

Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade¹

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Abstract: Bird predators (glaucous-winged gulls [*Larus glaucescens*], American black oystercatchers [*Haematopus bachmani*], and northwestern crows [*Corvus caurinus*]) were excluded over a period of 2 years with large, wide-mesh cages in the lower intertidal zone of Tatoosh Island, Washington State, U.S.A. to determine their direct and indirect effects on sea urchin (*Strongylocentrotus purpuratus*) abundance and macro-algal abundance and diversity. Bird predation directly reduced urchin abundance by 45-59%. By reducing urchin grazing, birds indirectly increased algal cover 24-fold, and increased algal taxonomic richness 6-fold across all replicates. Path analysis further supported the hypothesis that birds indirectly affected algal cover via a trophic cascade, and indicated that variation in algal taxonomic richness was strongly affected by sea urchin effects on algal cover in a non-linear way, but was only weakly influenced by the independent effects of selective foraging by sea urchins. Taxonomic richness increased with increasing algal cover at low levels of algal cover, but in a diminishing fashion as algal cover increased, consistent with the intermediate disturbance hypothesis. The results indicate that trophic cascades are important in this lower intertidal community and that predators may indirectly affect the diversity of guilds at lower trophic levels by controlling the abundance of keystone consumers.

Keywords: *Corvus caurinus*, *Haematopus bachmani*, indirect effects, keystone species, *Larus glaucescens*, path analysis, species diversity, *Strongylocentrotus purpuratus*.

Résumé: Au cours d'une période de deux ans, les oiseaux prédateurs (le goéland à ailes grises [*Larus glaucescens*], le huîtrier de Bachman [*Haematopus bachmani*] et la corneille d'Alaska [*Corvus caurinus*]) ont été exclus, grâce à des cages à grandes mailles, de la zone intertidale basse de l'île Tatoosh (état de Washington, É.-U.) afin de déterminer les effets directs et indirects de leur prédation sur l'abondance de l'oursin de mer (*Strongylocentrotus purpuratus*) et l'abondance et la diversité des macroalgues. La prédation par les oiseaux a réduit le nombre d'oursins dans une proportion de 45 à 59 %. En diminuant le nombre d'oursins et ainsi la pression de broutement de ces organismes phycophages, les oiseaux ont contribué de façon indirecte à augmenter le couvert (par un facteur de 24) et la richesse taxonomique (par un facteur de 6) des algues et ce, dans toutes les répétitions. Une analyse de parcours soutient l'hypothèse voulant que les oiseaux affectent de façon indirecte le couvert en algues via une chaîne trophique. L'analyse indique également que la richesse taxonomique des algues est fortement affectée d'une façon non linéaire par l'impact des oursins sur le couvert en algues, mais est faiblement influencée par la quête sélective de nourriture de la part des oursins. La richesse taxonomique augmente avec le couvert en algues lorsque ce dernier est réduit. Le taux d'augmentation de la richesse diminue toutefois à mesure que le couvert augmente. Cela est en accord avec l'hypothèse des perturbations intermédiaires. Ces résultats indiquent que les chaînes trophiques sont importantes dans cette communauté intertidale basse et que les prédateurs peuvent affecter de façon indirecte la diversité des guildes des niveaux trophiques inférieurs en contrôlant l'abondance des consommateurs ayant un rôle-clé dans l'écosystème.

Mots-clés: *Corvus caurinus*, *Haematopus bachmani*, effets indirects, espèces-clés, *Larus glaucescens*, analyse de parcours, diversité spécifique, *Strongylocentrotus purpuratus*.

Introduction

Since the hypothesis of Hairston, Smith, & Slobodkin (1960) was proposed, ecologists have been interested in the degree to which consumers, by reducing populations of their prey, can indirectly affect the populations sizes of species at lower trophic positions in a food web. Subsequent mathematical models of multi-trophic systems predict such effects for simple food chains (Smith, 1969; Rosenzweig, 1973; Fretwell, 1977; 1987; Oksanen *et al.*, 1981), although their existence in food webs has been questioned because of the possible compensatory effects of interspecific competition (Strong, 1992). Evidence has now begun accumulating that such indirect effects (indirect effects are defined here as an effect of one species on another that requires a third species to arise; see Wootton, 1994b), usually referred to as trophic cascades (Paine, 1980; Carpenter, Kitchell & Hodgson, 1985), can be important in a variety of natural communities, based on evidence from both experimental

manipulations (e.g. Kajak, Andrezejewski & Wojik, 1968; Shapiro, 1979; Carpenter, Kitchell & Hodgson, 1985; Power, Matthews & Stewart, 1985; Power, 1990; Turner & Mittelbach, 1990; Spiller & Schoener, 1990; Brönmark, Klosiewski & Stein, 1992; Martin *et al.*, 1992; Wootton, 1992; 1994b; Wootton & Power, 1993; Marquis & Whelan, 1994) and observed responses to predator and parasite invasion (e.g. Estes & Palmisano, 1974; Sinclair, 1979; Duggins, 1980). The question remains as to how frequently trophic cascades are important to natural communities as taxonomic membership and physical conditions change.

Consumers are also thought to have important effects on species composition within a trophic level. For example, experimental reductions of the starfish *Pisaster ochraceus* results in reduced diversity of space-occupying organisms (Paine, 1966; 1974), whereas removing some grazers enhances algal diversity, observations leading to the intermediate disturbance hypothesis (Paine & Vadas, 1969; Connell, 1977; Lubchenco, 1978). Whether diversity increases, decreases or is unaffected by such "keystone" consumers is determined by two factors: the intensity of

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consumption and the selectivity of consumption. When the intensity of consumption is high, the production of prey may not offset losses, whereas moderate consumption can make resources available to all prey species. Selective foraging can augment or counteract these effects, depending on whether consumers concentrate on competitively dominant or inferior species, respectively. Additionally, if consumers at higher trophic positions within a food web feed upon "keystone species," they might indirectly affect the diversity, as well as the abundance of species near the bottom of the food web.

Previous experiments have shown that sea urchins can have a strong impact on algal abundance and diversity in nearshore marine communities (*e.g.* Kitching & Ebling, 1961; Paine & Vadas, 1969; Ogden, Brown & Salesky, 1973; Dayton, 1975; Duggins, 1980; Harrold & Pearse, 1987; but see Ebeling, Laur & Rowley, 1985; Harrold & Reed, 1985; Prince, 1995), and that subtidal predators can modify their impact. Important subtidal predators include sea otters (*Enhydra lutris*) in Alaska (Estes & Palmasano, 1974; Duggins, 1980), the sun star (*Pycnopodia helianthoides*) along the Pacific coast of North America (Paine & Vadas, 1969; Dayton, 1973; Duggins, 1981), the California sheephead (*Semicossyphus pulcher*) along the southern California coast (Nelson & Vance, 1979; Cowen, 1983), and possibly American lobsters (*Homarus americanus*) along the Atlantic coast of North America (Breen & Mann, 1976; but see Elner & Vadas, 1990). The importance of these predators on urchin populations may not be consistent in all habitats, however, because of geographically limited ranges (*e.g.* sea otters), and because wave action and desiccation risk may render these predators ineffective in intertidal areas. Despite this potential refuge from predators, algae, rather than sea urchins, typically dominate lower intertidal shores (Stephenson & Stephenson, 1972; Paine, 1980). One possible cause of this pattern could be that bird predation becomes important in intertidal communities, reducing sea urchin populations and causing a trophic cascade to the algae. Observational estimates of urchin consumption rates suggest that birds (glaucous-winged gulls [*Larus glaucescens*], American black oystercatchers [*Haematopus bachmani*], and northwestern crows [*Corvus caurinus*] can potentially reduce sea urchin densities (Lubchenco, 1978; Irons, Anthony & Estes, 1986; Wootton, in review). In this paper I experimentally examine whether birds indeed affect urchin densities, and whether this impact cascades down to affect algal abundance. Additionally, I examine whether birds indirectly affect algal diversity, as well as the relative importance of selective foraging *versus* consumption intensity by sea urchins on any observed patterns of algal diversity.

Methods and study site

The study was conducted in the lower intertidal zone (below mean low water) on Tatoosh Island, 0.5 km off of the northwestern tip of Washington State, U.S.A. (48° 23' N, 124° 44' W). Tatoosh is characterized by extensive intertidal rock benches subject to heavy wave action, and its intertidal ecology has been extensively studied (see Paine, 1974; Paine & Levin, 1981; Leigh *et al.*, 1987; Wootton,

1992; 1993b; 1994a; and references therein for more detailed descriptions of the study site). My experiments on sea urchins were conducted on the north side of the island at the Hedophyllum Cove and East Beach sites (see Paine, 1988), lower intertidal areas exposed to moderate wave action because of the presence of several offshore rocks.

To examine the effect of bird predation, I experimentally excluded birds from feeding on purple sea urchins (*Strongylocentrotus purpuratus*) using prefabricated cages similar to those described elsewhere (Wootton, 1992; 1993a; 1993b; 1994a). The cages used in the sea urchin experiments differed from the cages in my previously-reported work in that they were almost twice as large (49 cm × 39 cm) and had larger-mesh sides (2.7 cm × 11 cm) and corners (6 cm × 11 cm). Each cage was paired with an adjacent open control area of the same size, and each treatment pair was replicated eight times. At the beginning of the experiment, plots were dominated by high densities (approximately 240 m⁻²) of sea urchins in an "urchin barren" consisting of crustose coralline algae but no macroalgae. The experiment was started on 1 July 1988, and was censused on 3 July 1989 and 23 June 1990. At each census, the number of sea urchins was recorded in each treatment. Additionally, in 1990, the species identity and total amount (percent cover) of fleshy algae was measured in each treatment using a quadrat subdivided into 135 units.

As in any cage experiment, possible cage artifacts need to be considered. Prior work has shown that cages of similar design but smaller mesh size do not have appreciable artifactual effects on intertidal organisms (Wootton, 1992; 1993a; 1993b; 1994a). Sea urchins do not present the same opportunity as other intertidal organisms to experimentally test for cage artifacts, however, because they do not occur in intertidal microhabitats (*e.g.* vertical walls) where birds are obviously absent. Several features of the cages reduce the chances of cage artifacts. First, large holes at the corners allow urchins to move into or out of the cage if they desire, so urchin movement is not artificially constrained. Second, large starfish predators (*Pycnopodia helianthoides* and *Pisaster ochraceus*) have gained access to cages with smaller mesh sizes than those used here (J. T. Wootton & R. T. Paine, pers. observ.), so the cages did not exclude them in these experiments. Other large predators (sea otters, crabs) were absent from the intertidal community of Tatoosh during the study, although a sea otter population introduced in the vicinity of Cape Alava, Washington, has expanded its range to include Tatoosh since 1992 (J. T. Wootton, pers. observ.). Finally, cage artifacts do not appear important for the patterns of algal abundance reported here, because algae has exhibited lush growth both under cages and in uncaged areas in the absence of sea urchins at my study sites (R. T. Paine, pers. comm.).

Differences between treatments in sea urchin density and algal cover were analyzed with Wilcoxon paired ranks tests (Sokal & Rohlf, 1981). Non-parametric tests were used because of violations of normality assumptions. To test whether bird predation indirectly affected the taxonomic composition of fleshy algae, I compared the cumulative frequency distribution (*i.e.* the fraction of total algal cover comprised of each taxa) pooled across all treatments using a Kolmogorov-Smirnov test (Sokal & Rohlf, 1981).

I also applied path analysis (Wright, 1934; Sokal & Rohlf, 1981; Hayduk, 1987) to the data in order to estimate the strength of both direct and indirect pathways from birds to sea urchins and algae, and the relative contribution of changes in the intensity of consumption *versus* the selectivity of consumption (see Wootton, 1994a, for application of the technique to ecological data). Path analysis, a statistical technique designed specifically to tease apart the relative strength of direct and indirect causal pathways between pairs of variables, is essentially a series of multiple regression analyses in which each partial regression coefficient is standardized by the ratio of standard deviations of the independent and dependent variables involved. Path coefficients provide an index of the sign of the effect of a causal variable on a target variable, and of the relative amount of variation accounted for by different variables. The relative importance of indirect pathways between two variables, relative to direct pathways, can be evaluated by multiplying path coefficients within a causal chain together. A key feature of path analysis is that the regression analyses are dictated *a priori* by an underlying mechanistic hypothesis of how the variables are causally related through direct interactions. Alternative hypotheses may yield differing results, but can be evaluated against one another to determine which ones do not adequately fit the data (Hayduk, 1987; Wootton, 1994a).

My path analysis was structured with the following causal hypothesis, based upon natural history observations and theoretical expectations (Figure 1). First, birds feed on sea urchins, but have no obvious direct interactions targeted toward algae. Second, sea urchins feed directly on algae, both reducing algal abundance and potentially affecting taxonomic composition via selective feeding (see Vadas, 1977). Third, algal abundance potentially affects taxonomic composition by affecting the intensity of competition and the probability of finding a new algal taxon. Therefore, the relationship between algal diversity and algal cover might be non-linear (hump-shaped function) if increasing algal

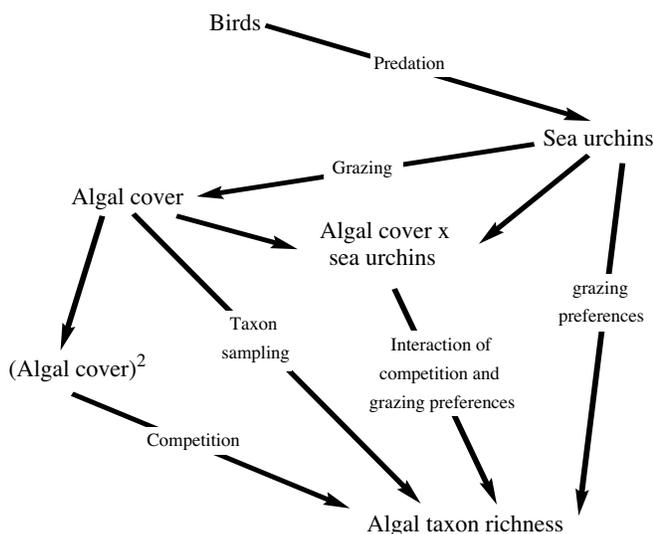


FIGURE 1. Qualitative diagram of causal relationships assumed in path analysis, based upon natural history observations and theoretical expectations of the intermediate disturbance and keystone predation hypotheses (see text).

cover at low abundance levels increases the sample of taxa drawn from the total available taxon pool but increasing algal cover at high abundance levels intensifies competition, leading to competitive exclusion. Fourth, algal cover and urchin density might interact to affect algal diversity if selective foraging by sea urchins is only important at high algal cover where competition would be intense. Therefore, to derive values for the path analysis, (multiple) linear regression was performed as follows: 1) birds (treatment level) on sea urchins, 2) sea urchins on algal cover, and 3) sea urchins, algal cover, squared algal cover, and the product of algal cover and sea urchin density on algal diversity. To derive path coefficients, (partial) regression coefficients were standardized by the ratio of standard deviations of the independent to dependent variable. Sea urchin densities were log-transformed to meet linearity assumptions of the regressions. For the diversity analysis, the four dependent variables used were designed to tease apart the potential importance of factors in the following way: 1) linear effects of algal cover reflect variation in diversity arising from stochastic "sampling" of the regional taxon pool through patterns of colonization and extinction, 2) negative quadratic effects of algal cover reflect increasing negative effects of competition on algal diversity at higher cover levels, 3) linear effects of urchin diversity reflect a direct reduction of taxonomic diversity by selective urchin grazing, and 4) multiplicative effects of algal cover and urchin grazing reflect the interactive effects of selective grazing by sea urchins on taxa of differing competitive ability when competition among algal taxa potentially becomes intense at high algal cover.

Results

Birds had an important effect on sea urchin abundance. Although urchin abundance did not differ between treatments at the start of the experiment (Wilcoxon paired ranks test, $P > 0.7$), urchins were 59% lower after 1 year and 45% lower after 2 years in the presence of bird predators compared to the absence of bird predators (Figure 2, Wilcoxon paired ranks tests, $P < 0.02$ and $P < 0.03$, respectively). I directly observed glaucous-winged gulls, American black oystercatchers, and northwestern crows feeding on sea urchins during the course of the experiment. Gulls and crows were more obvious in their feeding activities, consuming urchins by prying them from the rocks and moving them to a near-by area to either hammer a hole through the test with their beak or to crack open the test by flying up and dropping the urchin on the rocks below. Oystercatchers have not been previously reported to feed on sea urchins, perhaps because their feeding activity is more subtle. They deftly snip off the tube feet and turn the urchin over, cutting a neat hole through the Aristotle's lantern and extracting the meat; the urchin is rarely lifted from the rocks.

Birds caused a trophic cascade, indirectly enhancing the presence of algae by reducing sea urchin densities. In comparing treatment means, average algal abundance (% cover) was 24 times higher in the presence of birds feeding on sea urchins ($15.74 \pm 21.94\%$, range 0-63.7%) than where birds were excluded ($0.65 \pm 0.18\%$, range 0-5.2%, Wilcoxon paired ranks test, $P < 0.05$).

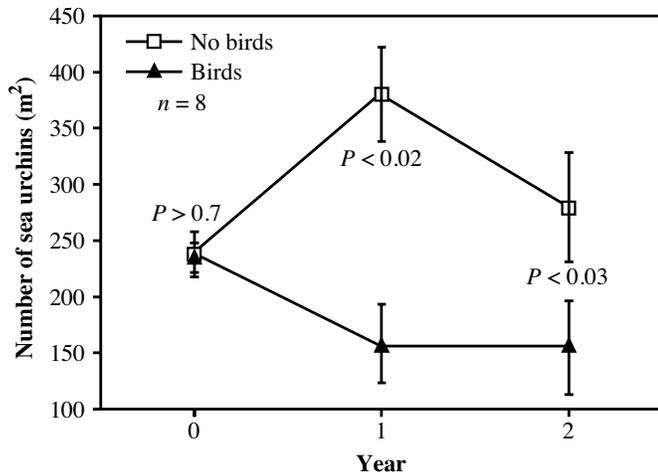


FIGURE 2. Sea urchin densities (mean \pm SE) in plots exposed to birds (triangles) and where birds were excluded with cages (squares) at the beginning of the experiment and after one and two years.

Birds also indirectly affected the taxonomic composition of fleshy macroalgae. In the absence of birds, only filamentous red algae occurred, but six taxa occurred in the presence of birds (filamentous red algae, the green alga *Acrosiphonia*, and the kelps *Nereocystis*, *Laminaria*, *Costaria*, and *Hedophyllum*; Figure 3). Cumulative frequency distributions indicated that taxonomic richness was significantly higher in the presence of birds (Kolmogorov-Smirnov test, $P = 0.006$), and Simpson's diversity index for macroalgae across all replicates in treatments without birds was 0 whereas it was 0.757 in the presence of birds.

Path analysis also indicated a trophic cascade from birds to algae, and suggested that birds indirectly affected overall algal diversity largely through changes in algal abundance, rather than through effects of selective grazing by sea urchins (Figure 4a). Birds had relatively strong effects on sea urchins and sea urchins in turn had relatively strong effects on algal cover consistent with a trophic cascade. Substantial variation remained, however, for both sea urchins (57.1%) and algal cover (41.8%), largely reflecting differences among local sites. Algal species richness had a strong ($r^2 = 0.920$) non-linear relationship with algal cover and sea urchin density. Diversity increased linearly but declined with the square of algal cover. Thus, algal cover had increasingly negative impacts on algal

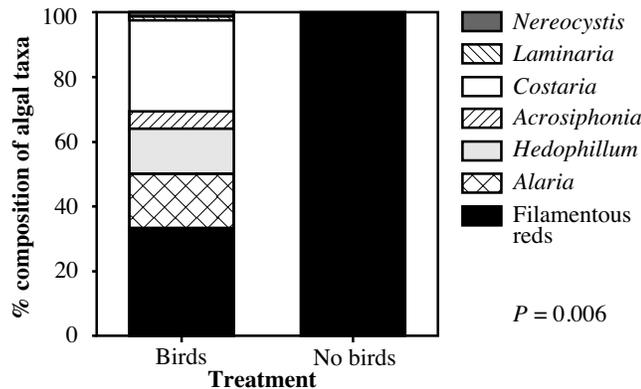


FIGURE 3. The percentage of total algal cover comprised of different algal taxa pooled across all replicates.

richness, consistent with competitive limitation of algal diversity at high levels but the loss of species at low levels because of sampling processes. In contrast, direct effects of sea urchins on algal taxonomic richness were estimated to be virtually non-existent (Figure 4a). However, there were moderate positive effects of sea urchin-algal cover interactions on algal richness. Such a pattern is consistent with selective foraging by sea urchins that enhances algal diversity as the potential for competition increases. Overall, however, pathways from sea urchins to algal diversity were far stronger when passing through algal cover than other pathways reflecting selective foraging.

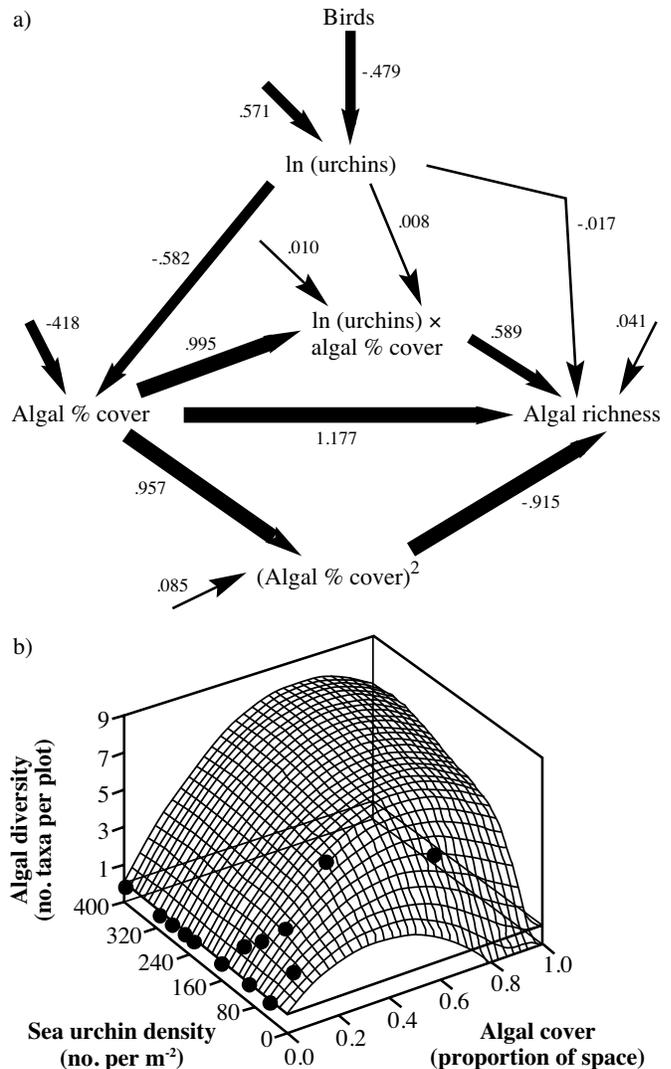


FIGURE 4. Indirect effects of bird predation on algal diversity. a) Path analysis describing the relationships of variation in bird abundance, sea urchin abundance, algal cover, the interaction of algal cover and sea urchin abundance, and algal diversity, given the causal relationships hypothesized in Figure 1. Sea urchin abundance was log-transformed to meet linearity assumptions. Arrows without variables at their base describe the proportion of unexplained variance for each target variable, numbers beside arrows represent path coefficients, which give a relative measure of the strength of association between variables. b) Surface of best fit ($r^2 = 0.920$) describing the relationship between algal cover, sea urchin abundance, and algal taxonomic diversity derived from the multiple regression analysis underlying the path analysis. Points represent results from the bird exclusion experiment used to fit the surface.

The surface plot of the independent and interactive relationship between algal cover and urchin abundance on algal taxonomic richness, derived from the best-fit regression equation, also provides some insights into the potential effects of selective foraging and changes in abundance produced by a consumer (Figure 4b). For a given level of algal cover, the selective foraging activities of a few urchins promote an increase of algal taxonomic richness, and do so more strongly at high levels of algal cover, but adding large numbers of urchins has little additional effect. In contrast, changes in algal cover are associated with changes in algal diversity across all levels of urchin density. Thus, algal cover exhibited consistent associations with changes in diversity in the path analysis, but little effect of selective urchin foraging was detected because urchin populations did not approach local extinction in the experiment.

Two related cautions need to be applied to the results in Figure 4. First, there was an unavoidable lack of data points under conditions of both high algal cover and high sea urchin abundance. This circumstance is rarely, if ever, found under natural conditions or obtained under experimental conditions. Consequently, the shape of the curve under these conditions is an extrapolation from the function fit to data points meeting other conditions and should be viewed with caution. As a further consequence, there was a high degree of colinearity among algal cover, the square of algal cover, and the product of algal cover and urchin density. Therefore, the relative magnitude of path coefficients associated with these variables and algal diversity is quite sensitive to error terms and the relative importance of the pathways could change with further data. It should be noted, however, that because all of these pathways are largely determined by algal cover, this feature does not affect the conclusion that sea urchin effects were largely mediated by changing algal cover, rather than through selective foraging.

Discussion

Bird predation on sea urchins indirectly contributes to the dominance of algae in the lower intertidal zone of Tatoosh Island. Where I excluded birds, sea urchin populations were 59% and 45% greater after 1 and 2 years, respectively. Feeding observations of birds are in accord with these results (Wootton, in review); based on estimates of individual feeding rates, bird densities, and sea urchin densities in the intertidal zone, birds were predicted to reduce sea urchin populations by 42% over the course of a year, with gulls, oystercatchers, and crows contributing 83%, 11%, and 6% to the annual consumption, respectively.

An alternative explanation to direct predation for the differences in sea urchin densities between treatments might be that sea urchins behaviorally select areas where they will minimize their chances of bird predation. Distinguishing between these two hypotheses experimentally is not straightforward, but several lines of evidence indicate that direct predation is the more likely mechanism. First, consumption rates of birds are quantitatively similar to those required to produce the observed differences (Wootton, in review). Second, there is no clear evidence that sea urchins are capable of assessing bird predation risk

in different areas and responding accordingly. They exhibit no obvious behavioral response to the presence of birds moving through an area, nor to other highly mobile vertebrates, such as human investigators. Indeed, avian predation risk at a local scale varies so quickly that it would be difficult for sea urchins to respond appropriately. It is possible that an increase in overhead cover might be a surrogate indicator of reduced predation risk if such cover made sea urchins harder to detect, but *Strongylocentrotus purpuratus* are usually found in areas that they have cleared of macroalgae, and they show no obvious migrations into adjacent areas with cover to avoid predation under those circumstances. Third, I did not note any of the observed changes between treatments over behaviorally-relevant time scales (e.g. between subsequent spring tide series), but only observed effects after a year or more of experimentation.

In association with reductions in sea urchin density, algae increased 24-fold in the presence of bird predators, indicating a strong trophic cascade. This interpretation is supported by numerous experimental manipulations of sea urchins at both this intertidal site (Paine, 1992) and in other habitats (e.g. Kitching & Ebling, 1961; Paine & Vadas 1969; Ogden, Brown & Salesky, 1973; Dayton 1975; Duggins 1980) that caused subsequent increases in the cover of their macro-algal food resource.

The magnitudes of the direct and indirect interactions found in this experiment are relevant to issues concerning the relative importance of direct and indirect effects in ecological communities in general. For example, Schoener (1993) has suggested that, because of environmental variability, the effects of manipulating a species should become damped out as the number of intervening pathways of interaction to another species increases, and thus, that indirect effects should generally be weaker than direct effects. In contrast to this hypothesis, the indirect effect of birds on algae in this experiment was actually magnified (i.e. the proportional change in mean values between treatments was approximately 12 times greater) compared to the direct effect on sea urchins. Because sea urchins are such devastating grazers, even moderate effects of bird predation on sea urchins causes strong changes in algal abundance. Thus, these results are more in line with the theoretical analyses of Levine (1976) and Yodzis (1988), who showed that the magnitude of indirect effects can often overshadow those of direct effects (see also Wootton, 1992; 1994a). It should be noted, however, that the units of measure being compared (sea urchin individuals *versus* area covered by algae) are not the same. Ideally, the magnitude of effects should be estimated by comparing the same units of measure, such as biomass of different populations or trophic levels. In this case, biomass should scale to a first approximation linearly with the number of sea urchins (assuming no shifts in size structure), but to the 3/2 power with algal area (assuming isometry), so the effect might be magnified still further if I had been able to use similar units.

Several other factors may interact to strengthen the effects of birds on sea urchin and macro-algal populations. First, the effects of birds would likely disappear in the absence of the large starfish *Pisaster*, because the preferred prey of the starfish, the mussel *Mytilus californianus*,

competitively excludes both sea urchins and algae independent of the effects of birds (Paine, 1966; 1974). Similarly, the effects might be eliminated with the invasion of sea otters, because sea otters would more efficiently remove the urchins before the birds did. Indeed, Irons, Anthony & Estes (1986) found that glaucous-winged gulls switched from a diet of sea urchins to one of fish when sea otters invaded areas in Alaska.

The effects of birds are probably magnified over time by a second factor, the sporadic recruitment events that sea urchins exhibit on Tatoosh Island. Purple sea urchins have not recruited in large numbers to Tatoosh Island since the early 1980's (J. T. Wootton, pers. observ.; R. T. Paine, pers. comm.), and consequently, chronic predation by birds and other predators becomes compounded over time. In fact, the dense local sea urchin populations that characterized the study site when my experiments began have subsequently disappeared, a pattern mirrored across all sites at Tatoosh.

The impact of birds on urchin populations appear to act in concert with a third factor, the subtidal activities of the sun star, *Pycnopodia*. *Pycnopodia* induces an escape response in sea urchins, causing a "stampede" of urchins into other areas (Paine & Vadas, 1969; Dayton, 1973). Because *Pycnopodia* is extremely rare in the intertidal zone (possibly in part because of heavy bird predation; see Wootton, in review), there tends to be a net movement of sea urchins into the intertidal zone where bird predation can have an impact. Indeed, the patterns of sea urchin population dynamics in the experiments (Figure 2) lend support to this view, particularly during the first year. Despite the absence of a large recruitment pulse of first-year individuals, sea urchin populations tended to increase under cages from initial densities, whereas they declined in the face of bird predation. Therefore, the difference between treatments was magnified when compared to the rates of decline derived from considering initial densities alone.

Bird predation on sea urchins also had an indirect keystone effect on macro-algal diversity, causing a 6-fold increase in overall taxonomic richness across all replicates and increasing average taxonomic diversity 15-fold. The increase in algal diversity in the face of bird predation mirrors the results observed by Paine & Vadas (1969) when they experimentally removed sea urchins from tidepools. Effects of consumers on diversity could be mediated both directly through consumer selectivity, and indirectly through reductions in competitive intensity. There is little evidence to support important effects on overall levels of algal diversity through grazer selectivity, in spite of evidence that selectivity occurs (Vadas, 1977). Virtually no variation in algal richness was associated with the density of sea urchins when changes in algal cover were accounted for (Figure 4). Whether algal selectivity could have a detectable effect at lower sea urchin densities and higher algal cover levels than those observed in this study remains an open question. It is possible that particularly favored taxa were still suppressed by grazing across all of the densities examined in this study. This possibility seems unlikely, however, because the three taxa most preferred by sea urchins in feeding trials (*Nereocystis*, *Costaria*, and *Laminaria*; see Vadas, 1977) were present in control areas in my experiments.

Two caveats need to be applied to the conclusion that changing algal cover, rather than consumer selectivity, is the primary driving force in affecting observed diversity patterns. First, if algal cover correlates with selectivity, as optimal foraging theory often predicts (e.g. MacArthur & Pianka, 1966), then the effects of such changes in selectivity can not be assessed in my analysis and hence the role of selective foraging might be underestimated. In this scenario, selectivity would act to reduce diversity, rather than promote diversity as in the keystone predation hypothesis. Second, although selective foraging may not affect the overall relationship of algal taxonomic richness to bird and sea urchin densities, it almost certainly plays a key role in shaping the pattern of taxonomic composition as diversity changes. The algae that are first eliminated from the plots with high sea urchin densities (Figure 3) are those that sea urchins prefer in feeding trials (Vadas, 1977)

In contrast to direct selectivity by sea urchins, macro-algal abundance appeared to play an extremely important role in determining the taxonomic richness of macro-algae. The combined effects of sea urchin density and algal cover explained more than 90% of the variation in algal diversity, but path coefficients associated with algal cover, which roughly correspond to the proportional contribution of each variable to the total variance explained, ranged from 180-310 times higher than those associated with the effects of sea urchin selectivity. The relationship between algal diversity and algal cover fit a quadratic equation, with both a strong positive linear relationship, and a strong negative relationship to squared algal cover. Therefore, a humped-shaped curve fit the diversity data well, suggestive that intermediate levels of grazing promote algal diversity as proposed by Paine & Vadas (1969) and demonstrated in intertidal communities in New England by Lubchenco (1978). Intense sea urchin grazing clearly drives species out of the system, whereas intense competition may exclude algal taxa when sea urchins are absent.

In summary, bird predation can have important effects on sea urchins in lower intertidal communities, effects which cascade down to indirectly affect macro-algal abundance and diversity. Whether this is a general feature of intertidal communities remains to be seen. Tatoosh Island has a major glaucous-winged gull breeding colony and, although these birds largely feed upon fish during the breeding season (Wootton, in review), bird predation intensity might be unusually high. Nevertheless, birds can be regularly observed feeding upon sea urchins along mainland coastal areas (Lubchenco, 1978; Irons, Irons & Estes, 1986; J. T. Wootton, pers. observ.). Furthermore, lower bird predation rates may be offset by another group of actively foraging terrestrial organisms: mammals. Feeding observations along the mainland coast of Washington state suggest that raccoons (*Procyon lotor*) may have an impact upon sea urchins comparable to birds where they have access to the intertidal (J. T. Wootton & C. A. Pfister, unpubl.). Thus, terrestrial-based predators as a whole may still have a major impact on the structure of the lower intertidal, providing another example of important trophic cascades in natural communities.

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