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Zonation of two barnacle species not determined by competition

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Two barnacle species (*Semibalanus cariosus* and *Chthamalus challengeri*) were studied during two years at Hokkaido, northern Japan, to find the interspecies boundary and to determine whether interspecific competition (interference and pre-emption) is important in maintaining the zonation in our study system. Both barnacle species showed tide level dependent distribution patterns in the boundary zone. *Semibalanus cariosus* was dominant at lower levels; this pattern was determined by post-recruitment mortality. This mortality pattern seemed to be set by physical stress because recruitment density and survival rate were not correlated with the cover of other species, and mortality was higher in higher zones where physical stress is more severe. *Chthamalus challengeri* was dominant at higher levels; this pattern was determined by recruitment. The recruitment density and survival rate of this species were not affected by the covers of other species, thus, neither interference nor pre-emption significantly affected the distribution pattern. Interspecific competition appears to be less important in organizing barnacle communities in our study area than in previously studied areas, however, the recruitment process is of major importance.

INTRODUCTION

Species inhabiting the rocky intertidal habitats occur in distinct vertical zones (Connell, 1961a,b, 1970; Hoshiai, 1964; Hoshiai et al., 1965; Lubchenco et al., 1984; Underwood & Denley, 1984; Menge & Farrell, 1989). Several authors have demonstrated that the boundary between neighbouring vertical zones are set by processes such as competition (Connell, 1961b; Hoshiai, 1964; Menge, 1976; Wethey, 1983) and predation (Connell, 1961a, 1970; Paine, 1974).

The importance of recruitment has been recognized in populations and communities in marine systems since the late 1970s (see Underwood & Denley, 1984; Connell, 1985; Menge & Sutherland, 1987). Recruitment-limited communities have been found mainly in rocky-intertidal habitats, especially barnacle communities (Denley & Underwood, 1979; Grosberg, 1982; Underwood & Denley, 1984; Roughgarden, 1986). However, there are fewer reports of recruitment-limited communities than of competition- and predation-limited communities. Only a few works have revealed that recruitment-limitation causes zonation (Denley & Underwood, 1979; Grosberg, 1982; Underwood & Denley, 1984).

Can we therefore conclude that the major maintenance processes of the boundary of zonations are competition and predation? To date, most studies of the maintenance of boundary zones were conducted in a few, limited areas (western Europe, east and west coasts of the USA). Considering that most ecologists now support a pluralistic view of community ecology, we believe that more varied habitats must be examined before we can infer that competition and predation are the key factors responsible for maintaining boundary zones.

The specific objectives of the present study are, firstly, to describe the tide level dependent distribution patterns of two intertidal barnacle species, and determine which population process (recruitment, post-recruitment mortality) is responsible for the maintenance of boundary, and, secondly, to determine if interspecific competition is important for maintaining the interspecific boundary of each barnacle zone. Interspecific competition is considered to be an important process in maintaining barnacle communities (e.g. Connell, 1961a,b), and two major types of competition are known: (1) pre-emption (Denley & Underwood, 1979; Underwood & Denley, 1984); and (2) interference (Connell, 1961b; Wethey, 1983). The data was analysed to test the importance of both of these effects.

STUDY SITE AND ORGANISMS

The study was conducted at Hiura, southern Hokkaido, Japan (41°44″N 141°04″E). Several rows of breakwaters are located parallel to the shoreline in the higher part of the intertidal habitat (>60 cm relative to mean tide level, MTL). The breakwaters are formed by large concrete structures called tetrapods. The range of extreme tides is about 1 m. Tetrapod surfaces were covered with two barnacle species, *Semibalanus cariosus* and *Chthamalus challengeri*. The percentage cover by the two species was lower than those reported for other major barnacle populations and communities in temperate areas (Connell, 1961a,b, 1970; Bertness, 1989; Farrell, 1991); bare substrate was always present. In upper part of barnacle zone, only *C. challengeri* occurred on the tetrapod surfaces. Both *S. cariosus* and *C. challengeri* occurred together in lower part (a horizontal band 35 cm in width in the intertidal). *Semibalanus cariosus* was rare on natural hard substratum and its distribution was very patchy. In contrast, *C. challengeri* was also common on natural hard substrata; this species was the dominant space occupant in the highest intertidal area.

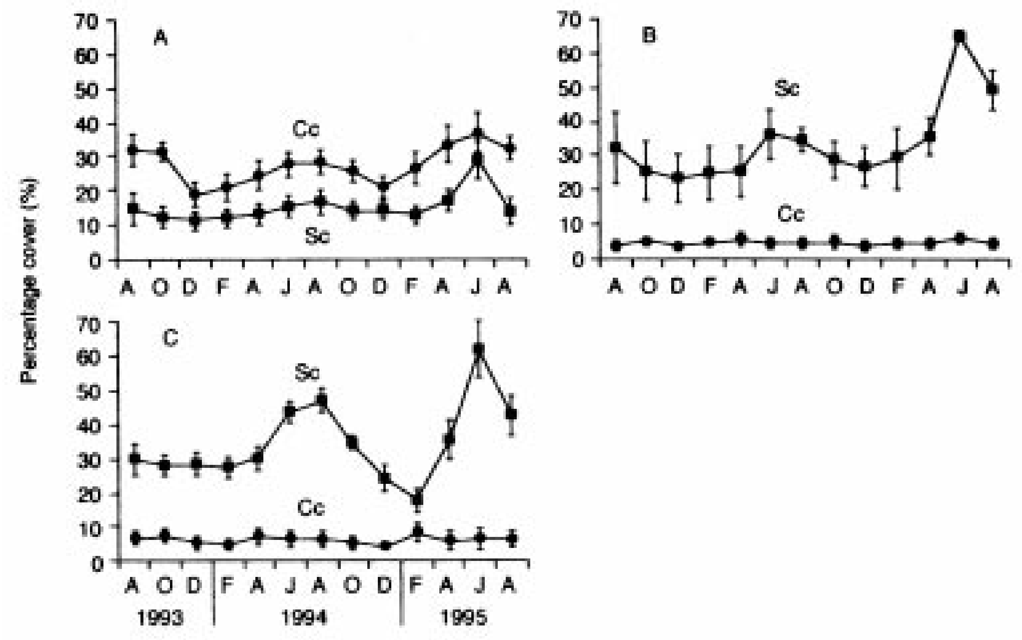

Figure 1. *Chthamalus challengeri* and *Semibalanus cariosus*: seasonal changes in percentage cover of barnacles in three tide zones (A) high, (B) mid, (C) low. Vertical bars indicate ±1 SE. (Cc, *Chthamalus challengeri*; Sc, *Semibalanus cariosus*.)

Table 1. *(A)* Chthamalus challengeri *and (B)* Semibalanus cariosus*: RM-ANOVA of the effect of tide level on percentage cover.*

(A) *Chthamalus challengeri* (arcsin transformed).

Source	df	MS	*F*	*P*
Tide level (TL)	2	4194.343	44.314	<0.001
Error	53	94.651		
Year (Y)	1	9.478	0.529	ns
TL×Y	2	24.009	1.339	ns
Error (year)	53	17.927		

Sheffe test (P=0.05)
Tide level: H > M=L

(B) *Semibalanus cariosus* (arcsin transformed).

Source	df	MS	*F*	*P*
Tide level (TL)	2	3105.850	16.420	<0.001
Error	53	189.147		
Year (Y)	1	711.730	16.848	<0.001
TL×Y	2	25.792	0.611	ns
Error (year)	53	42.243		

Sheffe test (P=0.05)
Tide level: H < M=L

ns, not significant; MS, mean square.

Table 2. *(A)* Chthamalus challengeri *and (B)* Semibalanus cariosus*: RM-ANOVA of the effect of tide level on yearly recruitment.*

(A) *Chthamalus challengeri*.

Source	df	MS	*F*	*P*
Tide level (TL)	2	66715	9.812	<0.01
Error	8	6799		
Year (Y)	1	15376	19.212	<0.01
TL×Y	2	3192	3.988	ns
Error (year)	8	800		

Sheffe test (P=0.05)
Tide level: H > M=L

(B) *Semibalanus cariosus*.

Source	df	MS	*F*	*P*
Tide level (TL)	2	0.108	2.291	ns
Error	11	0.047		
Year (Y)	1	6.415	691.4	<0.001
TL×Y	2	0.001	0.155	ns
Error (year)	11	0.009		

ns, not significant; MS, mean square.

It has been documented that intraspecific crowding in *S. cariosus* populations generates severely elongated individuals (e.g. Dayton, 1971), but no such individuals were observed.

Mobile animals commonly found on the tetrapod surfaces included the hervbivorous gastropods *Littorina brevicula*, *Neritrema sitkana*, *Lottia kogamogai*, *L. tenuisculpta*, *Notoacmaea concinna*. The carnivorous gastropod *Nucella freycineti* was occasionally found.

MATERIALS AND METHODS

To minimize the effects of distance from shore and of hydrodynamics, 20 10×10 cm quadrats were placed on the tetrapods so that the surface planes were perpendicular to the shoreline. All quadrats were set randomly in a narrow tidal range (35 cm) in the interspecies boundary zone. The tide level was divided into three zones: a high zone (2–14 cm relative to MTL, with eight 10×10 cm quadrats); a mid zone (14–24 cm relative to MTL, with five quadrats); and a low zone (24–37 cm relative to MTL, with seven quadrats). A division of the tide level was

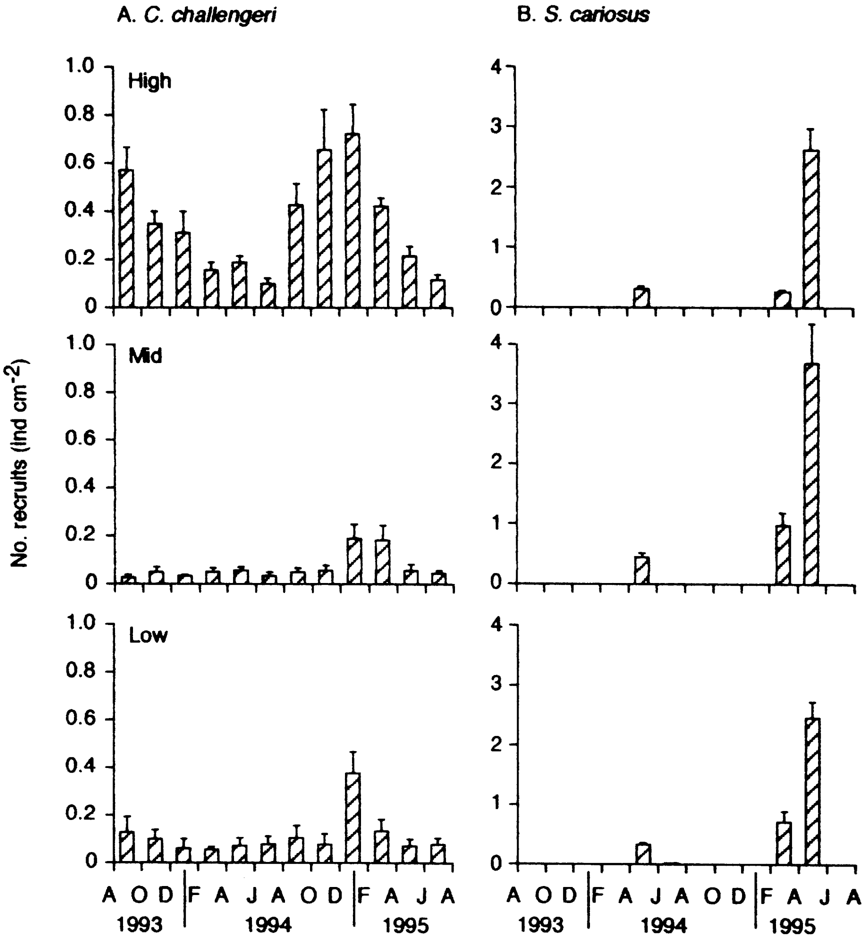

Figure 2. (A) *Chthamalus challengeri* and (B) *Semibalanus cariosus*: seasonal changes in recruitment of barnacles in three tide zones. Vertical bars indicate ±1 SE.

completed after setting of quadrats, and quadrat replicates were therefore unbalanced consequently. Quadrats were marked with stainless steel nails in August 1993 and photographed bimonthly from August 1993 to August 1995.

Percentage cover of *Semibalanus cariosus* and of *Chthamalus challengeri* was estimated by placing a clear plastic overlay with 225 evenly spaced dots over the photographs and counting the number of dots that occurred directly over each species. Each individual was identified and then followed on all photographs in the survey.

Recruitment was defined to occur when the basal diameter of a newly settled barnacle recognized in photographs reached 1 mm. Settlement size of *C. challengeri* and *S. cariosus* are 0.5 and 1 mm, respectively. For *C. challengeri*, it takes one month to grow to this size in average in our region. Bimonthly recruitment counts were made of the number of new recruits found at each census. Unfocused photographs were excluded in these counts. Yearly recruitment was estimated as the yearly total of bimonthly recruitment for two periods (August 1993 – August 1994 (year 1), and August 1994 – August 1995 (year 2)).

Opercular diameter was measured from photographs with an electronic digital caliper under a binocular and then calculated to actual size. To determine the seasonal pattern of growth, bimonthly growth of individuals that recruited in June (*S. cariosus*) and December (*C. challengeri*) in 1993 and survived to the last census were examined. For comparisons of yearly growth among three tide zones, the initial and final diameters of barnacles that survived in year 1 and year 2 were measured.

Bimonthly survivorship was estimated as the percentage of individuals that survived through each two-month census interval. Yearly survivorship was calculated as the percentage of individuals that survived through year 1 and year 2.

To compare the percentage cover, yearly recruitment and yearly survivorship among the three tide zones and among the two census years, repeated measures of analysis of variance (RM-ANOVA) was conducted. We used three months data per year (October, February, and June) for cover analyses. When necessary, data were transformed appropriately to meet the assumption of homogeneity of variance (Bartlett test, $P=0.05$). However, this assumption for cover data of *C. challengeri* could not be met even after arcsin transformation, this violation was marginal ($0.01 < P < 0.05$). When ANOVA results were statistically significant, a Scheffe test was used to determine which means differed significantly. To compare yearly growth among the three tide zones and among the two census years, regressions of final opercular diameter to initial diameter for year 1 and year 2 were estimated for each tide zone and then two-way analysis of covariance (ANCOVA) was conducted.

To detect the effects of pre-emption and interference, relationships between recruitment density, survivorship and cover were investigated. First, for the purpose of

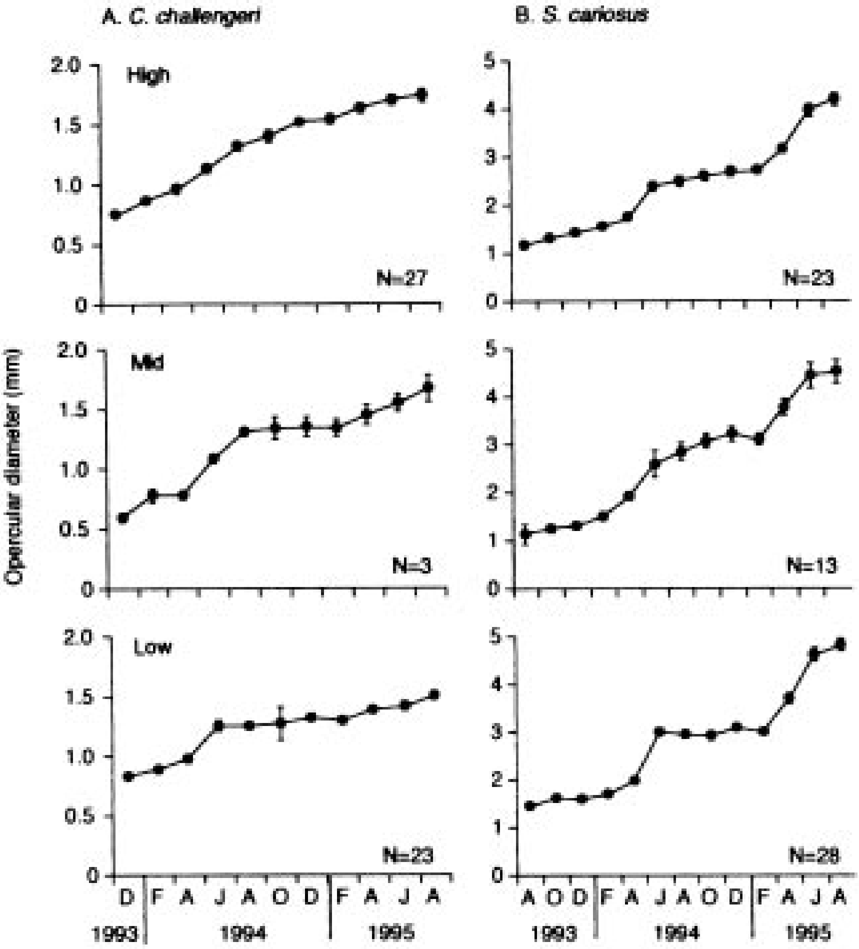

Figure 3. (A) *Chthamalus challengeri* and (B) *Semibalanus cariosus*: seasonal changes in opercular diameter (mm) of barnacles in three tide zones. Vertical bars indicate ±1 SE.

detecting the pre-emption effect on recruitment density by other species, effects of cover of bare space and other species on recruitment density were investigated. Data from just before the peak recruitment season (August data for *C. challengeri*, April (1994) and February (1995) data for *S. cariosus*) were used to estimate the cover of bare space and other species. Second, to detect interference with other species, the relationships between the cover of other species and the survival rate in the major growth season (February–June) were investigated. Bimonthly average values of cover data and four-month survival rate were analysed. In both investigations, to separate the effects of tide level and year, all relationships were evaluated for each tide level and each one-year period.

RESULTS

Distribution pattern and interspecies boundary

Tide level dependent distribution patterns were observed for both species; *Chthamalus challengeri* dominated in the high zone, and *Semibalanus cariosus* dominated in mid and low zones (Figure 1). Percentage cover of both species showed similar seasonal variations (Figure 1). Barnacle cover increased from winter to summer, and decreased from summer to winter. Seasonal variation of *S. cariosus* was larger at lower tide levels. On the other hand, variation of *C. challengeri* was larger at higher tide levels. The extent of seasonal variation of both barnacles appeared to differ annually. Although the cover of both species fluctuated temporally, the boundary between both species was maintained at a constant tide level; between the high and mid zones, through the census period.

These spatial and temporal distribution patterns were statistically significant (Table 1). Percentage cover varied significantly with tide level for both species; cover of *C. challengeri* in the high zone was higher than in the mid and low zones, in contrast, *S. cariosus* in the high zone was lower than in the mid and low zones (Table 1). Significant effect of year was observed only for *S. cariosus* (Table 1).

Recruitment

Recruitment of both species showed seasonal patterns (Figure 2). *Chthamalus challengeri* recruited year round, with a peak between autumn and winter. The seasonal pattern of *S. cariosus* was very clear; recruitment occurred only in spring (from February to June). In 1994, recruitment was low and occurred during a short period (from April to June). In 1995, however, recruitment was much higher and occurred during a longer period (from February to June). Recruitment in each

Table 3. *(A)* Chthamalus challengeri *and (B)* Semibalanus cariosus*: ANCOVA for yearly growth of opercular diameter of barnacles. The main effects are year and tide level; the covariate is the initial opercular diameter in each year period.*

(A) *Chthamalus challengeri* (year 1).				
Source	df	MS	*F*	*P*
Initial size (IS)	1	3.103	89.392	<0.001
Tide level (TL)	2	0.040	1.153	ns
IS×TL	2	0.023	0.665	ns
Error	107	0.035		
(B) *Semibalanus cariosus*.				
Source	df	MS	*F*	*P*
Initial size (IS)	1	588.52	16815	<0.001
Year (Y)	1	2.067	8.648	<0.01
Tide level (TL)	2	0.212	0.886	ns
IS×Y	1	0.142	0.593	ns
IS×TL	2	0.078	0.328	ns
Y×TL	2	0.431	1.804	ns
IS×Y×TL	2	0.364	1.522	ns
Error	158	0.239		

ns, not significant; MS, mean square.

species showed similar seasonal patterns among the three tide zones.

The effect of tide level on yearly recruitment was significant only for *C. challengeri* (Table 2); recruitment of this species in the high zone was significantly higher than in the mid and low zones. In both species, the total yearly recruitment varied significantly between years (Table 2), the total yearly recruitment in 1994–1995 was higher than in 1993–1994 (Table 2, Figure 2).

Growth

Growth of the opercular diameter of *S. cariosus* had a clearer seasonality than for *C. challengeri* (Figure 3). Both species grew throughout the year, with major growth occurring just after the phytoplankton bloom (February–March) season from February to June.

Yearly growth of opercular diameter did not differ among the three tide zones for either species (Table 3). For *S. cariosus* significant difference of interannual growth was observed. Yearly growth of *C. challengeri* was not analysed in year 2, since there were no significant linear correlations between initial and final opercular diameter in the high and mid zones.

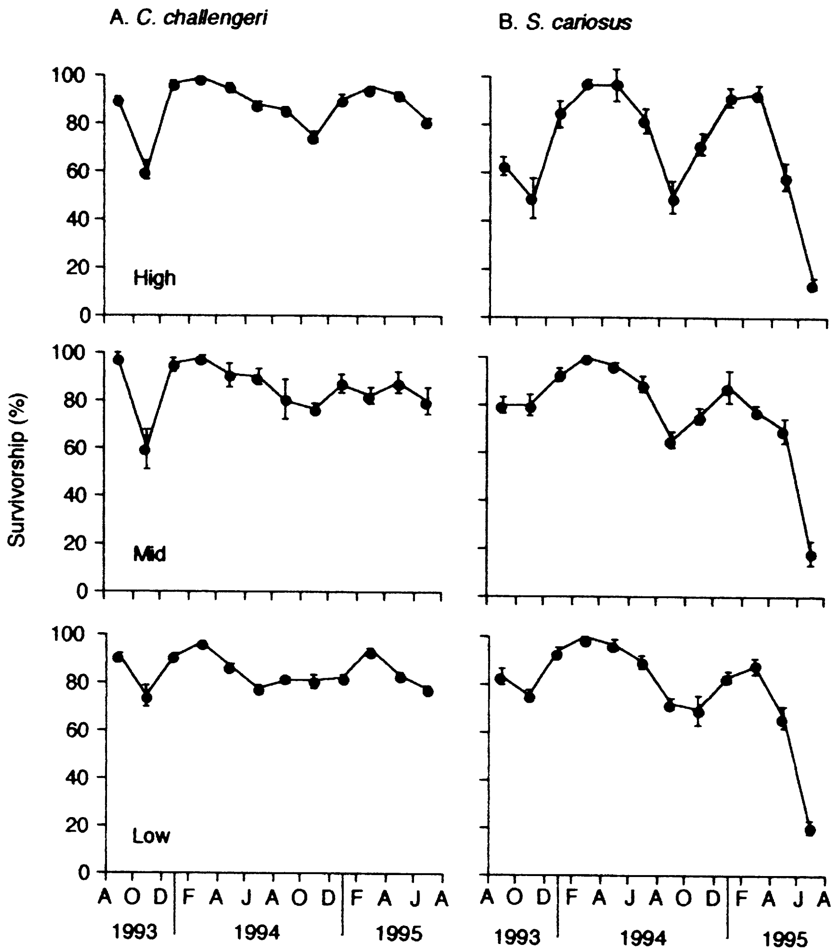

Figure 4. (A) *Chthamalus challengeri* and (B) *Semibalanus cariosus*: seasonal changes in survivorship of barnacles in three tide zones. Vertical bars indicate ±1 SE.

Table 4. *(A)* Chthamalus challengeri *and (B)* Semibalanus cariosus*: RM-ANOVA of the effect of tide level on yearly survivorship.*

Source	df	MS	F	P
(A) *Chthamalus challengeri.*				
Tide level (TL)	2	234.72	1.031	ns
Error	13	227.58		
Year (Y)	1	344.50	2.041	ns
TL×Y	2	45.00	0.267	ns
Error (year)	13	168.78		
(B) *Semibalanus cariosus.*				
Tide level (TL)	2	2472.9	8.788	<0.01
Error	13	281.4		
Year (Y)	1	896.4	8.730	<0.05
TL×Y	2	101.3	0.987	ns
Error (year)	13	102.7		
Sheffe test (P=0.05)				
Tide level: H<L, H=M, M=L				

ns, not significant; MS, mean square.

Survivorship

Seasonal variation of survivorship of both species showed similar patterns (Figure 4). Both species survived well from winter to summer, but survivorship decreased from summer to winter. This pattern was clearer in the high zone than in the mid and low zones for *C. challengeri*. Survivorship of *S. cariosus* was lowest from June to August in 1995, just after heavy recruitment in all three tide zones.

For *C. challengeri*, tide level, year and the interaction between these factors had no significant effect on yearly survivorship (Table 4). On the contrary, survivorship of *S. cariosus* differed among the three tide zones and two census years; survivorship in the high zone was lower than in the low zones, and yearly survivorship was higher in 1993–1994 than in 1994–1995 (Table 4, Figure 4). The interaction between tide level and year did not affect survivorship (Table 4).

Effects of cover on recruitment and survivorship

Annual recruitment density of *C. challengeri* was not correlated significantly with bare space (Figure 5). A significant negative relationship was observed between recruitment density and *S. cariosus* cover only in the mid zone in year 2 (Figure 5). For *S. cariosus*, a significant positive relationship was observed in the mid zone in year 2, and negative relationships occurred in the high zone in year 1, and in the low zone in year 2 (Figure 5).

For the relationship between survival rate and other species cover, no significant correlation occurred for *C. challengeri*, however, a significant correlation was observed for *S. cariosus* in the high zone in year 2 (Figure 6).

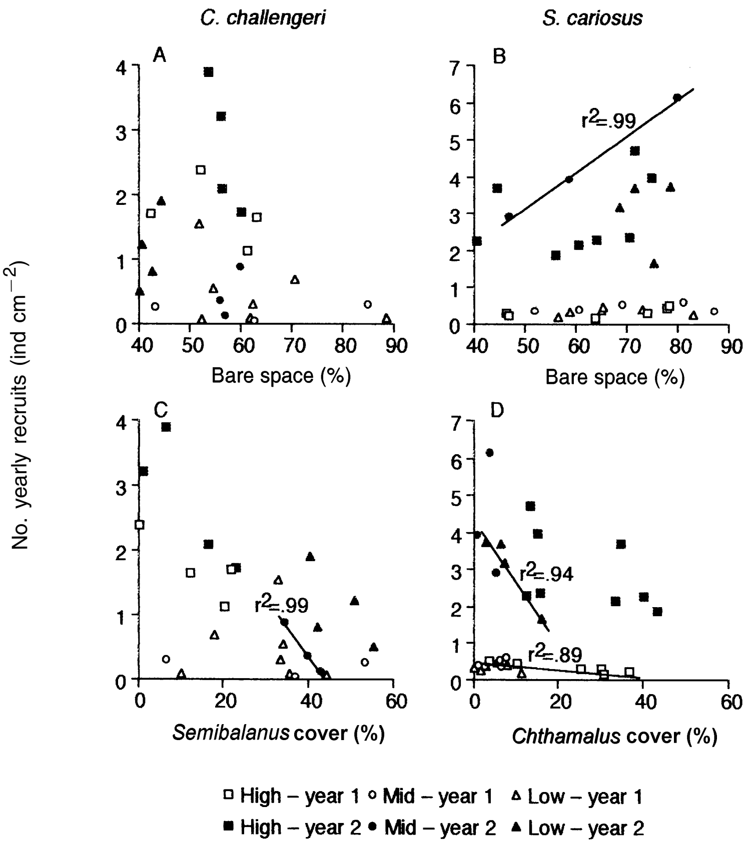

Figure 5. *Chthamalus challengeri* and *Semibalanus cariosus*: the relationship between annual recruitment density and bare space (A & B) and between annual recruitment density and cover of other species (C & D) in two 1-y periods. Bare space and barnacle cover were counted at the beginning of the recruitment period.

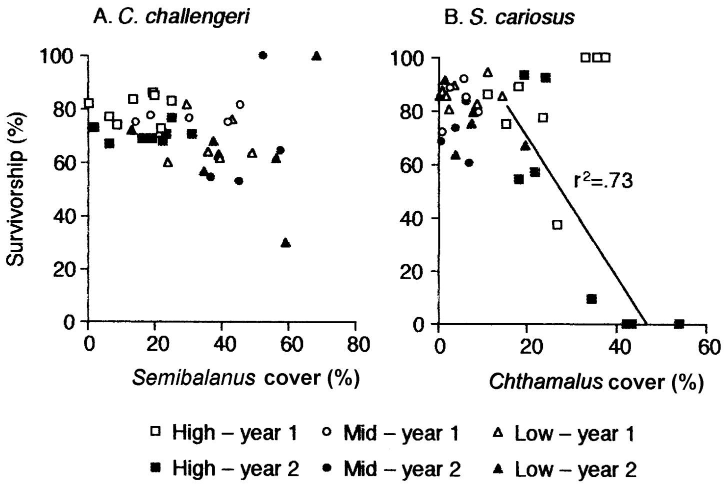

Figure 6. (A) *Chthamalus challengeri* and (B) *Semibalanus cariosus*: the relationship between the survivorship in a period of growth and barnacle cover in two 1-y periods. Barnacle cover was calculated as the mean value of each 1-y period.

DISCUSSION

Maintenance process of upper limit of distribution for Semibalanus cariosus

Semibalanus cariosus dominated in mid and low zones in the interspecies boundary zone (Figure 1, Table 1). In the boundary zone, recruitment density and growth rate did not vary in such a tide level dependent manner (Tables 2 & 3). On the other hand, survival rates decreased with increasing tide level (Table 4). This suggests that the tide level dependent distribution of *S. cariosus* was determined by survival processes after recruitment.

If pre-emption by other species is important for maintaining tide level dependent distribution, a negative relationship might be observed in zones that other species dominate; thus a significant negative correlation would be expected in the high zone for *S. cariosus*. However, such a negative correlation was not consistently observed (Figure 5). In terms of interference, the results indicate that a significant negative relationship between survival rate and other species cover occurred in the high zone in year 2 (Figure 6). However, this correlation was due to the occasional invasion of a carnivorous snail in four plots (personal observation) and was not the result of interference competition with *Chthamalus challengeri*. These correlation analyses are not conclusive due to the small number of replications. However, available space (=bare space) existed in all plots in both years (Figures 5 & 6), further suggesting interspecific competition is not an important factor in determining the upper limit of the *S. cariosus* zone.

Physical factors such as heat and desiccation (Connell, 1961a,b; Wethey, 1983, 1984; Bertness, 1989) and lack of recruitment (Denley & Underwood, 1979; Grosberg, 1982; Underwood & Denley, 1984) determine the upper limit of the vertical distribution of barnacles. Mortality of recruits of *S. cariosus* increased in the upper margin of their distribution. Such a mortality pattern is similarly seen for *S. balanoides* and is considered to be due to physical factors, such as heat and desiccation in summer (Connell, 1961a; Wethey, 1983). Although the spatial scales investigated are different between their studies and this one, these results are similar to those reported for *S. balanoides*. Thus, the distribution pattern of *S. cariosus* is considered to be determined by physical factors.

Maintenance process of lower limit of distribution for Chthamalus challengeri

Chthamalus challengeri dominated in a high zone in the interspecies boundary zone (Figure 1, Table 1). In this area, recruitment density varied in the same tide level dependent manner as percentage cover (Table 2). On the other hand, growth rate and survival rate did not vary in such a manner (Tables 3 & 4). This suggests that the tide level dependent distribution of *C. challengeri* was determined by the recruitment process.

If pre-emption by *S. cariosus* is important for maintaining tide level dependent distribution, a negative relationship might be observed in mid and low zones. However, a significant negative relationship was observed only in the mid zone in year 2 (Figure 5). In terms of interference, there was no significant negative relationship between survival rate and the cover of other species (Figure 6), suggesting that interference was unimportant. As mentioned before, these analyses are not conclusive. However, bare space was available in all plots in both years for *C. challengeri* (Figures 5 & 6), suggesting that interspecific competition is not an important factor in determining the lower limit of the *C. challengeri* zone.

Biological interactions, such as interspecific competition, predation (Connell, 1961a,b; 1970; Menge, 1976; Wethey, 1983) and lack of recruitment (Denley & Underwood, 1979; Grosberg, 1982; Underwood & Denley, 1984), determine the lower limit of vertical distribution of barnacles. Thus, in the case of *C. challengeri*, the tide level dependent distribution pattern is considered to be determined by recruitment.

Maintenance process of the interspecies boundary

Previous studies of barnacle communities in western Europe (Southward & Crisp, 1956; Southward, 1967; Connell, 1961a,b) and on the east coast of the USA

(Wethey, 1983, 1984) have shown that interspecific competition is an important process in maintaining interspecies boundaries. However, in the present barnacle community, interspecific competition appears to be of minor importance.

It is considered that balanoid barnacles are generally superior competitors to chthamaloid barnacles (Stanley & Newman, 1980), however, no evidence was found that *S. cariosus* eliminated *C. challengeri* competitively. Although the abundance of *S. cariosus* fluctuated widely (about two-fold), the lower limit of the distribution of *C. challengeri* was maintained between high and mid zones through the study period (Figure 1). This pattern was set by the recruitment process.

These findings suggest that interspecific competition is less important in maintaining the interspecies boundary in a barnacle community than reported in previous works and that the recruitment process is the most important factor in this study site. However, the period of this study (2-y) might not be long enough to test the possibility that other community maintenance processes, such as competition and predation, might exist. It might be important to conduct a long term study to confirm that recruitment is always important in this system. Also, experimental studies are needed to further strengthen our conclusions.

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