Ecology, 69(2), 1988, pp. 400–407

SETTLEMENT CUES AND DETERMINATION OF THE VERTICAL LIMIT OF AN INTERTIDAL BARNACLE[1]

PETER T. RAIMONDI
Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA

Abstract. The settlement behavior of the barnacle *Chthamalus anisopoma* near its upper intertidal limit was investigated using field surveys and experiments. The upper limit of *Chthamalus* was found to be extremely variable, ranging from 1.5 to 2.6 m above MLW.

Chthamalus showed increased settlement in response to chemical cues produced by several species whose vertical distributions overlapped with its vertical distribution. Within a single species there was significantly more settlement in response to cues associated with *Nerita funiculata* that occurred with *Chthamalus* than to *N. funiculata* that occurred only above the vertical limit of *Chthamalus*. Another species that induced settlement, *Acanthina angelica*, is the major predator of adult *Chthamalus*. *Acanthina* may be a good settlement cue because it is a reliable indicator of the vertical distribution of *Chthamalus* and because (1) the clusters of *Acanthina* that induced settlement may move away before the new barnacles become edible; and (2) *Chthamalus* can develop a predator-resistant morphology in response to *Acanthina*. I was also able to induce *Chthamalus* recruitment into areas well above their normal upper limits using a conspecific extract, indicating that conspecifics function as a strong settlement cue.

The evolution of larval attraction to settlement cues should be dependent on the reliability of the cues and the consequences of not using them. Reliable cues and harsh consequences should lead to the development of "strong" (i.e., attractive) cues. However, reliable cues may be conservative; their absence may not indicate a "bad" settlement site. Therefore, a variable distribution of strong settlement cues could lead to temporal and spatial variability in a species regardless of other factors such as pre- and postsettlement physical conditions or biological interactions.

Key words: barnacles; Chthamalus anisopoma; *Gulf of California; recruitment; settlement; settlement cues; variable distributions.*

INTRODUCTION

The settlement patterns of marine invertebrates vary greatly in both time and space (Connell 1961, 1985, Caffey 1985, Wethey 1985). Storms (H. M. Caffey, *personal communication*), tidal amplitude (De Wolf 1973), and days before the maximum tidal amplitude (Shanks 1983) have all been correlated with temporal patterns of settlement for intertidal species. Water movement (Crisp 1955), surface texture (Barnes 1956), light (Barnes et al. 1951), and the presence of conspecifics (Knight-Jones and Stevenson 1950, Knight-Jones 1953, Wethey 1984) and other indicator species (Strathmann et al. 1981) have been found to be important determinants of local spatial patterns of intertidal barnacles.

For sessile species these settlement patterns are critical for survival, since relocation following settlement is impossible. It is particularly important for larvae to settle between the upper and lower vertical limits at which the species can survive and reproduce. These limits are usually determined by either physical (upper limit) or biological (lower limit) factors (Connell 1961). Strathmann and Branscomb (1979) argued that cues that indicate the upper limits of a species' distribution were more reliable guides for settlement than those that indicate a lower limit because physical stress is less variable temporally and spatially than is biological stress.

The degree to which a species has evolved to use a particular settlement cue is probably related both to the reliability of the cue and to the consequences of not using it. The "strength" of a settlement cue is defined here as the extent to which it influences settlement choice. This definition is different from the standard usage of strength of a cue; it incorporates the larva's response to the cue and the sensitivity of its detection system.

Chthamalus anisopoma, an acorn barnacle, is the dominant midintertidal species in the northern Gulf of California (Dungan 1985). It is a relatively small barnacle, which seldom exceeds a basal diameter of 1 cm (Brusca 1980). Recruitment of larvae occurs from March through November with the majority settling during the summer months (Malusa 1983). Dungan (1985) found that it was susceptible to desiccation in the summer and reasoned that its upper limits were

[1] Manuscript received 24 June 1986; revised and accepted 12 June 1987.

TABLE 1. Numbers of *Chthamalus anisopoma* settling per day to 64-cm² plates on which a possible cue was applied (treatment), compared with plates to which seawater was applied (control. *P* values are from *t* tests, df = 4 for all comparisons, except df = 10 for *T. mariana*.

Cue organism			Mean *Chthamalus* settlement (no./plate)		
Species	Normal tidal range (m)	Description	Cue	Seawater	*P*
A) Organisms that induced settlement					
Chthamalus anisopoma	+0.0 to +2.6	Barnacle	290	98	<.01
Nerita funiculata	+1.0 to +4.3	Herbivorous gastropod	266	13	<.005
Acanthina angelica	+0.6 to +3.0	Predatory gastropod	80	13	<.05
Palythoa ignota	<+0.6	Zoanthid coelenterate	349	54	<.025
Tegula mariana	<+1.0	Herbivorous gastropod	31	14	<.01
B) Organisms that did not induce settlement					
Tegula rugosa	+2.4 to +4.3	Herbivorous gastropod	120	133	>.50
Calothrix crustacea	+2.0 to +4.6	Blue-green bacterium	44	49	>.50
Corallina sp.	<0.0	Red alga	10	10	>.50

set by mortality caused by excessive periods of exposure. Therefore, natural selection might be expected to produce behaviors in which *Chthamalus* would choose not to settle above certain levels. The use of reliable settlement cues is one such behavior.

In this study I examined the types of settlement cues *Chthamalus* uses and the strength of each cue. The results show that certain species within the barnacle's vertical range induce settlement. I conclude by speculating on the relationship between the upper limits of a sessile species' distribution and the strength of its settlement cues.

METHODS

Study site

All experiments were conducted at Punta Pelicano, a large granite shore on the eastern side of the northern Gulf of California, ≈8 km northwest of Puerto Penasco in Sonora, Mexico. The northern Gulf is known for its extreme tidal amplitude (up to 8 m) (Brusca 1980, Levinton 1982), strong seasonality (Hendrickson 1973), and its high diversity and endemism (Brusca 1980). Near the upper limits of its vertical distribution, *Chthamalus anisopoma* is generally restricted to very gently sloping, flat surfaces that typically occur on the tops of large granite outcrops or boulders.

Upper limits of Chthamalus anisopoma

To determine the mean upper limit of *Chthamalus anisopoma* I measured the tidal height of the upper boundary of 19 patches of *Chthamalus* in April 1986. Rather than occurring continuously along the intertidal zone at Punta Pelicano, *Chthamalus* is found in large patches. Each patch surveyed had a distinct upper boundary, and all patches were of similar aspect and slope. At each patch a ruled pole was placed at the upper limit of *Chthamalus* and was leveled with respect to a marker position of known tidal height.

Cues to settlement on experimental plates

Marine invertebrate larvae have been shown to settle preferentially in response to a variety of stimuli (see reviews by Meadows and Campbell 1972, Crisp 1974). The settlement behavior of barnacles has been particularly well studied (Knight-Jones 1953, Crisp and Barnes 1954, Crisp 1961, Crisp and Meadows 1962, 1963). Strathmann and Branscomb (1979) have suggested that organisms associated with the upper limits of the distribution of *Balanus cariosus* could function as settlement cues, allowing cyprids to avoid unfavorable sites in which they could not survive to maturity. To my knowledge there has been no direct evidence of this phenomenon in the field (but see Douros 1985). In the summer of 1984 I examined the possibility that *Chthamalus anisopoma* at Punta Pelicano used settlement cues.

Each trial used six 8 × 8 cm plexiglass settlement plates. Plexiglass plates were used because of their uniformity and because the cyprids of this species are very small and sometimes difficult to detect on natural substrate. All plates had 100 evenly spaced holes, each 2.5 mm in diameter and 2 mm deep, which simulated pits in natural substrate. On the three experimental plates a single "cue" was applied at both the morning and evening low tide during a 24-h period in a spring tide sequence. The organisms used as cues were the dominant species between 0 and 4 m above mean low water (MLW) and included four species of gastropods, one barnacle, a colonial anemone, a blue-green bacterium, and a coralline red alga (see Table 1). The normal tidal ranges of the organisms given in Table 1 are from presence–absence surveys done at several locations at Punta Pelicano (also see Brusca 1980).

Enough individuals of each species of gastropod were placed on each plate to cover >75% of its surface. These were allowed to attach to the plate and crawl off, leaving mucus trails. The other organisms were crushed and mixed with seawater, and the extract was painted on the plates with a brush. A treatment was applied to three plates, and fresh seawater was applied to three control plates during the morning and evening low tides. Both the experimental and control plates were attached to six randomly chosen sites at 1 m above MLW. Each trial lasted for 24 h, after which the plates were picked up and examined using a dissecting microscope for the number of *Chthamalus* settlers. Connell (1985) has defined settlement as the number of larvae attaching, whereas recruitment is the number present after some postsettlement mortality has occurred. I measured settlement over a 24-h period to avoid postsettlement loss. Differences between settlement on experimental and control plates were compared using *t* tests.

In the summer of 1985 I compared the settlement response of *Chthamalus* with the presence of individuals from two populations of *Nerita funiculata*. Individual *Nerita* tend to remain within narrow vertical limits (P. T. Raimondi, *personal observation*); some occur strictly above the *Chthamalus* zone, while others occur within it. If they acquire from the substrate substances that differ by tidal height, then *Nerita* from different heights may provide different cues and so may vary in the strength with which they induce barnacle settlement. Twenty-five *Nerita* that occurred within the *Chthamalus* zone were placed at +1 above m MLW on three plexiglass plates and allowed to crawl off. On three other plates the same procedure was followed with *Nerita* collected well above the *Chthamalus* zone. Treatments were randomly assigned to plates. The plates were put out at morning low tide and were collected 24 h later and examined for the number of *Chthamalus* settlers. The data were compared using a *t* test.

Recruitment induction on natural substrate within the Chthamalus *zone*

Although barnacles <1 d old are difficult to see on the natural granite substrate, they can be counted as recruits after a week of growth. In order to examine the effect of barnacle extract on *Chthamalus* recruitment to natural substrate I performed the following experiment. On 25 August 1984 I cleared and sterilized ten 10 × 10 cm sites on a large horizontal shelf dominated by *Chthamalus*. These sites were located at 1 m above MLW. In all experiments described in this paper sites were sterilized with concentrated NaOH and were rinsed thoroughly with seawater and scrubbed with a wire brush during the subsequent low tide to remove any residual NaOH. Five sites were randomly assigned as treatment sites, the other five were control sites. At each morning low tide from 26 to 30 August I applied a crushed barnacle–seawater mixture to the treatment sites and seawater to the control sites. On 8 September I sampled the sites using a 25-power field microscope with a field of vision of 0.5 cm^2. At each site I sampled four random locations for recruits. I used the number of recruits per square centimetre at each site for comparison by a *t* test.

The settlement behavior of *Chthamalus* in relation to barnacle extract might be in response to an individual chemical or to interactions of several chemicals released when I crushed the organisms. These would be biologically unimportant and experimentally confusing if they were never released naturally. In order to determine whether settlement is induced by living *Chthamalus* I performed the following experiment. In July 1984 I attached eight 7 × 7 × 3 cm stones to an intertidal reef at +1 m above MLW; these stones were intially sterilized with NaOH. Over the next year they developed a thick cover of *Chthamalus*. On 20 June 1985 I removed all of the barnacles from four control stones (chosen randomly) and from a 5 × 5 cm square in the middle of the other stones (treatment stones). The cleared area on each of the treatment stones and a similarly sized area on each of the control stones were sterilized with NaOH. The stones were reattached to the reef at +1 m above MLW with treatment and control sites picked randomly. Two weeks later I sampled the cleared and sterilized areas on the stones for recruitment using the field microscope. The edges of the cleared areas were not sampled to avoid a possible effect of the relief provided by the bordering barnacles on the treatment stones. Recruitment on treatment and on control stones were compared using a *t* test.

Recruitment induction on natural substrate above the Chthamalus *zone*

One way to assess the strength of a settlement cue is to determine whether settlement can be induced by it onto an area outside the normal settlement range of the organism. I conducted two experiments in which I attempted to induce settlement of *Chthamalus* onto sites that were above the upper limit of mature barnacles. In the first experiment, in July 1984, I examined two factors that might determine the upper limits of *Chthamalus* settlement: pre-emption of space by the blue-green bacterium *Calothrix crustacea*, and the lack of an appropriate settlement cue. The area above the barnacle zone often is partiallly covered with *Calothrix*. Sixteen 10 × 10 cm sites completely covered by *Calothrix* ≈0.5 m above the *Chthamalus* zone were selected. Of these, eight were chosen randomly, and all *Calothrix* was removed using NaOH; eight were left as controls. Out of each set of *Calothrix* removals and controls, four sites were randomly selected to receive crushed barnacle extract; the remaining four of each group received seawater. Thus the experiment was set up in a factorial design where each combination of treatments was performed on four replicates. The sites were sterilized on 17 July 1984. Barnacle extract or seawater was applied on 18 and 28 July. I sampled the sites using the field microscope three times between 1 August and 8 December 1984. The data were compared using a repeated-measures ANOVA procedure.

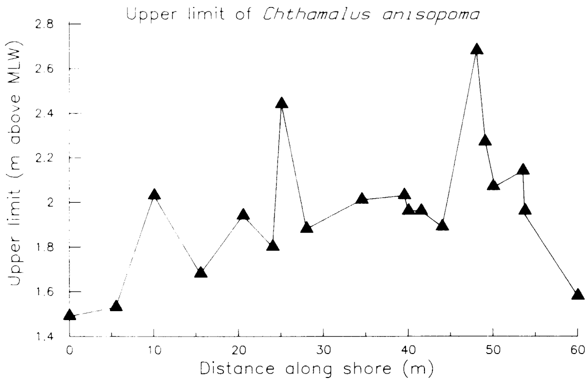

FIG. 1. Tidal heights (m above MLW) of the upper limits of all patches of *Chthamalus anisopoma* along a 60-m length of shore.

In the second experiment, in August 1984, I attempted to induce settlement at an even greater height than in the experiment described above. The presence of *Calothrix* was not used as a factor, based upon the results obtained from the first experiment. Four sites at each of two levels, 1 and 2 m above the observed upper limit of *Chthamalus,* were sterilized with NaOH on 12 August 1984. The experimental sites (n = 2 at each level) received barnacle extract, and the controls (n = 2 at each level) received seawater on 13 August. All sites were sampled microscopically on 30 August. Data were analyzed using an ANOVA procedure.

Settlement as a function of distance from an applied cue

If barnacle larvae can detect a settlement cue from a great distance, then inducement onto an area well above their vertical limit might only be a demonstration of their ability to swim towards a cue. Given the turbulent hydrodynamic conditions on rocky shores it seems improbable that long-range detection is possible. Under laboratory conditions Knight-Jones (1953) and Crisp (1974) both found that physical contact with a cue was necessary before *Balanus balanoides* would initiate settlement, and concluded that water-borne inducers were unlikely.

If the chemical inducer is "drawing" larvae towards it from long distances then settlement on similar surfaces should decrease as a function of distance from the inducer. However, if the cue is attractive for only a short distance then settlement should be concentrated at the site where the cue was applied. On 27 August 1984 I attached 12 of the plexiglass plates described above to the reef at +1 m above MLW. The pits on each plate were grouped into four sets of 25, each in one quadrant of the plate. Six plates were randomly designated treatment plates, the others, controls. These "far-from-cue" control plates were located no closer than 2 m from treatment plates. On two of the four quadrants of each treatment plate I applied crushed barnacle extract; on the other two "near-cue" quadrants seawater was applied. The far-from-cue control plates received only seawater. Twenty-four hours later I sampled all plates for settlement. For analysis I calculated the mean number of barnacles per quadrant for both the quadrants with and without the extract on treatment plates, and for all quadrants on the control plates. One control plate was lost, so there were six replicates of both cue and near-cue quadrant means, and five far-from-cue controls. To determine whether there were significant differences in settlement at short distances from cues, I compared cue and near-cue quadrant means using a paired t test. To assess whether cues operated at further distances, I used a t test to compare near-cue with far-from-cue quadrant means.

RESULTS

Upper limits of Chthamalus anisopoma

The observed upper limit of adult *Chthamalus* on large boulders ranged from 1.48 to 2.68 m above MLW (Fig. 1). The variability did not seem to be associated with any geomorphic characteristic of the shore; bare sites adjacent to and very similar to those with barnacles were common.

Cues to settlement on experimental plates

Of the eight organisms tested for the ability to induce *Chthamalus* settlement, five increased settlement on experimental plates as compared with controls (Table 1). These five co-occur with *Chthamalus* over at least part of its vertical range. The three species that had no significant effect on barnacle settlement have little spatial overlap with adult *Chthamalus.* Two congeneric species differed in their ability to induce settlement. *Tegula mariana,* which co-occurs with *Chthamalus,* induced settlement, whereas *Tegula rugosa,* which is found above the distribution of *Chthamalus,* did not.

Chthamalus settled in significantly greater numbers on plates exposed to *Nerita funiculata* that lived within the *Chthamalus* zone (mean ± SD = 36.7 ± 7.6 *Chthamalus*), than on plates exposed to *Nerita* that lived outside it (25.7 ± 4.5 *Chthamalus*; t = 2.27 on log-transformed data, df = 4, one-tailed $P < .05$).

Recruitment induction on natural substrate within the Chthamalus *zone*

Significantly more *Chthamalus* recruited to sites where a crushed barnacle–seawater mixture was applied than to sites where only seawater was applied (17.4 ± 2.51 *Chthamalus*/cm^2 vs. 12.2 ± 2.84/cm^2; t = 3.06, df = 8, $P < .01$). This indicates that barnacle extract is effective on natural substrates as well as on artificial plates.

Significantly more *Chthamalus* recruited to cleared areas on stones with barnacles than to similar areas on stones without barnacles (34.78 ± 5.06 vs. 11.71 ± 3.16 *Chthamalus*/cm^2; t = 7.63, df = 6, $P < .0005$).

TABLE 2. The effect of presence vs. absence of barnacle extract and *Calothrix* (blue-green bacterium) on recruitment to sites on natural substrate 0.5 m above the normal distribution of *Chthamalus* (repeated-measures ANOVA).

Source	df	SS	*F*	*P*
Calothrix (A)	1	130.02	46.69	<.0001
Barnacle extract (B)	1	117.19	42.08	<.0001
A × B interaction	1	117.19	42.08	<.0001
Error	12	33.42		
Time (C)	2	97.01	31.08	<.0001
A × C interaction	2	97.01	31.08	<.0001
B × C interaction	2	90.59	29.02	<.0001
A × B × C interaction	2	90.59	29.02	<.0001
Error	24	37.46		
Total	47	810.48		

Thus whole barnacles are settlement inducers; therefore it is unlikely that the inducement property of extract is an artifact of the crushing of barnacles.

Recruitment induction on natural substrate above the Chthamalus *zone*

Chemical attractant cues appear to be the main determinant of the upper limit of *Chthamalus* settlement (Table 2 and Fig. 2). The results indicate that: (1) no *Chthamalus* recruited to areas with *Calothrix* regardless of whether barnacle extract had been applied, (2) where *Calothrix* was removed there were significantly more recruits, on 1 and 30 August, on the sites where barnacle extract was applied than on control sites. By 8 December all the barnacles that had been present on 30 August had died, and there were no new recruits. The response was quite strong to barnacle extract; the density of recruits on these sites on 1 August was similar to that found in the middle of the barnacle zone. In contrast there were only a few recruits on sterilized sites to which seawater had been applied (Figs. 2 and 3). Since extract was applied only on 18 and 25 July the recruitment between 1 and 30 August on experimental sites was probably in response to those barnacles that had recruited between 18 July and 1 August. This is another indication that the settlement cue is not an artifact associated with the production of the extract.

In the second experiment higher on the shore, no *Chthamalus* recruited to control sites where seawater had been applied, and there was significantly more recruitment to experimental sites that were 1 m above the *Chthamalus* zone than to those 2 m above the zone (Table 3). This, in part, might be due to a shorter immersion time, and hence less potential for settlement, at the higher level. All barnacles were dead by 8 December 1984.

The results of the first experiment suggest that *Chthamalus* do not recruit to areas that are covered by *Calothrix*. The results of both experiments indicate that barnacle extract is a powerful settlement cue since it induced *Chthamalus* to settle into areas where they could not survive.

Settlement as a function of distance from an applied cue

Chthamalus settled in significantly greater numbers in quadrants where the cue had been applied than in adjacent near-cue quadrants on the same plate where seawater had been applied (10.83 vs. 4.33 *Chthamalus* per quadrant; SE = 1.24, df = 5, paired $t = 5.25$, $P < .005$). There was no difference between settlement in these near-cue quadrants and in the far-from-cue control quadrants ($\bar{X} \pm$ SE: 4.33 ± 0.78 vs. 3.1 ± 0.69 per *Chthamalus* quadrant; df = 9, $t = 1.15$, $P > .25$). These results indicate that contact is probably required for the cue to be effective.

DISCUSSION

For an intertidal species to survive it must not settle where conditions exceed its thermal or desiccation tolerances. The northern Gulf of California is one of the harshest intertidal areas in the world, with air temperatures exceeding 37° C throughout the summer. Furthermore, there is little relief from solar radiation since the lowest tides are during the daylight hours in the summer, and cloud cover is extremely sparse. Desiccation relief through wave splash is also unlikely; Lively and Raimondi (1987) showed that splash increased the total daily immersion time in the midintertidal by an average of only 12 min, which represents <2% of the average time of exposure at this height. In addition, rock surface temperatures are often much higher than the air temperature. I have recorded temperatures in the range of 45°–50° on midintertidal granite and basalt surfaces during the summer.

The summer is a particularly important period for *Chthamalus* because the bulk of its recruitment occurs

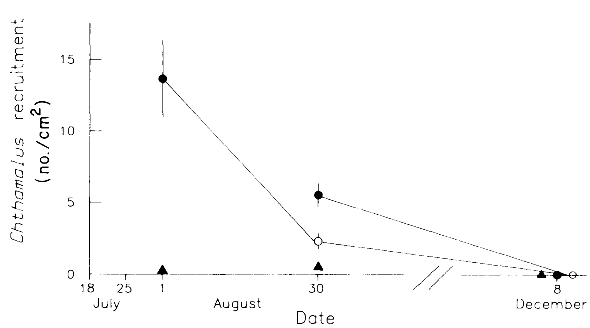

FIG. 2. *Chthamalus* recruits ($\bar{X} \pm$ 1 SE) and their survivorship on natural substrate 0.5 m above the adult upper limit. Sites were sterilized on 17 July, and barnacle extract and seawater were applied on 18 and 25 July. There was a significant difference ($P < .05$) between treatment and control sites on 1 and 30 August. ● = mean number of recruits on treatment sites (barnacle extract applied). ▲ = mean number of recruits on control sites (seawater applied). ○ = survivors from previous sample on treatment sites.

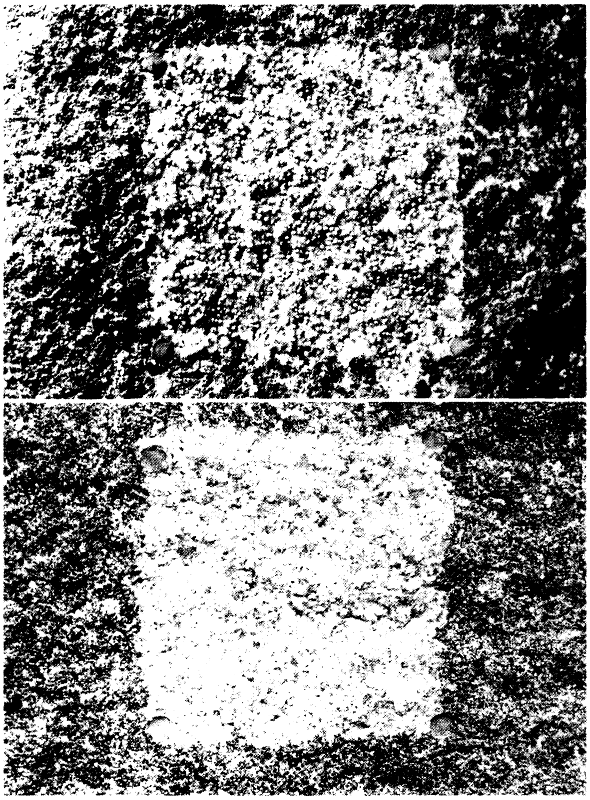

FIG. 3. Recruitment of *Chthamalus* to 10 × 10 cm sites sterilized on 17 July 1984, 0.5 m above the adult limit. Dark area around sites is *Calothrix crustacea*. (Top) site to which barnacle extract was intially applied. (Bottom) site to which seawater was initially applied.

then. In an experiment examining the desiccation/thermal resistance of *Chthamalus anisopoma*, in August 1982, Dungan (1985) found that all juveniles (<2 mm diameter) and 99% of larger individuals had died following 36 h of continuous exposure. This is very close to the longest period of exposure that *Chthamalus* would experience during the summer at its upper limit, ≈2.5 m above MLW (see Thomson 1970–1986). In addition, Lively and Raimondi (1987) showed that individual *Chthamalus* in low densities died in significantly greater numbers than those in high densities when subjected to the same desiccation/thermal stress. Since settlement above a certain level will almost certainly result in death before reproduction, and settlement next to conspecifics decreases the probability of death at high levels within the natural range, one would expect natural selection for settlement cues that indicate a safe upper limit (Strathmann and Branscomb 1979). This seems to have happened with *Chthamalus*. In areas above its distribution, it recruited only to sites where the extract had been applied or where barnacles had previously been induced to settle. Also, *Chthamalus* seems to be able to use several other indicator species as settlement cues, providing that their vertical distributions overlap its own (Table 1). Of the species that induced settlement, two were sessile filter feeders (*Chthamalus* and *Palythoa*), two were herbivorous gastropods (*Nerita* and *Tegula mariana*), and one was a predatory gastropod (*Acanthina*). An interesting result is that settlement was greater in response to *Nerita* found within the *Chthamalus* zone than outside it. This indicates that the cue may have been either traces of the barnacle or substrate that had been picked up by the inducing organism. The noninducing species were a red alga, a blue-green bacterium, and a herbivorous gastropod (*Tegula rugosa*). Both the blue-green bacterium and red alga preclude settlement by *Chthamalus*.

It is surprising that *Acanthina* induces settlement, since it is the major predator of *Chthamalus* in the northern gulf. However, *Acanthina* is a very reliable indicator of the distribution of adult *Chthamalus*, and the risk of predation to a barnacle settling in response to *Acanthina* is decreased by two factors. First, *Acanthina* occur in clusters that shift together over time (Turk 1981); an individual barnacle settling in response to *Acanthina* may not be subject to an increased risk of predation when it reaches a size that *Acanthina* will eat, ≈4 wk later, following settlement. Connell (1961) also noted that newly settled barnacles were not preyed upon by gastropod predators. The dense clusters of snails (up to 150/m^2) usually kill a large fraction of the adult barnacles in an area and then migrate in mass to another area (P. T. Raimondi, *personal observation*). This would have the additional effect of decreasing intraspecific competition between newly settled barnacles and residents. Second, *Chthamalus* has been shown to develop a predation-resistant morphology in response to the presence of *Acanthina* in the 1st 1–3 wk following settlement (Lively 1986).

Virtually no *Chthamalus* settled in areas above the

TABLE 3. The effect of barnacle extract on the numbers of *Chthamalus* settling above their normal zone.

A) Recruitment of *Chthamalus*, by treatment combination (mean ± SD).

Treatment	Height above upper limit of *Chthamalus*: 1 m	2 m
	Density of *Chthamalus* recruits (no./cm^2)	
Seawater	0.0 ± 0.00	0.0 ± 0.00
Barnacle extract	5.50 ± 1.41	1.75 ± 0.35

B) ANOVA table

Source	df	SS	*F*	*P*
Tide height	1	8.00	25.60	.0072
Barnacle extract	1	28.125	90.00	.0007
Interaction	1	8.00	25.60	.0072
Error	4	1.25		
Total	7	43.375		

natural distribution of adults unless I first applied a settlement cue. Using a cue, crushed barnacle extract, I was able to elevate the upper limit of newly settled *Chthamalus* by 2 m. This indicates how dependent *Chthamalus* is on cues. It also suggests that the upper limit of *Chthamalus* is not determined by the supply of potential settlers in the plankton (see Grosberg 1982). It is possible that planktonic larvae were drawn into these high areas by a potent and long-lived, water-borne cue, but I believe this to be unlikely. Settlement inducers for other barnacles require contact with the larvae before they are effective (Knight-Jones 1953, Crisp 1974). Furthermore, the results of the experiment testing settlement as a function of distance from a cue indicate that induction requires contact with the cue.

Strong settlement cues should act to reduce the margin of error in choosing a settlement site. Also, the strength of these cues should be related both to their reliability (Strathmann and Branscomb 1979) and to the consequences incurred by not using them. However, reliable cues may also be conservative, that is, their presence indicates a safe site on which to settle, but their absence does not indicate an unsafe one. This could lead to a patchy distribution of a species in time and space dependent on the variation in distribution of cues but independent of other environmental variability. The upper limit of the distribution of adult *Chthamalus* at Punta Pelicano is extremely variable (Fig. 1). The results of this study indicate that this variability may have resulted from the distribution of cues at the time of settlement.

Acknowledgments

I would like to thank Bill Douros, Melissa Hart, Liz Meer, and Katrina Mangin for invaluable field assistance. Carla D'Antonio, Mark Carr, Joseph Connell, Sally Holbrook, Dave Lohse, William Murdoch, Steve Pennings, Allan Stewart-Oaten, Richard Strathmann, Wayne Sousa, and an anonymous reviewer criticized drafts and/or helped with experimental designs. Thanks also to Gayle Balderson and Hal and Evelyn Mckenzie who allowed me to live in their homes in Punta Pelicano. I would also like to thank Peggy Turk, Rick Boyer, and the Center for Deserts and Oceans. Una agradecimiento especial para mis amigos en Mexico, Brazos, Manos Rapidos, los hijos del Ramon y Patti, y Osa. And finally to Curt Lively for giving me help and inspiration in all phases of my research; Thanks Buddy.

Literature Cited

Barnes, H. 1956. Surface roughness and the settlement of *Balanus balanoides* L. Archivum Societatis Zoologicae-Botanicae Fennicae Vanamo **10**:2.

Barnes, H., D. J. Crisp, and H. T. Powell. 1951. Observations on the orientation of some species of barnacles. Journal of Animal Ecology **20**:227–241.

Brusca, R. C. 1980. Common intertidal invertebrates of the Gulf of California. Second edition. University of Arizona Press, Tucson, Arizona, USA.

Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecological Monographs **55**:313–332.

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs **31**:61–104.

———. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. Journal of Experimental Marine Biology and Ecology **93**:11–45.

Crisp, D. J. 1955. The behaviour of barnacle cyprids in relation to water movement over a surface. Journal of Experimental Biology **32**:569–590.

———. 1961. Territorial behaviour in barnacle settlement. Journal of Experimental Biology **38**:429–446.

———. 1974. Factors influencing the settlement of marine invertebrate larvae. Pages 177–265 *in* P. T. Grant and A. M. Mackie, editors. Chemoreception in marine organisms. Academic Press, London, England.

Crisp, D. J., and H. Barnes. 1954. The orientation and distribution of barnacles at settlement with particular reference to surface contour. Journal of Animal Ecology **23**:142–162.

Crisp, D. J., and P. S. Meadows. 1962. The chemical basis of gregariousness in cirripedes. Proceedings of the Royal Society of London, Biological Sciences **156**:500–520.

Crisp, D. J., and P. S. Meadows. 1963. Absorbed layers: the stimulus to settlement in barnacles. Proceedings of the Royal Society of London, Biological Sciences **158**:364–387.

De Wolf, P. 1973. Ecological observations on the mechanisms of dispersal of barnacle larvae during planktonic life and settling. Netherlands Journal of Sea Reserach **6**:1–129.

Douros, W. J. 1985. Density, growth, reproduction and recruitment in an intertidal abalone: effects of intraspecific competition and prehistoric predation. Thesis. University of California, Santa Barbara, California, USA.

Dungan, M. L. 1985. Competition, and the morphology, ecology, and evolution of acorn barnacles: an experimental test. Paleobiology **11**:165–173.

Grosberg, R. K. 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical zonation of adults. Ecology **63**:894–899.

Hendrickson, J. R. 1973. Study of the marine environment in the northern Gulf of California. Final report, National Technical Information Service Publication N74-16008, Washington, D.C., USA.

Knight-Jones, E. W. 1953. Laboratory experiments on gregariousness during settling in *Balanus balanoides* and other barnacles. Journal of Experimental Biology **30**:584–598.

Knight-Jones, E. W., and J. P. Stevenson. 1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. Journal of the Marine Biological Association of the United Kingdom **29**:281–297.

Levinton, J. S. 1982. Marine ecology. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Lively, C. M. 1986. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma.* Evolution **40**: 232–242.

Lively, C. M., and P. T. Raimondi. 1987. The effects of competition, predation, and desiccation on an intertidal mussel–barnacle community. Oecologia (Berlin), *in press.*

Malusa, J. R. 1983. Comparative reproductive ecology of two species of intertidal barnacles. Thesis. San Diego State University, San Diego, California, USA.

Meadows, P. S., and J. I. Campbell. 1972. Habitat selection by marine invertebrates. Advances in Marine Biology **10**: 271–382.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series **13**:311–315.

Strathmann, R. R., and E. S. Branscomb. 1979. Adequacy of cues to favorable sites used by settling larvae of two intertidal barnacles. Pages 77–89 *in* S. E. Stanger, editor.

Reproductive ecology of marine invertebrates. University of South Carolina Press, Columbia, South Carolina, USA.

Strathmann, R. R., E. S. Branscomb, and K. Vedder. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. Oecologia (Berlin) **48**: 13–18.

Thomson, D. A. 1970–1986. Tide calendar of the northern Gulf of California. Printing and Reproductions, University of Arizona, Tucson, Arizona, USA.

Turk, M. 1981. Intertidal migration and formation of breeding clusters of labial spined morphs of the thaid gastropod, *Acanthina angelica*. Thesis. University of Arizona, Tucson, Arizona, USA.

Wethey, D. S. 1984. Spatial patterns in barnacle settlement: day to day changes during the settlement season. Journal of the Marine Biological Association of the United Kingdom **64**:687–698.

———. 1985. Local and regional variation in settlement and survival in the intertidal barnacle *Semibalanus balanoides*: patterns and consequences. Pages 194–202 *in* P. G. Moore and R. Seed, editors. The ecology of rocky coasts. Hodder and Stoughten, Sevenoaks, Kent, England.