PREDICTING DIRECT AND INDIRECT EFFECTS:
AN INTEGRATED APPROACH USING EXPERIMENTS
AND PATH ANALYSIS[1]

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Abstract. Determining the strengths of interactions among species in natural communities presents a major challenge to ecology. Using an approach combining experimental perturbations and path analysis, I examined the mechanisms by which birds directly and indirectly affected other members of an intertidal community, evaluated alternative causal hypotheses, and predicted whether interactions among other unmanipulated species would be strong or weak. Comparing treatments with *t* tests indicated that excluding bird predators with cages caused increases in *Pollicipes polymerus*, and declines in *Nucella* spp., *Mytilus californianus*, and *Semibalanus cariosus*. However, these conclusions provided no insight into the underlying mechanisms causing the differences. Path analysis permitted insight into the causal mechanisms by making a variety of predictions about the strength of direct interactions: (a) Bird predation negatively affects *Pollicipes*, but not *Nucella*, *Leptasterias*, or *Mytilus*; (b) *Pollicipes* reduces *Semibalanus* and *Mytilus* abundance because of space competition; (c) *Mytilus* reduces *Semibalanus* cover through competition for space; and (d) as prey species, *Semibalanus* and *Pollicipes* enhance *Nucella* density, but *Nucella* predation does not have important effects on *Semibalanus* or *Pollicipes*. Based on the estimated strength of direct interactions, the importance of indirect effects among species could also be predicted. In experiments manipulating *Nucella*, *Pollicipes*, *Semibalanus*, and birds independently of one another, I tested 11 of the interactions predicted by the path analysis; all were supported. Path analysis in conjunction with limited experiments may provide an efficient means to predict important direct and indirect interactions among unmanipulated species within ecological communities.

Key words: bird predation; community interaction webs; indirect mutualism; interaction strength; intertidal communities; Larus glaucescens; Mytilus californianus; Nucella; Pollicipes polymerus; Semibalanus cariosus; space competition.

INTRODUCTION

Ecological communities have long been viewed as complex interdependent sets of organisms (Darwin 1859, Forbes 1887, Elton 1927, Clements 1936, Hutchinson 1959, Hairston et al. 1960). This view implies that a species is likely not only to affect the abundance and distribution of those species with which it directly interacts, but also to influence indirectly other members of the community via chains of direct interactions or by changing the nature of direct interactions. I define "direct interactions" as those in which species physically interact (e.g., consumption, territoriality, interference competition, pollination), and "indirect interactions" as those effects of one species on another that do not involve physical interaction. Until recently, indirect effects of species were not well investigated, in part, because the complexity of the mathematics in modeling multi-species systems often makes them hard

to analyze. With the recent rise in ecological field experimentation, indirect effects of species on other members of the community have become increasingly apparent (e.g., Connell 1961, Paine 1966, 1980, Dayton 1971, Davidson et al. 1984, Dethier and Duggins 1984, Power et al. 1985, Sih et al. 1985, Dungan 1986, Hay 1986, Kerfoot and Sih 1987, Schmitt 1987, Carpenter 1988, Kneib 1988, Pfister and Hay 1988, Schoener 1989, Fairweather 1990, Petraitis 1990, Power 1990, Turner and Mittlebach 1990, Strauss 1991, Wootton 1992, 1993*a, b*).

The possibility of indirect effects makes mechanistic interpretation of results from experiments on species pairs difficult (Bender et al. 1984). For example, species that share resources are expected to negatively affect each other via competition. One species may indirectly enhance a second species on the same trophic level, however, if it primarily consumes species that compete with the preferred prey of the second species ("indirect mutualism," Levine 1976, Paine 1980, Vandermeer 1980, Davidson et al. 1984, Dethier and Duggins 1984, Boucher 1985). Therefore monitoring the responses of other members of the community while performing species perturbation experiments is advisable (Connell

1983, Dungan 1986). Predicting strongly interacting species—those species that both directly and indirectly influence other members of a community—is important because when they are affected by changes in the environment, many other species will be impacted indirectly. Progress in understanding and predicting indirect effects may be greatly facilitated by performing community manipulations and examining the characteristics of species interactions that either result or fail to result in indirect effects on other species. Unfortunately an exhaustive experimental analysis requires

$$\sum_{r=1}^{n} n!/[r!(n-r)!]$$

treatments in an n-species community, which can become logistically very difficult to carry out while maintaining adequate replication. Furthermore, although experiments on artificial communities with few species provide valuable insights into the forms that direct and indirect effects can take, they also indicate that extrapolating results from experiments between species pairs to whole communities may not be successful (Wilbur 1972, Neill 1974, Wilbur and Fauth 1990, Wootton 1993a; but see Pomerantz 1981, Case and Bender 1981). Additionally, it may be technically unfeasible or ethically unjustified (e.g., endangered species) to manipulate some members of a community. Hence, alternative methods are required to predict the role that experimentally untractable species play within a community. Although experimentally manipulating all possible combinations of species gives a definitive description of how species interact with one another, this approach does not *predict* which species interactions are most important within a community.

An alternative approach to manipulating all possible species combinations is to perform manipulations of suspected key species within a naturally occurring community, and monitor the response of the other community members. Links between species can then be inferred by analyzing how populations of other species in the community vary.

Path analysis is a promising statistical technique for assessing covariation among species in the investigation of community structure. It can perform two functions. First, it can suggest which of several alternative hypotheses describing the relationships among variables is most likely to be correct (Sokal and Rohlf 1981, Maddox and Antonovics 1983, Hayduk 1987, Johnson et al. 1991, Mitchell 1992). Second, given a particular hypothesis about the causal relationships among variables, it estimates the relative strengths of direct and indirect interactions among variables (Wright 1934, Arnold 1972, Power 1972, Johnson 1975, Li 1975, Sokal and Rohlf 1981, Dillon and Goldstein 1984, Schemske and Horvitz 1988, Crespi and Bookstein 1989, Sinervo 1990, Wilbur and Fauth 1990, Johnson

et al. 1991, Kingsolver and Schemske 1991, Mitchell 1992).

Community interaction webs represent qualitative hypotheses about causal relationships among variables. A community interaction web includes both links between consumers and their prey, as in traditional food webs, and also links representing other potential direct interactions, notably interference competition (the "cross-links" of Paine 1980). Thus, a solid understanding of the natural history of a system is critical to deriving an appropriate interaction web. The definition of direct effects used above is particularly helpful in this regard. Physically interacting organisms can usually be observed directly, making construction of an interaction web relatively easy. Also, experiments with species pairs in isolation can provide further information, where necessary, without performing all possible species manipulations, particularly when the nature of the interaction is difficult to observe (e.g., chemical signals).

Path analysis is, in effect, a sequence of multiple regressions and correlations structured by an a priori hypothesis. Because path analysis requires an a priori hypothesis, it can be used as a tool to predict important interactions in the community. Because path analysis is composed of multiple regression and correlation analyses, it contains the assumptions inherent in regression and correlation (i.e., linearity, additivity, uncorrelated residuals). In its simplest form, path analysis also assumes no reciprocal causation (i.e., species A affects species B, and species B affects species A). However, techniques are available to apply to path analysis where reciprocal causation is suspected to be important (Tukey 1954, Turner and Stevens 1959, Wright 1960b, Hayduk 1987).

Experimentally manipulating a species or environmental variable, then assessing the covariation among species via path analysis, is logistically much more feasible than experimentally examining all possible species combinations, and provides much stronger inference than studies employing regression techniques alone. The initial perturbations are known and treatments are randomly assigned; thus differences among treatments are unlikely to be the result of unknown factors. Qualitative knowledge of the community interaction web further strengthens the causal inference given to the conclusions from such an analysis. It is important to emphasize, however, that because correlation does not prove causation, the conclusions following from the second step in the analysis should be treated as predictions that point to the most important experiments to be conducted next, not as conclusions to be set in stone.

Here I present work in an intertidal community using a combined experimental and path analysis approach to (1) examine some processes that cause, and fail to cause, indirect effects, (2) predict strongly interacting species within the community beyond those species

that are experimentally manipulated, and (3) test how accurately path analysis predicts strongly and weakly interacting species. In particular I consider the direct and indirect effects of avian predators on predatory snails and their food resources.

NATURAL HISTORY

The middle intertidal assemblage on wave-exposed, rocky shores of Washington state is usually dominated by a band of the mussel *Mytilus californianus* with interspersed gaps filled by plants and sessile, filter-feeding invertebrates, notably acorn barnacles (*Semibalanus cariosus* and *Balanus glandula*), blue mussels (*Mytilus trossulus,* formerly considered *M. edulis,* MacDonald and Koehn 1988) and goose barnacles (*Pollicipes polymerus*) (Dayton 1971, Paine and Levin 1981). This assemblage occurs above the effective feeding range of the starfish *Pisaster ocraceous* (Paine 1966, 1974), and covers a tidal span between 1.3 and 0.2 m above mean low low water (MLLW) at my study site. A number of mobile invertebrates live within the matrix of sessile species (Suchanek 1979), notably herbivorous limpets (*Lottia* spp.) and predatory dogwhelks (*Nucella* spp.). The effects of birds on limpets and algae within this assemblage have been reported elsewhere (Wootton 1992, 1993a). The sessile invertebrates feed upon plankton, not other intertidal organisms, and therefore do not compete with mobile intertidal consumers for food. However, competition for attachment space on the rocks is an important interaction among the sessile species (Dayton 1971, Paine 1974, 1980, Paine and Levin 1981). The larger *Pollicipes* and *Mytilus californianus* represent later successional stages in mussel bed gaps, and are frequently seen overgrowing acorn barnacles (Paine 1974, Paine and Levin 1981; J. T. Wootton, *personal observation*). *Pollicipes* and *M. californianus* also interact with each other. By holding space, *Pollicipes* potentially inhibits the invasion of *M. californianus* (Paine 1974, Wootton 1990, 1992, 1993b).

Three species of predatory dogwhelks, *Nucella emarginata, N. canaliculata,* and *N. lamellosa,* are conspicuous predators in the middle intertidal zone of Washington state coastal communities, and attain densities ranging from 50 to 370 snails/m². These predatory snails feed upon many intertidal invertebrates (Dayton 1971, Palmer 1983, 1984, West 1986, Wootton 1990), particularly three groups of sessile filter feeders: acorn barnacles, goose barnacles, and blue mussels. *Nucella* lay benthic egg capsules that produce crawl-away larvae. Thus, they have no planktonic stage that sessile filter feeders can consume. *Nucella* are preyed upon by birds, notably Glaucous-winged Gulls (*Larus glaucescens*), Black Oystercatchers (*Haematopus bachmani*), and Northwestern Crows (*Corvus caurinus*) (Zach 1978, Wootton 1990; J. T. Wootton, *personal observation*). On English shores, *Nucella lapillus* density can be greatly reduced by Purple Sandpipers (*Calidris maritima*); thus one might expect birds to be important predators on
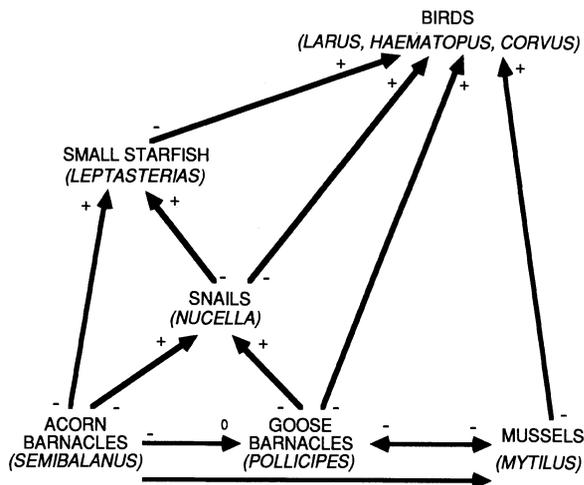

FIG. 1. Community interaction web upon which the path analysis in this study of a rocky intertidal assemblage in Washington state is based. Horizontal arrows represent competition for space and point to the winner. Other arrows represent predator–prey links, with the arrow indicating the direction of energy or nutrient flow.

Nucella in other areas (Feare 1970). *Nucella* is preyed upon by, and shares acorn barnacles as a food resource with, the small starfish *Leptasterias hexactis* (Menge 1972).

Aside from feeding on *Nucella,* gulls feed heavily on *Pollicipes* (Wootton 1990). Gulls and Black Oystercatchers also feed upon *Mytilus californianus* and small starfish (Marsh 1986, Wootton 1990; J. T. Wootton, *personal observation*). From this summary of natural history, a community interaction web can be constructed as a starting point for path analysis (Fig. 1).

INITIAL EXPERIMENTS: EFFECTS OF BIRDS

Study site and methods

I conducted the study on Tatoosh Island (48°23′ N, 124°44′ W), a 6-ha island 0.5 km off the northwest corner of Washington state. I placed experiments on the Simon's Landing site at tidal heights spanning 0.7 to 1.1 m above MLLW (mean low low water) to examine the effects of bird predation on other members of the intertidal community. Using prefabricated cages, I excluded bird predators from portions of five 1.5-yr-old gaps (>1 m²) in the mussel bed that contained newly settled *Pollicipes* (29.0 ± 6.3% cover [$\bar{X}$ ± 1 SD]). Cages were vinyl-covered wire letter baskets turned upside-down and strapped to the rocks, and measured 29 × 34 × 7.5 cm with 4 × 2.5 cm mesh on the top, 7.5 × 2.5 cm on the sides. Further details of cage design are presented in Wootton (1990, 1992, 1993b). I paired each cage with an adjacent 29 × 34 cm unmanipulated control area in each gap. Experiments began in May 1987 and were censused in June 1988 and 1989. At each census I measured the percentage cover of sessile organisms using a 29 × 34 cm quadrat divided into
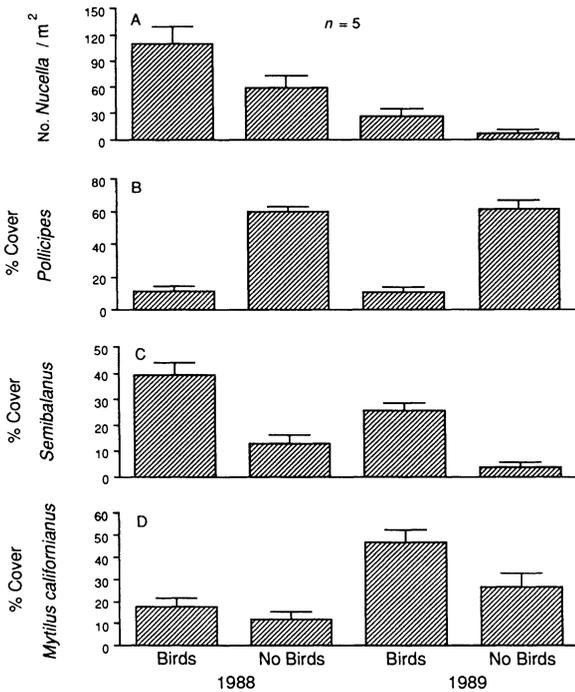
FIG. 2. Difference in the abundance of invertebrates after 1 and 2 yr in bird exclusion treatments. $n = 5$ pairs of plots. (A) Density (no./m²) of *Nucella* spp., (B) percentage cover of *Pollicipes polymerus*, (C) percentage cover of *Semibalanus cariosus*, (D) percentage cover of *Mytilus californianus*. Error bars = 1 SE.

100 squares, and counted individuals of mobile species.

I also conducted an experiment to test for effects that the cage rim might have on the movement of *Nucella* into and out of cages. In this experiment the mesh roof and sides were removed from the cages, leaving just the basal rim surrounding the plot, and an adjacent unmanipulated plot was randomly designated as a control. Birds thus had access to both treatments (Wootton 1993a; J. T. Wootton, *personal observations*), but the cage rim, that portion of the cage that potentially interfered with snail movement, remained. Five replicates were placed in gaps with newly settled *Pollicipes*, and were censused after 2 yr. I conducted another experiment testing for cage artifacts by placing cages on vertical walls, where the physical presence of the cage remained the same, but where birds could not feed in control plots. Results of this experiment have been

reported elsewhere (Wootton 1992); no cage artifacts were detected in the vertical-wall experiment.

Initially, statistical analysis of the experiments was conducted with paired t tests to test for differences between treatments within the same gap. To avoid dependence between census dates, I analyzed the mean abundance of species averaged over the 1988 and 1989 censuses of each plot. All data were tested for normality using Lilliefors test (Lilliefors 1967).

Results: comparison of treatment differences

The net effect of bird predation on *Nucella* density was not negative as expected in a predator–prey relationship. Instead, *Nucella* density was 1.9 times higher in control areas exposed to bird predation than in areas under cages after 1 yr, and 4.3 times higher than protected plots after 2 yr (Fig. 2A, mean difference between treatments $\overline{\Delta X} \pm 1$ SD = 35.5 $\pm$ 16.0 snails/m², paired t test, $P = .008$). The presence of a cage rim did not affect the abundance of *Nucella* (Table 1).

The proportion of the rock area covered by different sessile species changed in the absence of birds. *Pollicipes* covered more than 5.5 times the space under cages as in controls (Fig. 2B, $\overline{\Delta X} \pm 1$ SD = 49.8 $\pm$ 10.5% cover, paired t test, $P < .001$). *Semibalanus* covered 3.1 times more space after 1 yr and 6.7 times more space after 2 yr in controls compared to under cages (Fig. 2C, $\overline{\Delta X}$: 24.2 $\pm$ 6.4% cover, paired t test, $P = .001$). *Mytilus californianus* did not decline in the presence of its avian predators, but covered 42% more space after 1 yr and 77% more space after 2 yr in controls compared to caged plots (Fig. 2D, $\overline{\Delta X}$: 13.0 $\pm$ 7.2% cover, paired t test, $P = .016$). The cover of sessile species did not differ between treatments in the cage rim experiments (Table 1).

In summary, comparing treatment means yielded the following conclusions: (1) *Nucella, Mytilus californianus,* and *Semibalanus* decreased where I excluded birds, and (2) *Pollicipes* increased where I excluded birds. Therefore, these results provide the static consequences of an experimental manipulation, but they do not provide any insight into *why* these results were obtained.

With a qualitative knowledge of how species interact in this community (Fig. 1), at least three hypotheses can be formulated that are consistent with t test results (Fig. 3). First (hypothesis 1), bird predation reduced the abundance of *Pollicipes,* causing *Semibalanus* and

TABLE 1. Results from cage rim experiments run for 2 yr. Data show abundances in rim and control treatments and difference between paired treatments for each variable (means $\pm$ 1 SD). P values based on paired t tests ($n = 5$).

Variable	Rim	Control	Difference	P
Nucella density (no./m²)	1.2 $\pm$ 1.3	3.6 $\pm$ 5.9	−2.4 $\pm$ 5.6	.388
Pollicipes % cover	7.6 $\pm$ 6.2	11.0 $\pm$ 16.6	−3.4 $\pm$ 11.2	.534
Mytilus % cover	23.2 $\pm$ 25.8	22.0 $\pm$ 23.4	1.2 $\pm$ 6.3	.692
Semibalanus % cover	33.8 $\pm$ 18.0	40.0 $\pm$ 29.7	−6.2 $\pm$ 15.1	.409

Mytilus californianus to increase following their release from space competition. In turn, the increase in *Semibalanus* elevated *Nucella* abundance by enhancing its food supply, assuming that acorn barnacles are a relatively more important food item to *Nucella* than are goose barnacles. Second (hypothesis 2), bird predation lowered the abundance of small starfish (*Leptasterias*), reducing the predation pressure on *Nucella*. In turn, increased *Nucella* predation lowered the abundance of *Pollicipes*, causing increases in *Mytilus californianus* and *Semibalanus* through reduced space competition. Third (hypothesis 3), bird predation reduced small starfish, increasing *Semibalanus* by reducing predation by starfish. The increase of *Semibalanus* prey in turn raised the abundance of *Nucella*. Consequently, *Pollicipes* abundance declined because of increasing predation by *Nucella*, causing the release of *Mytilus californianus* from space competition.

Although the hypotheses derived from a qualitative knowledge of interactions among species narrow the range of possible mechanisms, at least two questions remain unanswered: (1) which of these hypotheses is likely to be correct, and (2) how important are the interactions that are not directly included in the causal chain of these hypotheses? By applying path analysis to the data derived from the bird manipulation experiment, we can obtain insight into these questions, and therefore derive better predictions about the importance of interactions that were not directly tested by the experiment.

PATH ANALYSIS OF BIRD MANIPULATIONS

Methods

Path analysis was carried out by conducting multiple regression on each species in a structured manner, determined by the specific causal hypothesis being assumed (Fig. 3), the specific treatments used in the experiments, and the other interactions diagramed in the community interaction web (Fig. 1). Aside from the anticipated species interactions in each hypothesis, I included relative tide height of the plots as a causal variable for all species, because time immersed in water was expected to affect the growth rate and mortality risk of marine species. Because I did not census small starfish in the initial experiments, if a hypothesis postulated an indirect effect of birds on other species through feeding on small starfish, I estimated a path coefficient for the entire indirect pathway by including bird treatment in the regression. For example, hypothesis 1 dictates that *Semibalanus* cover be regressed on *Pollicipes* cover, *Mytilus* cover, and tide height (Fig. 4A), but hypothesis 3 dictates that *Semibalanus* cover be regressed on birds and tide height (Fig. 4E). In all analyses *Nucella* density was transformed to $\ln(n + 1)$ to meet linearity assumptions.

I estimated path coefficients as the partial regression coefficients standardized by the ratio of the standard
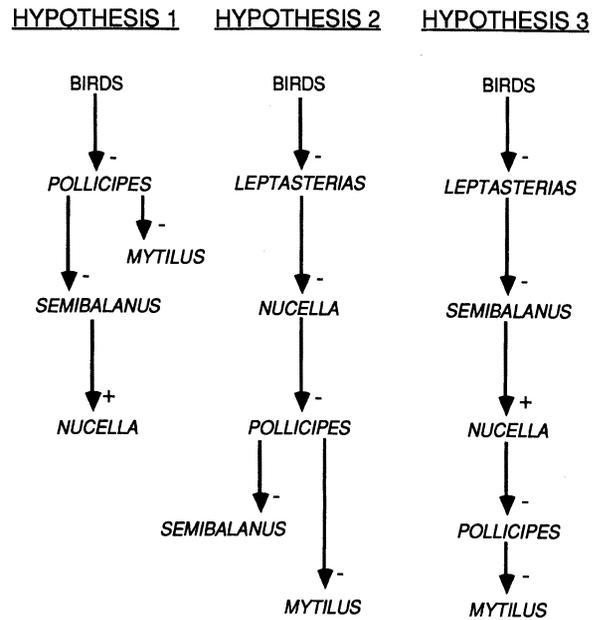

FIG. 3. Major causal links in three alternative hypotheses derived from Fig. 1 that can explain the results in Fig. 2. Arrows designate the direction of causality; signs adjacent to arrows represent direction of the effect (increase or decrease in abundance).

deviations of the independent and dependent variables (Table 2; Tukey 1954, Sokal and Rohlf 1981). For each causal hypothesis considered, I deemed paths important if the partial regression coefficients in the underlying multiple regressions were statistically different from zero ($P < .05$).

When performing the path analyses I examined the regression results to ensure that collinearity problems were not severe (see Myers [1986] for a clear discussion of the topic). If causal variables in a multiple regression are strongly collinear (i.e., strongly associated with each other), estimates of coefficients and their associated error terms can be highly sensitive to measurement errors. Therefore, when strong collinearity was indicated (high factor loading by two or more variables associated with a small eigenvalue; >90% of the variance in one independent variable explained by the other independent variables in a regression), I also performed path analysis after removing the collinear path with the smallest estimated path coefficient.

Although the three basic causal hypotheses that I examined did not imply reciprocal effects among variables, I also conducted path analyses incorporating possible reciprocal effects of *Nucella* on *Pollicipes* and *Semibalanus*, and of *Mytilus californianus* on *Pollicipes*. For example, to include a reciprocal interaction of *Mytilus californianus* on *Pollicipes* in hypothesis 1, I included *Mytilus californianus* cover as an independent variable in the regression along with birds and tide height (Fig. 4C).
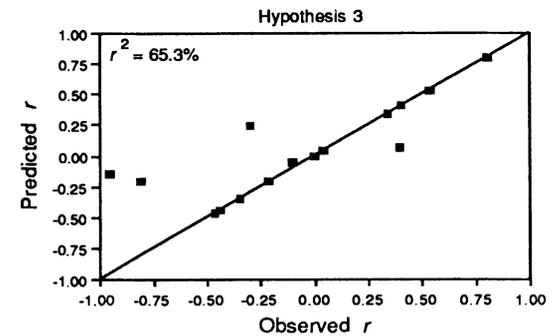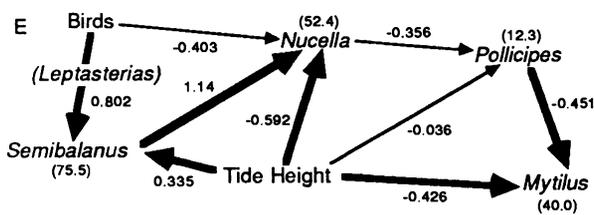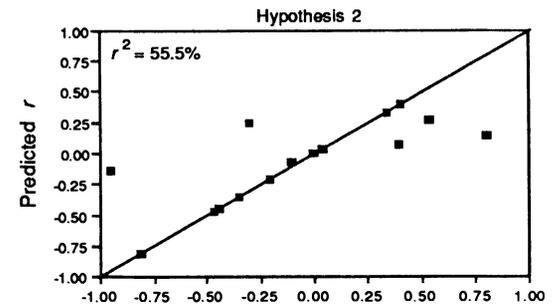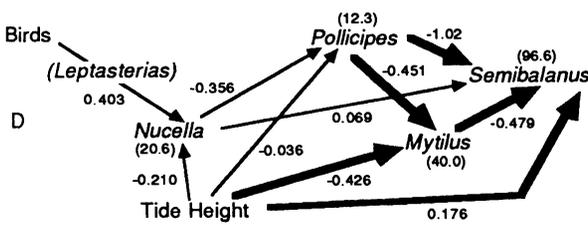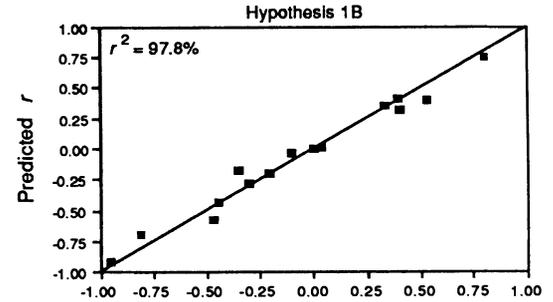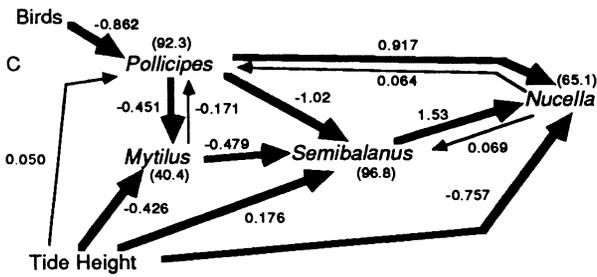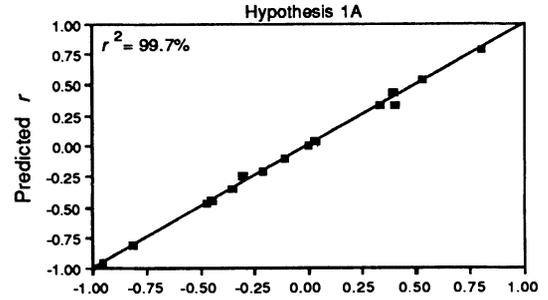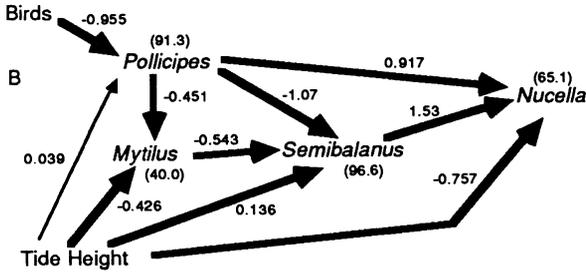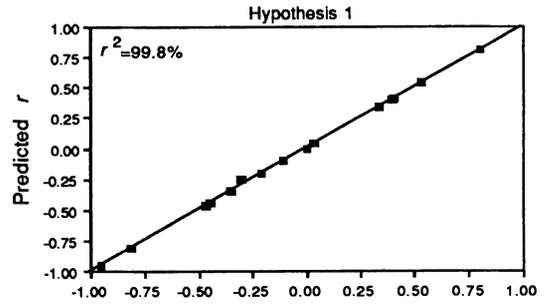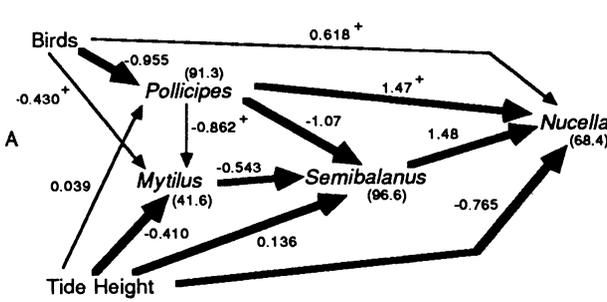
Path diagrams (Fig. 4) contain a variety of information (for detailed explanations see Wright 1934, 1960*a, b,* Tukey 1954, Turner and Stevens 1959, Li 1975, Sokal and Rohlf 1981, Dillon and Goldstein 1984). Paths can be evaluated either by path coefficients or by regression coefficients; each yields complementary pieces of information (Tukey 1954, Turner and Stevens 1959, Wright 1960*a*). Regression coefficients provide information about the functional relationships between pairs of variables, predicting how much the dependent variable changes with a given change in any of the different causal variables. Path coefficients indicate the strengths of association, providing a relative measure of the amount of variance explained by different causal variables, and the sign of the interaction. Unlike correlation coefficients, path coefficients are not constrained to lie between -1 and 1, but because the total proportion of variance explained is constrained, the absolute value of a path coefficient can only exceed 1 when indirect pathways of opposite sign exist, and when the amount of variation explained in the dependent variable is high.

To assess which of the hypotheses was most likely to explain the results of the experiment, I compared the variance–covariance (correlation) matrix predicted by each path analysis with the observed correlation matrix from the experimental data (Table 3). The closer the match between the predicted and observed correlation matrices, the more likely the associated path analysis correctly describes the system. Each model derived from a path analysis implies a specific, predicted correlation matrix, which I derived using the formula outlined in the Appendix. Basically, this formula predicts correlations among variables by adding together all paths between two variables and all paths through shared causal variables (Sokal and Rohlf 1981, Hayduk 1987). When pathways include chains of variables, the path coefficients of the component links are multiplied together. For example, the expected correlation between birds and *Mytilus* in hypothesis 1 (Fig. 4A) is the direct path between birds and *Mytilus* added to the indirect path from birds through *Pollicipes* to *Mytilus* ($-0.430 + [-0.955 \times -0.862] = 0.393$). Likewise, the expected correlation between *Pollicipes* and *Mytilus* is the direct path between *Pollicipes* and *Mytilus* plus the paths through their two shared causal variables, birds and tide height ($-0.862 + [-0.955 \times$

TABLE 2. Descriptive statistics of variables used in the path analysis of the bird manipulation experiments ($n = 20$).

Variable	Mean	SD	SS
Bird treatment	0.50	0.47	443.7
Pollicipes polymerus cover	35.50	26.76	14322.0
Mytilus californianus cover	25.60	16.97	5759.6
Semibalanus cariosus cover	20.30	15.48	4792.6
ln (*Nucella* density)	1.45	0.90	16.2
Tide height (metres above mean low low water)	0.87	0.16	0.52

$-0.430] + [0.039 \times -0.410] = -0.467$). I examined the relative fits of the predicted matrices of each path analysis to the observed correlation matrix by using the maximum-likelihood χ^2 formula presented in Hayduk (1987) (see Appendix).

Results of path analysis

The results of path analysis permitted a richer series of conclusions than would have been possible if I had only tested for statistical differences between treatments. First, path analysis indicated that the observed differences between cages and controls probably arose because bird predation reduced *Pollicipes* (hypothesis 1), rather than released *Nucella* and/or *Semibalanus* from predation by small starfish (hypotheses 2 and 3). The variation in observed correlation coefficients was matched by 99.8% of the variation in predicted correlation coefficients under hypothesis 1, but by only 55.5% of that predicted under hypothesis 2 and 65.3% of that predicted under hypothesis 3 (Fig. 4A, D, and E). Furthermore, the observed correlation matrix did not differ significantly from that expected under hypothesis 1 (maximum likelihood $\chi^2_5 = 2.62$, $P > .5$), but was significantly different from those expected under hypotheses 2 and 3 ($\chi^2_7 = 33.0$, $P < .001$ and $\chi^2_8 = 47.91$, $P < .001$, respectively). The poorer fits of hypotheses 2 and 3 in part reflected the fact that path analysis under these causal schemes did not predict strong paths between birds and several of the invertebrate species (Fig. 4D and E).

In all instances when both birds and *Pollicipes* were hypothesized to be causal variables, a high degree of collinearity was indicated. After eliminating links exhibiting high collinearity in hypothesis 1 to derive more stable path coefficients (hypothesis 1A), the fit re-

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FIG. 4. Path diagrams (left) and fits of predicted and observed correlation coefficients of each pair of variables (right) under five alternative structural hypotheses based on the results from bird exclusion experiments over 2 yr. Thick arrows represent statistically significant ($P < .05$) paths from multiple-regression analysis; thin arrows represent nonsignificant paths. Path coefficients are presented adjacent to paths. Total variance explained for each endogenous variable is presented in parentheses. Path coefficients highly sensitive to collinearity are indicated by $+$. (A) Hypothesis 1 (see Fig. 3), (B) Hypothesis 1A (Hypothesis 1 after removing high collinearity), (C) Hypothesis 1B (Hypothesis 1A with reciprocal loops included), (D) Hypothesis 2 (see Fig. 3), (E) Hypothesis 3 (see Fig. 3). The line $y = x$ is included on the graphs of model fits, indicating where points should fall in a perfectly fit model. Hypothesis 1A provides the best fit of models without strong collinearity.

TABLE 3. Observed correlations between variables from the bird manipulation experiments. Variable codes: P = *Pollicipes*, M = *Mytilus*, S = *Semibalanus*, N = *Nucella*, B = Birds, T = Tide height.

	P	M	S	N	B	T
P	1	−0.468	−0.809	−0.349	−0.955	0.039
M	−0.468	1	−0.103	−0.303	0.399	−0.444
S	−0.809	−0.103	1	0.532	0.802	0.335
N	−0.349	−0.303	0.532	1	0.403	−0.210
B	−0.955	0.399	0.802	0.403	1	0
T	0.039	−0.444	0.335	−0.210	0	1

mained high (r^2 = 99.7%, Fig. 4B), and the observed correlation matrix did not differ significantly from the expected matrix (χ^2_7 = 4.27, P > .5).

Models including reciprocal links did not perform better than hypothesis 1A. Adding reciprocal links from *Mytilus californianus* to *Pollicipes* and from *Nucella* to its two prey species reduced the fit in hypothesis 1B (r^2 = 97.8%, Fig. 4C, χ^2_4 = 34.02, P < .001). Both the reduced fit and the low estimated path coefficients indicated that these reciprocal interactions probably were not important in the experiments. Incorporating reciprocal links into the path analyses increased the fit of both hypotheses 2 and 3 (r^2 = 85.5% and 77.1%, respectively); however, neither matched the fit of hypothesis 1A, and both fits remained significantly poorer than expected by chance (χ^2_4 = 40.91, P < .001 and χ^2_3 = 50.63, P < .001, respectively).

TESTING THE PREDICTIONS OF PATH ANALYSIS

By assessing the importance of various direct and indirect pathways between variables, path analysis can predict which interactions within a community are likely to be important and which are not. This property of path analysis would be extremely useful to ecologists

TABLE 4. Predicted changes in target species abundance following particular manipulations based on hypothesis 1A favored by the path analysis (Fig. 4C), and the verbal causal hypotheses 2 and 3 (Fig. 3B and C).

Manipulation Target species	Predictions for hypotheses		
	1A	2	3
Reduce *Nucella*			
1) *Pollicipes*	0	+	+
2) *Semibalanus*	0	−	0
3) *Mytilus californianus*	0	−	−
Reduce *Semibalanus* independently of birds, *Pollicipes*, *Mytilus*			
4) *Nucella*	−	0	−
Reduce *Pollicipes* independently of birds			
5) *Semibalanus*	+	+	0
6) *Mytilus californianus*	+	+	+
7) *Nucella*	+	0	0
Reduce birds independently of *Pollicipes*			
8) *Semibalanus*	0	0	−
9) *Mytilus californianus*	0	0	0
10) *Nucella*	0	−	−
11) *Leptasterias*	None	+	+

if the predictions were accurate, but to my knowledge, the predictions of a path analysis have never been tested experimentally. I conducted a series of experiments that tested the predictions of the hypothesis (1A) that path analysis indicated as most likely to be correct, and thereby examined how much insight path analysis could provide into the important interactions within the community. By examining the included links and their estimated strengths in hypothesis 1A, at least 10 falsifiable predictions can be derived (Table 4). Furthermore, hypotheses 2 and 3 in their verbal form (see *Initial experiments: Results: comparison of treatment differences*) make distinguishing predictions in five cases (Table 4), and make the additional prediction that bird predation reduces the abundance of *Leptasterias*. I experimentally tested all of the predictions listed in Table 4.

Nucella *manipulations*

Methods.—I assessed the effects of *Nucella* on its prey species and on other members of the community with and without birds by removing *Nucella* at 2-wk intervals in caged and control treatments placed adjacent to each replicate pair of treatments in the bird manipulation experiments described above (see *Initial experiments: effects of birds: Study site and methods*). I initiated removal manipulations May 1987 and censused them at 1-yr and 2-yr intervals. Removing *Nucella* in these experiments probably did not eliminate its predation in plots completely because of migration from outside the experiments, but the treatment reduced *Nucella* predation pressure to at least half that of controls. *Nucella* treatments were crossed with bird treatments. This treatment was not motivated directly by the predictions of path analysis, but represents an independent assessment of *Nucella* effects for any given hypothesis because its results were not included in the original path analysis. I measured percentage cover of all sessile invertebrates in each treatment, and I also counted the number of individual *Pollicipes* per unit area within a sub-area of each plot (0.01 m² under cages, 0.064 m² in controls). I assessed differences between *Nucella* treatments in *Pollicipes*, *Mytilus californianus*, and *Semibalanus* cover and in *Pollicipes* density with paired *t* tests across both caged and uncaged treatments. Tests were one tailed, based upon the directional predictions made by the alternative hy-

potheses. To assure independence assumptions I analyzed data averaged from the 2 yr sampled. All data were tested for normality using Lilliefors test. Because some alternative hypotheses predicted no change in the percentage cover of particular species, I also estimated statistical power by determining the probability of failing to find a significant difference when a difference actually existed (i.e., a Type II error; see Cohen 1977, Sokal and Rohlf 1981, Toft and Shea 1983). Such analyses required that I set a specific minimum treatment effect that I felt would reflect a biologically meaningful change. I assessed what the probability of making a Type II error would be, given the observed variance among pairs of treatments, if the treatment actually caused a difference of 10% of the total cover available. This choice is relatively conservative, given that it was exceeded by all observed differences between treatments in the bird manipulations (Fig. 2).

Results. — Pollicipes cover did not increase when I removed Nucella (Fig. 5A, mean difference [$\overline{\Delta X} \pm 1$ SD] = $-1.50 \pm 4.05\%$ cover, $P > .5$). Given a difference of 10% cover of Pollicipes between treatments, the probability of making a Type II error (β) was $<.0005$. Nucella removal also had no significant effect on the average number of Pollicipes per unit area in plots with birds (paired t test, $P > .4$), but caused an 18% increase in Pollicipes density after 1 yr and a 35% increase after 2 yr when birds were excluded by cages (Fig. 5B, paired t test, $P < .03$). Thus Nucella predation negatively affected the population size of Pollicipes in the absence of birds, but because individuals compensated for reduced density by growing larger, its relative dominance within the sessile invertebrate community remained the same.

Removing Nucella did not reduce the percentage of area covered by Semibalanus (Fig. 5C, $\overline{\Delta X} \pm 1$ SD = $5.8 \pm 12.07\%$ cover, paired t test, $P > .5$, β for 10% difference = .26). Mytilus californianus cover also did not decline when I removed Nucella (Fig. 5D, $\overline{\Delta X}$: $-0.75 \pm 9.58\%$, paired t test, $P > .5$, β for 10% difference = .09).

To gain further insight into why sessile species did not vary with Nucella manipulations (e.g., because of weak effects vs. strong pathways of opposite sign), I conducted a second path analysis using bird presence, tide height, and Nucella treatment as externally controlled variables, that led to Semibalanus cover as the focal dependent variable. This path diagram provided no indication of important effects of Nucella treatment on space-occupying organisms (Fig. 6). As in the path analysis for the bird manipulation experiments, the percentage of variance explained for each species in the path diagram was high, ranging from 83 to 92%. Semibalanus cover again decreased strongly with increasing Pollicipes and Mytilus cover, but was not significantly associated with Nucella treatment or tide height. Mytilus cover declined with increasing Pollicipes cover and tide height, but was not associated with
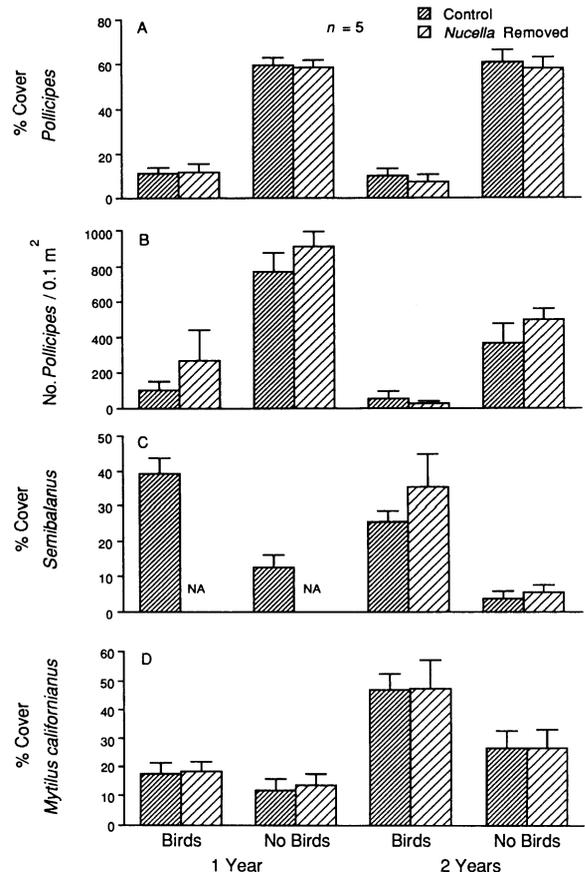

FIG. 5. Results of experiments removing Nucella at 2-wk intervals in the presence and absence of birds after 1 and 2 yr. Error bars = 1 SE, $N = 5$. (A) percentage cover of Pollicipes polymerus, (B) number of Pollicipes/0.1 m², (C) percentage cover of Semibalanus cariosus, (D) percentage cover of Mytilus californianus. Semibalanus cover was not recorded in Nucella-removal treatments in the first year of the experiment (NA).

Nucella removal treatment. Pollicipes cover declined in the presence of birds, but was not associated with tide height or Nucella treatment.

Semibalanus manipulations

Methods. — To test if Semibalanus increased Nucella density independently of Pollicipes, birds, or Mytilus californianus, I conducted the following experiment at the Simon's Landing site. In 29 × 34 cm plots within eight young gaps (<1 yr old) in the mussel bed, I reduced Semibalanus cover by ≈50% (Fig. 7A), leaving adjacent unmanipulated plots as controls. The gaps contained high cover of Semibalanus (Fig. 7A) but no Pollicipes or Mytilus californianus. This experiment, designed to test explicitly one prediction of the path analysis, was initiated on 10 June 1990, and censused on 6 August 1990. Treatments were compared using a paired t test after transforming Nucella densities to ln(n + 1) to meet normality assumptions. As with the Nu-
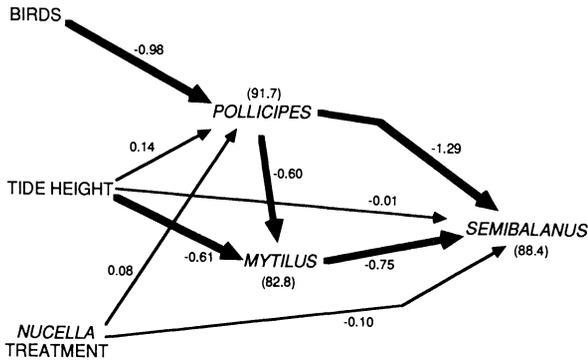
FIG. 6. Path diagram estimating the relative importance of direct and indirect effects of birds, *Nucella* treatment, tide height, and space competitors on *Semibalanus*, based on results of experiments crossing bird and *Nucella* density manipulations. Arrows designate the direction of causality; numbers adjacent to arrows represent the size of the abundance effect (path coefficients).

cella manipulation experiments, I examined statistical power given observed variances and assuming an average change of one snail per experimental plot (≈ 10 snails/m²). Again, this value is relatively conservative because differences observed in the bird manipulations exceeded one snail per plot.

Results. — Path analysis correctly predicted the response of *Nucella* to a change in *Semibalanus* cover. *Nucella* density declined by 58% when I reduced the cover of its prey species, *Semibalanus*, in the absence of *Pollicipes* and *Mytilus californianus* (Fig. 7B, $\overline{\Delta X} \pm$ 1 SD = 0.701 ± 0.552 for data transformed from n snails/m² to $\ln(n + 1)$, paired t test, $P < .005$, β for one snail per plot difference = .83).

Pollicipes *manipulations*

Methods. — To assess the independent effects of birds and *Pollicipes* on *Nucella, Semibalanus, Mytilus californianus,* and *Leptasterias,* I conducted the following experiments at the Strawberry Island and Finger sites on Tatoosh Island (see Paine and Levin [1981] for site descriptions). In each of six 1.5-yr-old gaps with newly settled *Pollicipes,* I created (1) a caged plot, (2) a caged plot with *Pollicipes* cover reduced to low levels (Fig. 8A), and (3) an uncaged plot with *Pollicipes* reduced to low levels (Fig. 8A). This experiment, designed to test explicitly seven predictions of the path analysis, was initiated on 26 May 1990, and censused on 26 June 1991. To assess the effects of *Pollicipes* independent of birds, I compared cage treatments with normal and reduced *Pollicipes* cover using one-tailed t tests, after assuring that normality assumptions were met using Lilliefors test. Similarly, to assess the effects of birds independent of *Pollicipes,* I compared *Pollicipes* removal treatments with and without cages. As in previously described experiments, I determined statistical power of the tests by assuming differences either of

10% total cover for sessile species or of one individual per plot for mobile species.

Results. — *Pollicipes* affected *Nucella, Semibalanus,* and *Mytilus californianus* independently of the presence of birds in the manner predicted by the path analysis. Under cages, when *Pollicipes* cover was reduced, *Nucella* density increased by a factor of 3.6 ($\overline{\Delta X} \pm 1$ SD = 22.01 ± 11.97 snails/m², paired t test, $P < .005$, Fig. 8B, β for one snail per plot difference = .48), *Semibalanus* cover increased by a factor of 6.9 ($\overline{\Delta X}$: 12.25 ± 8.77% cover, paired t test, $P < .01$, Fig. 8C, β for 10% cover difference = .24), and *Mytilus californianus* increased by a factor of 1.9 ($\overline{\Delta X}$: 18.50 ± 13.50% cover, paired t test, $P < .01$, Fig. 8D, β for 10% cover difference = .58; see also experiments in Wootton 1990, 1992).

Independent of their effects on *Pollicipes,* birds did not significantly increase *Nucella* density (Fig. 8B, $\overline{\Delta X}$ ± 1 SD of log-transformed data = 0.16 ± 1.18 individuals/m², paired t test, $P > .35$, β for one snail change per plot = .84), or *Semibalanus* cover (Fig. 8C, $\overline{\Delta X}$: −0.45 ± 0.73% cover [log-transformed data], paired t test, $P > .5$, β for 10% cover difference = .012), nor did they reduce *Mytilus californianus* cover (Fig. 8C, $\overline{\Delta X}$: −8.67 ± 14.50% cover, $P > .1$, β for 10% cover difference = .62). This result also provides further evidence that cage artifacts did not influence the abun-
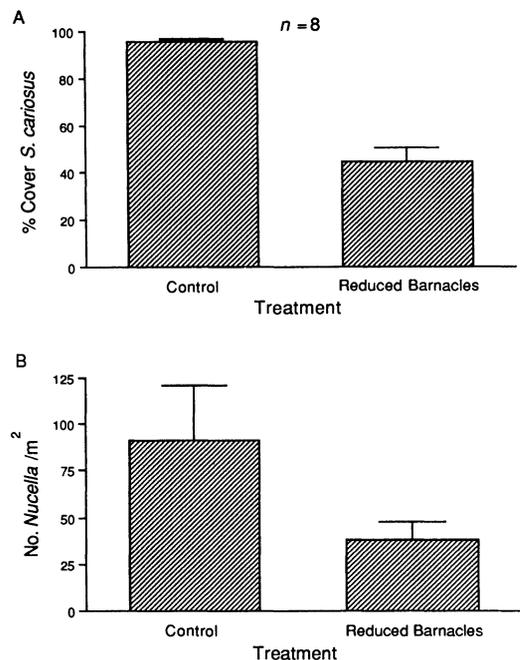

FIG. 7. Effects of reducing *Semibalanus cariosus* abundance on the abundance of its predators, *Nucella* spp. (A) Mean (and 1 SE) percentage area covered by *Semibalanus* in controls and areas where *Semibalanus* cover was experimentally reduced. (B) Mean (and 1 SE) density of *Nucella* in controls and reduced *Semibalanus* plots. $N = 8$.

dances of these species (see above and Wootton 1993*b*). Contrary to hypotheses 2 and 3, birds did not significantly reduce the abundance of *Leptasterias* (Fig. 8E, $\overline{\Delta X}$: $-0.17 \pm 1.59\%$ cover, paired t test, $P > .4$, β for one starfish per plot difference $= .67$).

DISCUSSION

Combining experimental manipulations, natural-history observations, and path analysis provided an efficient means to uncover the relative importance of direct and indirect pathways. Specifically, rather than reducing *Nucella* directly by predation, or indirectly increasing *Nucella* by feeding on *Leptasterias,* birds indirectly enhanced *Nucella* abundance by consuming *Pollicipes,* thereby releasing *Semibalanus,* the preferred prey of *Nucella,* from competition. The path analysis predicted four weak direct interactions: bird predation on *Nucella* and *Mytilus,* and *Nucella* predation on *Semibalanus* and *Pollicipes.* Three strong direct interactions were predicted: *Pollicipes* competition with both *Semibalanus* and *Mytilus,* and *Semibalanus* as food for *Nucella.* Path analysis also predicted the importance of four indirect interactions: a strong negative effect of *Pollicipes* on *Nucella,* little effect of birds on *Semibalanus* or *Mytilus* in the absence of a change in *Pollicipes,* and no effect of birds on other species by reducing *Leptasterias* numbers. My experiments verified all these predictions, and did not support any of the distinguishing predictions made by two alternative structural hypotheses that the path analysis did not favor. Statistical power tended to be lower when directional predictions were made by the hypothesis favored by path analysis (mean $\beta = .533 \pm .244$) than for the two alternative hypotheses (mean $\beta = .378 \pm .318$ and $.432 \pm .384$ for hypotheses 2 and 3, respectively); therefore the power of the experimental tests was not biased in favor of the path analysis predictions.

Pollicipes density increased where I experimentally reduced *Nucella* density (Fig. 2C), and *Nucella* density increased where either birds or I reduced *Pollicipes* abundance (Figs. 2A and 8B). The results of this reciprocal pair of species removals might suggest that *Nucella* and *Pollicipes* compete, but the mechanism leading to their reciprocal negative effects is not competition (see Schmitt [1987] for another example). The responses of associated species and qualitative observation of direct interactions suggest a different picture. Competition is an important but indirect part of the scenario, because space competition occurs among food resources of the predator. One could coin a new term such as "indirect competition" to describe this situation, but because the same reciprocal negative effects could occur in a number of ways as the signal of a perturbation is transmitted through the community web, ecology would soon be awash in terminology if new names were introduced for each different case. A more useful approach places species in the context of
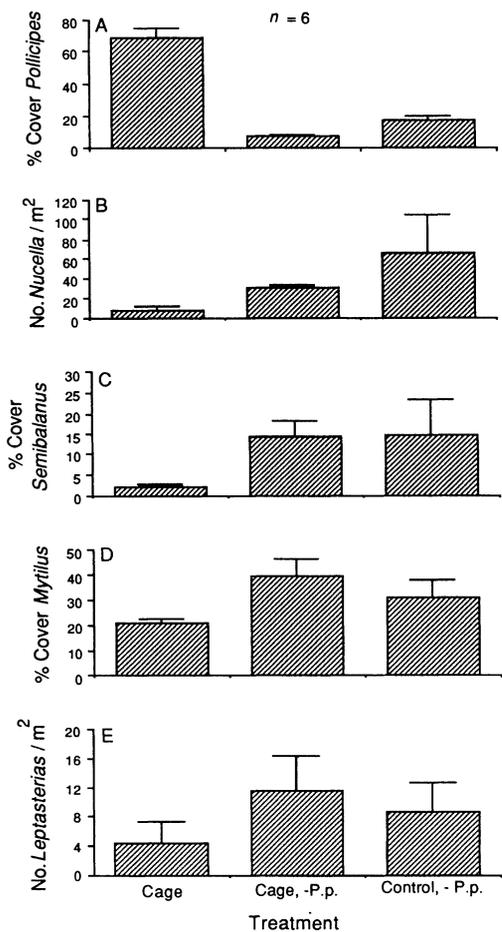

FIG. 8. Independent effects of *Pollicipes polymerus* and bird predators on the abundance of associated intertidal species. (A) *Pollicipes* percentage cover, (B) *Nucella* density, (C) *Semibalanus* percentage cover, (D) *Mytilus californianus* percentage cover, (E) *Leptasterias* density. Treatment symbols: Cage = no birds; Cage, $-$P.p. = no birds, reduced *Pollicipes*; Control, $-$P.p. = birds, reduced *Pollicipes.* Error bars = 1 SE; $N = 6$ plots.

an entire community rather than as one of a species pair and then traces chains of potential interactions, providing a more mechanistic and holistic understanding of how species affect each other.

In order to understand and predict why some species influence many other members of the community whereas other species do not, it is important to determine not only when and how indirect effects occur, but also when and why they do not occur. My experiments provide one such example. By feeding on *Pollicipes,* gulls dramatically affect the abundance of *Nucella, Mytilus californianus, Semibalanus,* several limpet (*Lottia*) species, and macroalgae (Wootton 1992, this study). In contrast, although *Nucella* predation can depress the density of *Pollicipes,* this reduction has no apparent effect on the rest of the community. The lack

of indirect effects can be traced to the indeterminant growth of *Pollicipes*. By growing larger, *Pollicipes* offsets the mild reduction in density caused by *Nucella*, and thus retains the same amount of space. *Nucella* predation has no indirect consequences for the abundance of other species because indirect effects related to *Pollicipes* are caused by changes in the amount of space it holds, not its density per se. Reduced intraspecific competition for space can counteract the relatively low predation rates of *Nucella*, but not the high rates of gull predation.

The *Nucella* removal experiments also provide two examples suggesting that the effects of some direct interactions can be obscured by other direct interactions. First, several experiments (Connell 1970, Dayton 1971) have clearly shown that *Nucella* can drastically reduce the cover of *Semibalanus*; however I found no such effect in my experiments (Fig. 5C). Instead differences in *Semibalanus* cover were strongly associated with differences in the cover of *Pollicipes* and *Mytilus californianus* (Figs. 4 and 6). In the experiments of Connell and Dayton, *Pollicipes* and *Mytilus californianus* were not present; thus *Nucella* predation rather than interspecific competition appeared important in their studies. Second, effects of *Nucella* on *Pollicipes* density were only apparent in caged plots; therefore, bird predation on *Pollicipes* obscured the already weak effects of *Nucella* predation.

By reducing the invasion rate of *Mytilus californianus*, *Pollicipes* affects the dynamics of succession described in Paine and Levin (1981). The detailed consequences of bird predation on *Pollicipes* are reported elsewhere (Wootton 1990, 1993b). Briefly, as mussels attain large size with time, the competitive effects of *Pollicipes* are reduced and the competitive effects of *Mytilus californianus* on *Pollicipes* become stronger. In the absence of birds *Mytilus californianus* eventually obtains dominance, but at a much slower rate than normal. In such cases as this, where size structure is suspected to play an important role, path analysis might require the incorporation of several size classes of a species.

Path analysis in conjunction with an experimental manipulation provided an accurate means of evaluating alternative structural hypotheses and predicting important interactions within the middle-intertidal community of Tatoosh Island. Some of the limitations of applying this approach should be recognized, however. First, the choice of the manipulated species is important. If the species chosen interacts strongly with other species, this technique will yield a large body of information on other important interactions within the community; little insight will be gained if a weakly interacting species is chosen. At present there are few concrete rules that can be applied to determine the best species to manipulate. Natural-history intuition seems to play a large role in determining the species on which experimental community ecologists choose to focus.

Thus, formalizing the factors that contribute to natural-history intuition represents a potentially useful endeavor. Tentative criteria might include species that exhibit dominance in abundance or biomass, species that have strong patterns of positive or negative association with other species, species that have high rates of resource consumption, or species that serve as resources for many other species. These criteria, however, do not guarantee that a strongly interacting species will be chosen (Paine 1980).

Second, as more possible interactions are included, replication must increase in order to maintain adequate degrees of freedom. Therefore the approach will be more successful if complex communities are organized into submodules of species (May 1974, Paine 1980) that can be examined somewhat independently of one another; further work is required to determine the reality of such submodules.

Third, path analysis varies in its ability to handle two basic types of indirect interactions, chains of direct interactions and modifications of interactions (see Wootton 1993a, and references therein). Chains of direct interactions form the basis for path analysis, so they are easily handled. Assessing the effects of a species that modifies how two other species interact is more difficult. When one variable modifies how a second variable interacts with a third, its effect can only be accounted for by including in the path analysis a variable with the particular functional form assumed to describe the joint effect of the two causal variables. For example, if two variables are assumed to act multiplicatively on a third, a new variable (the product of the two) could be included in the path analysis. However, using such variables increases the risk that linearity assumptions will be violated.

Fourth, when an important species is missing from the causal hypothesis underlying the path analysis (i.e., the underlying natural-history information is incomplete), the resulting predictions may be incorrect. This problem is shared with all methods that attempt prediction. The ability of path analysis to evaluate alternative hypotheses is useful in this regard when appropriate data are available. In some cases an alternative can be evaluated without data on particular species when information on a hypothesized causal variable is available. For example, I was able to partially evaluate the role that small starfish played in producing the patterns I observed by incorporating a direct link from birds to prey species of the starfish.

In this study I have shown how integrating experiments, natural-history observations (contained in a descriptive community-interaction web), and path analysis can be used to infer the importance of direct and indirect pathways through a community and thereby efficiently derive a functional web (sensu Paine 1980). The experiments presented above demonstrate that the presence of birds alters abundances of *Pollicipes, Mytilus, Semibalanus,* and *Nucella,* and that *Nucella* can

affect *Pollicipes* density in the mussel zone at Tatoosh Island. Path analysis structured by observations of direct interactions that are incorporated into a community interaction web provides predictions about the pathways through which birds affect other intertidal species. The conclusions from path analysis are strengthened greatly because much of the variance in the abundance of species can be traced to the original experimental perturbation, and the cause, nature, and point of action of the perturbation is known. The natural-history information underlying the community web may not be perfect, however, and as the structure of the path analysis depends on this knowledge, one cannot be sure that a given interpretation of direct and indirect effects is correct. The analysis suggests the subsequent critical experiments to perform without resorting to a vast multi-species manipulation. In conducting subsequent experiments, I found that path analysis correctly predicted the outcome in all 11 cases tested. Integration of experiments and path analysis is a promising approach for predicting important interactions within ecological communities.

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APPENDIX

FORMULAS USED TO CALCULATE AND TEST EXPECTED CORRELATION MATRICES OF DIFFERENT PATH DIAGRAMS (AFTER HAYDUK 1987)

I used the following formula to calculate an expected correlation matrix (Σ) (dashed lines represent the division of the Σ matrix into four submatrices):

$$\Sigma = \left[\begin{array}{c|c} (\mathbf{I} - \mathbf{B})^{-1}(\mathbf{\Gamma\Phi\Gamma'} + \mathbf{\Psi})(\mathbf{I} - \mathbf{B})^{-1'} & (\mathbf{I} - \mathbf{B})^{-1}\mathbf{\Gamma\Phi'} \\ \hline \mathbf{\Phi\Gamma'}(\mathbf{I} - \mathbf{B})^{-1'} & \mathbf{\Phi} \end{array} \right],$$

where $\mathbf{I}$ is an identity matrix, $\mathbf{B}$ is the matrix containing the path coefficients between the endogenous variables (variables affected by other variables in the path analysis, i.e., *Pollicipes, Mytilus californianus, Semibalanus,* and *Nucella*), $\mathbf{\Gamma}$ is the matrix containing the path coefficients between exogenous variables (variables without causal assumptions, i.e., birds, tide height) and the endogenous variables, $\mathbf{\Phi}$ is the correlation matrix between exogenous variables (= $\mathbf{I}$ when all are manipulated experimentally), $\mathbf{\Psi}$ is a matrix whose diagonal contains the errors in predicting the endogenous variables (i.e., $1 - R^2$ from the regression analyses), $\mathbf{X}'$ is the transpose of some matrix $\mathbf{X}$, and $\mathbf{X}^{-1}$ is the inverse of matrix $\mathbf{X}$. This

formula, simpler than the one presented in Hayduk (1987), assumes no correlation in error terms and no magnitude of measurement error.

I tested predicted correlation matricies (Σ) against observed correlation matrices ($\mathbf{S}$) using the maximum likelihood goodness of fit formula presented in Hayduk (1987):

$$[\text{tr}(\mathbf{S\Sigma}^{-1}) + \ln|\mathbf{\Sigma}| - \ln|\mathbf{S}| - v] N,$$

where $\text{tr}(\mathbf{S\Sigma}^{-1})$ is the sum of the diagonal elements in the matrix arising from the product of the observed and the inverse of the predicted correlation matrices, ln is the natural logarithm, $|\mathbf{\Sigma}|$ and $|\mathbf{S}|$ are the determinants of the predicted and observed correlation matrices, respectively, v is the number of variables in the path analysis, and N is the number of samples taken. The associated degrees of freedom are:

$$df = v(v + 1)/2 - t,$$

where t represents the total number of coefficients in $\mathbf{B}$, $\mathbf{\Gamma}$, $\mathbf{\Phi}$, and $\mathbf{\Psi}$ estimated from the regression analyses. This formula approximates a χ^2 distribution.