INDIRECT EFFECTS AND HABITAT USE IN AN INTERTIDAL COMMUNITY: INTERACTION CHAINS AND INTERACTION MODIFICATIONS

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Abstract.—Species may indirectly affect populations of other species in two basic ways. Interaction chains result from linked direct interactions between species pairs. Interaction modifications, emergent effects of a multispecies assemblage, result when a third species changes how a pair of other species interacts. Experiments and patterns of abundance in the upper zone of a rocky intertidal community provide examples of both types of indirect effects. By consuming limpets (Lottia digitalis), bird predators indirectly enhance acorn barnacle (Balanus glandula) abundance on horizontal rock benches because limpets dislodge or inadvertently consume young acorn barnacles, an example of an interaction chain. Because L. digitalis has a light-colored shell that is similar in color to barnacle shells, barnacles alter the bird-limpet interaction by changing the ability of birds to find limpets, an example of an interaction modification. Distinguishing between interaction chains and interaction modifications is important because interaction chains can be predicted with only a knowledge of pairwise species interactions while descriptions of interaction modifications require a knowledge of all species combinations involved, precluding a priori prediction. By classifying empirically determined indirect effects, the degree to which indirect effects can be predicted from a knowledge of pairwise interactions can be determined, and the mechanisms that cause interaction modifications can be identified to aid in future prediction.

Ecologists have long suggested that organisms within a community exhibit some degree of interdependence (Darwin 1859; Forbes 1887; Elton 1927; Clements 1936; Hutchinson 1959; Hairston et al. 1960). This view suggests that changes in the abundance of a species within the community will not only directly affect those species with which it physically interacts but also could indirectly alter the abundances of other species as a result of its direct interactions. As experimental manipulations of species abundances have become more common in ecology, many examples of indirect effects of one species on another have been detected (reviewed in Colwell and Fuentes 1975; Connell 1975, 1983; Schoener 1983; Sih et al. 1985; Kerfoot and Sih 1987). The next step for ecologists is to start developing methods that predict which species have important direct and indirect effects on other members of the community (Paine 1980, 1984). Toward this end, it is helpful to make a fundamental distinction between two types of indirect effects: interaction chains and interaction modifications. In this article I provide examples of each of these types of indirect effects.

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Interaction chains are indirect effects that result from a series of direct interactions between species pairs (fig. 1). Thus, one species directly alters the abundance of a second species, the change in the second species affects a third species, and so on. In mathematical terms, the functions describing the direct interactions between species pairs do not change as a result of the indirect interaction; only the abundances of the species change. For example, a predator may indirectly enhance the abundance of producers by reducing herbivore density (Hairston et al. 1960), or a predator may indirectly depress the population of a second consumer by reducing the abundance of a common prey species (exploitative competition).

Interaction modifications are indirect effects that result when a change in density of one species alters the nature of a direct interaction between two other species. In mathematical terms, it changes the function describing the direct interaction between a species pair. Therefore a species that indirectly influences another species in this manner directly affects the interaction between two species rather than the abundance of another species (fig. 1). For example, a predator could cause a behavioral shift in its prey that makes the prey more susceptible to another predator (Dayton 1973; Dinsmore 1973; Willis and Oniki 1978), unpalatable prey species may reduce predation intensity on palatable prey by reducing foraging profitability in a patch (Tahvanainen and Root 1972; Root 1973; Atsatt and O’Dowd 1976; Hay 1986; Pfister and Hay 1988), or a sessile species could alter the physical environment in which a predator searches for prey, changing the predator’s foraging efficiency (Werner et al. 1983; Wootton 1992; see below).

Interaction modifications have also been discussed under the term “higher-order interactions” (Vandermeer 1969; Neill 1974; Menge 1978; Case and Bender 1981; Pomerantz 1981; Abrams 1983; Wilbur and Fauth 1990), because early investigations concentrated on the question of whether species interactions could be described sufficiently by linear coefficients of the Lotka-Volterra competition equations without requiring nonlinear terms (Vandermeer 1969; Wilbur 1972; Neill 1974). In mathematics, the nonlinear parts of an equation are referred to as higher-order terms. Unfortunately, confusion has arisen because the observed deviations in community structure from that predicted by a linear model were originally assumed to be caused by an interdependence of the coefficients on the density of other members of the community (i.e., an interaction modification), whereas they can also be the result of a nonlinear direct interaction between a species pair (Pomerantz 1981). Therefore differentiating interaction modifications from other types of higher-order interactions seems useful.

Distinguishing interaction chains from interaction modifications is important because they are modeled theoretically and examined empirically in different ways (Vandermeer 1969; Wilbur 1972; Neill 1974; Menge 1978; Case and Bender 1981; Pomerantz 1981; Miller and Kerfoot 1987; Wilbur and Fauth 1990; Wootton 1990). Models of interaction chains are relatively easy to construct and to use in deriving predictions because they represent a series of pairwise interactions. Predictions of interaction chains can be made, therefore, by knowing only the direct relationships between species pairs in isolation.

Interaction modifications are an emergent property of a multispecies assem-
Fig. 1.—Diagram depicting the difference between interaction chain (top) and interaction modification (bottom) indirect effects. Dark arrows represent direct interactions between species pairs, the stippled arrow represents a third species indirectly changing the direct interaction between a species pair, and letters represent different species. In the interaction chain example, species C indirectly affects species A through a chain of direct interactions (interference competition between B and C, predation by A on B). In the interaction modification example, species C indirectly affects species A and B by changing a direct interaction between A and B (altering the rate at which species A feeds on species B).

blage and hence are more difficult to predict than interaction chains, because determining whether one species changes the interaction between two other species requires examining all species involved in all possible combinations (Bender et al. 1984). Therefore predicting a priori how species will interact when they occur together is not straightforward when some species indirectly influence others in this manner. At present, natural history intuition based on knowledge of a specific system provides the best avenue to predict interaction modifications, but
in the future, synthesizing empirical examples may aid in developing the ability to predict when they will occur. Identifying the relative frequency of these two types of indirect effects in experimental studies can help to determine whether descriptions of pairwise interactions will suffice to predict indirect effects, and it can aid in identifying the general mechanisms that typically cause interaction modifications.

If indirect effects are important, differences in the presence or absence of a species may explain the spatial variation of other species that it indirectly influences. Although much work has emphasized the effects of inter- and intraspecific competition on density patterns across habitats (MacArthur 1958; Fretwell 1972; Cody 1974; Werner and Hall 1976; Brown and Munger 1985; Pacala and Roughgarden 1985; Rosenzweig 1985; Wootton 1987), other interactions can also influence such patterns. For example, differences in predation pressure may also affect prey abundance in different areas (Paine 1974; Connell 1980; Frank 1982; Werner and Gilliam 1984; Mercurio et al. 1985; Power et al. 1985; Martin 1988). Predator pressure may differ among habitats for two reasons: (1) the predator may be present in some habitats but absent in others because of its inability to colonize or survive in those habitats and (2) foraging efficiency of the predator may vary between habitats. Differences in foraging efficiency could be caused by differences in physical characteristics of the habitat (e.g., physiological stress and topography; see Menge and Sutherland 1976) or could be the result of differences in the abundance of other species that indirectly affect the predator-prey relationship. Variation in predation pressure in turn may indirectly cause differences among habitats in the abundance of other species that interact with the prey species. Here I examine experimentally how differences in predator occurrence and foraging efficiency at different tidal heights on vertical walls and horizontal benches directly affect the abundance patterns of Lottia digitalis, an intertidal limpet. I also investigate how these direct effects of predation might indirectly affect acorn barnacle abundance.

THE STUDY SYSTEM

Lottia digitalis (formerly Collisella digitalis; see Lindberg 1986) is a common limpet species living in the upper intertidal zone of rocky shores along the Pacific Coast of North America (Frank 1965, 1982; Haven 1971, 1973; Breen 1972; Choot 1977; Ricketts et al. 1985; Hahn and Denny 1989). The density of these grazers differs characteristically among habitats as one moves either up or along the shore. Densities appear much greater on vertical walls than on horizontal benches (see Haven 1971; Frank 1982; Hahn and Denny 1989). Also, whereas individuals are commonly found at tidal heights of up to 1 m above the upper limit of acorn barnacles (Balanus glandula) on walls, they are almost never present at this level on horizontal benches (J. T. Wootton, personal observation; see below). Birds, notably black oystercatchers (Haematopus bachmani), glaucous-winged gulls (Larus glaucescens), black turnstones (Arenaria melanocephala), and surfbirds (Aphriza virgata), can feed heavily on limpets on horizontal surfaces but not on vertical walls (Frank 1982; Mercurio et al. 1985; Marsh 1986; Lindberg et al.
1987; Wootton 1990). Results of Mercurio et al. (1985) and Marsh (1986) from cage experiments conducted in British Columbia and Oregon suggested that birds could significantly reduce the densities of limpets. Frank (1982) and Hahn and Denny (1989), working in Oregon and California, respectively, observed feeding rates and compared limpet densities on vertical walls that were accessible and inaccessible to birds. They concluded that patterns of abundance in \textit{L. digitalis} on horizontal and vertical surfaces could be explained by bird predation but did not test this hypothesis experimentally.

The effect of bird predation on the distribution of \textit{L. digitalis} across tidal levels has not been investigated. The difference in the upper limit of limpets between horizontal and vertical surfaces suggests that it might be influenced by bird predation interacting with acorn barnacle cover. \textit{Lottia digitalis} is a light-shelled limpet with occasional dark lines and an irregular base; typically its shell is eroded on top. As a result, when these limpets occur on an acorn barnacle background, they appear very cryptic to the human eye. Therefore the upper tidal limit of \textit{L. digitalis} may be caused by a change in the efficiency of predation by birds. Limpets are essentially eliminated by birds above the barnacles because they are easily seen but persist in the barnacles as a result of crypsis. In this study, I test experimentally the hypothesis that birds are a factor setting the upper limit of \textit{L. digitalis} and additionally provide the first experimental evidence that the differences in density, as well as distributional patterns, between horizontal and vertical benches is the result of bird predation.

Any patterns of limpet abundance caused by differences in avian predation among habitats could also lead indirectly to variation in the abundance of intertidal species that interact with limpets. For example, experimentally removing limpets generally results in increased acorn barnacle abundance (Dayton 1971; Denley and Underwood 1979; Underwood et al. 1983; Tsuchiya 1984; Farrell 1988; Johnson and Strathman 1989). If limpets increase in the absence of avian predation, barnacles might exhibit a concomitant decline. I also present evidence that supports the hypothesis that bird predation can indirectly lead to habitat-specific differences in acorn barnacle cover.

METHODS AND STUDY SITE

I conducted the study on Tatoosh Island (48°24′N, 124°44′W), located 0.5 km off the northwestern tip of Washington State. Tatoosh is very wave exposed and exhibits a wide intertidal zone with well-defined zonation patterns on its large rock benches. Detailed descriptions of Tatoosh and some of its biology can be found in Paine (1974, 1988), Paine and Levin (1981), Leigh et al. (1987), and references therein. In the upper intertidal zone, the acorn barnacle \textit{Balanus glandula} dominates the community. The width of the \textit{B. glandula} zone generally covers 0.5–3.0 m vertically, and its upper limit ranges from 1.5 to 5.4 m above mean low water, depending on the degree of wave exposure at a site (Leigh et al. 1987). The major limpet consumers on Tatoosh are black oystercatchers and glaucous-winged gulls (Wootton 1990).

To document the patterns of limpet abundance I counted the number of limpets
in 31 × 31-cm quadrats haphazardly placed on vertical rock walls and on adjacent horizontal rock benches. Censuses were taken at all accessible sites on the island where horizontal benches and vertical walls were present in close proximity. At each census point along the shore, I sampled one quadrat 0.5 m above the upper limit of *B. glandula* and a second quadrat directly under the first one, 0.5 m below the *B. glandula* upper limit. The upper limit of *B. glandula* changes but provides a standard indicator of relative physical conditions (e.g., wave exposure, desiccation; see Lewis 1964; Leigh et al. 1987). By sampling quadrats on adjacent walls and benches, I insured that physical regimes of the habitats were similar. I also took a second series of 25 × 25-cm quadrats to examine the pattern of acorn barnacle abundance on horizontal and vertical surfaces and its relationship to limpet abundance. In these quadrats, placed 0.5 m below the upper limit of *B. glandula*, I estimated the number of limpets present and measured the percent area covered by barnacles by scoring the presence or absence of live barnacles under 81 points spaced systematically throughout the quadrat (2.5 cm apart).

To examine the effect of bird predation on limpet abundance, I experimentally excluded birds from areas using prefabricated cages. I constructed cages from vinyl-covered wire letter baskets (29 × 34 × 7.5 cm) placed upside down and strapped to the rocks with coated 14-gauge copper wire. The wide mesh of the roof (4 × 2.5 cm), much larger than that typically used in cage experiments, minimized differences in physical characteristics of the treatments. Each location contained three treatments. A cage treatment was made with half of the basket (29 × 17 cm in area) by removing a fraction of the basket roof and folding the remainder down to make a side wall. The other half of the basket, therefore, did not have a protective roof but did have a rim around the periphery. The rim-only treatment insured that no artifacts related to the presence of a potential physical barrier were important in the experiment. Finally a 29 × 17-cm area adjacent to the basket served as an unmanipulated control. I surrounded each treatment with a 2.5-cm band of copper-based antifouling paint to reduce limpet migration both among treatments and out of the experiments (see Cubit 1984).

Cages can potentially exclude any large-bodied mobile predator but represent only a manipulation of birds in this system. Large crabs (*Cancer* spp.) and sea otters (*Enhydra lutris*) are absent from the intertidal community of Tatoosh Island, and sea stars do not occur at the high tidal levels investigated here (Paine 1974, 1980; J. T. Wootton, personal observation). Although benthic-feeding fish (*Embiotoca lateralis*) have been observed in sheltered sections of the island on calm days (C. Pfister, personal communication), they probably do not feed effectively on the more wave-washed shores where the experiments were conducted. Furthermore, fish can feed on vertical walls, and therefore differences between cages and controls that result from fish predation should be apparent on both horizontal and vertical substrates.

My observations of birds attempting to feed under the cages in these and other experiments (Wootton 1990) suggested that cages protected most potential prey from bird predation. Additionally, in a preliminary experiment on a horizontal bench with two replicates, birds fed on limpets shortly after the experiments were started, before the tide was high enough to wash away the empty shells. In that
TWO TYPES OF INDIRECT EFFECTS

experiment, birds consumed one limpet under each of the two cages, eight in each of the two rim controls, nine in one control, and 10 in the other control. These observations indicated that, although effective, cages did not completely protect prey and that the rim control may have interfered slightly with bird predators.

I placed the three-treatment combinations testing for bird predation effects in six different habitats to examine the interaction of bird predation with barnacle cover and substrate angle. The habitat treatments (along with the coded abbreviations I will use below) were as follows: (1) on vertical walls 0.5 m above the upper limit of B. glandula (hv), (2) on vertical walls 0.5 m below the upper limit of B. glandula (hv), (3) on horizontal benches 0.5 m above the upper limit of B. glandula (hh), (4) on horizontal benches 0.5 m below the upper limit of B. glandula (bh), (5) on horizontal benches 0.5 m below the upper limit of B. glandula, with half the B. glandula removed (1/2bh), and (6) on horizontal benches 0.5 m below the upper limit of B. glandula with all B. glandula removed (0bh). To determine whether limpet migration might have affected the results, I placed a seventh cage within the barnacle zone on a horizontal surface at each replicate site but added no limpets. No limpets migrated into these plots during any experiment.

All habitat/cage combinations were executed at three different sites that contained adjacent horizontal and vertical substrates at the appropriate tidal height covering a large enough area to accommodate the experimental design (18 treatments). I added 10 L. digitalis to each treatment, a density (200/m²) that fell well within the range of natural densities observed on vertical walls. Limpets, typically ranging in size from 15 to 20 mm in length, were collected from vertical walls away from experimental sites and placed in a common bucket from which individuals were drawn randomly for each treatment and replicate to avoid any bias in size and home site. The transplanted limpets were checked after 24 h to insure that all had successfully attached to the rocks and did not experience any mortality due to handling. After starting the experiment, I made one posttreatment census when I next visited the island, a time period that varied from 9 to 87 d (median = 15 d) depending on weather conditions. After the termination of each experiment, I removed the remaining limpets, and arbitrarily reassigned cage and control treatments in each habitat and site. I initiated new experiments on November 11, 1985, and March 26, 1986 (one site each), on September 17, 1986, and October 3, 1986 (2 sites each), and on April 1, 1987, and April 18, 1987 (all three sites). Another limited series of experiments, initiated May 26, 1990, at all three sites, only included the habitat treatments on horizontal benches within the barnacle zone where I manipulated barnacle cover.

I designed the experimental treatments to test the following six predictions. (1) If cage artifacts enhanced limpet survival rates for reasons other than reduced avian predation (e.g., different physical environment, reduced fish predation), then limpet density should have been higher under cages than controls on vertical walls (where birds cannot feed) and higher in rim controls than in unmanipulated controls. (2) If bird predation reduced limpet abundance, limpet density should have been higher under cages than in controls on horizontal benches where birds
could feed, but not on vertical walls. (3) If tide height affected limpet survival, then limpet density should have been higher under cages at low tidal heights than under cages at high tidal heights, where desiccation would be more likely.

I expected barnacles to affect limpets independently of bird predation. At high densities, barnacles might interfere with the ability of limpets to feed or attach tightly to the rocks, reducing survival rates. In contrast, because barnacles increase water retention on the rock surface (J. T. Wootton, personal observation), the presence of barnacles might enhance limpet survival rates relative to plots without barnacles. Combining these hypotheses, I predicted (4) a significantly elevated survival rate of limpets under cages where half the barnacles were removed compared with caged plots without barnacles and with caged plots with normal barnacle densities.

If differences in barnacle cover affected the intensity of bird predation on limpets, (5) limpets in plots with barnacles and bird predation should survive at higher rates than those predicted from survival rates in plots with bird predation or barnacles alone. (6) Likewise, if differences in barnacle cover interact with bird predation to determine the upper tidal limit of limpets, then limpets exposed to bird predation without barnacles should exhibit low survival rates independent of tidal height.

The lack of normality prohibited use of an ANOVA to detect differences and interactions between barnacle and bird predation treatments, and the directional nature of the predictions also made use of ANOVA undesirable. Therefore, I compared the number of surviving limpets between treatments using paired t-tests for a priori hypotheses. Because each replicate was conducted in a blocked design of all 18 treatments, treatments testing specific hypotheses could be paired within each site in each block of experiments (e.g., comparing cage-control pairs within a habitat treatment, comparing cages between two habitats within a block). Pairing helped reduce the variance in results due to differences in location of the experimental sites and seasonal factors and controlled for effects of differences in the duration of the experiments. Additionally, although values for individual treatments were generally not distributed normally, differences between treatment pairs were approximately normal. When normality assumptions were not met, nonparametric statistics were used. Because the experiments were designed with a priori hypotheses in mind, I used a per-comparison error rate \( P < .05 \) in assessing statistical significance (see Day and Quinn 1989). Most tests were one tailed, reflecting the directional nature of the hypotheses tested.

To examine how barnacle cover interacted with bird predation intensity, I used paired t-tests to determine whether limpets in controls comprised a significantly higher proportion of the total number of limpets in a cage-control pair in the presence compared with the absence of barnacles for each replicate set of treatments. If barnacle cover did not affect avian predation intensity, then the proportion of limpets surviving in controls should have been the same across treatments manipulating barnacle cover. This method tests the following expected relationship of limpet survival rates among treatments: if the probability of survival under a given set of conditions, \( a \), changes by factor \( b \) (to \( ab \)) with a change in one
variable (e.g., birds) and by factor c (to ac) with a change in another variable
(e.g., barnacles), then in the absence of an interaction between variables, the
probability of surviving when both variables are changed is abc (see Wootton

To examine background mortality levels and the effect of differing durations
of the experiments on the results, I used linear regression to examine how the
number of surviving limpets varied with varying length of the experiment across
all treatments.

RESULTS

Quantitative surveys of *Lottia digitalis* density demonstrated the general distribu-
tion patterns noted above (fig. 2). *Lottia digitalis* was significantly more abun-
dant within quadrat samples taken from vertical walls than from horizontal
benches both above and within the B. glandula zone (Mann-Whitney U-tests, P
< .002). Additionally, patterns of limpet zonation suggested that they might be
mediated by avian predation. On vertical walls where birds could not feed (Frank
1982; Hahn and Denny 1989; J. T. Wootton, personal observation), limpets were
abundant both above and in the barnacle zone, and densities did not differ signifi-
cantly (U-test, P > .8). However, I found no limpets above the barnacle zone on
horizontal benches, whereas densities were maintained at moderate levels within
the barnacle zone (U-test, P < .025). Limpets sizes also differed between habi-
tats. The lengths of limpets on vertical walls were significantly greater than those
on horizontal benches (table 1, U-test, P < .0001).

Background limpet mortalities had little effect on the number of surviving lim-
pets at the end of each experiment. The number of limpets surviving at the end
of the experiment did not decline significantly with increasing experimental duration
(slope = 0.002, SE = 0.01, r² = 0.001, n = 216, P > .5). Therefore, comparing
the number of limpets remaining at the end of the experiment in different treat-
ments was not biased by variation in experimental duration. Furthermore, the
manipulated factors that caused significant changes in limpet survival rates during
the experiment were likely to be the most important factors influencing limpet
mortality and were likely to have had an impact on limpets in a strong pulse
within 9 d (the shortest duration of any experiments) rather than at constant low
levels over the duration of the experiments.

I detected no evidence of cage artifacts (fig. 3). *Lottia digitalis* survival did not
differ between pairs of cages and controls on vertical walls within or above the
barnacle zone (*hv* and *bv* treatments) or between pairs of rim controls and unma-
nipulated controls in any of the habitat treatments (paired *t*-tests, P > .05).

Birds appeared to strongly affect limpet survival rates on horizontal benches,
where they had access to control plots. On horizontal benches, limpet densities
were significantly greater under cages than in paired controls in all habitat treat-
ments, with densities under cages ranging from 2.1 to 7.8 times that of controls
(fig. 3, paired *t*-tests, all *P* < .005).

Tide height also affected limpet survival (fig. 3). Limpet density under cages
in the barnacle zone ranged from 1.4 to 2.7 times that under cages above the barnacle zone on both vertical walls and horizontal benches (hv vs. bv and hh vs. bh, 1/2bh or 0bh; paired t-tests, all $P < .01$).

Barnacles affected limpet survival independent of birds in the nonlinear manner predicted (fig. 3). Under cages in the plots on horizontal benches where I manipulated barnacle abundance, limpets in areas with reduced barnacle cover survived at a rate 1.5 times greater than those in areas without barnacles (1/2bh vs. 0bh, paired t-test, $P < .025$) and at a rate 1.2 times greater than those in areas with complete barnacle cover (bh vs. 1/2bh, paired t-tests, $P < .025$).
The presence of barnacles reduced the intensity of avian predation on limpets on horizontal benches. The proportion of limpets in the control of a cage-control pair was significantly lower in treatments without barnacles compared with those with barnacles (0bh vs. 1/2bh or bh; paired t-tests, $P < .004$; fig. 4), indicating that barnacles reduced the intensity of bird predation on limpets. Therefore, in controls (bird predation present), the number of limpets remaining was 5.4 times greater in the reduced barnacle treatment and 3 times greater in the barnacle treatment than in the no barnacle treatment (0bh vs. 1/2bh or bh; paired t-tests, $P < .01$). In contrast, limpet survival under cages was only 1.5 and 1.2 times greater than in the respective treatments with barnacles compared to barnacle removals.

The effect of barnacles on bird predation rates appeared to be strong enough to influence the upper tidal limit of L. digitalis on horizontal surfaces (fig. 3). Like limpets under cages, limpets in controls with barnacles present survived at higher rates (3.0–5.4 times as great) than limpets in controls above the barnacle zone (hh vs. bh or 1/2bh; paired t-tests, $P < .025$). In contrast, the survival of limpets in controls without barnacles did not differ at tidal levels above and below the barnacle zone (hh vs. 0bh; $\bar{X} = 0 \pm 1.54$, paired t-test, $P > 0.5$). Independent of tide height, by the end of each experimental period, L. digitalis without barnacles averaged less than one limpet in experimental arenas in the presence of bird predation, and the median probability of survival in these two treatments was zero.

Differences in avian predation pressure on limpets between horizontal and vertical habitats may have indirectly altered the abundance pattern of acorn bar-
Fig. 4.—Mean percentage (±1 SE) of surviving Lottia digitalis in cage-control pairs that are present in controls (exposed to bird predation) when the cover of acorn barnacles is experimentally varied. The significantly higher proportion of limpets remaining in controls in the presence of barnacles indicates that barnacle cover reduces the rate of bird predation on limpets.

nacles in the intertidal community. Barnacles covered three times as much area on horizontal benches ($\bar{X} = 51.9\% \pm 15.1\%, n = 17$), where birds reduced limpet abundance, than on vertical walls ($\bar{X} = 16.8\% \pm 12.6\%$, paired t-test, $P < .0001$). Furthermore, the percentage of area covered by barnacles declined significantly with increasing limpet abundance on vertical surfaces ($r = -0.43$, $P < .05$), where limpets spanned a wide range of densities ($\bar{X} = 25.5$ m$^{-2}$, range 9–55). However, on horizontal surfaces, where limpets occurred at uniformly low abundances ($\bar{X} = 5.5$ m$^{-2}$, range 0–19), the relationship between limpet abundance and the percentage of area covered by barnacles was not significant ($r = -0.13$, $P > .2$).

DISCUSSION

The differences in Lottia digitalis density among habitats described here appear to be caused primarily by differences in predation pressure. The reduction in limpet survival under controls compared to cages demonstrates experimentally that bird predation can negatively affect limpet abundance, as Mercurio et al. (1985) and Marsh (1986) have also found. My experiments also show that the differences in limpet density between horizontal and vertical walls can be explained largely by the presence or absence of avian predators in these habitats. Birds cannot feed on vertical walls, except where horizontal substrate affords them a place to stand (Frank 1982; Hahn and Denny 1989; J. T. Wootton, personal observation). Whereas limpets exposed to bird predation on horizontal benches exhibited low survival rates, limpets under cages and in controls on vertical walls...
survived at uniformly high levels. Additionally, L. digitalis density within the barnacle zone on vertical walls was 3.7 times that on horizontal walls, a value that agrees well with the range (2.1–7.8) of factor differences in survival rates I found between cage and control treatments in the bird exclusion experiments. Also, the difference in limpet size between habitats supports a bird predation hypothesis. Oystercatchers feed preferentially on larger limpets (Frank 1982; Marsh 1986; Hahn and Denny 1989; Wootton 1990, 1992); thus in areas where they forage, sizes, as well as densities, decline. These experimental and observational results verify that birds are one cause of the limpet abundance pattern observed between horizontal and vertical substrates, as was hypothesized by previous investigators (Frank 1982; Hahn and Denny 1989) from observational evidence. However, the number of limpets surviving under cages is lower on horizontal than vertical surfaces (fig. 3). These differences probably result largely because cages do not completely protect limpets from bird predation on horizontal benches (see Methods and Study Site). Nonetheless, other factors that differ between horizontal and vertical walls, such as increased shading, could also contribute to enhanced limpet abundance.

Bird predation also affects the vertical distribution of L. digitalis along the shore. Limpets occur naturally above the barnacle zone on vertical walls but not on horizontal benches. When birds are excluded from horizontal benches above the barnacle zone, limpet survival more than doubles (fig. 3). The presence of Balanus glandula reduces the severity of bird predation on L. digitalis. When birds are present, limpets survive 2.5–3.6 times better with barnacles than without barnacles when the effects of barnacles independent of bird predation are accounted for, and without barnacles, limpets uniformly exhibit very low survival rates independent of tide height. These results demonstrate that B. glandula has a positive indirect effect on L. digitalis by reducing avian predation rates.

The reduced predation intensity in the presence of barnacles could have two causes: (1) crypsis could reduce the rate of prey detection or (2) the barnacles could physically interfere with prey capture. The observed patterns in proportion of limpets found in controls between treatments with all barnacles and half the barnacles present (fig. 4) lends support to the first hypothesis. Because plots with all of the barnacles present contain fewer attachment sites between barnacles, more limpets have to attach on top of the barnacles, where any physical interference by barnacles on feeding birds should be reduced. However, the proportion of limpets in cage-control pairs that were present in controls was not higher in treatments where barnacle cover was reduced by 50% compared with treatments where all barnacles were left intact.

Factors other than avian predation also affect limpet mortality. The reduced survival with increasing tidal height of limpets under cages indicates that desiccation, heat stress, respiratory stress, or some other correlate of immersion time can directly alter limpet abundance. Factors related to tide height undoubtedly play an important role in determining the distributional limits and abundances of limpets, especially in areas without bird predators (Lewis 1964). Nevertheless, avian effects on limpet distribution appear more important on horizontal benches. In the absence of bird predators, limpets can survive at higher tidal heights than
they typically do in the presence of birds. Furthermore, in the presence of birds but the absence of barnacles, limpets are typically eliminated, independent of tidal height.

Aside from indirectly affecting limpets by altering the predation rate on them, barnacles also directly affect limpet survival in a complex, nonlinear manner (see also Hawkins and Hartnoll 1982; Tsuchiya 1984). Limpets survived best under cages when barnacles were partially removed. Completely removing barnacles may have enhanced desiccation stress on the limpets for two reasons. First, barnacles trap water and slow its runoff during low tide because they provide greater small-scale surface area and interstices for water to adhere. Therefore, small patches of bare rock in an area with barnacles remain moist throughout much of the low tide, whereas bare rock without surrounding barnacles quickly dries out (J. T. Wootton, personal observation). Second, by providing elevational relief, barnacles promote the development of a larger boundary layer, reducing convective water loss at the rock surface by reducing air movement. Such a boundary-layer effect could also reduce the stress of wave action on limpets at the rock’s surface. Other experiments have shown that barnacles can enhance the survival rates of limpets in Australia (Creese 1982), Great Britain (Hawkins and Hartnoll 1982), and Japan (Tsuchiya 1984).

Independent of bird predation, increasing barnacle cover from intermediate high levels had the opposite effect on limpet survival rates of increasing from no barnacles to intermediate abundances. Limpet survival was significantly reduced under cages with high barnacle cover compared with intermediate barnacle cover. High barnacle abundance may have provided a rough surface texture that was either difficult for limpets to forage on or reduced their ability to clamp down tightly to the surface, thereby detracting from their ability to conserve water during low tide or resist wave shock during high tide. Other studies have also found that barnacles negatively affect limpet performance (Branch 1976; Choat 1977; Creese 1982; Hawkins and Hartnoll 1982; Tsuchiya 1984; Dungan 1986).

Results of this study also relate to the general causes of zonation patterns in benthic marine systems. In intertidal communities, zonation patterns of organisms have been suggested to be generally set by biotic interactions at the bottom, physical stresses at the top (Connell 1972). This generalization is reasonable if all intertidal organisms are derived from taxa that evolved in marine environments; marine-adapted taxa are likely to find the environment more stressful as immersion time is reduced. However, not all members of intertidal communities have an evolutionary history of living in the ocean. Terrestrially adapted organisms experience a reversed gradient of physical stress, where the environment becomes more stressful with greater immersion time. The presence of terrestrially affiliated organisms means that strong biotic interactions might control the upper limits to intertidal distributions as well as lower limits. This experiment provides one example; birds control the upper limit of *L. digitalis* in habitats where birds are able to forage.

The effect of bird predation on *L. digitalis* appears to indirectly affect *B. glandula* abundance. Barnacle cover on vertical walls is one-third that on horizontal benches. Numerous experiments along Washington shores and elsewhere have
demonstrated that limpets negatively affect barnacle populations, probably by consuming or dislodging young barnacles from the rock (Dayton 1971; Denley and Underwood 1979; Underwood et al. 1983; Farrell 1988; Johnson and Strathman 1989). The negative relationship between limpet abundance and barnacle cover on vertical walls in my study further supports the hypothesis of a negative limpet effect across a wide range of limpet densities, and my bird exclusion experiments demonstrate that bird predation is a major cause of variation in limpet abundance between horizontal and vertical habitats. Given these patterns and experimental results, indirect effects of bird predation probably contribute to differences in barnacle abundance on horizontal and vertical surfaces.

This study provides examples of the two types of indirect effects (figs. 1 and 5). Balanus glandula indirectly affects L. digitalis populations by altering the consumption rate in the bird–L. digitalis predator-prey interaction. This indirect effect therefore represents an interaction modification because it arises from one species changing the mathematical relationship between two other directly interacting species. Finding evidence of crypsis, the apparent mechanism here, might be one good predictor of indirect effects via interaction modifications within a community (Colwell and Fuentes 1975). Examples of crypsis by one species in the presence of another species are frequently observed (Portman 1959; Wickler 1968; Owen 1980).

In contrast to the indirect effects of barnacles on limpets, the indirect effect of birds on barnacles represents an interaction chain, and its outcome can be predicted by knowing just the pairwise interactions. Birds directly reduce limpet densities via predation, and limpets directly reduce barnacle densities via interference competition or inadvertent predation (Dayton 1971; Denley and Underwood 1979; Underwood et al. 1983; Farrell 1988; Johnson and Strathman 1989). By following this chain of direct interactions, the straightforward prediction can be
made that barnacles will increase in the presence of birds. This prediction is supported by patterns of habitat occupancy on horizontal and vertical surfaces in the field.

The experiments and observations reported here provide evidence for both interaction chains and interaction modification indirect effects in natural communities. As more examples are documented, the relative importance of these two categories of indirect effects should become apparent, and some of the common circumstances under which they occur should be revealed. This information will provide one avenue of insight when one attempts to derive theories predicting the importance of direct and indirect interactions among species.

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