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INDIRECT EFFECTS, PREY SUSCEPTIBILITY, AND HABITAT SELECTION: IMPACTS OF BIRDS ON LIMPETS AND ALGAE[1]

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Abstract. I experimentally manipulated avian predation pressure in an intertidal community to determine its direct and indirect influence on the abundance and distribution of three limpets and their algal food source. Birds reduced the overall abundance of *Lottia digitalis* only; *L. strigatella* abundance increased and the abundance of *L. pelta*, the species most frequently consumed, did not change. Through crypsis, the goose barnacle *Pollicipes polymerus* and the mussel *Mytilus californianus* indirectly affected the abundance of *L. digitalis* and *L. pelta* in opposite ways by changing their risk of succumbing to bird predation. These limpets also exhibited strong habitat selection for their cryptic substrates. By altering the amount of preferred habitat, birds indirectly influenced limpet abundance: gull predation reduced the area covered by *P. polymerus*, releasing *M. californianus* from space competition. By consuming limpet grazers and reducing space competition, birds indirectly enhanced the abundance of algae. *L. strigatella* sizes generally fell below the range of limpet sizes consumed by birds. Consequently, birds indirectly increased *L. strigatella* density by reducing the intensity of exploitative competition with other limpet species; *L. strigatella* biomass declined significantly with increasing biomass of the other two limpets, and with decreasing algal cover. These results demonstrate that indirect effects and apparently adaptive behaviors can counteract (or reinforce) direct interactions between species pairs, suggesting that conclusions from short-term experiments emphasizing species pairs can be tenuous.

Key words: algae; crypsis; habitat selection; Haematopus bachmani; *herbivory; indirect effects;* Larus glaucescens; Lottia; Mytilus californianus; Pollicipes polymerus; *temporal scale.*

INTRODUCTION

Ecologists have long been interested in determining the causes of patterns in species abundance across different habitats, and have recently focused on the ecological and evolutionary roles that other species play in determining these patterns. Lately, attention has been drawn toward the relative importance of the direct effects (effects of one species on another as a consequence of a physical interaction between the two) and the indirect effects (effects that are not the result of a physical interaction) of species interactions on the distribution of species among habitats. The direct effects of one species on the distribution of another across habitats via interference competition (Connell 1961, 1983, Orians and Willson 1964, Davis 1973, Schoener 1983) and predation (Paine 1966, 1974, Connell 1980, Werner and Gilliam 1984, Mercurio et al. 1985, Sih et al. 1985, Martin 1988, McPeek 1990) have been investigated in detail, but the indirect effects of one species on the distribution of another, aside from exploitative competition (reviewed by Connell 1983, Schoener 1983), have been less studied, perhaps because indirect effects are often considered relatively unimportant compared to direct interactions (Yodzis 1988).

Although direct interactions may be more important to species populations than indirect effects because many (but not all; J. T. Wootton, *unpublished manuscript*) instances of indirect interactions arise from a series of direct interactions, this does not mean that indirect interactions are unimportant. The direct interactions impinging on a particular species may not be as strong as the direct interactions comprising an indirect effect (Paine 1966, 1980, Levine 1976, Bender et al. 1984, Davidson et al. 1984, Brown and Munger 1985, Yodzis 1988). Experiments focused on interacting pairs of species may not reveal important indirect effects on community structure, however, because indirect effects often operate via a third species, often take longer than direct effects to detect, and are often more difficult to detect experimentally (Davidson et al. 1984, Brown and Munger 1985). Despite the relative difficulty of detecting indirect effects, there is now a growing body of studies documenting important indirect interactions (Paine 1966, 1980, Estes and Palmisano 1974, Colwell and Fuentes 1975, Davidson et al. 1984, Brown and Munger 1985, Carpenter et al. 1985, Power et al. 1985, Sih et al. 1985, Hay 1986,

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Schmitt 1987, Carpenter 1988, Kneib 1988, Pfister and Hay 1988, Power 1990). Here I present experiments demonstrating that bird predation can influence the distribution and abundance of intertidal limpets and algae through a variety of direct and indirect interactions. I then compare the results of this longer term experiment with those of other experiments conducted over short time scales.

The study system

Limpet distributions in the mid-intertidal zone (Ricketts et al. 1985) of the west coast of North America appear to be separated between habitats through the influence of predation. In this zone *Lottia (Collisella) digitalis* (see Lindberg 1986 for a recent taxonomic treatment), a light-colored limpet, tends to occur on light-colored goose barnacles (*Pollicipes polymerus*), whereas *L. pelta*, a dark-colored species, occurs primarily on dark California mussels *Mytilus californianus* (Giesel 1970, Mercurio et al. 1985). Birds, particularly American Black Oystercatchers (*Haematopus bachmani*), can greatly reduce limpet densities, as shown by (1) studies of oystercatcher feeding rates (Hartwick 1976, Frank 1982, Lindberg et al. 1987, Wootton 1990), (2) censuses of apparently accessible and inaccessible habitats (Frank 1982, Hahn and Denny 1989), and (3) short-term (<1 yr) cage experiments (Mercurio et al. 1985, Marsh 1986*a*; J. T. Wootton, *unpublished manuscript*). Feeding observations suggest that Glaucous-winged Gulls (*Larus glaucescens*) also contribute significantly to limpet mortality (Wootton 1990).

Giesel (1970) proposed that *L. digitalis* persisted on *P. polymerus* in the face of bird predation because it cryptically matched its background. Experimental tests of interactions between predation rate and habitat have been equivocal. Hartwick (1981) found no evidence of color-dependent predation on rock substrates when he presented arrays of different-colored limpets to feeding oystercatchers. Mercurio et al. (1985) performed caging experiments on *L. pelta* and *L. digitalis* on different substrates. Their results indicated that *L. pelta* survived better on mussels than on barnacles when exposed to bird predation, and that both species survived better on their matching substrate in an area of low bird predation but high fish predation. Furthermore, Lindberg and Pearse (1990) showed that *L. digitalis* can modify its shell color to better match the substrate on which it occurs. *Lottia strigatella*, the third common species of limpet living in the *M. californianus/P. polymerus* zone, has not been investigated for responses to bird predation.

Previous experiments testing whether bird predation can lead to habitat separation were conducted in less than a day. Because many factors other than predation may influence limpet survival and reproduction, short-term studies may not be conducted over a sufficiently long time span to detect the overall importance of predation. Specifically, direct effects of intraspecific competition or indirect effects such as changes in the abundance of competitor or mutualist species following predation may offset the effects of predation over longer time scales. For example, birds differentially consume limpet species on eastern Pacific rocky intertidal communities (Frank 1982, Lindberg et al. 1987, Hahn and Denny 1989), altering the abundance of potential competitors. Birds also feed on the substrates (*P. polymerus* and *M. californianus*) upon which these limpets live (Marsh 1986*b*, Wootton 1990), possibly indirectly affecting predation susceptibility and habitat availability.

Methods

Simon's Landing, on the eastern side of Tatoosh Island (48°23′ N, 124°44′ W), Washington state, served as the study site (see Paine and Levin 1981 for a picture and a description of the island). Simon's Landing consists of a long, shallowly sloping intertidal bench that receives relatively strong wave wash.

To assess the role of predation in determining limpet distribution and density, I excluded bird predators from areas in large ($\approx$10 m^2), 1-yr-old gaps in the mussel bed, dominated by *P. polymerus*, the acorn barnacle *Semibalanus cariosus*, and foliose algae (mostly *Porphyra* and *Ulva* spp.; see Paine and Levin 1981) using cages made from vinyl-covered wire letter baskets (29 × 34 × 7.5 cm, with 4 × 2.5 cm mesh on the top, 7.5 × 2.5 cm mesh on the sides; Better Office Products, Carson, California) placed upside-down. I attached the baskets to the rock by strapping them at the corners with 2 mm diameter (14 gauge) insulated copper wire to stainless steel eyescrews embedded in the rock with wall anchors. The large mesh size of the cages allowed free access to mobile invertebrate predators (small snails, crabs, and starfish) with little alteration of the physical environment. Because of the large mesh size, some bird predation also occurred around the periphery beneath cages (J. T. Wootton, *personal observation*). I paired each cage (n = 15 replicates) with an immediately adjacent unmanipulated plot in the same gap to serve as a control area. Experiments began in May 1987, following gap formation, and were censused in July 1989.

Cage artifacts, such as physical alteration of the environment or exclusion of unintended predators, are always a concern in this type of experiment. To test for cage artifacts, I placed cages (n = 5 replicates) on vertical walls dominated by *P. polymerus*, and designated adjacent uncaged plots as paired controls; the vertical walls were accessible to any benthic-feeding fish (e.g., surfperch, *Embiotoca lateralis*), but not to birds (Hahn and Deny 1979, Frank 1982; J. T. Wootton, *personal observation*). Other experiments using this cage design have revealed no cage artifacts (J. T. Wootton 1990; *unpublished manuscript*).

The cages were unlikely to have inadvertently manipulated other large, mobile predators. Surfperch ap-

parently do not forage effectively in areas of high wave wash (Marsh 1986*b*; C. Pfister, *personal communication*), and any effects they might have would be detected in cages on vertical walls. Although the large starfish *Pisaster ochraceous* is an important predator in the lower intertidal zone, it cannot feed effectively within the mussel bed in the middle intertidal zone (Paine 1974, 1980, Paine and Levin 1981). Large crabs (*Cancer* spp.) and sea otters (*Enhydra lutris*) are not found near the intertidal zone of Tatoosh (Paine 1980; J. T. Wootton, *personal observation*).

I recorded the abundance of *L. digitalis, L. pelta,* and *L. strigatella* in all cage and control plots, and noted whether each individual *L. digitalis* or *L. pelta* was on *P. polymerus, M. californianus,* or another substrate. Because the plots were not destructively sampled, some limpets that occurred on the underside of mussels were probably not counted. As an index of habitat availability, I also measured the percent area covered by *P. polymerus* and *M. californianus* in each plot using a quadrat divided into 100 squares. Likewise I measured the percent area covered by foliose algae, an estimate of one limpet food source (Dayton 1971, Nicotri 1977, Lubchenco and Gaines 1981, Johnson 1989) that might increase if birds reduced limpet density.

I measured the shell lengths of *L. digitalis, L. pelta,* and *L. strigatella* in six of the replicates, and estimated mean limpet biomass in each using regressions of shell length on dry mass (R. T. Paine and J. T. Wootton, *unpublished data*):

$$\ln W_{L.d.} = -4.29 + 3.30 \ln S \quad (r^2 = 0.973),$$

$$\ln W_{L.p.} = -4.47 + 3.26 \ln S \quad (r^2 = 0.947), \quad \text{and}$$

$$\ln W_{L.s.} = -4.09 + 2.27 \ln S \quad (r^2 = 0.767),$$

where $W_{L.d.}$, $W_{L.p.}$ and $W_{L.s.}$ are dry tissue masses in grams of *L. digitalis, L. pelta,* and *L. strigatella,* respectively, and S represents shell length in centimetres. I estimated total limpet biomass per unit area for control vs. predator exclusion treatments by taking the product of the limpet density in each replicate and the mean biomass per individual of each treatment obtained from the size analysis.

To derive size distributions of limpets fed upon by birds, I noted areas where Black Oystercatchers were feeding, and thoroughly searched these areas for all of the empty shells left behind after the foraging bout. Oystercatchers only feed on limpets by removing them from the shell, rather than by swallowing them whole (Frank 1982, Lindberg et al. 1987, Hahn and Denny 1989, Wootton 1990), so that empty shells reflect the actual prey sizes taken. Any bias against my finding small limpets was probably slight given my efforts to thoroughly search an area, and would not be expected to differ between treatments within the experiments or in observations of limpets consumed by birds.

To assess whether limpets actively selected the sessile species upon which they appeared most cryptic, I conducted a series of habitat choice experiments. During 11–12 July 1991, I cleared all limpets from four areas (53 × 43 cm) covered by a mixture of *M. californianus* and *P. polymerus,* then introduced 40 *L. digitalis* and 40 *L. pelta* (12–16 mm in length) in a uniform pattern within each area. I then protected each plot with a cage made from a wire storage basket to insure that no confounding effects of selective predation by birds occurred, and censused those limpets remaining in the plot after 24 h to determine the substrate upon which they occurred.

To assess possible competition for space between the sessile species that the limpets lived upon, I conducted another set of experiments to determine whether *P. polymerus* negatively affected *M. californianus.* I removed *P. polymerus* from 29 × 34 cm plots consisting of a mixture of the two species, leaving adjacent 29 × 34 cm plots as paired controls. The five replicates were initiated in May 1987, and censused in October 1987.

Statistical analysis

For planned comparisons of limpet and algae density, I used Wilcoxon signed ranks tests for paired samples or (for normally distributed data) paired t tests. Most tests were two tailed, reflecting the possibility of observing indirect effects of unknown direction. Failure of normality and homogeneity of variance assumptions precluded the use of ANOVA to test for interactions between bird predation and habitat on limpet density. Furthermore, ANOVA does not test for interactions in a particular direction, but the bird predation × habitat interaction predicts a specific outcome (lower probabilities of predation on cryptic habitats). Instead, I used one-tailed Wilcoxon paired ranks tests to investigate the interaction, comparing the product of the densities on cryptic substrates without birds and on noncryptic substrates with birds to the product of the densities on noncryptic substrates without birds and on cryptic substrates with birds.

This test for an interaction between variables compares treatments in a similar way to a blocked ANOVA testing for an interaction, and can be explained as follows. Suppose N represents the density of limpets surviving in the absence of predators on a cryptic substrate, b is the proportional effect on N of bird predation, c is the proportional effect on N of switching from a cryptic to a noncryptic substrate in the absence of bird predation, and d is a factor describing the interaction between bird predation and habitat crypticity. Then the combined effect of introducing bird predation and changing to a noncryptic substrate should be bcd, and in the absence of an interaction ($d = 1$), the following relationship among limpet densities in the different treatments should hold:

$$N(bcdN) = (bN)(cN), \; d = 1. \qquad (1)$$

However, if bird predation on limpets is more intense

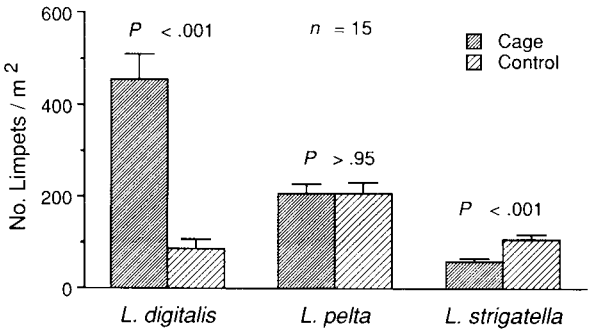

FIG. 1. Density of three limpet species (*Lottia digitalis*, *Lottia pelta*, and *Lottia strigatella*) in control plots (light bars) and plots protected from bird predation for two years via cages (dark bars) (means and 1 SE). $n = 15$.

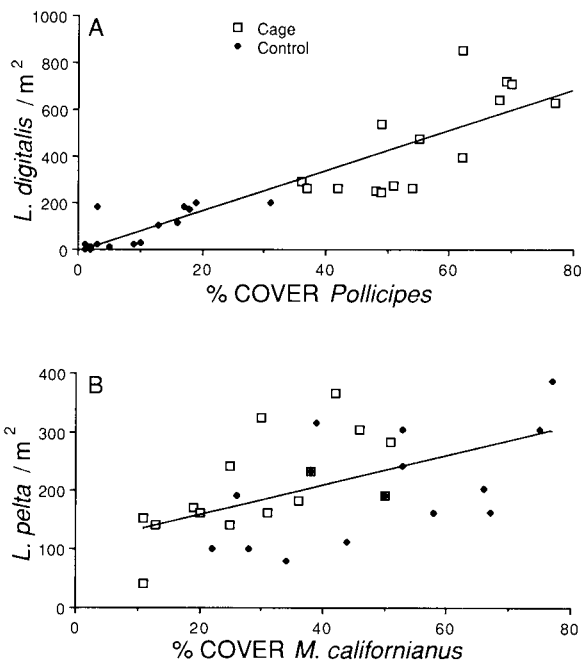

FIG 2. Limpet density plotted against percent cover of cryptic substrate species. □ represent cages, ◆ represent controls. Lines of best fit from linear regression. (A) *Lottia digitalis* density vs. percent cover of *Pollicipes polymerus* (*L.d.* = −1.37 + 0.86[*P.p.*], $r^2 = 0.81$), (B) *Lottia pelta* density vs. percent cover of *Mytilus californianus* (*L.p.* = 10.6 + 0.25[*M.c.*], $r^2 = 0.28$).

in noncryptic habitats ($d < 1$), then the proportional effect of bird predation and a noncryptic habitat on limpet density should be $< bc$, so the left-hand side of Eq. 1 should be lower than the right-hand side, yielding the following relationship among treatments:

(cryptic, no birds) × (noncryptic, birds)
< (noncryptic, no birds) × (cryptic, birds).

In some cases, I applied least squares linear regression techniques to the data. These analyses tested for relationships among species that were predicted by hypotheses of the likely mechanisms causing any observed indirect effects of bird predation. Where required, data were transformed with natural logarithms or by taking reciprocals to achieve linearity.

To examine effects of bird predation on limpet size distributions, I compared mean lengths of limpets in cages with those in control areas using t tests or Mann-Whitney U tests, depending on whether or not parametric assumptions were met. Then, based on the size distribution of victims of Black Oystercatcher predation, I divided limpets into susceptible and nonsusceptible sizes and compared the percentage of susceptible limpets between cages and controls to determine whether any observed differences in size distributions between treatments resulted from a reduction of bird-susceptible sizes in control treatments.

To determine whether limpets actively chose to reside on their apparently cryptic habitat, I used one-tailed binomial tests to determine whether the proportion of limpets on their cryptic substrates (i.e., *L. digitalis* on *P. polymerus* and *L. pelta* on *M. californianus*) was significantly greater than the proportion of area covered by each sessile species in the habitat selection experiments. I then used Fisher's method for combining probabilities from independent experiments (Sokal and Rohlf 1981:779) to determine whether limpets exhibited a consistent pattern of preference for their cryptic habitats across all experiments.

RESULTS

Overall abundance

Limpet abundance did not consistently increase with the experimental reduction of avian predation pressure. *Lottia digitalis* density was >5 times higher when protected from bird predators (Wilcoxon paired ranks test, $P = .001$, Fig. 1). In contrast, *L. strigatella* density almost doubled in the presence of bird predators (paired

TABLE 1. Abundances of limpets, and of their sessile invertebrate habitats, on vertical walls under cages and in controls, $n = 5$ replicates. P values from paired t tests.

Species	Cage		Control		P
	Mean	1 SD	Mean	1 SD	
Lottia digitalis (no./m²)	75.1	81.0	127.8	160.2	>.2
Lottia pelta (no./m²)	95.3	21.0	83.2	39.6	>.6
Lottia strigatella (no./m²)	26.4	23.3	48.7	61.5	>.2
Pollicipes polymerus (% cover)	41.6	12.5	49.0	12.8	>.2
Mytilus californianus (% cover)	5.8	7.3	8.8	6.2	>.1

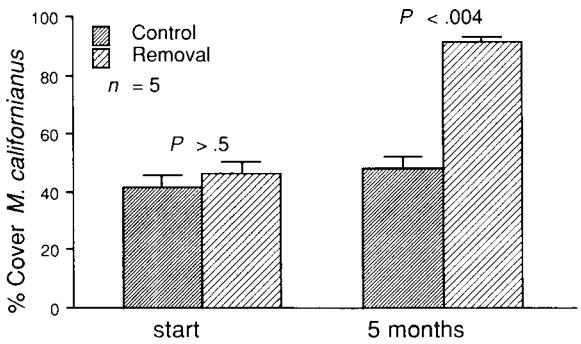

FIG. 3. The % area covered by *Mytilus californianus* in plots where *Pollicipes polymerus* was experimentally removed (darker bars) and in controls with *P. polymerus* (lighter bars) after 5 mo (means and 1 SE). $n = 5$.

t test, $P < .001$). Overall density of *L. pelta* did not differ significantly between treatments (paired *t* test, $P > .95$, Fig. 1). On vertical walls where birds could not forage, densities of the three limpet species and the sessile species comprising their habitat did not differ significantly between cage and control treatments (Table 1, paired *t* tests, all $P > .1$), thus I found no evidence of cage artifacts or important effects of fish predation. The difference in the effect of cages between horizontal and vertical substrates was not simply the result of lower statistical power. The means and standard deviations exhibited for the overall abundances of limpets and sessile species on horizontal benches would still be significantly different if they were derived from 5 rather than 15 replicates.

Habitat effects

L. digitalis and *L. pelta* abundance varied with the composition of sessile species dominating the community. *L. digitalis* density was correlated positively with *P. polymerus* cover (Fig. 2A, $r = 0.897$, $n = 30$, $P < .001$), whereas *L. pelta* density increased with *M. californianus* cover (Fig. 2B, $r = 0.528$, $n = 30$, $P < .01$).

Bird predators altered the habitat features (sessile species composition) where the limpets lived. Gull predation reduced goose barnacle cover; *P. polymerus* cover was higher under cages ($\bar{X} \pm 1$ SD $= 55.1 \pm 12.6\%$, $n = 15$) than in controls ($9.6 \pm 7.9\%$, paired *t* test, $P < .001$, Fig. 2A). Competition for space by *P. polymerus* reduced the abundance of *M. californianus*; *M. californianus* covered a significantly greater percentage of the area in plots where I removed *P. polymerus* compared to plots where *P. polymerus* remained intact (paired *t* test, $P < .004$, Fig. 3). Therefore, *M. californianus* covered a significantly higher percentage of the area in controls ($\bar{X} \pm 1$ SD $= 29.9 \pm 13.7\%$), where gulls fed on *P. polymerus*, compared to under cages ($48.7 \pm 17.6\%$, paired *t* test, $P < .001$, Fig. 2B).

The density of *L. digitalis* and *L. pelta* per unit area of habitat type changed between experimental treatments as expected under a hypothesis of bird predation. In comparison to controls, *L. digitalis* density increased when protected from bird predation on both cryptic (*P. polymerus*) and noncryptic substrates (Fig. 4, Wilcoxon test, $P < .065$ and $P < .004$, respectively). Although the overall density of *L. pelta* did not differ between treatments (Fig. 1), its density on both cryptic (*M. californianus*) and noncryptic habitats increased where I experimentally excluded birds, relative to controls (Fig. 4, paired *t* tests, $P < .01$ and $P < .004$, respectively).

The sessile species on which limpets occurred influenced the intensity of bird predation through crypsis. The effects of bird predation were significantly more severe on noncryptic substrates for both *L. digitalis* and *L. pelta*. When protected from bird predation, *L. digitalis* density increased by only 34% on cryptic *P. polymerus* habitats, but by 322% on non-*P. polymerus*

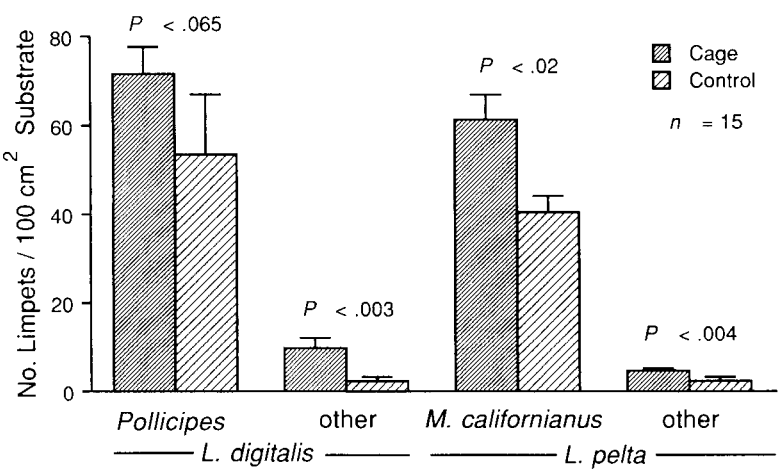

FIG. 4. Density of *Lottia digitalis* on *Pollicipes* and other substrates, and of *L. pelta* on *Mytilus californianus* and other substrates, in control plots (light bars) and plots protected from bird predation via cages (dark bars) (means and 1 SE). $n = 15$.

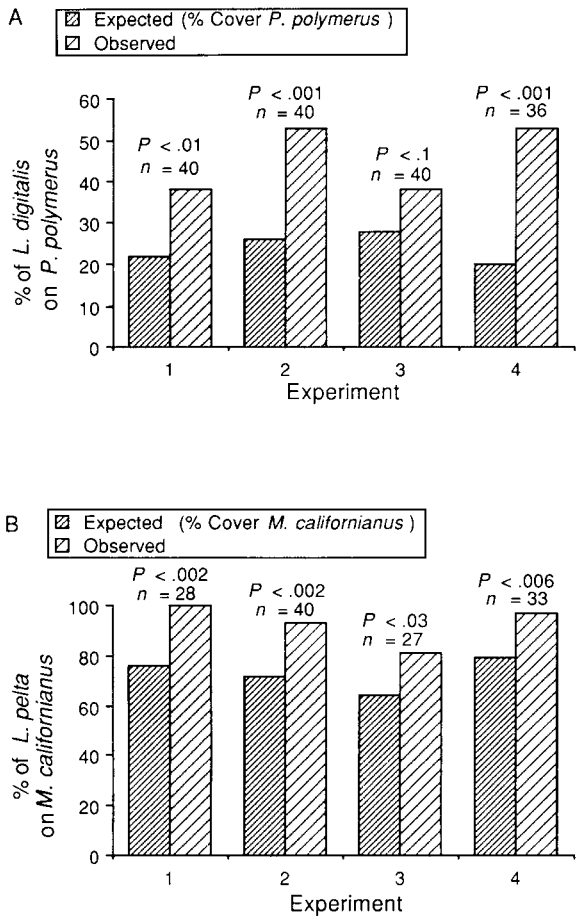

FIG. 5. Percentage of limpets on cryptic substrates (barnacles or mussels) after 24 h compared to the percentage of area covered by a substrate (= expected percentage of limpets on a cryptic substrate). Higher observed percentages indicate active habitat selection favoring the cryptic substrate. (A) *Lottia digitalis* on *Pollicipes polymerus*, (B) *Lottia pelta* on *Mytilus californianus*. n = number of limpets remaining after 24 h in each experiment.

habitats. Therefore, the product of *L. digitalis* densities on no bird-*P. polymerus* substrate and bird-non-*P. polymerus* substrate was significantly lower than the product of its densities on bird-*P. polymerus* substrate and no bird-non-*P. polymerus* substrate, indicating an important interaction between substrate crypticity and predation intensity (Fig. 4, Wilcoxon test, $P < .01$). Similarly, *L. pelta* density increased under cages by only 52% on cryptic *M. californianus* habitat, but by 91% on non-*M. californianus* habitat (Fig. 4). Therefore, the product of *L. pelta* densities on no bird-*M. californianus* substrate and bird-non-*M. californianus* substrate was significantly lower than the product of the densities on bird-*M. californianus* substrates and no bird-non-*M. californianus* substrate, again demonstrating an interaction between substrate crypticity and predation intensity (Fig. 4, Wilcoxon paired ranks test, $P = .045$).

Limpets preferentially selected the habitat that reduced their risk of predation by birds, a behavior expected to occur if the sessile species comprising the habitat indirectly affected limpet abundance by altering predation intensity. In all four 24-h habitat selection experiments, *L. digitalis* occurred on *P. polymerus* (Fig. 5A), and *L. pelta* occurred on *M. californianus* (Fig. 5B), at higher rates than expected on the basis of the proportional area covered by these substrates. With the exception of *L. digitalis* in experiment number 3 ($.05 < P < .1$), the percentage of limpets on cryptic substrates was significantly higher (one-tailed binomial tests, all $P < .03$) than the percentage of area covered by the cryptic substrate (Fig. 5), and combined probabilities from the four independent experiments indicated that the probability that the limpets were not actively choosing their cryptic substrate was very small (Fisher's method for combining probabilities, $P < .001$ for *L. digitalis* and for *L. pelta*). Consequently, where birds were excluded over a period of 2 yr, *L. digitalis* density was >10 times as high on *P. polymerus* as on non-*P. polymerus* substrates (Fig. 4, paired t test, $P < .0001$), and *L. pelta* density was almost 15 times as high on *M. californianus* as on non-*M. californianus* substrates (Fig. 4, Wilcoxon test, $P < .005$). Thus, the observed relationships between limpet abundance and the amount of area covered by the substrate on which they were most cryptic resulted from both reduced predation pressure and active habitat selection.

Size effects

Black Oystercatchers fed disproportionately on big limpets, and only consumed limpets 10 mm or more in length (Fig. 6A). Limpet sizes differed significantly between treatments in a manner consistent with the expected effects of Black Oystercatcher predation (Fig. 6B–E). In particular, lengths of *L. digitalis* under cages (mean ± 1 SD = 11.8 ± 0.3 mm) were 20% greater than in controls (9.8 ± 1.4 mm, U test, $P < .03$). Likewise, lengths of *L. pelta* under cages (9.8 ± 1.1 mm) averaged 15% greater than in controls (8.5 ± 0.3 mm, t test, $P < .04$). The percentage of limpets ≥10 mm was >1.7 times as high under cages as in controls (for *L. digitalis*, cage: 85.2 ± 6.2%, control: 47.7 ± 34.0%, U test, $P < .02$; for *L. pelta*, cage: 32.4 ± 12.3%, control: 16.8 ± 7.1%, t test, $P < .03$).

The combined size distribution of *L. strigatella* from cages and controls suggested that oystercatchers did not feed heavily on these limpets, unlike *L. digitalis* and *L. pelta*. Of all *L. strigatella* measured, 86.1% were <10 mm, and none were >11 mm (Fig. 6F).

Biomass effects

Total limpet biomass increased when bird predators were excluded. *L. digitalis* biomass was 7.9 times as high under cages (mean ± 1 SD = 2390 ± 1108 g) as in controls (303 ± 298 g, Wilcoxon test, $P = .001$),

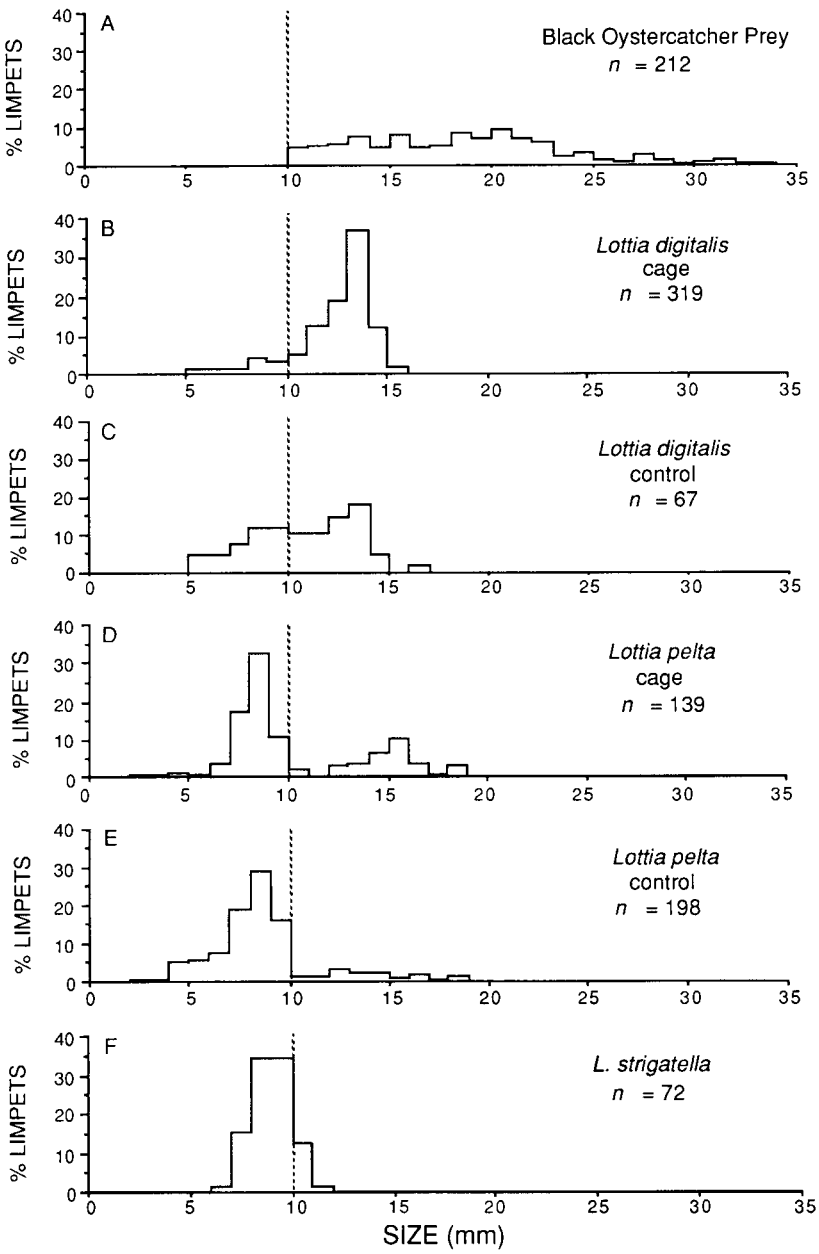

FIG. 6. The percentage of limpets measured as a function of their shell length pooled for all replicates measured. Dashed vertical line represents 10 mm, the lower limit of oystercatcher prey size. (A) Limpets fed upon by Black Oystercatchers, (B) *Lottia digitalis* under cages, (C) *L. digitalis* in control plots, (D) *L. pelta* under cages, (E) *L. pelta* in control plots, (F) *L. strigatella* in all treatments. n = number of limpets measured in six replicates.

whereas *L. pelta* biomass increased by a factor of 1.7 in cages (613 ± 252 g) relative to controls (355 ± 157 g, Wilcoxon test, $P = .002$).

L. strigatella biomass changed in a manner consistent with exploitative interspecific competition with the larger limpet species. *L. strigatella* biomass declined with increasing biomasses of the other two limpet species (multiple regression, $r^2 = 0.26$, $P < .025$), and increased with increasing cover of algae (linear regression, $r^2 = 0.21$, $P < .02$).

Effects on fleshy algae

Excluding birds reduced algal cover. The percent cover of foliose algae (mostly *Halosaccion glandiforme*, *Porphyra* spp., *Mastocarpus papillata*, and *Endocladia muricata*) increased 26-fold in controls compared to cages (Fig. 7, Wilcoxon test, $P < .001$). The amount of area covered by foliose algae declined significantly with increasing biomass of *L. digitalis* and *L. pelta* (reciprocal-transformed data, $r^2 = 0.399$, $P < .01$). The area covered by macroalgae also declined with increas-

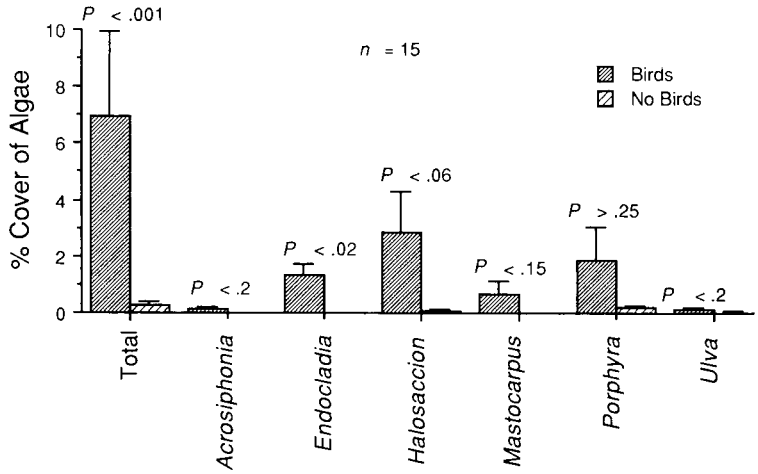

FIG. 7. Percent cover of fleshy algae (*Acrosiphonia coalita, Endocladia muricata, Halosaccion glandiforme, Mastocarpus papillata, Porphyra* spp., and *Ulva* spp.) in control plots with birds (dark bars) and caged plots without birds (light bars) (means and 1 SE). *P* values derived from Wilcoxon paired-ranks tests, $n = 15$.

ing cover of *P. polymerus* and *M. californianus* (log-transformed data, $r^2 = 0.572$, $P < .01$). Both grazer biomass and cover of space competitors was negatively correlated with algal cover in multiple regression ($r^2 = 0.637$; reciprocal-transformed grazer biomass: slope ± 1 SE = 1.24 ± 0.56, $t_{27} = 2.21$, $P < .05$), log-transformed competitor cover: slope ± 1 SE = −13.97 ± 4.19, $t_{27} = 3.34$, $P < .01$).

DISCUSSION

The direct effect of consumption of one species by another is expected to be a reduction in the density and biomass of the prey species. In the case of avian predation on limpets, observations (Hartwick 1976, Frank 1982, Hockey and Branch 1984, Lindberg et al. 1987, Hahn and Denny 1989, Wootton 1990) and short-term experiments (Mercurio et al. 1985, Marsh 1986*a*; J. T. Wootton, *unpublished manuscript*) all suggest that limpet abundance, biomass, and/or average size decline in the presence of birds. In the longer term experiments reported here, limpet abundance patterns did not completely agree with those expected on the basis of short-term observations and experiments. *L. digitalis* did show reduced abundance in the presence of bird predation; however, the two other limpet species did not (Fig. 1).

One explanation for these data is that bird predators were not particularly important to limpets in these experiments. However, detailed examination of the response of limpets and other members of the community instead indicated that indirect effects (e.g., crypsis, chains of predator–prey and interference interactions), strong habitat selection, and differences in susceptibility to predators all combined to offset, enhance, or overshadow the direct effects of predation on abundance (Fig. 8). Most of these processes take longer time periods to affect species abundances than does predation.

Several lines of evidence do point to important direct effects of predation by birds in the mid-intertidal community that I examined, as expected on the basis of short-term studies. In my experiment, the reduction of *L. digitalis* biomass, size (Fig. 6), density (Fig. 1), and substrate-specific density (Fig. 4) and reduction of *L. pelta* biomass, size (Fig. 6), and substrate-specific density (Fig. 4) in controls compared to cages follow the patterns expected under the bird predation hypothesis.

The apparent positive effect of birds on *L. strigatella* suggests an indirect interaction involving interspecific competition and predator escape. *L. strigatella* rarely grows larger than 10 mm on the Washington coast in the presence or absence of birds (Fig. 6), hence is not an important prey species for oystercatchers. Furthermore, the experiments of Choat (1977) demonstrate that the survivorship and tidal range of *L. strigatella* both increase in response to the removal of *L. digitalis*, indicating that these limpets compete. The hypothesis of competitive release predicts three patterns: (1) a negative association between *L. strigatella* biomass and the biomass of other limpet species, (2) a positive relationship between *L. strigatella* and its algal food source, and (3) a negative effect of algal abundance and the biomass of other limpet species. All three predictions are upheld; thus, when birds feed on *L. digitalis* and *L. pelta*, *L. strigatella* appears to undergo competitive release and increases in density.

Sessile organisms indirectly affect limpet abundance by changing the rate of bird predation upon limpets. The results of the experiments reported here and the short-term experiments of Mercurio et al. (1987) both show that bird predation intensity is reduced in those habitats comprised of sessile organisms on which the limpets appear more cryptic to visual predators. The effect of a particular sessile species depends on its color relative to the shell color of the limpet species; thus different species are favored on different substrates.

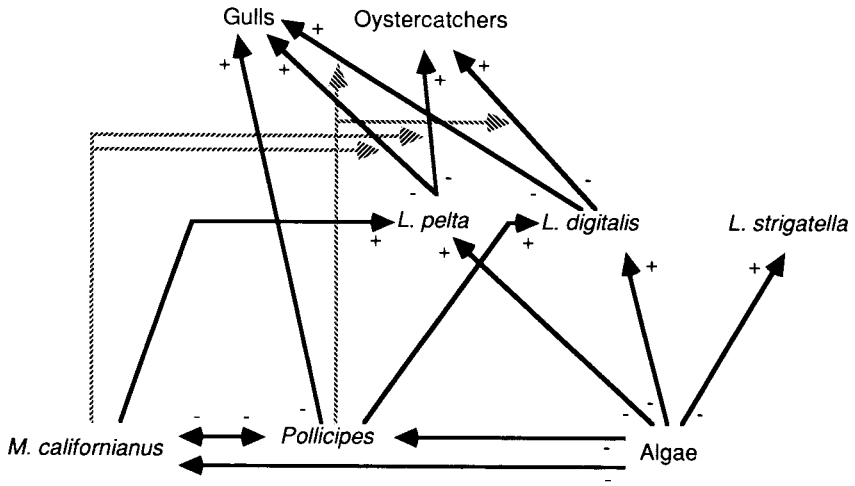

FIG. 8. Diagram of interactions affecting limpet abundance in the middle intertidal zone of Tatoosh Island. Solid arrows indicate direct interactions among species (e.g., predator–prey, interference competition, habitat preference). Stippled arrows indicate indirect interactions that act by modifying a direct interaction between two other species. Other indirect effects can be visualized by following chains of direct interactions.

This result would not be expected if the substrate species were physically interfering with feeding rates, rather than altering the efficiency of prey detection through crypsis. Under a hypothesis of physical interference, one substrate type would have consistently provided the best protection, independent of limpet species identity.

Bird predation provides a potentially strong selective pressure for habitat choice in *L. digitalis* and *L. pelta*. The differential removal by birds of limpets on mismatching habitats would favor behavioral selection of habitats of matching color. Additionally, limpet size distributions indicate that selection pressure favoring habitat choice might be stronger than that indicated by differences in limpet abundance alone, because the smaller limpets that remain following bird predation (Fig. 6) tend to be less fecund.

Limpets appeared to exhibit strong habitat selection in both 24-h substrate preference experiments and in the long-term bird exclusion experiments, tending to favor the substrate whose color they matched. In the absence of bird predation, *L. digitalis* still occurred at much higher densities on *P. polymerus* and likewise *L. pelta* occurred at higher densities on *M. californianus* (Figs. 4 and 5). Giesel (1970), Mercurio et al. (1985), and Byers (1989) also provided evidence of habitat preference by limpets, although they apparently did not exclude birds in their habitat selection experiments, raising the possibility of confounding selective predation.

L. pelta is affected by a complex interaction among processes, and therefore its density does not exhibit a net change in the presence of bird predation, despite the prevalence of this limpet in the diet of birds (Hartwick 1976, Frank 1982, Lindberg et al. 1987, Hahn and Denny 1989; J. T. Wootton, *personal observation*). Bird predation reduces *L. pelta* density in all habitats, and may represent a strong selection pressure promoting the evolution of habitat selection favoring *M. californianus* substrates. However, by also feeding on *P. polymerus*, gulls cause a competitive release of *M. californianus*, the habitat *L. pelta* preferentially selects. Removing *P. polymerus* enhanced the abundance of *M. californianus* (Fig. 3), thereby demonstrating strong interference competition between the two. Thus, permitting access to gulls reduced the abundance of their main prey species, *P. polymerus*, indirectly causing an increase in *M. californianus*. Therefore, the increase in preferred habitat offsets the decline in *L. pelta* density caused by oystercatcher and gull predation, leading to no net change in density.

The large decline of herbivorous limpet biomass in the presence of birds raises the possibility of other indirect effects of oystercatchers on the producers in the community, as envisioned by Hairston et al. (1960). A large body of experimental work demonstrates that when limpets are removed, benthic algae flourish (Dayton 1971, Lubchenco and Gaines 1981, Johnson 1989). Consistent with these studies, algal cover increases significantly in my experiments when bird predators are present (Fig. 7). The negative relationship between algal cover and limpet biomass across treatments supports a hypothesis of an indirect effect of bird predation on algae via a reduction in grazing pressure. A similar effect has been suggested for sea otters feeding on sea urchins (*Strongylocentrotus* spp., Estes and Palmisano 1974, Estes et al. 1978).

The positive indirect effects of predators on algae may have been caused not only by changes in grazing pressure, but also by changes in interference competition for space with sessile invertebrates. Specifically, gull predation alters the cover of *P. polymerus* and *M.*

californianus, thus reducing the overall abundance of potential space competitors (Paine 1966, 1974, Paine and Levin 1981). Algae occurred only on rock or acorn barnacle substrate. Consistent with the space competitor hypothesis, algal cover was correlated negatively with *P. polymerus* and *M. californianus* cover. Examining the relationship between algal cover and either (1) grazers or (2) space competitors with the other held constant suggested that both factors may be important; multiple regression revealed a significant negative relationship of algal cover to both grazers and space competitors. Therefore, birds may affect algal populations indirectly by two very different pathways.

The indirect effects detected in this experiment occur through two alternative processes: chains of direct interactions or modifications of direct interactions (Fig. 8; J. T. Wootton, *unpublished manuscript*). For example, birds feed on limpets and limpets feed on algae, therefore birds indirectly enhance algae through a chain of two direct consumer–prey interactions. In contrast, goose barnacles indirectly affect limpet abundance by changing the efficiency of bird predation, a modification of a predator–prey interaction. Identifying which of these two mechanisms of indirect effects occurs is important because predicting indirect effects arising from chains of direct interactions can be accomplished by just knowing pair-wise interactions, but a priori prediction of interaction modifications cannot (Vandermeer 1969, Wilbur 1972, Neill 1974, Case and Bender 1981, Pomerantz 1981, Abrams 1983, Miller and Kerfoot 1987, Wilbur and Fauth 1990; J. T. Wootton, *unpublished manuscript*). Therefore, determining the prevalence of these two processes in causing indirect effects provides information on whether models based on pairwise direct interactions are sufficient to predict community structure, and on the mechanisms, such as crypsis, that tend to modify direct interactions.

The long-term effects of birds on limpet density were not immediately predictable from short-term effects of direct predation on limpets (e.g., Mercurio et al. 1985, Marsh 1986*a*; J. T. Wootton, *unpublished manuscript*). Indirect effects of birds on preferred limpet habitat and on competitors for food offset or enhance direct effects of birds. Therefore short-term predation experiments may not detect compensating mechanisms related to size shifts, habitat selection, competition, or migration. As these and other experiments demonstrate (e.g., Davidson et al. 1984, Brown and Munger 1985), care must be taken that possible indirect effects that may develop over longer time spans are not ignored when interpreting results of short-term experiments.

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Literature Cited

Abrams, P. A. 1983. Arguments in favor of higher-order interactions. American Naturalist **121**:887–891.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65**:1–13.

Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology **66**:1545–1563.

Byers, B. A. 1989. Habitat choice polymorphism associated with cryptic shell-color polymorphism in the limpet *Lottia digitalis*. Veliger **32**:394–402.

Carpenter, S. R., editor. 1988. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634–639.

Case, T. J., and E. A. Bender. 1981. Testing for higher order interactions. American Naturalist **118**:920–929.

Choat, J. H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. Journal of Experimental Marine Biology and Ecology **26**: 1–26.

Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics **6**:281–310.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710–723.

———. 1980. Diversity and coevolution of competitors, or the ghost of competition past. Oikos **35**:169–192.

———. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist **122**:81–116.

Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology **65**:1780–1786.

Davis, J. 1973. Habitat preference and competition in wintering juncos and golden-crowned sparrows. Ecology **54**: 174–180.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **45**:137–159.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058–1060.

Estes, J. A., N. S. Smith, and J. F. Palmisano. 1978. Sea otter predation and community organization in the Western Aleutian Islands. Ecology **59**:822–847.

Frank, P. W. 1982. Effects of winter feeding on limpets by black oystercatchers, *Haematopus bachmani*. Ecology **63**: 1352–1362.

Giesel, J. T. 1970. On the maintenance of a shell pattern and behavior polymorphism in *Acmaea digitalis*. Evolution **24**:98–119.

Hahn, T., and M. Denny. 1989. Tenacity-mediated selective predation by oystercatchers on intertidal limpets and its role in maintaining habitat partitioning by *'Collisella' scabra* and *Lottia digitalis*. Marine Ecology Progress Series **53**: 1–10.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960.

Community structure, population control, and competition. American Naturalist **94**:421–425.

Hartwick, E. B. 1976. Foraging strategy of the black oystercatcher (*Haematopus bachmani* Audubon). Canadian Journal of Zoology **54**:142–155.

———. 1981. Size gradients and shell polymorphism in limpets with consideration of predation. Veliger **23**:254–264.

Hay, M. E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. American Naturalist **128**:617–641.

Hockey, P. A. R., and G. M. Branch. 1984. Oystercatchers and limpets: impact and implications. A preliminary assessment. Ardea **72**:199–206.

Johnson, L. E. 1989. Spatial and temporal influences on the recruitment of intertidal red algae. Dissertation. University of Washington, Seattle, Washington, USA.

Kneib, R. T. 1988. Testing for indirect effects of predation in an intertidal soft-bottom community. Ecology **69**:1795–1805.

Levine, S. H. 1976. Competitive interactions in ecosystems. American Naturalist **110**:903–910.

Lindberg, D. R. 1986. Name changes in the "Acmaeidae." Veliger **29**:142–148.

Lindberg, D. R., and J. S. Pearse. 1990. Experimental manipulation of shell color and morphology of the limpets *Lottia asmi* (Middendorff) and *Lottia digitalis* (Rathke) (Mollusca: Patellogastropoda). Journal of Experimental Marine Biology and Ecology **140**:173–185.

Lindberg, D. R., K. I. Warheit, and J. A. Estes. 1987. Prey preference and seasonal predation by oystercatchers on limpets at San Nicolas Island, California, USA. Marine Ecology Progress Series **38**:105–113.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant–herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics **12**:405–437.

Marsh, C. P. 1986*a*. Impact of avian predators on high intertidal limpet populations. Journal of Experimental Marine Biology and Ecology **104**:185–201.

———. 1986*b*. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. Ecology **67**:771–786.

Martin, T. E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? Evolutionary Ecology **2**:37–50.

McPeek, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology **71**:83–98.

Mercurio, K. S., A. R. Palmer, and R. B. Lowell. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology **66**:1417–1425.

Miller, T. E., and W. C. Kerfoot. 1987. Redefining indirect effects. Pages 33–37 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Neill, W. 1974. The community matrix and interdependence of the competition coefficients. American Naturalist **108**:399–408.

Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology **58**:1020–1032.

Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. Ecology **45**:736–745.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berlin) **15**:93–120.

———. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**: 667–685.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Pfister, C. A., and M. E. Hay. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. Oecologia (Berlin) **77**:118–129.

Pomerantz, M. J. 1981. Do "higher-order interactions" really exist? American Naturalist **117**:583–591.

Power, M. E. 1990. Effects of fish in river food webs. Science **250**:811–814.

Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology **66**:1448–1457.

Ricketts, E. F., J. C. Calvin, and J. W. Hedgpeth. 1985. Between Pacific tides. Stanford University Press, Stanford, California, USA.

Schmitt, R. J. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. Ecology **68**:1887–1897.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240–285.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition and prey communities: a review of field experiments. Annual Review of Ecology and Systematics **16**:269–311.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, New York, New York, USA.

Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with protozoa. Ecology **50**:362–371.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393–425.

Wilbur, H. M. 1972. Competition, predation, and the structure of the *Ambystoma–Rana sylvatica* community. Ecology **57**:3–21.

Wilbur, H. M., and J. E. Fauth. 1990. Experimental aquatic food webs: interactions between two predators and two prey. American Naturalist **135**:176–204.

Wootton, J. T. 1990. Direct and indirect effects of bird predation and excretion on the spatial and temporal patterns of intertidal species. Dissertation. University of Washington, Seattle, Washington, USA.

Yodzis, P. 1988. The indeterminancy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508–515.