible for the maintenance of low postrecruitment densities of barnacles and bivalves.

In another example, high recruitment occurs sporadically in the high zone in Oregon (*personal observations*), although no such event occurred during this study. Field observations indicate that most recruits are killed relatively quickly (e.g., within a few days) in these events, most probably due to heat and desiccation. Since such short-term phenomena could be easy
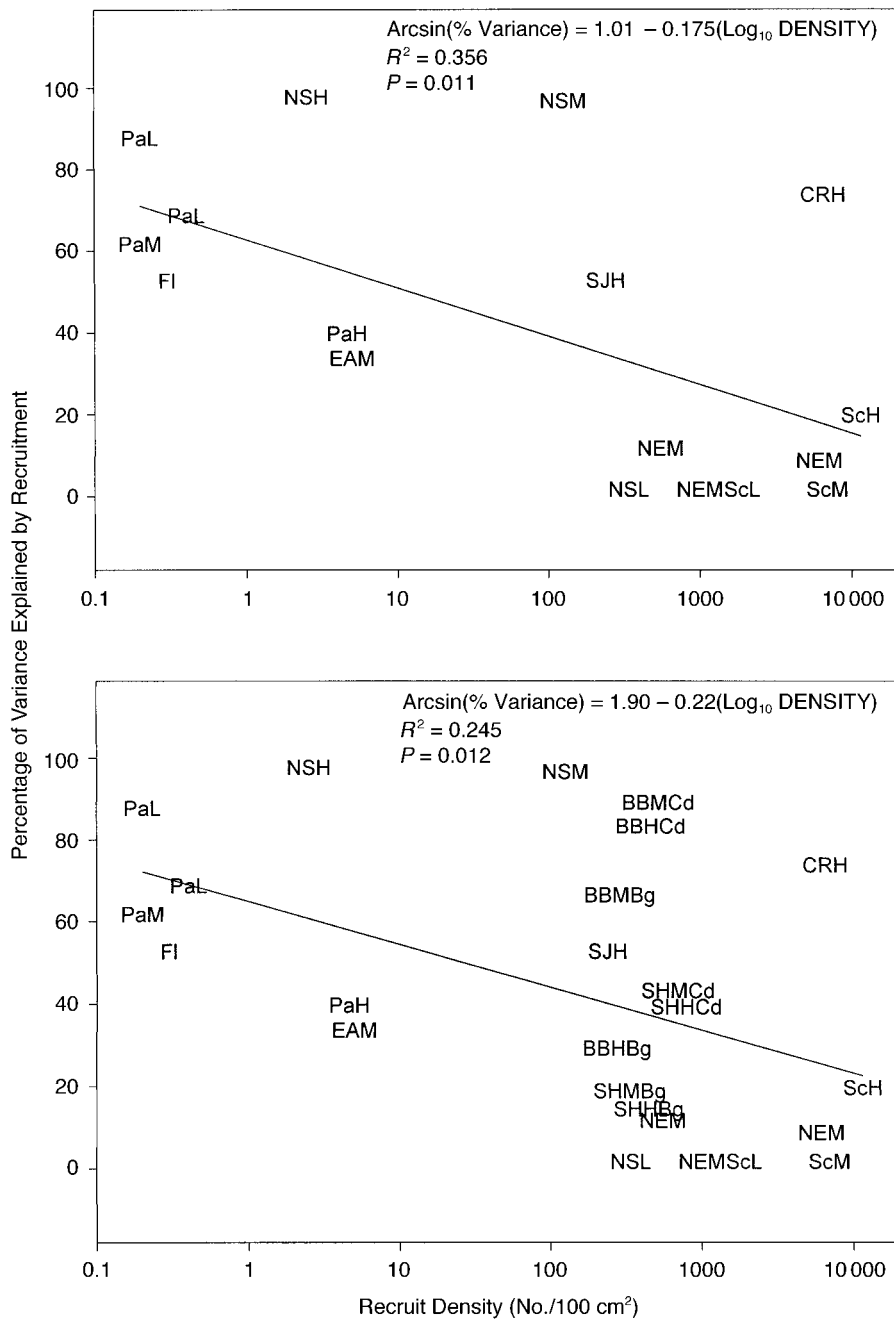
FIG. 13.   Global recruit density vs. R^2 relationships (A) without Oregon data and (B) with Oregon data. Regression equations, R^2, and P values are shown for both regressions. Data are shown by site, zone, and for Oregon. Site codes (first two letters in abbreviations: Pa, Panama; Fl, Florida; EA, Eastern Australia; NS, Nova Scotia; SJ, San Juan Islands; CR, Costa Rica; Sc, Scotland; NE, New England; BB, Boiler Bay; SH, Strawberry Hill. Zone codes (third letter in abbreviations): H, high zone; M, mid-zone; L, low zone. Species codes (fourth and fifth letters in abbreviations): Bg, *Balanus glandula*; Cd, *Chthamalus dalli*. See Table 5 for details.

to miss, it is possible that some habitats categorized as having low recruitment are in fact supplied with high numbers of larvae or settlers. Resolution of this issue will require approaches that evaluate the influence of multiple ecological processes integrated across both life stages, from larvae to adults, and time scales, from

days to years. The recent models of Connolly and Roughgarden (1998, 1999), that incorporate both larval/recruitment and postrecruitment processes into a coupled pelagic/benthic predictive framework is a promising step in this direction.

I conclude that, although density of recruits was of-

ten a strong determinant of density of adults, the magnitude of this relationship was context and species dependent, and was often modified by postrecruitment processes. As predicted by the recruit–adult hypothesis, adult abundance was strongly dependent on recruit density when recruitment was low, and this relationship weakened with high recruitment. Yet under some circumstances high recruit densities reliably predicted adult density (e.g., *Chthamalus*), and in others, when densities of recruits were low, postrecruitment factors were important determinants of densities of adults (Menge et al. 1986*a, b,* Menge 1991). These and similar results (e.g., Minchinton and Scheibling 1991, 1993, Hixon and Carr 1997, Connolly and Roughgarden 1998) suggest that further development of models of community regulation will depend on the integration of both recruitment and postrecruitment determinants of population densities. Identifying the conditions under which each will have an impact remains as a major challenge in the development of a broad predictive framework.

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