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PREDATION BY THE PILE PERCH, *RHACOCHILUS VACCA*, ON AGGREGATIONS OF THE GASTROPOD *LITTORINA SITKANA*

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ABSTRACT The pile perch, *Rhacochilus vacca* (Embiotocidae), is abundant on the Pacific Coast of North America and is known to crush hard-shelled prey with its heavy pharyngeal teeth. We investigated whether pile perch predation has the potential to limit or regulate populations of *Littorina sitkana*, a direct-developing gastropod found on wave-sheltered shores near Bamfield, British Columbia, Canada. Laboratory experiments showed that pile perch required an average of only 19.2 sec (SE = 5.61; n = 20) to crush and swallow a large *L. sitkana*, which resulted in consumption rates averaging 33.3 (SE = 6.27; n = 4) large snails per day. The snails had no size refuge from predation by adult fish because even small fish (fork length 21 cm) could crush the largest *L. sitkana* present on the shore (>11 mm shell width). Indeed, some fish showed a significant preference for large snails (shell width >6.3 mm) over small snails (3.35 mm < shell width < 4.0 mm). Our 1998 observations with SCUBA during daytime high tides showed that the density of pile perch foraging in the intertidal averaged 0.119 (SE = 0.0205; n = 20) individuals per square meter (estimated fork lengths 5–40 cm). However, the intertidal distribution of pile perch that were actually consuming prey was highly aggregated. In the field, we investigated whether predation by this fish on snails deployed onto boulders was density dependent. The fish swam parallel to the shore and located and consumed 40% of the patches of *L. sitkana* that we deployed (n = 70) within 50 min. This foraging behavior resulted in density-dependent predation on the deployed snails in only one of the three tidal cycles (or 2 of the 12 days) of our experiment. We offer several proximate reasons for the low frequency of density-dependent predation found in this study and conclude that the pile perch may not be an important regulating factor for *L. sitkana* populations at this site at the present time. However, the very high predation rates we observed suggest that this predatory fish is an important limiting factor at this site.

KEY WORDS: aggregative response, limiting factor, population regulation

INTRODUCTION

The factors that determine the distribution and abundance of marine invertebrates are still not well understood. Predation is known to be important in limiting the abundance of littorinid gastropods on rocky shores. Paine (1994) reviewed examples where predators had been excluded from rocky shores and concluded that such exclusions usually resulted in dramatic increases in the abundance of the competitive dominant. Many of the classic exclusion experiments he reviewed have involved slow-moving predators, such as gastropods or starfish. However, slow-moving predators are unable to move rapidly to high-density aggregations of their prey and are generally less tolerant to emersion than their prey (Newell 1970). As a result, they usually have a very local effect at the lower end of the intertidal distribution of their prey. In contrast, highly mobile predators, such as crabs and fish, can forage throughout the intertidal during a single high tide period and have been observed to feed more heavily on high-density aggregations of their prey (Boulding & Hay 1984, Behrens Yamada & Boulding 1996). Sinclair (1989) argues that only density-dependent factors can provide the negative feedback that can regulate a population at equilibrium. Consequently, highly mobile predators may be disproportionately important as regulating factors on rocky intertidal shores.

Two highly mobile predators, crabs and fish, can prey very heavily on littorinid gastropods on wave-sheltered shores of the northeastern Pacific, and it is not clear which predator type is more important. McCormack (1982) deployed *Littorina sitkana* into fenced areas of the intertidal and observed predation rates of up to 54% per daytime high tide period, which she attributed entirely to predation by pile perch (*Rhacochilus vacca*). Behrens Yamada and Boulding (1996) tethered *L. sitkana* in the intertidal zone and found predation rates of up to 77% per high tide period. They recovered diagnostic shell fragments that had been peeled by crabs from 40% of the dead snails of shell length 15–17.5 mm. Boulding et al. (1999) found predation rates on tethered *L. sitkana* to be up to 25% per high tide period and used shell fragments to attribute at least 52% of the predation of their largest size class to predation by crabs. The daily rates of predation reported above are too high for any *L. sitkana* population to sustain given their known reproductive rates (Behrens Yamada 1989). We hypothesize that these high predation rates represent a strong density-dependent response to local high-density patches of prey and present experiments here to test our hypothesis.

Foraging excursions into the intertidal during high tide have been well documented for large subtidal crabs such as *Cancer productus* (Boulding & Hay 1984, Robles et al. 1989, Behrens Yamada & Boulding 1996, Boulding et al. 1999). There is experimental evidence that predation by this crab species can be density dependent (Boulding & Hay 1984).

However, much less is known about the foraging behavior of the pile perch other than its extreme morphological specializations for crushing hard-shelled prey (Brett 1979). One of the major components consistently found in stomach analyses of pile perch are gastropod molluscs (Ellison et al. 1979, Haldorson & Moser 1979, Hueckel & Stayton 1982, Laur & Ebeling 1983, Stouder 1987). The only other surf perch that is common in the intertidal zone on the west coast of Vancouver Island and is known to eat gastropods is the striped perch (*Embiotoca lateralis*) (Lamb & Edgell 1986, E.G. Boulding Pers. Comm.). Striped perch stomachs sometimes contain gastropod mollusks, but soft bodied invertebrates such as amphipods, bryozoans, and isopods are much more prevalent (Haldorson & Moser 1979). The different feeding preferences of the two species are correlated with their mouth size and structure. The pile perch has extremely large pharyngeal plates, heavy blunt (pavement-like) pharyngeal teeth, and well-developed associated musculature for specialization in crushing and grinding (DeMartini 1969). The striped perch, however, has only moder-

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ately sized pharyngeal plates; smaller, more pointed pharyngeal teeth; and moderately developed musculature and is specialized for feeding on large whole prey (DeMartini 1969). For these reasons, we decided to focus on determining whether pile perch predation on patches of *L. sitkana* deployed onto a rocky intertidal shore was density dependent.

MATERIALS AND METHODS

Study Area

Our experimental site was located on a wave-sheltered boulder shore in front of Bamfield Marine Station (48°50′, 125°08′) in Barkley Sound, Vancouver Island, British Columbia, Canada. We chose the site because it was one of the sites ("Pebble Beach A," hereafter Pebble Beach) used by McCormack (1982) in her study of the role of pile perch in maintaining shore-level size gradients in *L. sitkana* populations.

Laboratory Feeding Experiments

Our laboratory feeding experiments were conducted in round fiberglass tanks at Bamfield Marine Station. The experimental tanks were either 1.22 or 1.83 m in diameter and were filled with free-flowing sea water to a depth of 0.914 m. The tanks were covered with plywood but were left open along a 20-mm crack to allow for low levels of light. The flow rate of seawater into the tanks was at least 1 l/s, and the water had a temperature of 10 ± 1°C and a salinity of 31‰.

The pile perch were collected by fishing with a hook baited with a whole mussel (*Mytilus trossulus*). Upon landing, the hook was carefully removed with pliers, and the fish was placed in a bucket of sea water and rapidly transported to 2.44-m diameter round holding tanks. The fish were then held for at least a week and maintained on a diet of *M. trossulus*. The total length of the fish collected ranged from 275–330 mm.

L. sitkana were collected from Seppings Island near Bamfield Marine Station. The large size-class of snails was also collected from nearby Second Beach. They were held in perforated containers in free-flowing sea water until used in the experiments. The size of the minimum diameter (shell width) of the snails was determined by passing them through a series of brass soil test sieves stacked so that the mesh size decreased from the top sieve to the bottom sieve.

Three different feeding experiments were conducted using one fish in each experimental tank. In the first experiment (Consumption Amount) we offered each of four pile perch 100 extra-large (>6.3 mm shell width) *L. sitkana* placed at the bottom of the tank. After 24 h we recorded the number of live snails above, at, and below the water line and then removed the live snails and the shell fragments from each tank. This experiment was continued for nine replicate days. We chose not to use repeated measures analysis of variance (ANOVA) because our primary objective was to compare the consumption rates of the different fish rather than trends over time. Instead, we used a one-way ANOVA with FISH as the factor and then used Bonferroni pairwise comparisons to determine whether some individual fish ate more than others. We used version 5 of the statistical package SYSTAT for this and all other statistical analyses (SYSTAT 1992).

In the second experiment (Size-Selection) we offered each of four pile perch 100 extra-large and 100 small (3.35 mm < shell width < 4.0 mm) *L. sitkana*. After 24 h we recorded the number of live snails of each size-class above, at, and below the water line. We then removed the live snails and the shell fragments from each tank. This experiment was conducted for 6 days. To analyze the data we used three-way ANOVA with DAY, FISH, and SIZE as the factors and included only the interaction we thought most important, FISH × SIZE, in our model. One fish did not eat and was excluded from further analysis.

In the third experiment (Consumption Rate) we opened the crack in the plywood cover to 10 cm and offered each of four pile perch 20 large *L. sitkana* (4.75 mm > shell width < 6.3 mm). We then used a stopwatch to record the time it took the fish to crush each snail. We noted that only certain fish would feed while being observed.

Field Transects

In 1998 we deployed two 50-m transect lines at Pebble Beach (below the *Fucus* zone) parallel to the depth contours at 0.8 m and 1.1 m above 0.0 datum (Canadian Hydrographic Services). The transects were surveyed for pile perch and striped perch densities. Counts were done using SCUBA during high tides of 3.0 m or greater such that the upper transect (1.1 m) was in at least 1.9 m of water. Two observers swam along the transect line, one on each side, for about 15 min recording fish densities and size classes within 2 m of their side of the line. Fish size-classes were divided into 5-cm intervals from a minimum length of 5 cm to a maximum length of 40 cm. A total of five surveys were done in July 1998. We did four similar transect surveys between June 28 and July 1, 1999, except that these transect lines were at 0.0 m and 1.3 m above 0.0 datum (Canadian Hydrographic Services). In 1999, we tested how good the divers were at estimating the total length of the fish by placing models of different sizes of fish underwater at distances from 2–6 m from each diver and asking her to estimate its total length.

We estimated the abundance and mean size of mollusc prey at Pebble Beach by counting and measuring the molluscs in five 10-cm × 10-cm quadrats sampled at random along a tape measure placed on the beach, parallel to the water's edge, at low tide. The sampling was repeated at 1.5 m, 2.2 m, 2.8 m, and 3.2 m above 0.0 m datum. Because only one *L. sitkana* was found in the quadrats, an additional search was done to find *L. sitkana* by walking along the entire beach at low tide and turning over rocks for a total of 2 h. The abundances were then compared with estimates of *L. sitkana* density done by McCormack at the same site in 1981.

Field Experiments

In 1999 we used SCUBA to deploy three high-density and three low-density replicate patches of snails each day at high tide for a total of 12 days. A container with either a high-density patch (n = 50 snails) or a low-density patch of *L. sitkana* (n = 5 snails) was chosen at random from the mesh bag carried by the divers. The divers opened the container, and the snails were placed on boulders along the 1.3-m depth transect line. We chose boulders that were flat on top, about 0.3–0.6 m in diameter and 0.3–0.5 m high, and cleared them of macroalgae. This clearing was done to reduce variance among replicates caused by the snails hiding more effectively on some rocks than on others. After 40–50 min the divers returned to the boulder, collected all the live snails and shell fragments from the boulder and surrounding area, and placed them in labeled containers.

All shell fragments we collected from our experimental boulders could be attributed to predation by fish and not by crabs. In our laboratory experiments we noted that pile perch preying on snails immediately spat out small broken pieces of shell body whorl. However, they swallowed the columella and later excreted it in a mucus-coated pellet onto the tank floor. All shell fragments found in our field experiment were small broken pieces, and no columellas were seen. We also did not see pelleted fragments of columellas, probably because fish retreated to the subtidal before defecating. This is distinct from shell fragments formed as a result of predation by crabs, which typically have either an intact columella with a spiral gouge up the body whorl or broken pieces of columella (Zipser & Vermeij 1978, Lawton & Hughes 1985, Behrens Yamada & Boulding 1996).

Upon returning to the laboratory we counted the number of replicate patches in which we found shell fragments. We also counted the percentage of live snails that we had deployed that were recovered. The data were analyzed with contingency table analysis and with ANOVA.

Contingency Table Analysis

The different dates of the experiment were categorized into three separate spring (or large) tide series: A, B, and C. Tide A refers to dives from June 28 to July 1, Tide B is from July 12 to July 14, and Tide C is from July 29 to August 3, 1999. We assumed predation by pile perch when we recovered shell fragments on or near the rocks where snails were deployed. First, tidal series A–C were compared with each other in a pairwise fashion to test for differences in the mean percentage of the deployed patches that experienced predation using Fisher's Exact Test. Tidal series B and C showed no differences in mean percentage predation per day; they were therefore lumped together. Differences in mean percentage predation between high- and low-density patches were then compared within the two new groups using Fisher's Exact Test.

ANOVA

We compared the mean percentage of snails we recovered in the high patches vs. the low patches across the 12 days using a factorial ANOVA model with date and treatment as the factors. We then used Fisher's Least Significant Difference test to determine which pairs of means were significantly different.

RESULTS

Laboratory Experiments

The four pile perch in the consumption experiment ate an average of 33.3 ± 6.3 snails per day (mean ± SE). The largest fish (total length = 330 mm) ate significantly more snails ($P < 0.006$) than one of the smallest fish (total length = 280 mm). We observed that when the *L. sitkana* were placed in the bottom of the tanks they eventually crawled up to or above the water line, which made them inaccessible to the fish. We therefore reanalyzed the data considering only the consumption rate of the snails found at or below the water line but got very similar patterns. The fish ate

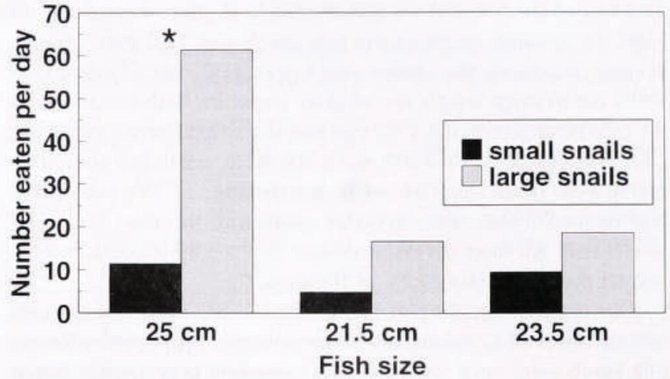

Figure 1. Size-selection for larger snails (*Littorina sitkana*) in the laboratory consumption experiment. *indicates a fish which ate significantly more large snails (Bonferroni pairwise comparisons, $P < 0.05$).

32–61% of the snails available with the largest fish again eating significantly more than the smallest fish ($P = 0.033$).

Only the largest of the three remaining pile perch (total length = 330 mm) in the size-selection experiment showed a significant preference for the extra-large size-class of *L. sitkana* over the smallest size-class (Fig. 1). There was a significant interaction between FISH and SIZE ($P < 0.001$) but no significant effect of DATE ($P = 0.319$).

The laboratory consumption experiment verified that the pile perch were very efficient predators on the snails, but only one fish would feed while being watched. One 250-mm fish required only 42.9 ± 8.02 sec (mean ± SE, $n = 19$) to consume each large *L. sitkana* (shell length 10 mm). The same fish became even more efficient at eating the snails by the next day and required only 19.2 ± 5.61 sec (mean ± SE; $n = 20$) to consume each snail.

Field Transects

The average density of pile perch in the intertidal at high tide was moderately low and was concentrated in the middle intertidal zone. In 1998, the average density of pile perch in the 0.8- and 1.1-m transects combined was an order of magnitude higher than the average density of striped perch (Table 1). In 1999, the densities of pile perch and striped perch in the 1.3-m transect were similar to those observed in the 0.8- and 1.1-m transects in the previous year (Table 1). However, in 1999 we also surveyed a 0.0-m transect where we observed no striped or pile perch (Table

TABLE 1.

Density of pile perch and striped perch in 1998 and 1999 in transects at Pebble Beach near Bamfield Marine Station.

Year	Species	Mean density	SE	n[d]
1998[a]	Pile perch	0.119/m^2	0.0205	20
	Striped perch	0.0205/m^2	0.0055	20
1999[b,c]	Pile perch	0.124/m^2	0.0221	16
	Striped perch	0.0275/m^2	0.00818	16

[a] Densities are taken from an average of 0.8 m and 1.1 m above 0.0 datum transects.

[b] Densities are taken from 1.3 m above 0.0 datum transect.

[c] No fish were seen at 0.0 m; $n = 6$.

[d] n is number of transects surveyed.

1). Most of the fish that we observed in both years were small. In 1998 the average length of the pile perch was 12.0 mm, and the average length of the striped perch was 11.2 mm (Table 2). In 1999, the average length was slightly larger for both species, with the pile perch averaging 15.2 mm and the striped perch averaging 13.5 mm (Table 2). In 1998 most fish were small, but some pile perch were more than 30 cm in length (Fig. 2). We found that experienced divers were good at estimating the total length of model fish. All three divers were able to place the models into the correct 5-cm size-class 95% of the time.

Our quadrat sampling of Pebble Beach estimated that the current densities of *L. sitkana* and other potential prey species for the pile perch were very low. The most common prey species found were the gastropods *L. scutulata* and *Tegula funebralis*, and even these were not abundant (Table 3). *L. sitkana* was especially rare, with only one found in the entire quadrat survey and only three more found after walking the entire beach. The density of mussels (*M. trossulus*) was very low, but the abundance of barnacles (*Balanus glandula*) was high.

Field Experiments

Contingency Table Analysis

A total of 40% of all the patches deployed in this experiment (n = 70) were found by fish within 50 min. We found that the number of patches where we found shell fragments (i.e., predation) was significantly higher in the second and third tidal series than the first (A vs. B: $P < 0.004$, df = 1, n = 41; A vs. C: $P < 0.036$, df = 1, n = 52). The percentage of patches in each tidal series where we found shell fragments is shown in Figure 3. The second and third tidal series were not significantly different from each other in the number of patches that experienced predation and were thus lumped together for analysis of treatment effects (B vs. C, P = 0.37, df = 1, n = 47). In the first tidal cycle, significantly more of the high-density treatments experienced predation (Table 4). In the second and third tidal series, there was no difference in the percentage of the patches that experienced predation between the high- and the low-density treatments (Table 4). The mean percentage predation in the low- and high-density treatments is shown in Figure 3 for each tidal series. In all patches where shell fragments were found, an average of 81 ± 0.06% (n = 26) of the snails deployed were eaten.

ANOVA

A significant DATE × TREATMENT interaction was found for the percentage of recovered snails (Table 5); therefore, we present

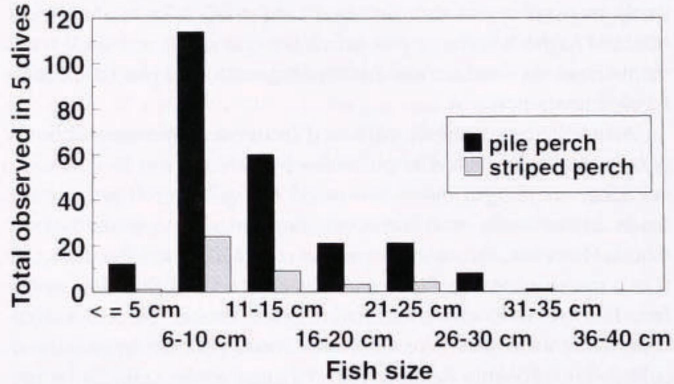

Figure 2. Size-distribution of the pile perch, *Rhacochilus vacca*, and the striped perch, *Embiotoca lateralis*, seen in intertidal transects in 1998.

only the interaction means (Fig. 4). We recovered a significantly lower proportion of snails from the high-density patches than from the low-density patches on 2 of the 12 days of the experiment (June 28 and July 13). We observed an inverse density-dependent trend on 3 days, but these were not significant (Fig. 4).

The divers made some additional observations on foraging pile perch. In 1998, divers at Pebble Beach watched two 35-cm pile perch consume a patch of deployed snails and noted that they required only 9 min to consume a total of 17 snails. As previously mentioned, in 1999, divers left the patches for at least half an hour after they had deployed the snails. However, by the third spring tidal series they noticed that some fish began to circle the divers before all the snails were deployed. Although divers were not present during the entire time that the snail patches were deployed, any predation that was observed was always by pile perch.

DISCUSSION

This study shows that pile perch were the major consumers of the large *L. sitkana* we deployed in the Pebble Beach intertidal during diurnal high tides. Striped perch were much less common in the field transects at Pebble Beach, and we did not observe striped perch eating the snails we deployed. The pile perch has previously been implicated as an important predator of littorinid gastropods on wave-sheltered shores of the Northeastern Pacific (McCormack 1982, Boulding et al. 1999). However, there has been some question about its importance because at some sites predation rates by

TABLE 2.

Mean size of pile perch and striped perch in 1998 and 1999 in transects at Pebble Beach near Bamfield Marine Station.

Year	Species	Mean size (cm)	SE	n
1998[a]	Pile perch	12.01	1.35	237
	Striped perch	11.17	1.14	41
1999[b]	Pile perch	15.2	1.63	99
	Striped perch	13.5	3.06	22

[a] Lengths are taken from an average of 0.8 m and 1.1 m above 0.0 datum transects.

[b] Lengths are taken from 1.3 m above 0.0 datum transect.

TABLE 3.

Abundance and mean size (shell length) of mollusc prey present at Pebble Beach near Bamfield Marine Station[a]

Tidal height[b]	Prey species[c]	Mean density (m^{-2}) ± SE	Mean size (mm) ± SE	n
1.5 m	*Littorina scutulata*	10.0 ± 3.36	5.21 ± 6.44	50
	Tegula funebralis	1.6 ± 1.16	12.60 ± 1.20	8
2.2 m	*Littorina scutulata*	15.6 ± 4.09	5.77 ± 5.90	78
2.8 m	*Littorina scutulata*	8.4 ± 2.42	5.59 ± 1.96	42
3.2 m	*Littorina scutulata*	4.4 ± 1.80	6.09 ± 0.50	22

[a] A total of five quadrats were done per tidal height.

[b] Tidal height above 0.0 datum.

[c] Also one *Littorina sitkana* shell length 9.0 mm.

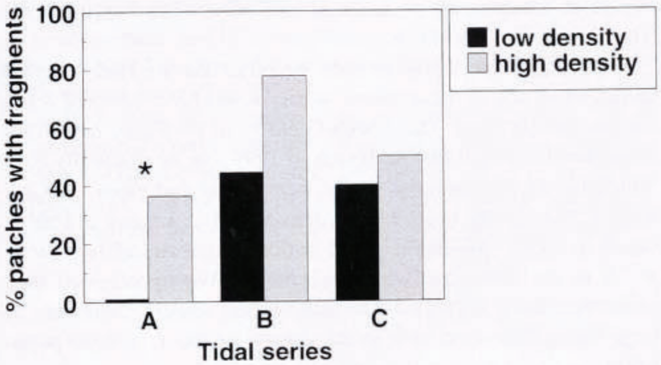

Figure 3. Percentage of snail patches deployed where shell fragments were found at Pebble Beach in high-density and low-density treatments for tidal series A (June 28 through July 1, 1999), B (July 12 through July 14, 1999), and C (July 28 through August 3, 1999). *Significant differences between densities (Fisher's Least Significant Difference test, $P < 0.05$).

pile perch have been estimated to be close to zero (Behrens Yamada & Boulding 1996). In our experiment the pile perch found 40% of the deployed patches of snails. Within the patches found by the fish, the consumption rate averaged 81%. This suggests that pile perch have the potential to severely limit the size of *L. sitkana* populations. We doubt that predation rates on the natural snail population on Pebble Beach are nearly so high because the population is currently at a very low density. However, natural populations of *L. sitkana* do occur at higher densities at other locations (McCormack 1982), and pile perch predation rates on these populations may be high.

Adult pile perch exhibited a very high foraging efficiency when feeding on large *L. sitkana*. The pile perch consumed snails at a very high rate (19.1 sec per snail). The largest fish showed a size preference for large snails, which makes it unlikely that certain size-classes of *L. sitkana* have a size refuge from pile perch. In addition, large pile perch were moderately abundant in the intertidal zone at high tide at Pebble Beach and reached fish densities of $0.119/m^2$. This is an order of magnitude higher than the only previously reported densities for pile perch of $0.0039–0.0109/m^2$ in kelp beds off southern California (Ebeling et al. 1980). These data suggest that the pile perch could be an important limiting factor for the population of *L. sitkana* at this site.

TABLE 4.

Number of high- and of low-density patches of *Littorina sitkana* deployed at Pebble Beach in 1999 that were recovered with and without shell fragments resulting from predation by pile perch.

Tide series	Patches with fragments	Patches without fragments	df	*P* value[d]
A,[a] High-density (50 snails)	0	12	1	
Low-density (5 snails)	4	7		0.037
B[b] & C[c], High-density (50 snails)	10	14	1	
Low-density (5 snails)	14	9		0.248

[a] Trials performed from June 28 through July 1, 1999.
[b] Trials performed from July 12 through July 14, 1999.
[c] Trials performed from July 28 through August 3, 1999.
[d] Probability values are from Fisher's Exact Test for particular tide series.

TABLE 5.

Analysis of Variance of percentage of snails recovered.[a] Factors are DATE (Date of Experiment) and DENSITY (Density of Snails).

Source	SS	df	MS	*F*	*P* value
DATE	8.469	11	0.770	3.827	0.001
DENSITY	0.760	1	0.760	3.777	0.058
DATE × DENSITY	4.833	11	0.439	2.184	0.032
Error	9.255	46	0.201	0.201	

[a] Percentage of live snails (*Littorina sitkana*) recovered after exposure to predation during one high tide period. Data were transformed with an angular transform before analysis.

When a pile perch found a patch of deployed snails in our field experiment, it ate the majority of the snails. Density-dependent predation can result from a predator finding high-density patches of prey more often or from the predator spending more time in high-density patches once they are found (Krebs & Davies 1991). Consumption rates were high in all patches that were found suggesting that the fish were not spending more time in high-density patches than in low-density patches. Therefore, any density-dependent predation we observed probably resulted from the fish finding high-density patches more easily than low-density patches. No work has been done specifically on the searching behavior of the pile perch, but they are known to be visual predators that feed during the day (Ellison et al. 1979). Many other benthivorous fishes that feed diurnally are know to use vision almost exclusively to find prey (Keenleyside 1979).

Our analysis by tidal series found significant density-dependent predation in the first tidal series (A) but not the second (B) and third (C). We doubt the lack of significance in tidal series B and C is due to low statistical power because sample sizes were smallest in tidal series A. Furthermore, we also observed a low frequency of density-dependent predation when we analyzed our experiment with ANOVA, detecting it on only 2 of the 12 days.

There may be several reasons why our study did not frequently detect density-dependant predation of *L. sitkana* by pile perch. In tidal series C, the divers noticed several large pile perch following them that consumed the snails as soon as they were deployed.

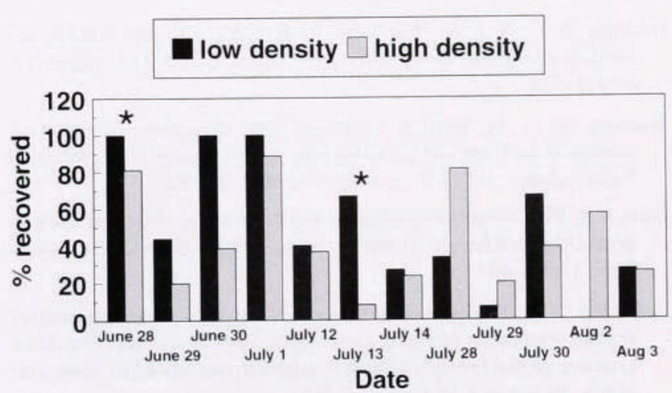

Figure 4. Mean percentage of snails (*Littorina sitkana*) recovered from the low- and high-density treatments on six different sampling dates. *Dates on which a significantly higher percentage of snails was recovered from the low-density treatment (Fisher's Least Significant Difference test, $P < 0.05$).

This suggests that the fish had become habituated to the divers and used their presence as a cue to find the patches of snails. This behavior may have made it difficult to detect density-dependent predation.

Another explanation for the low frequency of density-dependent predation is that the high consumption rate of snails by pile perch in both the high- and the low-density treatments made it difficult to detect subtle density-dependent predation. Our ability to detect density dependence was further reduced by our inability to distinguish snails that had been consumed from those that had simply migrated away from the top of the boulder. A single missing snail would affect the percentage recovered in the low-density treatment much more strongly than in the high-density treatment. For example, two snails migrating from the low density-treatment where a total of only five were deployed would result in a 60% recovery of snails, whereas two snails migrating from the high-density treatment would result in a 96% recovery.

In addition, the low-density treatments may have been in fact high density when compared with the present ambient density of possible prey species at this site. Almost no *L. sitkana* were found in our quadrats at Pebble Beach. Two other gastropod species were present at Pebble Beach, *L. scutulata* and *Tegula funebralis*, but neither are preferred prey of pile perch. Adult *Tegula* are rejected by pile perch (McCormack 1981), whereas the *L. scutulata* present on this beach averaged only 5.21 mm in shell length and are likely too small to be profitable. We suspect that the intense predation by pile perch at Pebble Beach keeps the densities of their preferred prey very low. Indeed, the low densities of potential prey items found there in 1999 cause us to question why the fish are venturing in the intertidal at all. The pile perch may be feeding on the barnacles there as was observed by our divers in 1998. Barnacles were reported to make up 56–75% of the stomach contents of large pile perch foraging on an artificial reef off the Washington coast (Hueckel & Stayton 1982).

Given the high predation rates we observed, we find it highly unlikely that any of the deployed snails would have survived if left out for another hour. The ambient density of prey may have been exceptionally low at Pebble Beach in 1999 that an unusually high proportion of the deployed snails were found and eaten. McCormack (1981) found much higher densities of *L. sitkana* at Pebble Beach in 1980 (10 snails/m^2 at 1.5 m tidal height and 970 snails/m^2 at 2.2 m in 1980) than we did (Table 3). We hypothesize that, rather than being regulated at an equilibrium density, there may be large fluctuations over time in the density of this *L. sitkana* population.

This study did not find predation by the pile perch on deployed patches of littorinid prey to be consistently density dependent. Consequently, we lack strong evidence that this predator has the potential to be an important regulating factor for the *L. sitkana* population at this site. Nevertheless, its high success rate at locating patches, its high foraging efficiency, and the high mortality rates we observed for the deployed prey suggests that the pile perch is an important limiting factor for the snail population at this site.

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