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PREDATOR-MEDIATED MICROHABITAT PARTITIONING BY TWO SPECIES OF VISUALLY CRYPTIC, INTERTIDAL LIMPETS^{1,4}

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Abstract. Two species of limpets appear to partition microhabitats according to substratum color within the mixed mussel-barnacle zone of the Pacific Northwest rocky intertidal. A predominantly light-shelled species, *Collisella digitalis*, occurs most commonly upon the light-colored skeletons of barnacles (*Pollicipes polymerus* and *Semibalanus cariosus*), while a predominantly dark-shelled species, *Collisella pelta*, occurs most commonly on the dark valves of mussels (*Mytilus californianus*). Field experiments revealed significantly higher mortality of limpets mismatched to their background, due to predation by both fish and birds. When given a choice, in the absence of predation, both species moved actively onto the substratum where they were most cryptic. Strong selection by visual predators appears to maintain the partitioning of space by these limpet species. Competitive interactions are not required to explain this microhabitat partitioning, although they cannot be ruled out as one of the original selection pressures.

Key words: *Acmaeidae; behavior; crypsis; distribution; Embiotocidae; field experiment; Gastropoda; resource partitioning; shell; variation; visual predation.*

INTRODUCTION

Differences in microhabitat use by otherwise sympatric species within a feeding guild are often interpreted as evidence for competitive displacement (MacArthur 1972, Huey et al. 1974, Schoener 1974, 1983, Fenchel 1975, Diamond 1978, Nevo 1979). Other selection pressures correlated with microhabitat differences, however, could also account for the same pattern (Connell 1980). We report here that predation by visual predators (fish and birds) appears to be a very strong selective force maintaining the preferential use of different microhabitats by two cryptically colored, rocky-shore limpet species. Thus, although the potential for competition may exist, competitive interactions need not be invoked to account for habitat partitioning by these species.

The acmaeid limpets *Collisella digitalis* (Rathke) and *Collisella pelta* (Rathke) are common inhabitants of rocky shores along the Pacific coast of North America (Morris et al. 1980). Although *C. digitalis* generally occurs above *C. pelta* on the shore (Carefoot 1977:134, Morris et al. 1980, Frank 1982), both species co-occur in the upper-mid intertidal (Carefoot 1977) and in mixed beds of *Mytilus californianus* and barnacles (Su-

chanek 1979). Within these mixed mussel-barnacle beds, *C. digitalis* has a predominantly light-colored shell with variable amounts and patterns of dark pigment; the shells of some individuals exhibit remarkable convergence with the color and patterning of *Pollicipes* skeletal plates (Giesel 1970). *C. pelta*, on the other hand, has a predominantly dark-colored, often black shell with variable patterns of lightly pigmented areas; here also, limpet shell color is often very similar to the brownish-black of *M. californianus* valves (R. B. Lowell, *personal observation*). Both graze upon a similar suite of diatom species (Nicotri 1974, 1977) and other microscopic algae, and these and related limpet species are preyed upon by a variety of predators (gastropods [Black 1978], octopus [Wells 1980], crabs [Chapin 1968, R. B. Lowell, *personal observation*], starfish [Menge 1972], fish [Mitchell 1953, Johnston 1954, Paine and Palmer 1978, Parry 1982], birds [Hartwick 1976, 1978, 1981, Simpson 1976, Frank 1982], and small mammals [Frank 1965]).

Because of their similar diets, experimental studies have frequently demonstrated that grazing gastropods compete for food when they occur together (Underwood 1978, 1979, and references therein). Coexistence of such potentially competing species should be possible only if subdivision occurs along some other resource axis. The simplicity of this logic is often used to justify the conclusion that, for many species, microhabitat partitioning is a direct result of competition, since space represents the most likely alternative re-

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source axis (Schoener 1974). Such a conclusion depends upon at least two assumptions: (1) that other factors (e.g., physical stresses, predation, parasitism) do not keep population sizes depressed to levels at which competition is no longer occurring, and (2) that these other factors vary independently among microhabitats and thus themselves do not account for the pattern. On the basis of the predation experiments discussed below, we question whether competition is required to account for microhabitat partitioning by *Collisella digitalis* and *C. pelta* when they co-occur in beds of *Mytilus californianus*.

METHODS

Observations on microhabitat use were obtained by collecting all limpets from 0.2×0.25 m quadrats placed within a mussel bed where several substratum types were available. A pair of quadrat samples was taken at each of two tidal heights (+2.5 m, +3.2 m above extreme low water, spring [ELWS], Canadian datum) within some very exposed mussel beds of Prasiola Pt. (48°49'N, 125°10'W) on the west coast of Vancouver Island, British Columbia, Canada, on 9 and 18 July 1981. Quadrats were placed to obtain as similar a proportion of substrata as possible; the approximate proportions of substrata represented by *Mytilus californianus*, *Pollicipes polymerus*, and *Semibalanus cariosus* in the quadrats at each height were: +2.5 m: 43, 43, and 14%; and +3.2 m: 30, 40, and 30%, respectively. Only limpets on exposed surfaces (i.e., potentially accessible to visual predators) were collected. The shell-length ranges of each limpet species for the lower and upper samples, respectively, were: *C. digitalis*: 5–12 mm, 3–12 mm; *C. strigatella*: 4–7 mm, 4–7 mm; *C. pelta*: 3–15 mm, 4–12 mm. As many limpets as possible were identified using shell features (Lindberg 1981). Although the shells of *Collisella digitalis* are quite distinctive, those of *C. pelta* and *C. strigatella* (Carpenter) (which now includes *C. paradigitalis* (Fritchman) of recent authors; D. Lindberg, *personal communication* November 1984) intergrade when small (<10 mm), so radulae were checked where necessary to aid in identification. Radular morphology of these latter two species also intergrades to some extent in Vancouver Island populations (R. B. Lowell, *personal observation*); however, individuals were assigned to species according to Lindberg (1981).

Following identification, individuals of each species were then ranked into three categories according to the predominant color of the shell: the fraction of the shell that was dark brown to black. Shells that were 0 to $\frac{1}{3}$ dark brown to black were scored as "light," those $\frac{1}{3}$ to $\frac{2}{3}$ dark brown to black were scored as "intermediate," and those $\frac{2}{3}$ to completely dark brown to black were scored as 'dark.' This method was used in preference to Giesel's (1970) for the different morphs of *C. digitalis*, because it could be applied uniformly to all three species in the present study.

Field experiments were conducted with limpets collected intertidally from Wizard Island (48°51'N, 125°09'W) in Barkley Sound on the west coast of Vancouver Island. *Collisella digitalis* and *C. pelta* ranging from 6.0 to 12.5 mm were pried from the rock and returned to the Bamfield Marine Station, where they were marked with a small notch on the shell margin using a hand-held electric grinder with a very fine bit, and returned to the field the following day. Because of the large number of individuals needed for the field experiments and because of the difficulty of identifying small limpets reliably using their shells, some darker *Collisella strigatella* were probably misidentified as *C. pelta*. Since *C. strigatella* formed only $\approx 13\%$ of the sample in the quadrat observations, and since the relevant variable in the predation experiments below was shell color, these misidentifications are not likely to have influenced the results. Further, only the darkest *C. pelta* were used in the experiments. Thus, since most shells of intermediate color were *C. strigatella*, misidentifications would have been at worst $\approx 5\%$.

Balanced two-way or unbalanced but proportional three-way analyses of variance were performed, where appropriate, on the frequency data following the procedures outlined in Sokal and Rohlf (1981). Where initial numbers of limpets were not the same for a comparison, frequencies were converted to arcsine-transformed proportions prior to analysis.

Predation by fish

Predation by two molluscivorous surfperch, *Damallichthys vacca* and *Embiotoca lateralis* (Embiotocidae), was examined by placing limpets on different natural substrata glued within a 75×75 cm wooden tray (Fig. 1). The tray was divided into four equal-sized quadrants within which were glued (with Sea Goin' 'Poxy Putty) either stones covered with barnacles (*Balanus glandula*), providing a light-colored substratum, or single, disarticulated valves of *Mytilus californianus*, providing a dark-colored substratum (i.e., two barnacle and two mussel quadrants). Each quadrant was surrounded, and exposed wood surfaces covered, with copper-based antifouling paint enhanced with copper filings; limpets will not cross this barrier (Cubit 1984). Thus limpets were not allowed to move between substratum types nor onto wood surfaces. The tray was deployed at $\approx +1.5$ m on the cobbled shore of Wisman's Bay, adjacent to the Bamfield Marine Station (48°50'N, 125°08'W) where, at high tide, both surfperch species were known to forage (McCormack 1982, R. B. Lowell, *personal observation*), and where few if any seabirds were observed to forage. Feeding by these fish was confirmed by observing the tray at high tide from a small boat with the aid of a facemask during preliminary experiments conducted 2 d immediately prior to the main experiments.

Experimental trials were initiated by introducing individuals of *C. digitalis* or *C. pelta* onto each substratum.

tum type in the tray at low tide; 40 individuals of each limpet species were placed on each of the two substratum types; thus both species were present in each trial, but only a single limpet species was present in each quadrant. On the following low tide (≈ 12 h later) the number of limpets remaining in each quadrant was counted. At the end of each trial, missing limpets were replaced to bring the totals in each treatment back up to 40. These experimental trials were repeated eight times on consecutive days. The location effects criticized by Hurlburt (1984) as "temporal pseudoreplication" were very unlikely to have been important here because the ambit of the predators exceeded the size of the tray by at least two orders of magnitude; thus all four quadrants were equally accessible to both fish predators at all times.

A control for the influence of other predators or handling disturbance to the limpets was conducted immediately following these feeding experiments using the same protocol, except that the tray was covered with a 7-mm mesh plastic netting (Vexar) spaced 5 cm above the edges of the tray to permit access by crabs or other predators. The control was repeated for three consecutive days.

Predation by birds

To determine whether limpets not matching their substratum were more likely to be removed by birds, light- and dark-colored limpets of comparable size ranges were introduced on different natural substrata on Wizard Island, where many seabirds were observed to roost and forage at low tide. Two experimental arenas were established, one at the lower edge of the zone of *Balanus glandula* immediately above the upper edge of the mussel bed, where there were no mussels (+2.97 m above ELWS, 0.6×0.6 m = light substratum), and the other within a continuous bed of *Mytilus californianus* that were largely free of epibiotic barnacles (+2.57 m above ELWS, 0.4×0.4 m = dark substratum). Each arena was surrounded, and divided in half diagonally, by 5 cm wide bands of copper-based antifouling paint supplemented with copper filings, and all naturally occurring limpets were removed. At low tide, 100 *C. digitalis* were placed on one half of the barnacle arena, while 100 *C. pelta* were placed on the other half. Only 50 limpets of each species were introduced into each half of the arena in the mussel bed because of its smaller size. On the following low tide (12 h later) the number of limpets remaining in each section of each arena was counted, and the shore within 1 m of each arena was searched for marked individuals. The experiment was repeated on seven consecutive days using newly introduced limpets each day. As with the fish experiments above, the repeated observations over time at the same sites were very unlikely to have resulted in a bias due to location effects (Hurlburt 1984) for two reasons: (1) the important comparison was between adjacent halves of the treatments on each sub-



FIG. 1. Two quadrants each of barnacle and mussel substrata in a wooden tray used to expose limpets to predation by surfperch, *Damalichthys vacca* and *Embiotoca lateralis*. Each quadrant is 35 cm on a side.

stratum type rather than between substratum types so access by predators would not have differed on this scale, and (2) the mobility of the predatory birds was much greater than the size of the arena on each substratum type, again ensuring equal predator access. In addition, limpets were replaced completely each day; thus the replicates over time were statistically independent.

To control for the effects of handling trauma and other predators, the above procedure was repeated, except that each arena was roofed over with 7-mm plastic mesh (Vexar) raised 2 cm above the substratum by small wooden posts glued to the rock with Sea Goin' Poxy Putty. Only 50 of each limpet species were used in each half of the controls; the control was repeated twice on consecutive days immediately following the experimental series.

Birds in the area of the experiments at low tide were observed from a distance of ≈ 70 m using either binoculars or a telephoto lens mounted on a camera.

Substratum preference experiments

To determine whether differences in substratum preference existed among limpets, two 20×20 cm arenas of mixed substratum type were delineated on Wizard Island, containing $\approx 50\%$ light-colored substrata (formed primarily of barnacles [*Balanus glandula*, *Semibalanus cariosus*] with some light-colored rock) and $\approx 50\%$ dark-colored substrata (formed mostly by the mussel *Mytilus edulis*, but including some dark-colored rock; Fig. 2). As above, each arena was surrounded with an ≈ 5 cm wide band of copper-based antifouling paint, supplemented with copper filings, to prevent immigration and emigration of limpets. Two coats were applied on successive low tides. Both barnacles and mussels were painted, when necessary, as part of the outline that formed the arena. Twenty light-colored *C. digitalis* and 20 dark-colored *C. pelta* were



FIG. 2. A mixed-substratum arena (*Mytilus edulis* = dark substratum, *Balanus glandula* = light substratum) used to monitor the movement of limpets initially placed on substrata of a color contrasting to their shells. The light-colored square of copper-based antifouling paint defines the perimeter of the arena (20 cm on a side).

placed on substrata of opposite color to their shell within each of these arenas. Following the introduction, the number of limpets occurring on each substratum type was recorded daily for 5 d both within the arenas and to a distance of 1 m in all directions. Marked limpets found outside the arenas were scored for substratum type but otherwise were not disturbed.

RESULTS

Field distributions

Three species of limpets were found in the replicate quadrat samples taken from mussel beds, and they were distributed nonrandomly among substratum types (Table 1). *Collisella digitalis* and *C. pelta* occurred in approximately equal numbers, while *C. strigatella* formed a significantly smaller proportion (13%) of the total from all four samples pooled ($P = .005$, Table 2). In these samples, no significant difference existed in the total number of all limpets from each substratum type ($P = .33$) nor from the different tidal heights ($P = .91$). However, a highly significant substratum \times limpet interaction ($P < .001$, Table 2) resulted from the

lighter shelled species, *C. digitalis*, being almost 270% as common on barnacles, while the darker shelled species (*C. pelta* and *C. strigatella*) were >400% as common on mussels as on barnacles. A significant limpet \times tidal height interaction ($P = .002$) revealed that *C. digitalis* were more common at the higher site while *C. pelta* were more common lower.

The mixed mussel-barnacle habitat we sampled quantitatively at only one site is nonetheless widely distributed along the Pacific coast (Ricketts et al. 1968, Carefoot 1977). Although additional quantitative samples were not taken because of the time required to identify small limpets reliably, qualitative observations at several different sites in Barkley Sound revealed the same substratum preferences (e.g., Owen Island, Benson Island, Bordelais Islets, Cape Beale, and Kirby Point [Dianna Island]; K.S. Mercurio, R. B. Lowell, *personal observation*). Furthermore, light *C. digitalis* associate with barnacles on the coast of Oregon (Giesel 1970) and dark *C. pelta* associate with mussels in California (Lindberg 1981); thus the substratum preference exhibited by these species appears to be a general feature of their biology.

Predation by fish

Fragments of limpet shells were observed commonly in the tray after each experimental replicate, reflecting mortality due to the surfperch, which crush the shells of their molluscan prey (Brett 1979) and often spit out a portion of the shell fragments prior to swallowing (McCormack 1982, R. B. Lowell, *personal observation*). In addition to *Damalichthys* and *Embiotoca* predation, occasional small crabs (*Hemigrapsus nudus* and *H. oregonensis*, 0.5–1.8 cm carapace width) probably also accounted for some limpet mortality in the tray. The number of crabs observed ranged from one to seven on different days; however, no more than four, whole, empty limpet shells were found on any one day. Whole, unoccupied limpet shells were scored as eaten, even though they had not been consumed by fish; these limpets were too large for the observed *Hemigrapsus* to have eaten normally; thus probably they were moribund or died due to handling trauma.

Significantly more limpets of both species disap-

TABLE 1. Frequencies of three limpet species found on different substrata within beds of *Mytilus californianus* (two replicates pooled at each tidal height). L = shell predominantly light colored. I = shell of intermediate color. D = shell predominantly dark colored.

Substratum	Tidal height (m)	<i>Collisella digitalis</i>			<i>Collisella pelta</i>			<i>Collisella strigatella</i>		
		L	I	D	L	I	D	L	I	D
<i>Mytilus californianus</i> (dark substratum)	+2.5	8	..*	4	78	1	7	7
	+3.2	31	3	26	6	6	8
<i>Pollicipes polymerus</i> (light substratum)	+2.5	37	1	9
	+3.2	41	1
<i>Semibalanus cariosus</i> (light substratum)	+2.5	2	3	5	...	3	...
	+3.2	28	5	1	6	...	2	4

* No individuals observed in this category.

TABLE 2. Three-way model I analysis of variance with replication of frequencies of limpets found on different substrata at different tidal heights (data from Table 1).†

Source of variation	df	F	P
Main effects			
Substrata	1	1.05	.33
Limpet species	2	8.60	.005**
Tidal height	1	0.01	.91
Two-way interactions			
Substratum × limpet	2	14.51	<.001***
Substratum × tidal height	1	2.19	.16
Limpet × tidal height	2	10.52	.002**
Three-way interaction	2	1.41	.28

** $P < .01$, *** $P < .001$.

† Because of the large number of zero cells in Table 1, the numbers of individuals for all shell colors were pooled within each limpet species and the frequencies of limpets on both barnacle substrata were pooled, yielding a $2 \times 3 \times 2$ factorial ANOVA. Any error introduced by this pooling is conservative, since it should decrease the apparent differences in substratum use among limpet species. All mean squares were tested over the error mean square (51.50, df = 12), as appropriate for model I ANOVAs.

peared from the experimental treatments than from the controls ($P < .001$); across treatments and substrata more *Collisella digitalis* disappeared than *C. pelta* ($P < .001$; Tables 3 and 4). When averaged across treatments and limpet species, there was no significant effect of substratum type on survival ($P = .75$, Table 4). However, a highly significant substratum × limpet interaction ($P < .001$) confirmed that limpet survival depended heavily on substratum type: *C. digitalis* were ≈60% more likely to disappear from mussels than barnacles, whereas *C. pelta* were almost 130% more likely to disappear from a barnacle substratum (Table 3). Further, the significant treatment × substratum × limpet interaction ($P = .012$) reflected the lack of a significant substratum × limpet interaction in the controls; although *C. digitalis* disappeared more rapidly than *C. pelta* in the controls, disappearance rates of both species were related only slightly if at all to substratum type (Table 3).

Predation by birds

Many seabirds were observed either roosting or foraging on Wizard Island. Some, including California

Gulls (*Larus californicus*), Black Oystercatchers (*Haematopus bachmani*), and Black Turnstones (*Arenaria melanophala*), were observed to feed on limpets in the vicinity of the marked arenas almost every day. Others observed in the vicinity, including the Western Sandpiper (*Ereunetes mauri*), and the Northwestern Crow (*Corvus daurinus*), did not appear to be feeding on limpets.

Significantly more limpets of both species disappeared from the experimental treatments in the barnacle arena than from the controls ($P < .001$; Tables 5 and 6). However, as in the experiments with surfperch predation, *C. digitalis* disappeared significantly less rapidly than *C. pelta* from the barnacle substratum in the unroofed treatments compared to the roofed treatments (treatment × limpet interaction, $P = .008$, Table 6). The treatment × limpet interaction was significant here, in contrast to the experiments with surfperch, because only results from a single substratum type (barnacles) were analyzed. The results from the mussel arenas could not be analyzed in the same manner, since the plastic mesh roof of the controls was torn off by waves on both days and time did not permit additional controls to be conducted. The average rate of disappearance of all limpets from the mussel arenas was comparable to, though somewhat less than that from the barnacle arenas (25 vs. 35%, Table 5). However, the disappearance rates of the two limpet species were not significantly different from each other ($t = 0.88$, $P = .40$; Table 5).

Some marked individuals were found outside their respective arenas, but these never formed >5% of the total in each experiment, and they were not counted as having been eaten.

Substratum preference

Although some limpets disappeared from both substratum-preference experiments, individuals of both species exhibited a striking tendency to move to the substratum type upon which they were most cryptic (Fig. 3). Within 24 h, >50% of the individuals were found on the "correct" (i.e., more cryptic) substratum for their shell color in three of the four cases, even though all limpets were started on a contrasting substratum type. After 5 d, only 3 of the 50 individuals remaining of both species were found on "incorrect"

TABLE 3. Mean number (\pm SE) of limpets missing and presumed dead after 12 h of exposure to predation.*

Treatment	Limpet	Substratum	
		Barnacle	Mussel
Unroofed (experimental)	<i>C. digitalis</i>	17.5 \pm 1.89	28.7 \pm 1.32
	<i>C. pelta</i>	15.4 \pm 3.13	6.7 \pm 2.17
Roofed (control)	<i>C. digitalis</i>	8.7 \pm 0.88	7.0 \pm 1.73
	<i>C. pelta</i>	2.3 \pm 0.33	1.0 \pm 0.58

* Primarily by the surfperch *Damalichthys vacca* and *Embiotoca lateralis*, but also by small shorecrabs, *Hemigrapsus*. Forty individuals of each limpet species were present initially on each of the two substratum types for each replicate. Number of replicates: experimental = 8; control = 3.

TABLE 4. Three-way model I analysis of variance with replication of the frequencies of limpets disappearing from different substrata due primarily to predation by surfperch (data from Table 3).†

Source of variation	df	F	P
Main effects			
Treatment	1	42.13	<.001***
Substratum	1	0.10	.75
Limpet species	1	38.09	<.001***
Two-way interactions			
Treatment × substratum	1	0.55	.46
Treatment × limpet	1	2.40	.13
Substratum × limpet	1	17.98	<.001***
Three-way interaction	1	7.06	.012*

* $P < .05$, *** $P < .001$.

† Because this was a pure model I ANOVA, all mean squares were tested over the error mean square (31.6, $df = 36$) and no corrections were required for the unequal but proportional cell sizes (Sokal and Rohlf 1981).

substrata ($\chi^2 = 39.1$, $P < .001$ from both replicates pooled; 2×2 contingency table on data from the last day).

Day-to-day variation in limpet number within the quadrats must have resulted from the overlooking of marked individuals, since no more than two marked limpets were recorded outside but within 1 m of the arenas, and since limpets would be very unlikely to move out of, then back into the arena.

DISCUSSION

Both surfperch and shorebirds appeared to remove selectively those limpets that were visually more conspicuous, a pattern of selection observed for other visual predators on gastropods (Heller 1979, Reimchen 1979; but see Hartwick 1981 for a possible exception). The conclusion that these predators, and not some other factors, were the primary agents of selective mortality in the field experiments is supported by three lines of evidence. First, when these predators were denied access to the limpets by a coarse (7 mm), plastic mesh roof in the three successful sets of controls, the differential mortality of *C. digitalis* or *C. pelta* either disappeared or decreased significantly, even though other benthic predators (crabs, starfish, snails) would have had access from the sides (Tables 3–6).

Second, these control treatments also demonstrated that differential mortality was not due entirely to trauma or damage associated with prying limpets off the rocks and transplanting them. Trauma may have been responsible for the greater mortality of *C. digitalis* in the controls for the surfperch experiments (Table 3), and thus some of the higher rate of mortality of the light-colored *C. digitalis* when placed on mussels. However, the mortality rate of *C. digitalis* when exposed to fish predators on a substratum of mussels was much higher than its mortality in the controls (Table 3).

Third, disappearance rates of limpets from the experimental arenas were high where differential mortality was demonstrated (mean = 53.7% on contrasting substrata vs. 26.3% on cryptic substrata, from Tables 3 and 5), even though it was measured over only 12-h intervals. With only a few exceptions, surfperch and shorebirds were the only predators observed feeding either in or in the immediate vicinity of the respective experimental arenas during these intervals. The few grapsid crabs observed in the arena of the surfperch experiments were probably feeding on moribund limpets; the more powerful cancrid crabs, *Cancer oregonensis* and *C. productus*, though known to forage in the intertidal in the vicinity (Boulding and Hay 1984; R. B. Lowell, *personal observation*), were not observed in or around the arenas at either site during these experiments. Although predation by surfperch or some other fish at high tide cannot be eliminated entirely for the experiments on Wizard Island, it is unlikely to have been as important a source of mortality as birds, because the experiments were conducted rather high on the shore (+2.6 and +3.0 m) where fish would have had limited access. Furthermore, Wizard Island is exposed to almost continuous, though often not powerful wave action, and this consistent wave surge would reduce substantially the ability of surfperch to position themselves for effective "suction removal" of limpets; to feed on limpets effectively, both surfperch must be able to remain stationary and oriented perpendicular to the substratum (R. B. Lowell, *personal observation*).

The rather striking results of the substratum choice experiments (Fig. 3) indicate that the preferential oc-

TABLE 5. Mean number (\pm SD) of limpets missing and presumed dead from both the barnacle and mussel arenas on Wizard Island after ≈ 12 h of exposure to predation.*

Treatment	Limpet species	
	<i>Collisella digitalis</i>	<i>Collisella pelta</i>
Unroofed, barnacle (experimental)	18.4 \pm 4.77	50.3 \pm 4.84
Roofed, barnacle (control)	1.0 \pm 1.00	0.0 \pm 0.0
Unroofed, mussel (experimental)	10.4 \pm 3.15	14.4 \pm 3.30
Roofed, mussel (control)	... †	... †

* Primarily by California Gulls (*Larus californicus*), Black Oystercatchers (*Haematopus bachmani*), and Black Turnstones (*Arenaria melanocephala*). On the barnacle substratum, the initial number of limpets was 100 in each replicate of the experimental groups and 50 in each replicate of the controls. On the mussel substratum, the initial number of limpets per replicate was 50 for both experimentals and controls. Number of replicates for both substratum types: experimentals = 7, controls = 2.

† The roofs were swept away by wave action in both attempts at a control on the mussel substratum; thus no data were obtained.

TABLE 6. Two-way model I analysis of variance with replication on the frequencies of limpets disappearing from a light-colored (barnacle) substratum *only*, due primarily to predation by seabirds.†

Source of variation	df	F	P
Main effects			
Roofed vs. unroofed	1	47.34	<.001***
Limpet species	1	17.71	<.001***
Treatment × limpet interaction			
	1	9.38	.008**

** $P < .01$, *** $P < .001$.

† Data from the barnacle substratum in Table 5 were transformed using the angular transformation on the percentage of limpets disappearing from each condition, since the initial numbers of limpets were different in the experimental and control groups. All mean squares were tested over the error mean square (64.3, df = 36).

currence in more cryptic microhabitats of both *Collisella digitalis* and *C. pelta* is maintained at least in part by active behavior in both species. These results are similar to Giesel's (1970) for the different shell morphs of *C. digitalis*; as discussed below, however, they do not permit identification of the agent(s) of selection favoring this behavior.

The predation experiments nonetheless clearly demonstrate the potential of selective predation by both fish and birds to sustain preferential use of cryptic microhabitats within *Mytilus californianus* beds by the limpets *C. digitalis* and *C. pelta*. The actual intensity of predation by either type of predator, however, is likely to depend on local conditions. As indicated above, in areas of sustained wave action, fish like the suction-feeding *Damalichthys vacca* and *Embiotoca lateralis* may have considerable difficulty maintaining the required orientation for successful feeding on limpets. Thus, on many more exposed shores with extensive beds of *Mytilus californianus*, wave action may effectively eliminate surfperches as important predators of limpets. On the other hand, on more sheltered shores mortality due to surfperch predation on both littorines (McCormack 1982) and limpets (R. B. Lowell, *personal observation*) can be very intense (> 50%/d and 40–100%/d, respectively, among animals placed in more accessible or less cryptic habitats). Intensity of predation by marine birds will also vary since it can be influenced greatly by local topographic conditions; at least some shorebirds cannot forage efficiently on steeply sloping or vertical shores (e.g., the black oystercatcher *Haematopus bachmani*; Hartwick 1978, Frank 1982). As a result of these environmental constraints, differential substratum use by *C. digitalis* and *C. pelta* will not be

Even though the intensity of selection may be patchy, however, it nonetheless could have exerted an important influence on the evolution of shell color and substratum preference in these species as a whole for two reasons. First, the mortality experienced by both limpets, when more conspicuous against the substratum, was substantial (Tables 3 and 5). Second, both species

have pelagic larvae; this results in the distribution over many patches of offspring whose parents have been exposed to intense selection only in a subset of these patches. Thus, in each generation, the average fitness of a given genotype will be based on its success over many patches.

We must emphasize that, as with many studies of this type, we are dealing with a subset of all the habitats occupied by both limpet species; although the mixed mussel-barnacle habitat is widespread (Ricketts et al. 1968, Carefoot 1977) and both limpet species commonly co-occur in it (Giesel 1970, Lindberg 1981), each species can and does occur in isolation in other habitat types (Carefoot 1977, Morris et al. 1980). The vertical range of *C. digitalis* extends higher in the intertidal; thus it can occur in the absence of *C. pelta* in the upper reaches of the *Balanus glandula* zone. Conversely, the range of *C. pelta* extends lower on the shore; thus it may be the only one of these two species found among the stipes of the mid and low intertidal kelps.

In addition, other differences exist between these limpet species. These differences suggest that interactions between them affecting their coexistence may be more complex than we have suggested. Both *Collisella digitalis* (Frank 1965, Breen 1972) and *C. pelta* (R. B. Lowell, *personal observation*) settle low in the intertidal and migrate upshore as they increase in size; individuals of intermediate size occur within and on mussel beds. In some areas (e.g., the Oregon coast) *C. digitalis* is polymorphic, with two rather distinct adult morphs occurring on different substrata: barnacles and rock (Giesel 1970). The largest adults of *C. pelta*, on the other hand, tend to occur under *Fucus* high on the

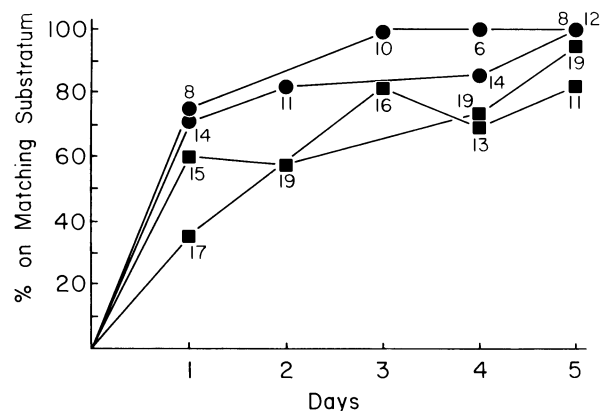


FIG. 3. Percent of limpets of each species found on the substratum type on which they were most cryptic, as a function of time. The light-colored *Collisella digitalis* (●) were initially released only on the dark-colored substratum (*Mytilus edulis*), while the dark-colored *C. pelta* (■) were initially released only on the light-colored substratum (*Balanus glandula*; see Fig. 2). Two replicates were conducted with 20 individuals of each species per replicate. Number of individuals found at each census is shown.

shore (R. B. Lowell, *personal observation*). One consequence of these distribution and life-history differences is that only a subset of morphs (in *C. digitalis*) or ages of individuals (in *C. pelta*) will co-occur together in mussel beds and be exposed to the selective predation we have described above. Hence, on an evolutionary time scale, many factors may have contributed to the observed ecological differences between these two limpet species. Nevertheless, on an ecological time scale, we feel that predation by visual predators is the overriding agent of selection maintaining the differential use by these species of microhabitats within beds of *Mytilus californianus*.

Although predation appears to play an important and possibly the important role in maintaining the partitioning of microhabitats by *C. digitalis* and *C. pelta* when they co-occur, competitive interactions between these species cannot be ruled out as a factor that may have favored habitat partitioning originally. Experimental studies have demonstrated frequently that microherbivorous gastropods compete for food when they are caged together (Underwood 1978, 1979, and references therein). However, it seems to us that, in the absence of predation, substratum differences alone would not permit coexistence of these two species if neither limpet species was favored over the other on either substratum type. For competitive interactions to lead to habitat partitioning in this system, some morphological or physiological constraints would have to reduce the feeding efficiency or increase the susceptibility to physiological stress of one species compared to the other on one substratum type and vice versa on the other. Possible differences that would favor habitat partitioning include: different availabilities of micro- or macroalgal food on which one or the other feeds more efficiently, differences in foot morphology (differential ability to adhere to smooth vs. rough surfaces), and differences in grazing apparatus (differential ability to remove microalgae from smooth vs. rough surfaces, susceptibility of radular teeth to wear). Both species appear to consume the same diatom species when they co-occur (Nicotri 1974, 1977), thus decreasing the likelihood that different food availabilities favor habitat partitioning, but no data exist to assess the importance of the latter two hypotheses.

Using the criterion of parsimony, we feel that visual predation is the most likely agent of selection responsible for the evolution of microhabitat partitioning by *Collisella digitalis* and *C. pelta* in mixed beds of barnacles and mussels. Predation by visual predators alone is sufficient to account for these differences in microhabitat use. An explanation of this pattern based on interspecific competition, however, requires both (1) that competition occurs, and (2) that some as yet undetermined constraint or constraints prevents a single limpet species from using both microhabitats more efficiently than the other potentially co-occurring species. To test the assertion that competition is not important

here, both the visual predators and one of the two limpet species would have to be removed to determine if the remaining species would "invade" the vacated microhabitat. Unfortunately, a negative result (i.e., no invasion) would obtain, since both species preferentially remain on or return to the substratum on which they are most cryptic (Fig. 3). Alternatively, one could also test for the presence of competition via caging experiments (e.g., Underwood 1978) with both species on each substratum type. A competitive interaction would almost certainly be demonstrated, yet such a result would also be ambiguous unless clear evidence of aggressive interactions (i.e., interference competition) were obtained, as observed for *Lottia gigantea* along the California coast (Stimson 1973); to our knowledge, such aggression has not been observed between *C. digitalis* and *C. pelta*. The demonstration of exploitative competition when two species that normally are allopatric (at least on the microhabitat scale) are placed in sympatry cannot be interpreted as evidence that competition either is or was the primary agent of selection behind the evolution of the microallopatric distribution, since factors other than competition could cause the same pattern. But of course, competition cannot be ruled out either. Thus the "ghost of competition past" (Connell 1980) cannot be exorcised.

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