

ESTIMATES AND TESTS OF PER CAPITA INTERACTION STRENGTH: DIET, ABUNDANCE, AND IMPACT OF INTERTIDALLY FORAGING BIRDS

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Abstract. Predicting the dynamics of natural food webs requires estimates of the strength of interactions among species. The ability to estimate per capita interaction strength from observational data is desirable because of the logistical difficulty of using experimental manipulations to obtain such measures for all species within complex natural communities. In this paper, I derive observational measures of per capita interaction strength having units matching those of dynamic food web models (per capita consumption and assimilation rates). I also highlight the difference between per capita interaction strength (a parameter used in theoretical models) and species impact (empirical measures of total species effect). I then use behavioral observations and population censuses in a rocky intertidal community to estimate both per capita interaction strengths and species impacts on invertebrate prey of Glaucous-winged Gulls (*Larus glaucescens*), American Black Oystercatchers (*Haematopus bachmani*), and Northwestern Crows (*Corvus caurinus*). Estimated per capita interaction strengths exhibited a skewed distribution with many weak interactions and few strong interactions: mean \pm 1 SD of \log_{10} (interaction strength) = -1.95 ± 1.40 (bird-day/m of shore)⁻¹. Per capita interaction strength correlated poorly ($r^2 = 0.152\text{--}0.157$) and nonlinearly with both consumption rates and percentage contribution of a prey species to the diet. Using my observational estimates of per capita interaction strengths, I predicted the species impact of bird predation on different prey taxa. Predictions included strong effects of birds on goose barnacles (*Pollicipes polymerus*), limpets (*Lottia* and *Tectura* spp.), sea urchins (*Strongylocentrotus* spp.), and large starfish (*Pycnopodia helianthoides* and *Solaster stimpsoni*), but little effect on mussels (*Mytilus californianus* and *M. trossulus*), dogwhelk snails (*Nucella* spp.), and acorn barnacles (*Semibalanus cariosus*). I compared nine of the predictions with 126 results of experimental manipulations of birds. The predictions agreed both qualitatively and quantitatively with the experimental results. These findings suggest that observational measures of interaction strength that have units matching those of dynamical food web models may be reasonable to use in estimating those found in natural communities.

Key words: communities; *Corvus caurinus*; *Larus glaucescens*; food webs; foraging behavior; *Haematopus bachmani*; population dynamics; predation; rocky intertidal; species interactions.

INTRODUCTION

A central goal of ecology is to understand and predict the dynamics of natural communities. One key to attaining this goal is the successful application of models of natural food webs. In his seminal book, May (1973) identified three types of information that are minimally required to construct food web models: the number of species in the community, the presence or absence of trophic interactions between the species (termed linkage), and the strength of interactions between species. The first two types of data are easier to obtain from field investigations than the third, and have spawned a plethora of descriptive studies of how patterns of linkage vary with number of species (e.g., Briand and Cohen 1984, Cohen 1989, Martinez 1991). Estimating in-

teraction strength in natural communities is much more difficult and, consequently, it has been ignored in these descriptive food web studies. Yet, interaction strength is critical both to understanding how communities function and to developing models that predict the dynamics of natural systems (Paine 1980, 1988a).

Little progress has been made on the problem of determining interaction strengths in natural systems. In his discussion of food webs, Paine (1980) noted two types of commonly collected data that have been suggested to reflect interaction strength: relative abundance in the diet and relative energetic contribution to the diet (used in many ecosystem models of energy flow, e.g., Teal 1962, Patten 1982, Higashi and Patten 1989). In comparing these measures with results of experimental manipulations of consumers in the rocky intertidal zone of Washington State, Paine (1980) found that these measures did not predict the importance of particular consumer–resource interactions within the community (see also Dayton 1984, Polis 1994). For example, the low incidence of the mussel *Mytilus cal-*

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TABLE 1. Variable definitions used in this paper.

Variable	Definition
A) Variables used in equations	
N	number or density of target species
t	elapsed time
N_t	number or density of target species after time t
R_i	number or density of resource species i
P_j	number or density of consumer species j
B	number or density of birds
$b_{i,N}$	conversion efficiency of resource species i into species N
$c_{N,i}$	per capita consumption rate of species N by consumer species i
B) Measured variables	
ρ	consumption rate of actively foraging birds
ϕ	fraction of birds at low tide actually foraging
δ	total prey density
λ	proportion of time that tide is low
β	bird density
A_m	mean average bird density in month m
d_m	number of days in month m
l_m	mean minutes of daylight in month m

ifornianus in the diet of the starfish *Pisaster ochraceus* did not reflect the experimentally documented importance of *Pisaster* predation on *Mytilus* populations (Paine 1966, 1974). Consequently, Paine (1980, 1992) argued that interaction strength is most feasibly estimated by experimentally manipulating a target species and comparing the subsequent differences in populations of other species between treatments.

Unfortunately, conducting experimental manipulations of all members of a natural community is logistically difficult, if not impossible, so the experimental approach may be limited to examining particular species in specific systems. Furthermore, indirect effects of the manipulation (reviewed in Wootton 1994c) may confound the experimental measurement of the strength of direct interactions. For these reasons, the ability to estimate interaction strength from observational data would be extremely useful. Such observational approaches, however, need first to be applied in experimentally tractable systems where their utility can be tested before they are extended to other situations. In this paper, I identify observational measures that should reflect interaction strength, based upon considerations of dynamic food web models. I then present estimates of interaction strengths between intertidal birds and their invertebrate prey, based upon observational data, and test how well these estimates of interaction strength match those based upon experimental manipulations of bird predation.

OBSERVATIONAL ESTIMATES OF INTERACTION STRENGTH AND SPECIES IMPACT

What sort of observational data might best reflect the strength of interactions in natural food webs? The answer to this question should lie in examining the general form of predator–prey equations. In the simplest case, the dynamics of a food web element (N) can be described as:

$$\left(\frac{1}{N}\right)\frac{dN}{dt} = \sum_{i=1}^r b_{i,N}c_{i,N}R_i - \sum_{j=1}^p c_{N,j}P_j, \quad (1)$$

where R_i is the abundance of the i th resource species available to species N , and P_j is the abundance of the j th predator species that feeds on species N , $c_{Y,X}$ is a function describing the per capita consumption rate of species X on species Y , and $b_{i,N}$ is the efficiency with which species i is converted into species N . Thus, $b_{i,N}c_{i,N}$ represents the per capita interaction strength of resource R_i on species N , and $c_{N,i}$ represents the per capita interaction strength of consumer P_j on species N (Table 1).

It is important to note that the concept of interaction strength can take on at least four different meanings within ecology (M. S. Laska and J. T. Wootton, *unpublished manuscript*), all of which are valid from a theoretical standpoint. For example, May (1973; see also Yodzis 1989, Schoener 1993) designated elements in a Jacobian matrix evaluated at equilibrium as measures of interaction strength, which, although related, are quite different from the per capita parameters in dynamic equations estimated here. I prefer to examine the latter (see also MacArthur 1972, Paine 1992, Fagan and Hurd 1994) because they require no assumptions about whether or not the community is at equilibrium, and because all other concepts of interaction strength ultimately can be derived from these parameters. (As an aside, L. Goldwasser [*personal communication*] has pointed out that elements of a Jacobian matrix need not be evaluated at equilibrium, but I know of no explicit theoretical definitions of interaction strength based upon Jacobian elements that do not make equilibrium assumptions). For the rest of this paper, any reference to interaction strength will refer to the per capita parameters from dynamic food web equations.

For the purpose of clarity, I will refer to another concept of interaction strength, most frequently used

in empirical investigations, as *species impact*. Species impact can be defined as the effect of one species on another over some time interval. It is this value that is normally measured in field experiments manipulating the presence or absence of a species, and that most directly applies to the question of what effect a species has on a system. For sufficiently short time periods (i.e., when indirect effects are not important), $c_{Nj}P_j$ represents the per capita species impact on species N of the total population of predator species P_j , and $b_{iN}c_{iN}R_i$ represents the per capita species impact on species N of the total population of prey species R_i , for the food web equations presented. Note that large species impacts can result from large per capita interaction strengths, from large population sizes, or from a combination of both factors. Consequently, another advantage of concentrating on per capita interaction strengths is that they will show much less variation than will total species impacts as population sizes change.

Observational measures used to estimate either per capita interaction strength or species impact should have the same units as the variables in the food web model described. What are the appropriate units? Eq. 1 has units of t^{-1} , so per capita effects of a total population should also be expressed as t^{-1} . For the case of predator species, then, c_{Nj} (per capita predator interaction strength) should have units of $t^{-1}P_j^{-1}$, where t is a unit of time. In the case of prey species, $b_{iN}c_{iN}$ (per capita prey interaction strength) should have units $t^{-1}R_i^{-1}$. Therefore, because c_{iN} should have units $t^{-1}N^{-1}$, b_{iN} should have units NR_i^{-1} .

In examining its units of measure, it is not surprising that diet representation fails to reflect experimentally determined interaction strengths or species impacts. Diet representation, expressed either as individuals consumed or energy consumed, has units of resources consumed per predator per unit time: $R_i t^{-1} N^{-1}$ or $N t^{-1} P_j^{-1}$. When expressed as a percentage of the diet, the units become the amount of a given resource consumed per total resources consumed per predator per unit time $R_i (\sum R_i)^{-1} t^{-1} N^{-1}$. None of these units corresponds to those of either per capita interaction strength or total species impact of a population in dynamic models. For example, to properly estimate the effects of a prey population on its consumer, diet data must be multiplied by conversion efficiency (units of predator produced per prey consumed) and divided by prey density. This is not straightforward for diet measures based upon numbers of prey consumed, since prey may vary in such attributes as body size or mass-specific energy content. If diets are expressed in a common energetic currency, however, consumption rate, after it is standardized by the total energy content of each prey in the system, might roughly approximate the importance of prey to predators if energy is more or less equally extractable from all prey items. Similarly, to properly estimate the species impact of a predator population on its prey, diet data must be multiplied by predator

abundance and divided by prey abundance. Therefore, unless all prey populations have equal abundance, diets will not directly reflect predator impact.

It is of interest to determine whether or not observationally derived estimates of per capita interaction strengths and species impacts reasonably reflect those determined from experimental manipulations. In the following sections, I evaluate the usefulness of observationally derived estimates of per capita interaction strength and species impact in an experimentally tractable intertidal community.

BIRDS IN THE INTERTIDAL COMMUNITY: NATURAL HISTORY

Birds are conspicuous predators in intertidal communities throughout the world. Because their extreme mobility makes them difficult to manipulate experimentally, and their relatively low densities might suggest low impacts on other species, the effects of birds on intertidal community structure have only recently been considered (Schneider 1978, Frank 1982, Hockey and Branch 1984, Quammen 1984, Mercurio et al. 1985, Marsh 1986a, b, Hahn and Denny 1989, Wootton 1990, 1992, 1993a, b, 1994a, 1995, Good 1992, Dumas and Witman 1993, Meese 1993). Birds may exert an impact on community structure disproportionate to their density and biomass because, as active endotherms, they exhibit much higher metabolic rates than marine invertebrate predators. One way of assessing what effect birds exert on intertidal communities is to document avian diets and patterns of abundance, and from these, estimate the amount of prey consumed relative to the prey populations available (e.g., Gibb 1956, Drinnan 1958, Davidson 1967, Feare 1970, Heppleston 1971, Cantin et al. 1974, Goss-Custard 1977, O'Connor and Brown 1977, Hartwick and Blaylock 1979). Although, in many cases, these estimates from feeding observations may be the only ones available to determine potential impacts of predator species, I have developed methods to experimentally manipulate avian predators in rocky intertidal communities (Wootton 1990, 1992, 1993a, b, 1994a). Therefore, I can determine the accuracy of the estimates derived from the observational methods used here to assess their potential usefulness in other studies.

At least 17 species of birds forage intertidally on Tatoosh Island, the main study area (Table 2). Three species, Glaucous-winged Gulls (*Larus glaucescens*), Black Oystercatchers (*Haematopus bachmani*), and Northwestern Crows (*Corvus caurinus*) are relatively abundant throughout the year and, therefore, probably have the most important impact on other members of the intertidal community. Black Turnstones (*Arenaria melanocephala*) and Wandering Tattlers (*Heteroscelus incanus*) also occur, but in low numbers.

Few detailed accounts exist of the diets of the three major intertidal bird species present on Tatoosh. Glaucous-winged Gull diet information, derived from the

TABLE 2. Birds observed foraging in the intertidal zone on Tatoosh Island, Washington, USA.

Species	Major prey
Glaucous-winged Gull	<i>Pollicipes, Strongylocentrotus, Lottia, Katharina</i>
Black Oystercatcher	<i>Lottia, Mytilus, Strongylocentrotus</i>
Northwestern Crow	isopods, <i>Lottia, Strongylocentrotus</i>
Black Turnstone	amphipods, <i>Semibalanus, Balanus, Lottia, Littorina</i>
Surfbird	<i>Littorina, Mytilus, Semibalanus, Balanus, Lottia</i>
Black Brant	<i>Ulva</i>
Western Sandpiper	isopods, amphipods, chironomids, <i>Littorina</i>
Wandering Tattler	chironomids, amphipods, small molluscs
Savannah Sparrow	chironomids
Song Sparrow	chironomids
Fox Sparrow	chironomids
Snow Bunting	chironomids
Lapland Longspur	chironomids
Water Pipit	chironomids
Winter Wren	chironomids
Great Blue Heron	fish
Harlequin Duck	amphipods, small snails, <i>Mytilus</i>

analysis of hard parts contained in regurgitated pellets is available from Alaska (Trapp 1979, Murphy et al. 1984, Irons et al. 1986) and from Vancouver Island, British Columbia (Vermeer 1982). Analysis of pellets does not necessarily provide an accurate picture of the diet, however, because different prey items contain different amounts of indigestible material. Irons et al. (1986) also provide data on gull diets based on feeding observations: sea urchins (*Strongylocentrotus polycanthus*) dominated the diet on islands without sea otters (*Enhydra lutris*), but fish predominated on islands with sea otters.

Black Oystercatcher diets have been documented by Hartwick (1975) in British Columbia and Frank (1982) in Oregon. They found that oystercatchers consumed limpets and mussels, but the relative contribution differed between study sites; oystercatcher diets contained few mussels in Oregon, but up to 40% mussels in British Columbia. Zach (1978) provided information on foraging strategies of crows dropping snails (*Nucella lamellosa*), but no general record of Northwestern Crow diets is available.

STUDY SITE AND GENERAL METHODS

Study site

The study was largely conducted on Tatoosh Island, a 6-ha rocky island located 0.5 km off the northwest corner of the Olympic Peninsula in Washington State. Tatoosh consists of a main island, with several large sub-islands to the north and west (see Paine and Levin 1981, Paine 1988b). The community ecology of Tatoosh and several nearby mainland shores has been studied extensively (e.g., Paine 1966, 1974, 1976, 1977, 1979, 1980, 1984, 1988b, Paine and Vadas 1969, Dayton 1971, 1975, Suchanek 1979, Paine and Levin 1981, Sebens 1981, Dethier 1984, Leigh et al. 1987, Johnson 1989, Pfister 1993). This background knowledge provides an ideal context in which to place avian predators, because the biology of so many members of the community is known. As an offshore island cur-

rently without impacts from human (aside from researchers) or other terrestrial mammal inhabitants, Tatoosh supports an abundant breeding-bird fauna. I also made limited censuses at Shi-shi Beach, a mainland beach site just north of the Olympic National Park (see Dayton 1971, Suchanek 1979, Dethier 1984, Johnson 1989, Pfister 1993), to provide a comparison between mainland shores and offshore islands.

Methods

General population patterns.—I censused relative population size on the entire island by counting all gulls, oystercatchers, and crows seen from seven points around the perimeter of the main island once or twice a month between 1985 and 1990. The area observed in the counts represented an estimated 60% of the known gull colony area, because the outer sides of some sub-islands were not observable from the main island. I did not include nestlings in the censuses because they were difficult to count accurately.

Diets and consumption rates.—At points throughout 1986–1993, I examined bird diets in two ways. First, I made quantitative estimates of diet composition with the aid of a 15–45× spotting scope by observing actively foraging individuals in the middle and lower intertidal zone (i.e., in or below the mussel zone) over timed intervals, and identifying the type of prey taken at three wave-exposed sites (Toad Point, the west cliff of the main island, and Simon's Landing), and in a more wave-sheltered site (the east side of the Beach and North Island; see Paine and Levin 1981, Paine 1988b for location of the sites). From these data, I estimated consumption rates of each prey item as number of prey consumed per actively foraging bird per minute (designated ρ). Feeding rates for gulls and oystercatchers were calculated independently for wave-exposed and wave-sheltered sites, but data were insufficient to do so for crows. I also calculated the rate at which adult oystercatchers fed nestlings. In calculating annual consumption rates, I assumed nestlings

were fed from mid-June through mid-August. Second, I supplemented the quantitative diet data with incidental feeding observations and analysis of nest middens and regurgitated pellets to provide a qualitative list of dietary items for gulls and oystercatchers.

Activity patterns.—I made behavioral observations throughout 1985–1989 to determine the proportion of time that birds present in the intertidal zone spent foraging. During observation periods, I scanned the middle and lower intertidal zone at 10-min intervals, scoring the behavior of each individual into five general activity categories: searching for food, feeding, preening, loafing or sleeping, and interacting with other birds. From these data, I could derive the proportion of time a bird present in the intertidal actively foraged (i.e., either was searching for food or feeding, designated ϕ).

Intertidal abundance of birds.—I counted the number of birds present in the lower and middle intertidal zone to estimate the density of birds potentially foraging there over the course of the tide. During 1987–1991, I made counts along a total of 340 m of shore covering three locations on Tatoosh (see Paine and Levin 1981, Paine 1988b): Toad Point, Simon's Landing, and Strawberry Island (including all of the south side and the south half of the east side). Counts were also made along 100 m of shore at Shi-shi beach. These areas represent four of my five major study sites for intertidal experiments (Wootton 1990, 1992, 1993a, b, 1994a, 1995).

A subset of counts made at 30-min intervals throughout low tide provided information on how bird abundance in the middle and lower intertidal zone changed over the course of the low tide cycle (i.e., 3.5 h before to 3.5 h after low tide). The mean number of birds from each census provided an estimate of the number of birds present per minute per meter of shore during the entire 7-h low tide period. I then used multiple regression to derive general relationships between the number of birds counted at a particular point in the tidal cycle, the total number of birds counted over the course of the tidal cycle, and the time of the census relative to the time of low tide. Specifically, for each bird species, I regressed the number of birds counted at a particular point in time against the total number of birds counted over the course of the tidal cycle, the product of the total number of birds counted and the relative census time, and the product of the total number of birds counted and the square of relative census time. The form of the regression model was chosen because (1) single-point observations are expected to be directly related to the mean number of birds present over the low tide period; (2) the number of birds present in the intertidal zone is likely to interact with the tidal stage, such that more birds are present when the tide is lower because there is more area available for foraging as well as more foraging birds present; and (3) the pattern of bird presence may not be strictly symmetrical around the

low tide point for a variety of reasons, including bird satiation or changes in prey behavior as the stress from being emerged increases. A constant was not included in the model because, a priori, no birds will be seen at any point in the tidal cycle when there are no foraging birds present over the entire tidal cycle. When any of the terms in the regression did not contribute significantly to the explanatory power of the regression model, they were dropped.

To maximize the information on bird abundance that I could obtain throughout the year, I made most counts at only one time point during the tidal cycle, rather than continuously throughout the tidal cycle. I then estimated mean bird abundance over the course of the tidal cycle from these single time-point counts using the relationships from the complete tidal cycle counts described.

To calculate the cumulative annual abundance of birds in the intertidal zone, I derived mean abundance from the point and complete tidal cycle counts for each month, then used the mean monthly values to estimate annual bird foraging in the intertidal zone. Analyzing monthly means rather than the overall count mean was necessary because of lower census effort in winter compared to summer, and because the amount of potential foraging time for birds changed seasonally with changing day length. My observations indicate that birds do not forage in the intertidal on Tatoosh at night. Therefore, I estimated the annual number of bird-minutes per meter of shore (designated β) as:

$$\sum_{m=1}^{12} A_m d_m I_m, \quad (2)$$

where A_m is the mean abundance of birds in the intertidal zone during low tide in the m th month, d_m is the number of days in the m th month, and I_m is the mean number of minutes of daylight per day in the m th month.

Estimating interaction strength and species impact.—To estimate per capita interaction strength of birds on their prey ($c_{N,B}$ in Eq. 1, where B represents the effect of birds), I combined the observational information described with measurements of prey abundance per meter of shoreline on Tatoosh (Suchanek 1979, Wootton 1992, 1993a, b, 1994a, 1995, Paine 1992; J. T. Wootton, unpublished data), yielding:

$$-\rho \phi (1/\delta)\lambda, \quad (3)$$

where ρ is the consumption rate by actively foraging birds at low tide, ϕ is the fraction of birds at low tide that are actively foraging, δ is total prey density, and λ is the proportion of time that the tide is low enough for the middle or lower intertidal zone to be exposed to bird predators (Table 1). To estimate λ , I integrated the duration of time that the top of a given tidal zone was exposed at low tide on Tatoosh Island over a representative year (1989, the median year of the study), using "Tides and Currents for Windows" software

(Nautical Software, Beaverton, Oregon). For organisms whose range extended into the middle intertidal zone (*Mytilus californianus* zone), I used the tidal height of the upper limit of the mussel bed (1.7 m; Leigh et al. 1987), whereas for organisms restricted to the lowest parts of the intertidal zone, specifically sea urchins and large starfish, I used the tidal height of the lower limit of *Hedophyllum sessile* (0.3 m; Leigh et al. 1987). To estimate species impact, I multiplied Eq. 3 by bird density (β), derived from the observational measures, and by elapsed time in years (t), yielding:

$$-\rho \phi (1/\delta)\lambda\beta t. \quad (4)$$

Experimental tests of species impact.—I assessed the utility of observational data to predict the importance of different species interactions by comparing predicted species impacts based upon my observational data to observed species impacts from experimental manipulations of bird predators in the intertidal zones of Tatoosh Island and Shi-shi Beach. I excluded birds from some portions of the intertidal community using large-mesh, prefabricated cages, and compared these areas to adjacent control plots where birds had access to their prey. Cages in most experiments, constructed from vinyl-covered wire letter baskets (Better Office Products, Carson, California), were $29 \times 34 \times 7.5$ cm in dimension, with 4×2.5 cm mesh on top and 7.5×2.5 cm mesh on the sides. In experiments examining the effects of purple sea urchins (*Strongylocentrotus purpuratus*), larger cages constructed from vinyl-covered wire computer paper baskets ($34 \times 44 \times 11$ cm in dimension, with 4×2.5 cm mesh on top and 11×2.5 cm mesh on the sides) were used. Because the large mesh of the cages minimally affects the physical environment and does not constrain access by mobile intertidal invertebrates, no appreciable cage artifacts have been detected in experiments manipulating the presence or absence of the bottom rim, the mesh size of the roof, or the presence or absence of cages in microhabitats where birds cannot forage (e.g., vertical walls; for further details, see Wootton 1990, 1992, 1993a, b, 1994a, 1995).

For each experiment, I compared the available abundance data in each cage–control pair after 1 yr for every species known, on the basis of feeding observations and nest midden analysis, to be consumed by birds. The available experimental data afforded nine situations to compare with observational measures: (1) goose barnacles (*Pollicipes polymerus*) on wave-exposed shores of Tatoosh (Wootton 1993b); (2) goose barnacles on exposed shores of Shi-shi Beach (Wootton 1990); (3) limpets (*Lottia digitalis* and *Lottia pelta*) on exposed shores of Tatoosh (Wootton 1992); (4) California mussels (*Mytilus californianus*) on exposed shores of Tatoosh (Wootton 1994a); (5) blue mussels (*Mytilus trossulus*) on exposed shores of Tatoosh (Wootton 1990); (6) dogwhelk snails (*Nucella emarginata* and *Nucella canaliculata*) on exposed shores of

Tatoosh (Wootton 1994a); (7) six-armed starfish (*Lep-tasterias hexactis*) on exposed shores of Tatoosh (Wootton 1994a); (8) acorn barnacles (*Semibalanus cariosus*) on exposed shores of Tatoosh (Wootton 1994a); and (9) purple sea urchins on sheltered shores of Tatoosh (Wootton 1995). For all but one species (*S. cariosus*), experimental data were available because preliminary observations of bird feeding and prey remains, made before the quantitative analysis of interaction strength presented here, led me to believe that birds might have detectable effects on these species.

Experimental results were compared to observational estimates of short-term species impact, derived from Eq. 4. Because effects can only be measured empirically over discrete time intervals, field tests cannot be easily applied to Eq. 1, which is based upon instantaneous rates (Wootton 1994b). Consequently, the observational predictions and experimental results were applied to the most frequently used discrete-time analog (see Van der Vaart 1973, Comins and Hassel 1976, Hofbauer et al. 1987, Billick and Case 1994, Wootton 1994b):

$$N_t = N_0 \exp \left\{ \left[\left(\sum_{i=1}^r b_{iN} c_{iN} R_i \right) - \left(\sum_{j=1}^{p-1} c_{Nj} P_j \right) - (c_{N,B} B) \right] t \right\}, \quad (5)$$

where N_t represents prey density at time t , N_0 represents the initial density of prey N , B is the density of birds, and $c_{N,B}$ is the per capita interaction strength of birds on N . All other variables are defined as in Eq. 1 (Table 1). For the purposes of analysis, I have separated bird effects from the rest of the consumer terms in Eq. 5. The total species impact of birds can be expressed as the ratio of prey densities after some time t in the presence ($B > 0$) to the absence ($B = 0$) of birds. Applying Eq. 5 and simplifying, this expression becomes:

$$\frac{N_{t,B>0}}{N_{t,B=0}} = e^{-c_{N,B} B t}, \quad (6a)$$

or

$$\ln \left[\frac{N_{t,B>0}}{N_{t,B=0}} \right] = -c_{N,B} B t. \quad (6b)$$

The expression ($-c_{N,B} B t$), represents total bird impact after some elapsed time t , and therefore can be compared directly to Eq. 4.

Following Eq. 6b, short-term species impacts were derived in the experimental comparisons by taking the log ratio of control to cage abundances. To avoid the problems of taking logs of zero or of dividing by zero for some experimental results, the comparisons were made on $\ln[(N_{\text{control}} + 1)/(N_{\text{cage}} + 1)]$. Additionally, species in two sets of experiments were censused after 4 mo (Wootton 1990) and 2 yr (Wootton 1992), respectively, rather than over a 1-yr time interval. To allow direct comparisons with the other experimental results,

these results were standardized to a 1-yr time interval by dividing by the elapsed time in years, following Eq. 6b.

I included the results of every bird manipulation experiment that I conducted between 1985 and 1991 (Wootton 1990, 1992, 1993a, b, 1994a, 1995), with certain restrictions dictated by the underlying theory. Specifically, Eqs. 5 and 6 assume that indirect effects are absent over the time period being investigated. Consequently, I only included experimental results where known indirect effects would be absent. For indirect effects arising as chains of direct interactions (i.e., birds eating goose barnacles, goose barnacles affecting other species), I used only experiments in which the intermediary species (goose barnacles) was either naturally absent (Wootton 1990) or was experimentally held to constant levels (Wootton 1994a). To factor out the indirect effects resulting from sessile species (i.e., goose barnacles and mussels) modifying the interaction of birds on their prey (i.e., limpets) via crypsis (Wootton 1992), I compared the responses of the prey on each sessile habitat type within each cage-control pair, and then took the mean response of the prey across each habitat type. In total, 126 experimental results were available to use in the comparison with observational estimates of species impact.

To assess the utility of predictions derived from observational data applied to Eq. 4, I plotted these results against the observed species impacts from the experimental manipulations. Using linear regression, I examined the plotted relationship, both to determine whether or not there was a significant relationship, at the $\alpha = 0.05$ level, between observed and predicted values, and to test whether or not the relationship deviated from the expected relationship $\text{Observed} = \text{Predicted}$. I compared the predicted mean species impact both with the nine observed mean species responses and with all 126 experimental results. Additionally, because examination of the plot residuals indicated that the variance in the experimental results was not independent of predicted values, I applied linear regression on the data, weighted by the inverse of the variance in each of the nine situations being compared to stabilize the variance across all predicted values (Snedecor and Cochran 1980). In this case, I used linear regression to estimate the parameters in the equation $\text{Weight} \times \text{Observed} = \text{Weight} \times \text{constant} + \text{Weight} \times \text{slope} \times \text{Predicted}$, which simplifies to the relationship $\text{Observed} = \text{constant} + \text{slope} \times \text{Predicted}$.

RESULTS

Bird population patterns

Population sizes of the major avian predators varied seasonally and between study sites. Glaucous-winged Gull abundance on standardized censuses varied from low levels (≈ 500 birds) in winter, to high levels (≈ 2500 birds) in summer (Fig. 1A). The majority of

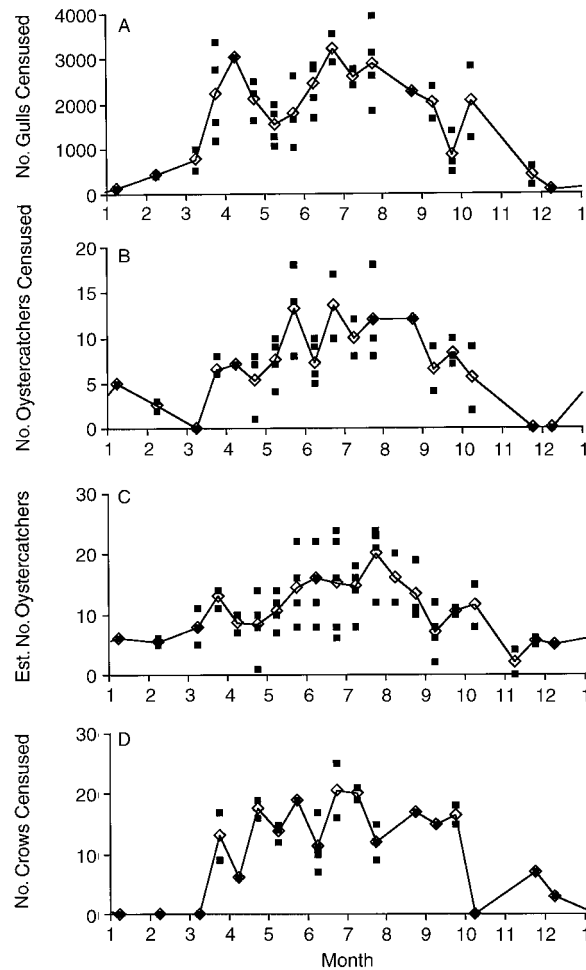


FIG. 1. Estimates of relative bird population sizes on Tatoosh Island over a year. Black squares represent individual sample points; open diamonds connected by lines represent the mean number of counts at biweekly intervals. Total numbers of birds are given for (A) Glaucous-winged Gulls, counted from standardized census points along the top of the island; (B) Black Oystercatchers and (D) Northwestern Crows, both from standardized censuses; and (C) the total Black Oystercatcher population on the island, estimated by the number seen while walking throughout the intertidal zone associated with Tatoosh.

gulls arrived at Tatoosh in late March, established territories, commenced breeding in late May and early June, and fledged young in July. The pattern of abundance on Tatoosh was opposite that seen on mainland sites without large nesting colonies. Sporadic censuses of gulls on exposed intertidal benches at Shi-shi beach showed relatively high abundance during the winter and very low abundance during the summer breeding season (Fig. 2B, Table 3). The movement of gulls from coastal beaches to the Tatoosh breeding grounds and the initiation of breeding coincide with the seasonal shift in water masses off the Washington coast that results in nutrient-rich water with an abundant supply of small fish and pelagic crustaceans.

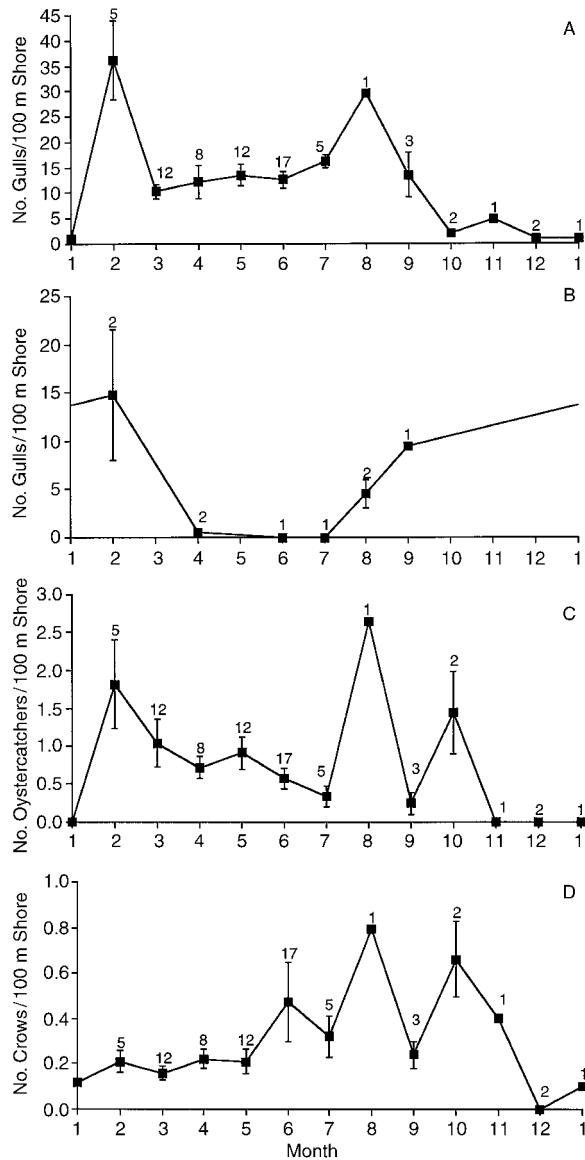


FIG. 2. Mean number (with ± 1 SE bars) of birds present in the intertidal zone per 100 m of shoreline during low tide over the course of a year. Sample sizes are given above points for (A) Glaucous-winged Gulls on Tatoosh Island; (B) Glaucous-winged Gulls on Shi-shi beach, a mainland site; (C) Black Oystercatchers on Tatoosh; and (D) Northwestern Crows on Tattosh.

Like gulls, oystercatchers showed a seasonal pattern of abundance on Tatoosh, breeding in relatively high densities during the summer and dispersing along the coast in winter (Fig. 1B, C). Eleven pairs of oystercatchers typically bred on Tatoosh; they initiated nesting in mid-May through mid-July, generally producing nestlings from mid-June to mid-August. Crow populations showed a seasonal fluctuation in size similar to that of gulls and oystercatchers, with higher populations in summer than in winter (Fig. 1D).

Population patterns: intertidal zone

Bird abundance in the intertidal zone varied significantly over the course of the tidal cycle. The relationships between abundance at a given point in the tidal cycle, cumulative abundance, and time of observation relative to the time of low tide were highly significant ($P < 0.00001$) for all three bird species, with fits ranging from excellent ($r^2 = 0.929$) for gulls to good ($r^2 = 0.576-0.569$) for oystercatchers and crows, respectively (Fig. 3). Oystercatchers and crows probably had lower fits because their abundances tended to be lower and, therefore, varied less on different sampling dates. Patterns of intertidal abundance varied with bird species; gulls and crows exhibited a symmetrical increase in intertidal abundance around low tide as more of the intertidal zone was exposed (Fig. 3), whereas oystercatchers showed no such humped pattern of abundance around low tide, but instead tended to increase as the tidal cycle proceeded.

Gull abundance in the Tatoosh intertidal zone over the course of a year corresponded to changes in total abundance (Fig. 2A), but the seasonal variation was not as great. Proportionately one-third as many gulls occurred intertidally, relative to my index of total gull abundance on Tatoosh, in summer vs. winter (Fig. 4; t test, $df = 67$, $P = 0.0013$). This reflects a shift in the relative importance of pelagic fishes in the diet, associated with the increase in fish availability in the water column during the breeding season (T. Wootton, *personal observation*). Annual gull abundance in the middle intertidal zone during daylight low tides was an estimated 22 057 gull-min/m of shore on Tatoosh, and 10 899 gull-min/m of shore on Shi-shi beach (Table 3).

Oystercatcher and crow abundance in the intertidal zone also paralleled their abundance on Tatoosh (Fig. 2C, D). Mean oystercatcher abundance in the intertidal zone was 1 bird/180 m of shore, and total oystercatcher pressure was an estimated 1053 oystercatcher-min/m of shore per year (Table 3). Additionally, oystercatchers foraged for their nestlings during 528 of the total bird-min/m of shore per year (mid-June through mid-August). Mean crow abundance in the intertidal zone was 1 bird/297 m of shore, and mean crow pressure in the intertidal zone was 659 min/m of shore per year (Table 3).

Activity patterns

Gulls in the intertidal zone spent 33.5% of their time either feeding or searching for food (Fig. 5A). A surprisingly large percentage (55.8%) of gulls spent time either sleeping or resting in the intertidal zone.

Oystercatchers in the intertidal zone spent 31.4% of their time searching and feeding (Fig. 5B). Like gulls, they also spent a large percentage of their time (48.1%) loafing and sleeping in the intertidal zone. The time oystercatchers spent interacting with other birds, most-

TABLE 3. Monthly estimates of bird abundance (bird-minutes/m of shore) in the mid- and lower intertidal zone during daylight hours, and mean no. daylight minutes per day. Totals represent estimated annual bird-minutes/m of intertidal shore ($= \lambda\beta$).

Month	Daylight (min)	Gulls		Oyster- catchers	Crows
		Tatoosh	Shi-shi		
January	536	75	1539	0	0
February	610	3568	1709	128	35
March	717	1615	1157	115	32
April	820	1754	116	94	42
May	867	2099	55	124	43
June	949	2077	0	69	80
July	933	2840	0	50	78
August	854	4440	805	285	163
September	757	2693	1458	52	35
October	661	252	1468	136	149
November	561	555	1320	0	0
December	508	89	1352	0	0
Totals		22 057	10 979	1053	659

ly other oystercatchers, was more than six times that of gulls ($\chi^2 = 15.1$, $df = 4$, $P < 0.005$).

In contrast to gulls and oystercatchers, crows in the intertidal zone concentrated primarily on foraging; 84.2% of their time in the intertidal zone was spent either searching for food or feeding (Fig. 5C).

Feeding patterns

Gulls fed on at least 32 species of intertidal organisms (Table 4), particularly molluscs, crustaceans, and echinoderms. Feeding observations demonstrated distinct differences in gull diets in different habitats. On shores exposed to heavy wave wash, >88% of the intertidal organisms taken were goose barnacles (*Pollicipes polymerus*) (Table 5). Gulls fed on *Pollicipes* by grabbing the "head" (capitulum) of the barnacle with their beaks and pulling until the barnacle was separated from the rock, or, more commonly, until the capitulum was separated from the stalk. Gulls consumed *Pollicipes* at a rapid rate, which averaged 2.01 individuals eaten per foraging bird per minute during low tide (Table 5). The diet changed to a more equitable composition on less exposed shores, where *Pollicipes* is rare (Table 5), even though the different types of sites were <300 m from each other. On sheltered shores, major prey items included purple and green sea urchins (*Strongylocentrotus purpuratus* and *S. droebachiensis*), limpets (*Lottia* and *Tectura* spp.), nemerteans (*Amphiporous* spp.), and polychaete worms (usually *Nereis vexillosa*).

The diets of adult oystercatchers were comprised primarily of limpets (*Lottia* and *Tectura* spp.) in both wave-exposed (81.6% of diet) and sheltered (78.9% of diet) sites (Table 5). Oystercatchers consumed limpets with great efficiency, often reaching rates of 1 limpet/10 s, with a mean of 0.52 and 0.68 limpets/min per foraging oystercatcher at exposed and sheltered sites, respectively (Table 5). Multiplying this rate by the mean fraction of intertidal oystercatchers that were actively foraging yielded a value of 0.16 to 0.21 limpets/min per intertidal oystercatcher, which is half as great

as rates found in other studies of 0.37 (Frank 1982) and of 0.39 limpets/min per oystercatcher (Lindberg et al. 1987). At sheltered sites, purple sea urchins (*S. purpuratus*) also became an important (16.9%) component of the diet (Table 5). Oystercatchers also consumed lesser amounts (< 10% of the diet) of mussels (*Mytilus californianus*), crabs (especially *Oedignathus inermis* and *Petrolisthes* spp.), chitons, and nereid worms (Table 5). Oystercatchers obtained limpets and chitons with a quick, sharp blow under the edge of the shell with their chisel-like bill, flipping the mollusc over, and then deftly snipping the muscles attached to the shell, sometimes detaching the shell completely with a violent shake of the head. They fed on mussels by quickly stabbing gaping individuals and cutting the adductor muscles before the shell could be closed. Oystercatchers consumed sea urchins by snipping off the tube feet to detach them, then puncturing through the soft tissue surrounding the Aristotle's Lantern to gain access to the meat.

Diets of nestling oystercatchers differed greatly from those of adults (Table 5). Whereas limpets continued to provide a relatively large portion of the diet (28.9%), other large prey types were included with much greater frequency, particularly mussels (18.4%) and crabs (35.5%). Additionally, adult oystercatchers foraged preferentially on large limpets (Wootton 1992; see also Frank 1982, Hockey and Branch 1984, Marsh 1986a, Hahn and Denny 1989), but limpets fed to nestlings were significantly larger than limpets consumed by adults (Fig. 6; adults: 18.8 ± 5.1 mm limpet length, mean ± 1 SD, $n = 187$; nestlings: 21.1 ± 4.4 mm limpet length, $n = 670$; t test: $df = 855$, $P < 0.001$). The rate at which adults fed themselves (0.6–0.9 items/min) was substantially higher than that (0.1 items/min) at which they fed their nestlings (Table 5).

Crows foraging in the intertidal zone consumed isopods (*Idotea*), sea urchins (*Strongylocentrotus* spp.), and limpets (*Lottia* and *Tectura* spp.) at moderate rates (< 1 prey item/10 min, Table 5). Crows also fed upon

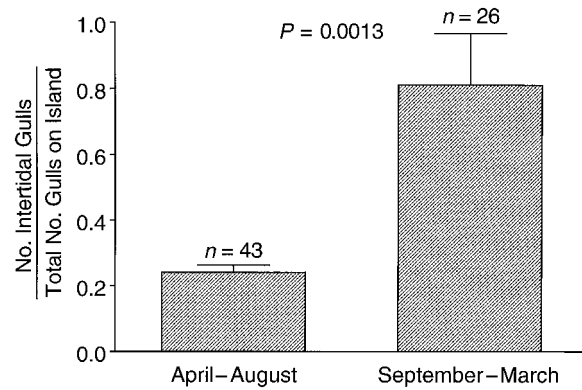
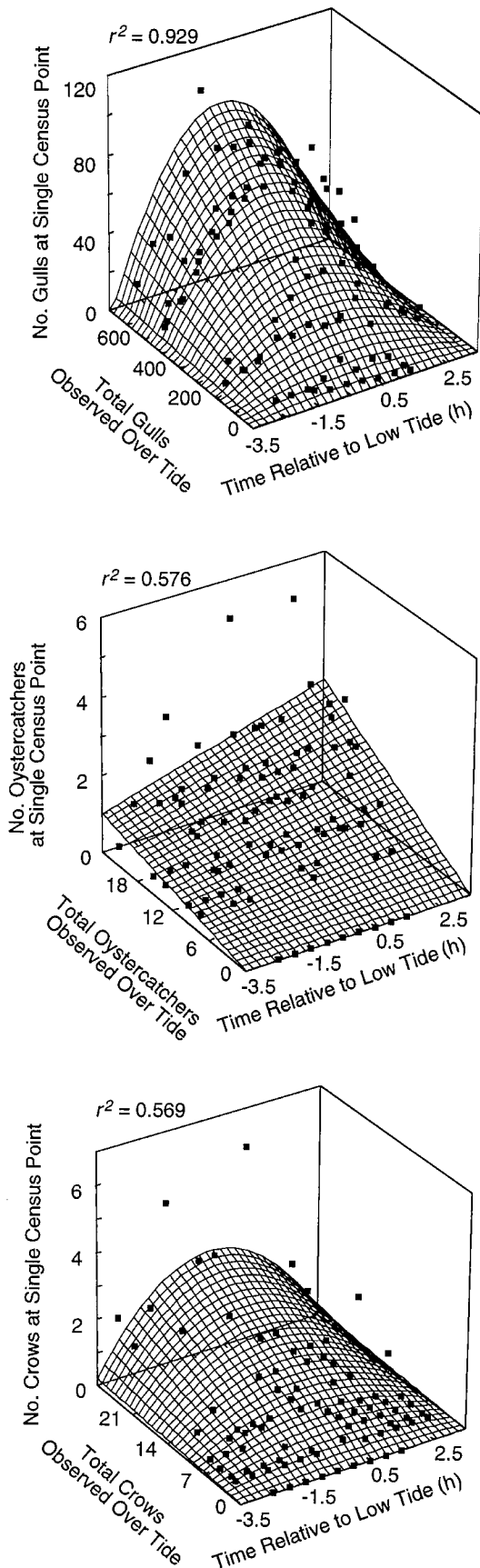


FIG. 4. Mean (± 1 SE) ratio of the no. gulls present in the intertidal zone during low tide to the total no. gulls counted on Tatoosh Island from standardized census points along the top of the island. The ratio presents one measure of the relative importance of intertidally derived (vs. pelagically derived) food for the Tatoosh Island gull population. The ratio during the summer is 31% of the ratio found during the winter (t test, $df = 67$, $P = 0.0013$). Values of n are the number of censuses.

neriid worms, small crabs, and intertidal fishes: Pholidae (gunnels) and Stichaeidae (pricklebacks) living either in rock cracks or among sessile invertebrates (Table 5).

Per capita interaction strengths

Estimates of per capita interaction strengths of birds on their prey ranged from very strong: 2.83 (bird-day/m of shore) $^{-1}$ to very weak: 0.00001 (bird-day/m of shore) $^{-1}$ (Table 6). Interaction strengths (Fig. 7A) exhibited a strongly skewed distribution, with many weak interactions and few strong interactions. Log transformation produced an approximately lognormal distribution ($\log_{10}[\text{interaction strength}] = -1.95 \pm 1.40$, mean ± 1 SD; Lilliefors' test for normality: $df = 50$, $P > 0.3$; Fig. 7E).

The association between interaction strength and either consumption rate or the percentage in the diet of the prey was poor and exhibited a very nonlinear relationship. Extremely strong interaction strengths were typically associated with rare components of the diet, whereas items that comprised the majority of the diet were not associated with the largest interaction strengths (Fig. 8A, B). When all variables were log-transformed, however, a slight positive association was

←

Fig. 3. Data on Glaucous-winged Gulls (top), American Black Oystercatchers (middle), and Northwestern Crows (bottom) in 340 m of intertidal zone from censuses taken throughout eight entire low-tide cycles. Plots show the relationship between no. birds censused at a given point in time, total cumulative no. birds observed over the course of the tidal cycle, and time of the census relative to low tide. Surfaces of best fit, derived from nonlinear regression, were used to estimate the total cumulative no. birds from a wider series of censuses taken at single points during a tidal cycle.

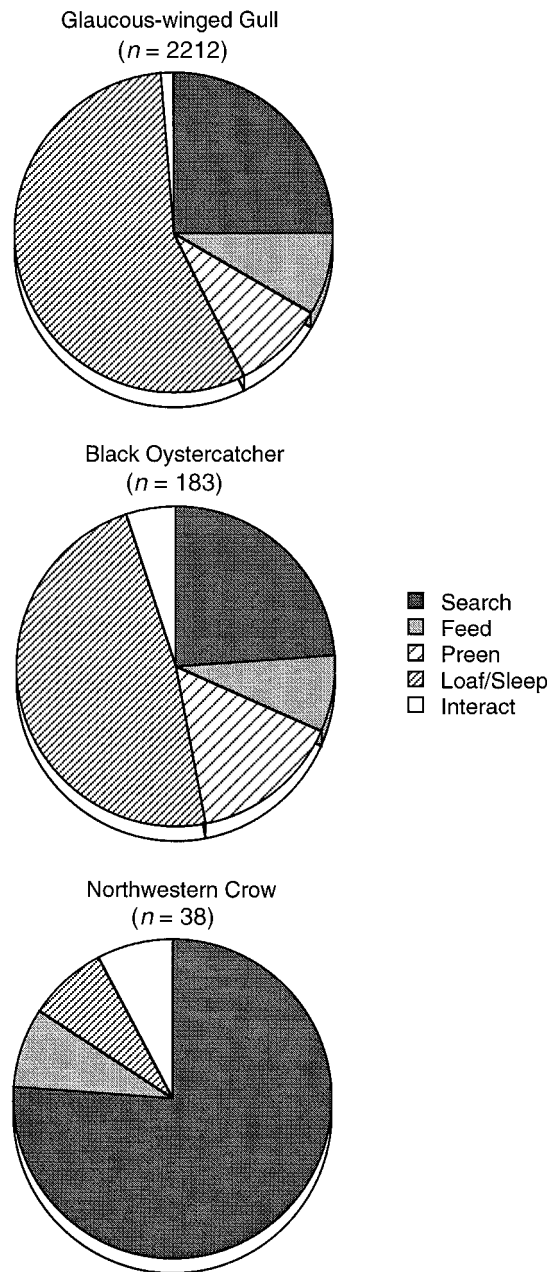


FIG. 5. The percentage of birds (with sample size, *n*) in the intertidal zone engaged in five behavioral activities: searching for food, feeding, preening, loafing or sleeping, and interacting with other birds.

detected between interaction strength and both consumption rate and percentage of diet (Pearson correlation coefficients, *df* = 49, *P* < 0.005; Fig. 8C, D), but the correspondence between the two was very weak (*r*² = 0.152 and 0.157, respectively).

Estimated total species impact and experimental comparisons

Observational estimates of short-term species impact predicted that birds have varied effects on their inter-

TABLE 4. Intertidal species consumed by Glaucous-winged Gulls on Tatoosh Island, based on data from feeding observations, regurgitated pellets, and nest middens.

Nemerteans	
	<i>Amphiporus</i> spp.
Molluscs	
	<i>Acmaea mitra</i>
	<i>Cryptochiton stelleri</i>
	<i>Katharina tunicata</i>
	<i>Lottia digitalis</i>
	<i>L. pelta</i>
	<i>Mopalia muscosa</i>
	<i>M. ciliata</i>
	<i>Mytilus californianus</i>
	<i>M. trossulus</i>
	<i>Nucella canaliculata</i>
	<i>N. emarginata</i>
	<i>N. lamellosa</i>
	<i>Tectura scutum</i>
	<i>Tegula funebris</i>
Polychaetes	
	<i>Nereis vexillosa</i>
Crustaceans	
	<i>Hemigrapsus nudus</i>
	<i>Oedignathus inermis</i>
	<i>Petrolisthes eriomerus</i>
	<i>Petrolisthes cinctipes</i>
	<i>Pollicipes polymerus</i>
	<i>Semibalanus cariosus</i>
Echinoderms	
	<i>Cucumaria pseudocurata</i>
	<i>Dermasterias imbricata</i>
	<i>Leptasterias hexactis</i>
	<i>Orthasterias koehleri</i>
	<i>Pisaster ochraceus</i>
	<i>Pycnopodia helianthoides</i>
	<i>Solaster stimpsoni</i>
	<i>Strongylocentrotus droebachiensis</i>
	<i>S. franciscanus</i>
	<i>S. purpuratus</i>

tidal prey species. Several species of invertebrates were predicted to be strongly affected by bird predation (Table 7). Over the course of a year, birds were predicted to reduce goose barnacle abundance by 71% on Tatoosh and by 46% at Shi-shi Beach, based upon Eqs. 4 and 6. Birds were also predicted to reduce limpet abundance by 25% on wave-exposed shores, and to lower purple urchin abundance by 36%. However, many invertebrate prey species were not expected to be strongly affected (<1% reduction), including California mussels, blue mussels, dogwhelks, six-armed starfish, and acorn barnacles on wave-exposed shores at Tatoosh.

Estimated annual species impacts based upon observational data agreed well with experimental assessments of direct effects of bird predation. Bird manipulation experiments resulted in significant impacts on goose barnacles at Tatoosh (Wootton 1993b), goose barnacles at Shi-shi Beach (Wootton 1990), limpets at Tatoosh (Wootton 1992), and purple sea urchins at Tatoosh (Wootton 1995). Birds had no significant direct effects on dogwhelk snails (Wootton 1994a), California mussels (Wootton 1994a), blue mussels (Wootton

TABLE 5. Consumption rate (no. consumed per foraging bird per minute) of actively foraging intertidal birds under different situations (wave-exposed vs. wave-sheltered shores, adults vs. nestlings).

Prey	GWG		BOC			NW Crow
	Exposed	Sheltered	Exposed	Young	Sheltered	
<i>Amphiporous</i> spp.	0.004	0.088	0	0	0	0.010
<i>Katharina tunicata</i>	0.013	0.026	0	0	0	0
<i>Mopalia</i> spp.	0	0	0.002	0	0	0
<i>Lottia</i> and <i>Tectura</i> spp.	0.009	0.026	0.52	0.04	0.68	0.14
<i>Nucella</i> spp.	0	0	0	0.002	0	0
<i>Tegula funebris</i>	0	0	0	0.002	0	0
<i>Mytilus californianus</i>	0.004	0	0.025	0.026	0	0
<i>M. trossulus</i>	0	0	0.003	0	0	0
<i>Nereis vexillosa</i>	0.022	0.035	0.018	0.013	0.012	0.069
<i>Idotea</i> spp.	0.009	0	0.007	0	0	0.17
Amphipods	0	0	0.002	0	0	0
<i>Pollicipes polymerus</i>	2.01	0	0.010	0.002	0	0.010
<i>Semibalanus cariosus</i>	0	0	0	0	0	0
Small crabs	0.009	0.018	0.036	0.049	0	0.059
<i>Leptasterias hexactis</i>	0	0.026	0	0	0	0
<i>Pisaster ochraceus</i>	0	0.026	0	0	0	0
<i>Pycnopodia helianthoides</i>	0.004	0.018	0	0	0	0
<i>Solaster stimpsoni</i>	0	0.009	0	0	0	0
<i>Strongylocentrotus purpuratus</i>	0	0.062	0	0	0.15	0.079
<i>S. droebachiensis</i>	0	0.070	0	0	0	0.020
<i>S. franciscanus</i>	0	0	0	0	0.012	0
<i>Cucumaria</i> spp.	0.017	0.008	0	0	0	0
Intertidal fish	0	0	0	0	0	0.040
Unidentified	0.16	0.044	0.015	0.005	0.012	0.059
Total no. items consumed	524	52	386	76	71	66
Total no. min observed	231.8	345.5	610.1	546.0	82.4	101.0

Note: GWG, Glaucous-winged Gull; BOC, American Black Oystercatcher; NW Crow, Northwestern Crow. Rates are for adult birds unless otherwise noted.

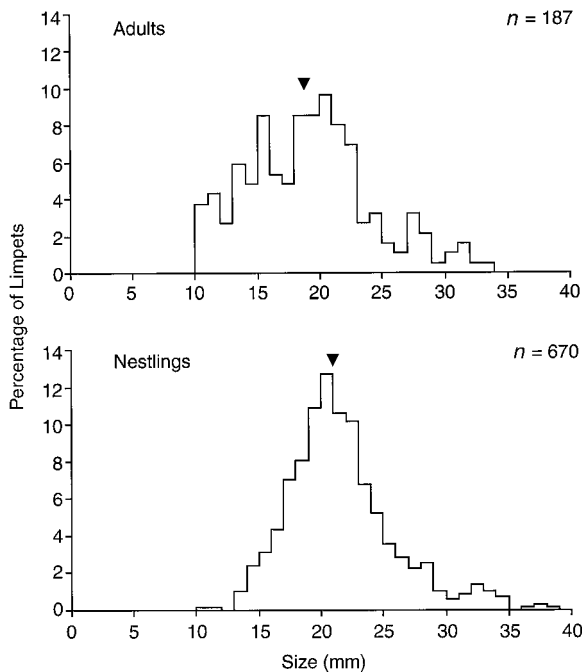


FIG. 6. Size-frequency plots of shell lengths of limpets consumed by adults (upper graph: shells collected from intertidal feeding areas), and fed to nestlings (lower graph: shells collected from nest middens). Nestlings were fed significantly larger limpets than those consumed by adults ($P < 0.001$). Sample sizes are given in the upper right corner of each graph; means are represented by inverted black triangles.

1990), acorn barnacles (Wootton 1994a), or six-armed starfish (Wootton 1994a). Observational estimates agreed well quantitatively, as well as qualitatively, with experimental results (Fig. 9, Table 8). Observed and predicted species impacts were significantly associated with each other (Table 8; all $P < 0.02$). Furthermore, the predicted species impact did not differ significantly from the observed species impact in any of the available comparisons (Fig. 9). Consequently, the best fit relationship between predicted and observed species impact did not differ significantly from the line $y = x$ (linear regression, Table 8), indicating that the observational measures I used were good estimates of short-term species impacts that were uncovered experimentally.

DISCUSSION

Estimates and experimental tests of species impacts

Observational estimates of interaction strength and species impact indicated that avian predators can have an important impact on dynamics of the rocky intertidal community of Tatoosh Island, despite their relatively low abundance compared to other intertidal organisms. In particular, my calculations predicted that bird predators reduce populations of goose barnacles, limpets, and sea urchins. Alternative calculations based upon energetics also support this conclusion. Given the mean observed densities of intertidally foraging birds and

TABLE 6. Estimated interaction strengths ([no. prey consumed] [total no. prey]⁻¹ [bird]⁻¹ [d]⁻¹ [m of shore]) of bird predators on their prey under different situations. Values are presented in scientific notation.

Prey	GWG		BOC†		NW Crow
	Exposed	Sheltered	Exposed	Sheltered	
<i>Amphiporous</i> spp.	1.1×10^{-3}	-2.3×10^{-2}	0	0	6.5×10^{-3}
<i>Katharina tunicata</i>	3.1×10^{-2}	6.2×10^{-2}	0	0	0
<i>Mopalia</i> spp.	0	0	2.9×10^{-3}	0	0
<i>Lottia</i> and <i>Tectura</i> spp.	1.3×10^{-3}	3.9×10^{-3}	7.5×10^{-2}	9.8×10^{-2}	5.2×10^{-2}
<i>Nucella</i> spp.	0	0	8.8×10^{-4}	8.8×10^{-4}	0
<i>Tegula funebris</i>	0	0	8.6×10^{-2}	8.6×10^{-2}	0
<i>Mytilus californianus</i>	6.3×10^{-5}	0	5.2×10^{-4}	1.8×10^{-4}	0
<i>M. trossulus</i>	0	0	1.3×10^{-4}	0	0
<i>Nereis vexillosa</i>	2.8×10^{-2}	4.5×10^{-2}	2.9×10^{-2}	2.2×10^{-2}	2.2×10^{-1}
<i>Idotea</i> spp.	7.4×10^{-3}	0	5.3×10^{-3}	0	3.65×10^{-1}
Amphipods	0	0	5.4×10^{-6}	0	0
<i>Pollicipes polymerus</i>	2.8×10^{-2}	0	1.4×10^{-4}	1.2×10^{-5}	3.4×10^{-4}
<i>Semibalanus cariosus</i>	0	0	0	0	0
Small crabs	1.8×10^{-3}	3.6×10^{-3}	1.2×10^{-2}	4.8×10^{-3}	3.1×10^{-2}
<i>Leptasterias hexactis</i>	0	1.9×10^{-2}	0	0	0
<i>Pisaster ochraceus</i>	0	1.6×10^{-1}	0	0	0
<i>Pycnopodia helianthoides</i>	6.9×10^{-1}	2.8	0	0	0
<i>Solaster stimpsoni</i>	0	1.8	0	0	0
<i>Strongylocentrotus purpuratus</i>	0	8.3×10^{-3}	0	2.1×10^{-1}	2.7×10^{-2}
<i>S. droebachiensis</i>	0	2.5	0	0	1.8
<i>S. franciscanus</i>	0	0	0	1.4	0
<i>Cucumaria</i> spp.	1.4×10^{-4}	7.2×10^{-5}	0	0	0
Intertidal fish	0	0	0	0	6.3×10^{-1}

Note: Bird species codes are as in Table 5.

† Values include combined adult and nestling impacts.

estimates of daily energy requirements derived from the allometric relationship of Nagy (1987), the populations of intertidally foraging Glaucous-winged Gulls, American Black Oystercatchers, and Northwestern Crows would require 143, 6.4, and 2.4 KJ/d, respectively. By comparison, the energetic requirement for the total population of the starfish *Pisaster ochraceus*, which is known to have a major impact on the system (Paine 1966, 1974), is ≈ 25.5 KJ/d, based upon data on densities (Paine 1974) and metabolic requirements (Menge and Menge 1974).

Observational estimates of species impact also suggested that bird predation could have negative impacts at Shi-shi beach as well as at Tatoosh. For example, birds were predicted to reduce goose barnacle populations by 46% over the course of the year. The comparison is of interest, because most of the local gull population nests on Tatoosh but disperses to winter on mainland beaches. Consequently, bird effects might be unusually high on Tatoosh. Although total gull populations at Tatoosh attain much greater sizes, the disparity in impact, relative to mainland beaches, appears to be reduced because proportionally fewer gulls forage intertidally during the breeding season (Fig. 4), a pattern correlated with shifts to a diet dominated more by pelagic fish (J. T. Wootton, *personal observation*).

Experiments indicated that observational estimates with the proper units of per capita interaction strength and species impact can reasonably estimate the true direct effects of consumers in a natural system. For species that I examined in experimental manipulations, those prey species predicted to show little effect of

birds did not differ between treatments, whereas those prey species predicted to be strongly affected exhibited differences between treatments that were similar, both qualitatively and quantitatively, to observational predictions. Few studies have simultaneously estimated species impacts from observational data and experimentally tested the predictions. Bengston et al. (1976) and Székely and Bamberger (1992) estimated effects of birds on lumbricid worms and chironomid larvae, respectively, and their predicted impacts matched the results of experimental exclusions quite well.

Observational estimates of species impact also predicted that bird predation should strongly impact several other species of prey that could not be examined in my experiments (Table 7). Green urchin (*Strongylocentrotus droebachiensis*) populations are expected to be reduced by 27% per day on wave-sheltered shores at Tatoosh. This prediction is in accord with observations that $\approx 10\%$ of bird-consumed urchin tests that wash up on the beaches of Tatoosh are green urchins, even though they comprise an extremely small fraction of the living urchin population ($\approx 0.1\%$; J. T. Wootton, *personal observation*; R. T. Paine, *unpublished data*). Red sea urchins (*Strongylocentrotus franciscanus*), were also predicted to show smaller, but important, declines (22% per year) as a result of bird predation. The rarity of both of these sea urchin species in the intertidal zone has prevented experimental manipulations to assess the impacts of avian predation to date.

Birds are also likely to affect the abundance and distribution of large starfish (Table 7). Intertidal populations of *Pycnopodia helianthoides* and *Solaster*

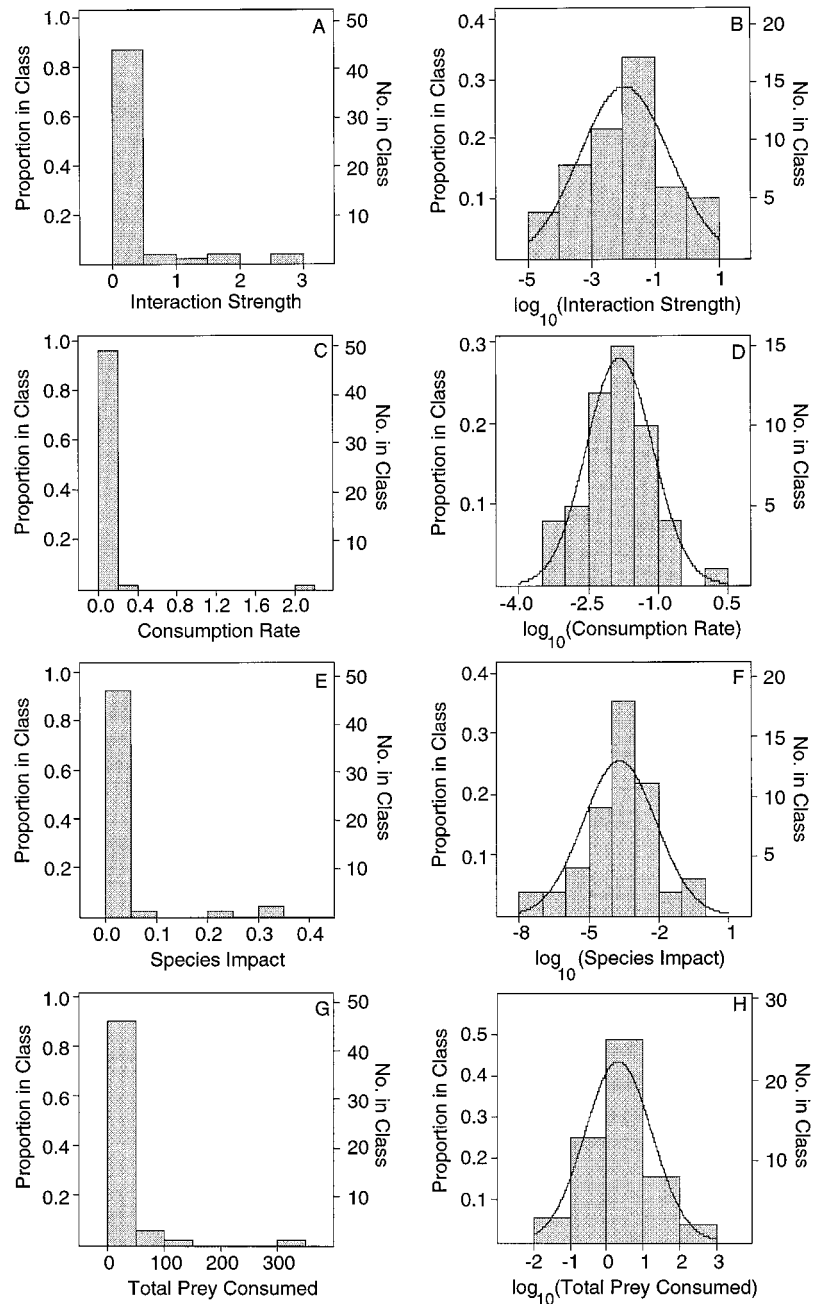


FIG. 7. Frequency distribution of four different indices of estimated interaction strengths (per capita interaction strength, consumption rate, per capita species impact, and total prey consumption) presented both on untransformed scales (A, C, E, and G, respectively), and on \log_{10} scales (B, D, F, and H, respectively). Curves in the log-transformed graphs represent the expected pattern if the distributions follow lognormal distributions. All nontransformed patterns were highly skewed (all skewness indices > 2.8) and significantly different from a normal distribution (Lilliefors' tests, $df = 50$, all $P < 0.0001$). All log-transformed patterns were relatively symmetrical (all skewness indices between -0.27 and 0.22) and did not differ significantly from a lognormal distribution (Lilliefors' tests, $df = 50$, all $P > 0.1$).

stimpsoni are predicted to show declines of 29% and 20% per day, respectively, in wave-sheltered sites. These starfish are quite rare in the intertidal zone of Tatoosh (≈ 0.09 and 0.065 intertidal individuals/m of shore, respectively), yet are frequently found eaten by birds (J. T. Wootton, *personal observation*). Popula-

tions of a third species of starfish that is consumed by birds (Table 4), *Orthasterias koehleri*, may also be strongly affected. This species is extremely rare in the intertidal zone (≈ 0.025 intertidal individuals per meter of shore), making any consumption difficult to detect over the duration of my observations. However, I fre-

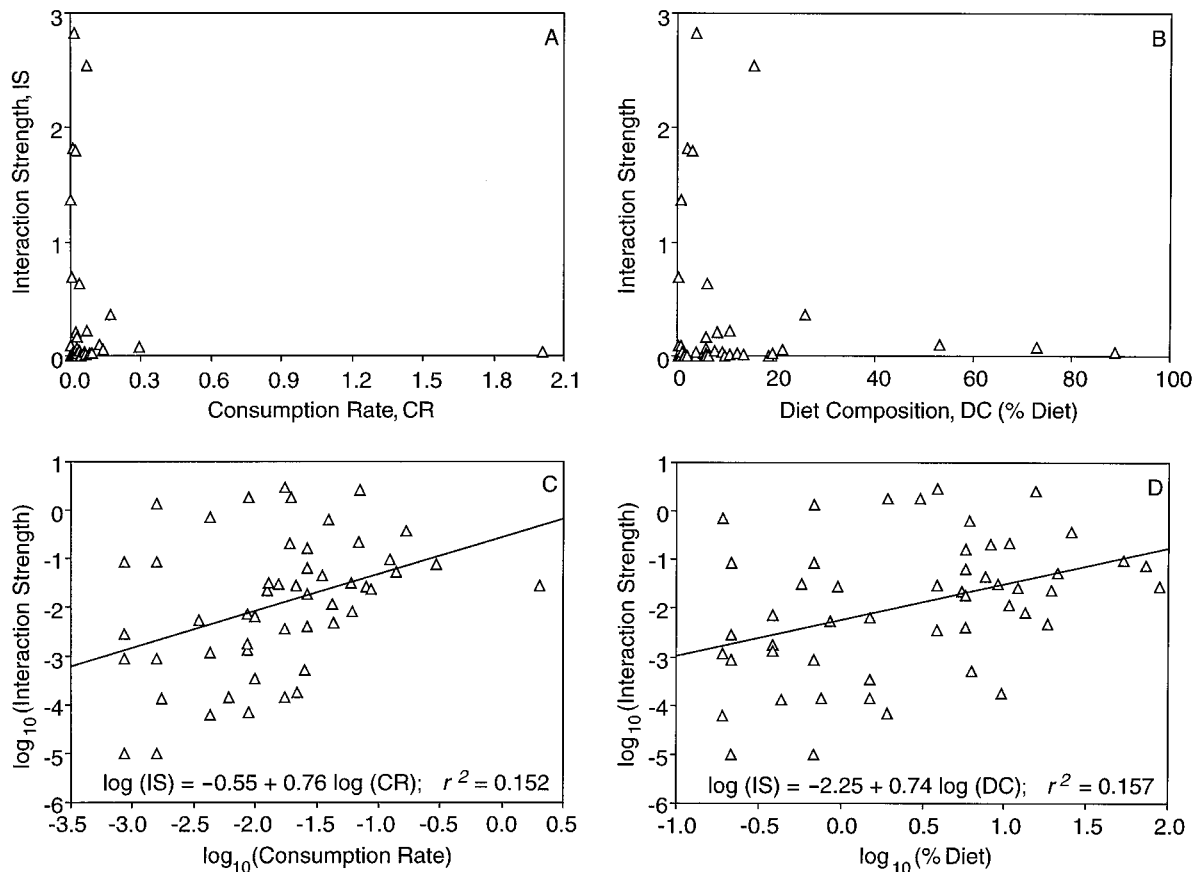


FIG. 8. Relationship between estimated interaction strength and dietary measures: (A) untransformed relationship between interaction strength and consumption rate; (B) untransformed relationship to percentage of a prey type in the diet; (C) \log_{10} -transformed relationship with consumption rate; and (D) \log_{10} -transformed relationship with percentage of a prey type in the diet. Statistically significant ($P < 0.05$) lines of best fit and their equations are included.

TABLE 7. Estimated daily percentage decline in populations of prey species in response to all bird predation on wave-exposed and wave-sheltered shores on Tatoosh Island.

Prey	Exposed	Sheltered
<i>Amphiporous</i> spp.	0.016	0.28
<i>Katharina tunicata</i>	0.37	0.76
<i>Mopalia</i> spp.	0.0017	0
<i>Lottia</i> and <i>Tectura</i> spp.	0.079	0.12
<i>Nucella</i> spp.	0.00051	0.00051
<i>Tegula funebris</i>	0.050	0.050
<i>Mytilus californianus</i>	0.0011	0.0010
<i>M. trossulus</i>	0.000077	0
<i>Nereis vexillosa</i>	0.43	0.64
<i>Idotea</i> spp.	0.23	0.13
Amphipods	0.0000031	0
<i>Pollicipes polymerus</i>	0.34	0.00013
<i>Semibalanus cariosus</i>	0	0
Small crabs	0.040	0.058
<i>Leptasterias hexactis</i>	0	0.23
<i>Pisaster ochraceus</i>	0	2.0
<i>Pycnopodia helianthoides</i>	8.1	29.3
<i>Solaster stimpsoni</i>	0	20.0
<i>Strongylocentrotus purpuratus</i>	0.010	0.12
<i>S. droebachiensis</i>	0.66	27.3
<i>S. franciscanus</i>	0	0.070
<i>Cucumaria</i> spp.	0.0017	0.00088
Intertidal fish	0.23	0.23

quently find individuals that have been preyed upon by birds. Had I observed only one instance of predation by gulls on this species, estimated interaction strength would have been $0.62 \text{ (bird-day/m-shore)}^{-1}$, and predicted losses due to bird predation on sheltered shores would have been on the order of 46% of the population per day. Clearly, more observations are necessary to better pin down the magnitude of predation effects on this and other rare species. The magnitude of estimated rates of loss of intertidal *Pycnopodia*, *Solaster*, and possibly *Orthasterias* is sufficient to explain the near absence of these soft-bodied starfish in the intertidal zone of Tatoosh. Experimental tests of this hypothesis are difficult, however, because of the rarity, large size, and mobility of these animals. It should also be noted that these starfish can have fairly large subtidal populations that do not experience bird predation. Hence, birds may have little effect on their total population sizes, but rather may set up a source-sink relationship in subtidal and intertidal habitats, respectively.

Several other groups of intertidal organisms are predicted to experience strong population effects by birds (Table 7). These include nemertians (largely *Amphi-*

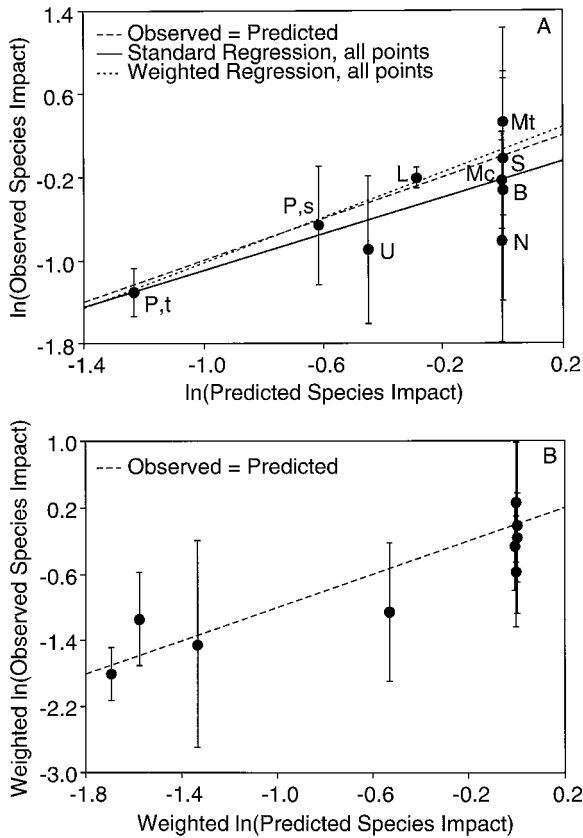


FIG. 9. Plot of predicted annual effects of bird predation on invertebrate prey from observational data vs. mean (and 95% CI) of observed effects in 126 results of experimental manipulations examining nine different taxa/situations. Observed species impact is defined as $\ln[(\text{control} + 1)/(\text{cage} + 1)]$, where cage and control values are densities (for mobile species) or percent area covered (for sessile species) in paired cage and control plots in the experimental studies outlined in the *Methods*. (A) Untransformed data. (B) Data weighted to stabilize the variance. The dashed line represents the expected relationship (Observed = Predicted), the solid line represents the line of best fit in standard regression, and the dotted line represents the line of best fit in weighted regression. All nine 95% CI encompass the line Observed = Predicted. Species codes are: B, acorn barnacles (*Semibalanus cariosus*); L, limpets (*Lottia* spp.); Mc, California mussels (*Mytilus californianus*); Mt, blue mussels (*Mytilus trossulus*); N, dogwhelk snails (*Nucella* spp.); P_s, goose barnacles (*Policipes polymerus*) at Shi-shi Beach; P_t, goose barnacles at Tatoosh Island; S, six-armed starfish (*Leptasterias hexactis*); U, purple sea urchins (*Strongylocentrotus purpuratus*).

porus spp.; 64% loss per year in sheltered sites), large isopods (*Idotea* spp., ranging from 38% to 56% per year in sheltered and exposed sites, respectively), large polychaetes (*Nereis vexillosa*; 79% to 90% per year in exposed and sheltered sites, respectively), the grazing snail *Tegula funebris* (17% per year), and small eel-like fish (Pholidae and Stichaeidae; 57% loss per year). Several of these taxa are sufficiently abundant to provide an experimental test of the observational predictions, if intertidal communities (e.g., mussel beds) are destructively sampled after experimental manipulations of birds. This analysis, however, has not accounted for the fact that some of these taxa have several reproductive bouts per year (e.g., *Idotea*; J. Reusink, *personal communication*), so the estimated predation impact may only be observed in short-term experiments.

Diet and behavioral patterns

Observations of avian behavioral activity in the intertidal zone exhibited different patterns among bird species (Fig. 5), corresponding to differences in their life-styles. Gulls and oystercatchers spent about one-third of their time in the intertidal zone foraging, but spent a surprisingly large amount of time ($\approx 50\%$) loafing or sleeping. Gulls may spend a large amount of time loafing and sleeping in the intertidal zone, because most other open areas on the island are aggressively defended nesting territories, and offer little opportunity for relaxing (J. T. Wootton, *personal observation*). Unlike gulls, oystercatchers incorporate intertidal feeding areas in their territories. Loafing and sleeping in the intertidal zone may place oystercatchers in a better position to defend their territory, and their presence alone may discourage intruding birds. Consistent with this difference in territorial behavior, the amount of time oystercatchers in the intertidal zone spent interacting with each other was more than six times greater than that spent by gulls. In contrast to gulls and oystercatchers, crows spent almost all of their time foraging in the intertidal zone. Crows do not defend intertidal territories, and their nests are sufficiently dispersed that aggression on the completely terrestrial portions of the island is reduced. Thus, there is little reason for crows to be present in the intertidal zone except to forage.

Differences in intertidal abundance patterns during a tidal cycle (Fig. 3) can also be linked to differences in aggressive behavior among species. Oystercatchers exhibit no marked peak in abundance when the tide

TABLE 8. Summary of regression analyses between observationally derived predictions and experimentally derived observations, where c is the constant and s is the slope of best fit, and r^2 is the proportion of variance explained by the regression. Probabilities in the last three columns represent the probability that the condition inside the parentheses holds.

Data	c (1 SE)	s (1 SE)	r^2	$P(c = 0)$	$P(s = 0)$	$P(s = 1)$
Means	-0.203 (0.145)	0.901 (0.294)	0.573	0.204	0.018	0.745
All points	-0.219 (0.128)	0.877 (0.180)	0.161	0.090	<0.00001	0.497
Weighted means	0.037 (0.097)	1.068 (0.234)	0.883	0.695	0.0026	0.781
All weighted points	0.062 (0.063)	1.089 (0.125)	0.558	0.336	<0.00001	0.476

drops to its lowest level. By defending intertidal territories, individuals restrict conspecifics from utilizing the larger foraging area available at low tide. In contrast, gulls and crows do not establish intertidal territories, and, consequently, their abundance increases as more potential prey become exposed when the tide goes out. Causes for the slow increase in oystercatcher abundance over the entire tidal cycle are more subtle, but probably relate to changes in prey behavior that occur over time in response to the stress of being exposed to air (J. T. Wootton, *personal observation*). As the tide comes in, mussels cease to keep their shells tightly clamped together, and gastropods cease to keep their shells tightly clamped down to the rock surface, presumably to facilitate water exchange and hasten a return to a more favorable physiological state. The resulting gaps in the shell armor increase the accessibility of the meat for oystercatchers, permitting more successful foraging during these times.

The diet composition of adult and nestling oystercatchers varied greatly, with adults consuming much smaller species, and smaller size classes within species, than they fed to their nestlings (Fig. 6, Table 5; Hartwick 1975). Adults consume prey as soon as it is captured, but must transport food to the nestlings. The shift to increasing food size with increasing transportation time agrees with the general predictions of central-place foraging theory (Orians and Pearson 1979), and may represent an adaptive foraging strategy that increases the amount of energy gained per unit time. Additionally, delivering food to the nest in large loads may lower the number of trips made to the nest, reducing the risk that predators will discover the nestlings. Delivery of larger food items to the nest may also explain, in part, why adults could feed nestlings at a much lower rate than they feed themselves.

Gulls exhibited distinct differences in diet on wave-exposed vs. wave-sheltered shores. *Pollicipes* comprised the bulk of the diet on exposed shores, whereas most of the items taken on sheltered shores were urchins, limpets, and worms (Table 4). The shift in diet was associated with a change in the community composition. *Pollicipes*, the most frequently consumed prey on wave-exposed shores, is uncommon on sheltered shores with less wave motion, because it depends on water motion for food delivery. Where *Pollicipes* is not available, other foods become important in the diet. Other studies on gull diets have found similar changes with changing prey availability. Vermeer (1982) found that a high percentage of regurgitated pellets contained *Pollicipes* on the west coast of Vancouver Island, where *Pollicipes* is abundant, but that garbage dominated the diets of gulls on the east coast, where *Pollicipes* is uncommon. *Pollicipes* does not occur in the Aleutian Islands, where other prey dominate (Trapp 1979, Irons et al. 1986). Sea urchins are prevalent in gull diets in areas without sea otters (*Enhydra lutris*), but are greatly reduced where sea otters are present (Estes and Pal-

misano 1974); gulls switch to fish as a consequence. Sea otters were not present at this site during my study.

Per capita interaction strength

Estimates of per capita interaction strength, expressed on a per day basis, varied over five orders of magnitude and were approximately log-normally distributed, with a mean magnitude of 0.011 (predator-day/m of shore). The strongly skewed distribution found in this study, derived from observational data, is interesting because it is similar in form to distributions of per capita interaction strength reported from experimental manipulations by Paine (1992), examining the effects of a suite of intertidal grazers on algae, and by Fagan and Hurd (1994), investigating the effects of a mantid predator on a suite of arthropod prey. The similarities in distributions between these studies might suggest a possible generality to the shape of the distribution of interaction strengths in natural communities, and raise the question of whether or not properties of communities change with changes in the distribution of interaction strength. For example, studies investigating model communities often randomly assign interaction strengths based upon a normal, rather than a lognormal, distribution (e.g., May 1973). Skewed distributions of interaction strength might be indicative of relatively modular structure in communities, a feature that tends to promote community stability (May 1973).

Goldwasser and Roughgarden (1993) introduced an alternative measure of interaction strength, the total number of prey consumed by the entire predator population per day. In their study, the distribution of their measure of interaction strength was also highly skewed, with few strong interactions and many weak interactions. However, the correspondence of their result with those described here is difficult to determine, because of the different definitions of interaction strength. To investigate this issue, I examined the distributions derived from my observational data, describing four different possible metrics of interaction strength (Fig. 7): per capita interaction strength (per predator per day), consumption rates (prey per predator per minute), per capita species impact (per day), and total prey consumption (number of prey per day). Interestingly, all metrics exhibited a highly skewed, approximately log-normal distribution, despite the fact that these measures did not all correlate tightly or linearly with each other. Thus, interaction strength, regardless of the specific index used, might generally be distributed in a highly skewed manner. This question requires further empirical investigation.

It might also be tempting to draw tentative conclusions about community stability by relating the observed mean interaction strength to theoretical predictions relating the number of species in a community, the density of interactions among species, and interaction strength (May 1973). Several cautions need to be applied to any attempt to draw conclusions from the

mean magnitude of estimated interaction strengths presented here. First, the interaction strengths that I have estimated come from a single system and a single group of predators, which are unusual in their high activity levels and metabolic demands. Therefore, overall interaction strengths in the intertidal at Tatoosh might be lower. Second, my analysis centered on the effects of consumers on their resources; the magnitude of other types of effects probably vary. For example, the interaction strengths that I estimated would have to be adjusted by some index of digestive efficiency to estimate the interaction strengths of prey on their consumers. Since assimilation efficiency is usually < 1 , interaction strengths of prey on consumers are likely to be lower. On the other hand, strengths of nontrophic direct interactions, such as interference competition, might be either stronger or weaker. Third, the issue of appropriate time units is problematic. My estimates are derived from measurements taken over a discrete time interval, and therefore depend on the time scale assumed. For example, if one tries to parameterize models with a yearly rather than a daily scale, the interaction strength estimates are multiplied by 365. Although this change does not affect the predicted dynamics of the system, the magnitude of interaction strengths is clearly affected, complicating comparisons with other studies. Thus, future comparisons to studies in other systems will require a uniform choice of time units. Finally, most theoretical treatments rescale interaction strength by dividing by the strength of intraspecific interactions (May 1973). As it is currently unclear what the magnitudes of intraspecific interactions among the prey are, let alone whether they are even present, applying mean interaction strength estimates to stability questions is not appropriate at this time.

My analysis further highlights the problems of using diet composition or energy flow as an index of interaction strength or species impact. The relationships between interaction strength and several indices of diet were very nonlinear, and the strength of the association was weak, explaining only $\approx 15\%$ of the variance even after log transformations. Similar conclusions hold for estimated species impacts. Although some strong effects were associated with substantial contributions to avian diets (e.g., *Pollicipes* and *Lottia*), large effects were also expected for relatively rare elements in the diets (e.g., sea urchins, large starfish, nereid worms, and eel-like fish). In estimating interaction strength in food web studies, species abundance, consumption rates, and assimilation efficiency must all be accounted for.

Conclusions

Developing methods to estimate interaction strength in the field is critical to making progress in understanding and predicting the dynamics of natural systems. This study has shown that combining observational data to produce measures with theoretically appropriate

units can provide a means to predict the per capita interaction strengths and species impacts of natural systems. The estimates presented here can still be considered relatively crude, in that they were assumed constant (i.e., linear). Further precision could also have been made by noting foraging patterns at finer spatial scales (e.g., in mussel beds vs. gaps, at different tidal levels), and by taking data over a range of estimated prey densities to account for nonlinearities. More extensive observations would yield better estimates of predation effects on rare species (e.g., *Orthasterias*). Despite these limitations, predictions matched the results of experimental manipulations reasonably well. Thus, observational data may provide a viable way to estimate interaction strength and species impact. The observational approach will require further application and experimental testing, however, before its utility is known. Additionally, it is not clear what types of observational data might be applied to estimate the strength of nontrophic types of interactions such as interference competition. This issue deserves further investigation, but may represent a major limitation to the approach.

Successfully estimating interaction strength in the field ultimately will require the application of several different approaches. On the one hand, observational data can often be taken quickly, and when numerous experiments are not feasible. For example, using observational data allowed me to estimate the independent effects of gulls, oystercatchers, and crows. In contrast, although I could experimentally manipulate all birds at once, there was no feasible way to manipulate each species separately. In other cases, experimental estimates might be more tractable, for example when one is interested in extremely small organisms that are difficult to observe. Statistical approaches such as path analysis (see, e.g., Wootton 1994a) could also be applied to long-term census data to obtain estimates of interaction strength, as long as the structure of the analyses agrees with the structure of the motivating theory (Wootton 1994c), in much the same way that observational units and experimental data must match those of theoretical variables. A combination of these approaches will aid our efforts to estimate interaction strengths and to check our estimates with independent data. Estimates of per capita interaction strength, in turn, will be key to unraveling and predicting the dynamics of natural systems.

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