

AN ABSTRACT OF THE THESIS OF

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Title: The Role of Avian Predators in an Oregon Rocky Intertidal
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Birds affected the community structure of an Oregon rocky shore by preying upon mussels (Mytilus spp.) and limpets (Collisella spp.). The impact of such predation is potentially great, as mussels are the competitively dominant mid-intertidal space-occupiers, and limpets are important herbivores in this community.

Prey selection by birds reflects differences in bill morphology and foraging tactics. For example, Surfbird (Aphriza virgata) uses its stout bill to tug upright, firmly attached prey (e.g. mussels and gooseneck barnacles [Pollicipes polymerus]) from the substrate. The Black Turnstone (Arenaria melanocephala), with its chisel-shaped bill, uses a hammering tactic to eat firmly attached prey that are 1) compressed in shape and can be dislodged, or 2) have protective shells that can be broken by a turnstone bill. In addition, the Black Turnstone employs a push behavior to feed in clumps of algae containing mobile arthropods.

Bird exclusion cages tested the effects of bird predation on 1) rates of mussel recolonization in patches (50 x 50 cm clearings), and 2)

densities of small-sized limpets (≤ 10 mm in length) on upper intertidal mudstone benches. Four of six exclusion experiments showed that birds had a significant effect on mussel recruitment. These experiments suggested that the impact of avian predators had a significant effect on mussel densities when 1) the substrate was relatively smooth, 2) other mortality agents were insignificant, and 3) mussels were of intermediate size (11-30 mm long).

Another series of exclusion experiments demonstrated that birds decreased densities of limpets 5-10 mm long, but not densities of smaller sized limpets. Experiments in which limpets were added to protected and unprotected plots indicated that bird predation varied seasonally; and that emigration, in addition to predation, may be responsible for the general absence of larger limpets on high intertidal mudstone benches.

THE ROLE OF AVIAN PREDATORS
IN AN OREGON ROCKY INTERTIDAL COMMUNITY

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THE ROLE OF AVIAN PREDATORS IN AN OREGON ROCKY INTERTIDAL COMMUNITY

Chapter I.

GENERAL INTRODUCTION

During the last two decades the rocky intertidal communities of the northeastern Pacific have been studied intensively (e.g. Paine 1966, 1974, 1980, Connell 1970, Menge and Menge 1974, Estes et al. 1978). Much of this research has focused on how biotic interactions alter distributions and relative abundances of dominant space-occupiers. Several of these studies have demonstrated that predators may significantly alter the appearance of a rocky intertidal community, either by feeding preferentially on a dominant space-occupier (e.g. Paine 1966, 1974) or by reducing the density of a dominant herbivore (e.g. Estes et al. 1978). Until recently, however, the impact of bird predation on densities of rocky shore invertebrates has largely been ignored. The objective of this study is to provide the information necessary to evaluate if and how predation by some birds alters invertebrate densities in a rocky intertidal community on the Oregon coast.

The study consists of two parts. In the first part I examine prey selection by the common species of birds that foraged in the intertidal zone. This provides information on the types of invertebrates that are most greatly affected by bird predation. Much of this part of the study focuses on the foraging tactics of two species of sandpipers that are

common along rocky shores, but about which little diet information has been published (see Chapter II). In addition to providing diet information on these two species of sandpipers, the results of this part of the study illustrate how bill morphology, foraging behavior, and prey selection are interrelated.

In the second part of this study I measure the impact of avian predators with a series of exclosure experiments. Observations on prey selection by birds indicate that both mussels (a dominant space-occupier) and limpets (a common herbivore) regularly comprise a large proportion of the diets of several species of birds. Consequently, I conducted two separate sets of exclosure experiments. The first set of experiments examines the impact of bird predation on mussels that settled in moderate-sized clearings in a mussel bed (see Chapter III); the second set of experiments tests if bird predation significantly decreases limpet densities on flat, high intertidal benches (see Chapter IV). These experiments also consider factors, such as prey density and substrate heterogeneity, that influence the impact of bird predation.

When combined, information about prey selection and estimates of predation intensity provides the background necessary to make inferences about the conditions under which bird predation has its greatest effect (see Chapter V). This synthesis, in turn, provides direction for future studies on bird predation in rocky intertidal communities.

Chapter II.

COMPLEMENTARITY IN THE FORAGING TACTICS OF TWO SPECIES OF
SANDPIPERS: AN EXAMPLE OF NON-COMPETITIVE RESOURCE PARTITIONING?

ABSTRACT

The Surfbird (Aphriza virgata) and Black Turnstone (Arenaria melanocephala) commonly forage together as mixed-species flocks in rocky intertidal habitats of the Pacific Northwest. These two species are similar in body weight and bill length, but have distinct prey preferences and foraging tactics.

Dissimilarities in the diets of the two species were verified by multinomial classification models. Surfbirds ate primarily mussels (Mytilus spp.) and gooseneck barnacles (Pollicipes polymerus), whereas Black Turnstones ate primarily limpets (Collisella sp.) and small, mobile arthropods. Both species regularly ate the acorn barnacle, Balanus glandula, but turnstones selected a wider size range of barnacles than did Surfbirds. Turnstones usually ate only the soft parts of the barnacle, whereas Surfbirds always swallowed barnacles intact.

Interspecific differences in foraging tactics account for observed differences in prey selection by the two species. The Surfbird uses its stout bill to tug upright, firmly attached prey (e.g. mussels and gooseneck barnacles) from the substrate. The Black Turnstone, with its chisel-shaped bill, uses a hammering tactic to eat firmly attached prey

that are 1) compressed in shape and can be dislodged, or 2) have protective shells that can be broken by a turnstone bill. In addition, the Black Turnstone employs a push behavior to feed in clumps of algae containing mobile arthropods.

Resource partitioning by Surfbirds and Black Turnstones appears to be the result of bill morphologies that are adapted for exploiting attached prey with different shapes. This complementarity in prey selection appears to be better explained by a noncompetitive hypothesis based on energetic efficiency rather than the conventional explanation of interspecific competition.

INTRODUCTION

The feeding ecology of shorebird assemblages has received increasing attention during the last decade (e.g. Baker and Baker 1973, Goss-Custard et al. 1977, Pienkowski 1980, Evans et al. 1979). Interest in these assemblages stems in part from the ease of quantifying both the behaviors of the birds and the distribution and abundance of their prey (Wiens 1979, Strauch and Abele 1979). More importantly, the characteristics of the shorebirds and their environment provide a means by which to address ecological questions relating to foraging theory, predator-prey interactions, and the organization of multiple-species assemblages (Wiens 1979). In this study I address the latter question by examining how two species of shorebirds respond to a common set of resources.

The Surfbird (Aphriza virgata) and the Black Turnstone (Arenaria melanocephala) are the two most common shorebirds found on rocky shores of the Oregon coast and usually co-occur in mixed species feeding flocks (see Figure 1; Gabrielson and Jewett 1940, Bent 1929). Although both are subarctic nesters (A.O.U. 1957), they are absent from the Oregon coast for only two months (early May through early July; C. Marsh, personal observation; 4 yrs. of monthly observations). These two species are more similar to one another in size and general appearance than either is to the other species of shorebirds found on rocky shores (i.e., the Black Oystercatcher Haematopus bachmani, the Wandering Tattler Heteroscelus incanum, and the Rock Sandpiper Calidris

ptilocnemis). The Surfbird, however, is slightly larger than the Black Turnstone (Gabrielson and Jewett 1940).

Niche exploitation patterns of coexisting species can be studied in a variety of ways. In the past two decades many studies have used predictions of niche theory as a basis for such comparative studies (see Pianka 1976, 1980 for reviews). Use of niche theory in this context, however, has two shortcomings. First, interspecific comparisons must be restricted to only one or two resource axes (Pianka 1976). In some studies such an assumption may result in oversimplification or misinterpretation (Leisler and Thaler 1982). Second, the predictions of niche theory are unfalsifiable. Consequently, the results of studies based on niche theory are ambiguous (Colwell and Futuyma 1971, Wiens 1977, Brown 1981). Thus, rather than placing this study under the constraints of current niche theory, I focused on the "adaptive modes" (sensu Root 1967) of the Surfbird and Black Turnstone.

This study differs from most other comparative diet studies in several ways. First, I compared interspecific versus intraspecific variation in diets to determine if observed interspecific differences were consistent or were biased by high intraspecific variation of diet. Second, I provide evidence that the critical resource parameter for prey selection is prey shape rather than one of the resource axes most commonly used (i.e., prey size, prey taxon, or prey location along a habitat gradient; see Pianka 1980). Third, I propose that the observed interspecific differences are better explained by a non-competitive mechanism (the energetic efficiency hypothesis) rather than by interspecific competition.

THE STUDY SITE

This study was conducted along a 2-km section of exposed rocky shore at Seal Rock, Lincoln County, Oregon (44°, 29.8'N, 124°, 5.2'W). The site is an isolated outcrop, flanked by sandy beaches for 24 km to the south and 23 km to the north. The intertidal substrate is largely sandstone with several basaltic dikes varying in size from one to several meters in height and width. Large, offshore basaltic rocks moderate the wave action along some sections of the shore. Sand movement over the flatter sandstone portions of the intertidal zone occurs throughout the year. The physical heterogeneity of this area results in a high diversity of intertidal microhabitats. General descriptions of rocky intertidal regions of the Pacific Northwest can be found in Carefoot (1977) and Ricketts et al. (1968).

MATERIALS AND METHODS

Collection of diet information

I collected 21 Surfbirds and 18 Black Turnstones from January 1979 through March 1981. Two Surfbird stomachs contained less than 10 prey items and were not included in the analyses. A comparison of formalin-injected stomachs with uninjected stomachs indicated that prevention of digestion by immediate injection of formalin was not necessary. Major prey were known to be either calcareous or heavily sclerotized, and appeared to be broken down in the stomach by mechanical grinding. All birds were put on ice within 30 minutes after collection. Stomach contents were removed immediately upon return to the lab (1 to 2 hours later). All prey were identified; and if intact, measured to the nearest 0.1 mm with an ocular micrometer. Prey items were considered to be recently swallowed (and were noted as such) if they were intact and unchipped. Lengths for snails (e.g. Littorina spp. and Lacuna marmorata) were in some cases estimated from whorl height by regression techniques. Similarly, shell heights of some gooseneck barnacles (Pollicipes polymerus) were estimated by regression from shell basal widths. Measurements from collected birds included weight, empty stomach weight, and three bill measurements (culmen length, basal height, and distal height 5 mm from the tip). Throughout this paper, I refer to kinds of prey as prey types and individual prey as prey items to avoid the ambiguity of the word "prey."

In several instances it was possible to observe a bird feeding in a restricted area, collect the bird, and census the prey remaining at the feeding site. Prey abundance was successfully measured in this manner for more Surfbirds than Black Turnstones, as turnstones frequently hunted over a large area in a short time period. Prey abundance was censused over a 300-800 cm² area depending on the walking rate of the collected bird. No attempt was made to measure prey abundance when the effective foraging area was not known. For comparative purposes, all data are expressed as density per 0.1 m².

Fecal samples were also collected to substantiate diet differences based on stomach samples. Fecal samples appear to provide a suitable method of prey determination because all major prey are either calcareous or heavily sclerotized. Over 60 fecal samples were examined before this study to gain expertise in identification of prey types from fragments. Feces from the two species are easily separated by size. Fecal samples were collected from February 1979 to March 1981 from areas where flocks had previously been observed foraging. To obtain as representative set of samples as possible, no more than 10 (and usually five or less) fecal samples were taken from a given feeding site. A second set of samples was collected during a 2-day period in September 1981 to test the results of a classification model derived from the first set of samples. In this case no more than three samples were taken from a given feeding site.

Conclusions of the study are based on between-species comparisons so that prey-specific digestion rates should not significantly bias the data, as these should be similar for both species. Handling times (on

the order of seconds) are similar for all prey types so arguments by Fairweather and Underwood (1983) are not applicable. Nemerteans were the only prey that could not be detected in stomach and fecal samples. Consequently, nemerteans were not included in the diet comparison, although both species were observed to eat them occasionally.

Statistical treatment of diet information

I used classification analysis to test for interspecific differences in diet (see Ramsey and Marsh in press). This approach has several advantages over other statistical methods commonly used for diet comparisons. First, it provides a measure of intraspecific as well as interspecific variability. Second, it classifies prey types according to their contribution to observed diet differences between species. Third, it does not assume that data follow a multinormal distribution.

The questions addressed by classification models are different than those addressed by overlap measures. Classification models are intended to test the validity of observed interspecific differences, rather than to estimate an overlap measure of the diets of the two species. Also, by ranking the prey types according to their contribution, a classification model focuses on qualitative differences in prey selection, whereas comparisons using overlap measures focus on quantitative differences in the diets of the two species.

A classification model assigns a sample as belonging to one of the two species by determining whether the contents of the sample more closely resemble that of the average sample from predator A or

predator B. The success of a classification model is determined by the percent of samples it classifies correctly. In other words, the accuracy of a classification model depends not only on the differences in the average diets of the two species, but on the consistency of these differences among the samples of the two species. The "overall average certainty of correct classification" provides a measure of the consistency of interspecific differences; and therefore, represents a measure of confidence that correct identification of a particular set of samples could be made by the model. It does not, however, provide information about the actual success of the classification model.

Prey types are ranked by a classification model according to their contribution to the dissimilarity of the diets of the two species. For example, if a prey type is almost always found in samples of predator A but never in samples of predator B, there is a high probability that a sample with that prey type is from predator A. The contribution of each prey type is ranked in two ways: 1) the relative predictive power they add to the model (its model factor); and 2) its contribution to the discrimination of a given set of samples (expressed as a dissimilarity index).

The model factors are the basis of the classification models and are Bayesian estimators (i.e., they are a posteriori estimates of the parameters of interest). The occurrence of a prey type in Surfbird versus Black Turnstone diets is expressed as a ratio. The model factor of a prey type is the logarithm of this ratio (hereafter referred to as its log odds). Log odds, rather than probabilities, are used as model factors because the former are additive, but the latter are not. When

comparing the magnitudes of the model factors, however, they are converted from log odds to probabilities for easier interpretation. Steps of calculation depend on the type of classification model being used (see Ramsey and Marsh MS).

The relative contribution of a prey type to the discrimination of a particular set of samples depends on both the model factor and the dissimilarity index of the prey type. For example, a prey type may be highly indicative of a particular predator species, but due to its rarity, it may contribute little to the discrimination of a particular set of samples (i.e., the dissimilarity index). On the other hand, a prey type may be abundant in a set of samples, but it may not contribute to the discrimination of the set of samples because of its being equally abundant in samples of both species (i.e., a model factor with a low value).

Two types of classification models were employed in this analysis. A multinormal classification model (hereafter referred to as Model 1) was used with the stomach samples, because this model incorporated information about the relative importance of a prey type in the sample. In Model 1 the measure of the occurrence rate of a prey type represents the average proportion that the prey type comprised in a set of a stomach samples. Here the model factor of prey type x is interpreted as the probability of correctly identifying a sample knowing only that the identity of one item from the sample was of prey type x .

The independent binomial classification model (hereafter referred to as Model 2) was used with the fecal samples, and is based upon presence/absence of a prey type in a sample. The model factors of Model 2 were calculated using the average percent of samples that contain a certain prey type. It can be interpreted as the probability of correctly identifying a fecal sample knowing only that the sample contained that prey type. Model 2 also assumes independence among the occurrence of the different prey types. Therefore, before accepting the conclusions of Model 2, Fisher's Exact Test is used to test for independence among all combinations of prey types.

Comparison of Foraging Tactics

I compared the foraging tactics of the Surfbird and Black Turnstone by quantifying the relative occurrence of certain feeding behaviors among individuals of the two species. During the first two years of fieldwork with these two shorebird species, I formed the opinion that the Surfbird and Black Turnstone used different foraging tactics. My observations indicated that Surfbirds obtained many of their prey by forcibly tugging attached prey from the substrate. Black Turnstones were observed to use a hammering attack either to dislodge attached prey or to chisel them open. I tested this hypothesis by enlisting the aid of three observers who were unfamiliar with shorebirds. I used naive observers instead of making behavioral observations myself to eliminate the possible bias of my preconceived expectations. Each was taught field identification of all the shorebirds present on the outer coast;

afterward, each was tested to verify that his/her identifications were accurate.

Six feeding behaviors were defined as follows:

1) tugging - A bird grabs a prey and forcibly pulls on it. This behavior is usually detected by movement of the bird's body and tail because more than just a simple bill motion is required to remove the prey from the substrate.

2) hammering - A bird strikes or chisels at the substrate or a prey in "woodpecker-like" fashion; sequential hammers are distinct behaviors and are not in rapid succession.

3) pecking - A bird moves the bill toward and away from the substrate or prey without any noticeable effort. The bill does not penetrate the substrate or enter a crack or crevice more than one-half of its length.

4) rapid pecking - This behavior is similar to pecking, but it is done at such a speed that an observer cannot readily count the individual actions.

5) probing - The bill penetrates the substrate or enters a crack or crevice to more than one-half of its length.

6) pushing - The head and bill are used to push an object (usually an alga) aside or upward.

Each observer was equipped with a cassette tape recorder and a spotting scope (either a 20x or 20x - 45x zoom). Each was instructed to describe the feeding behavior of as many individuals of each species as

possible on each of the five following substrates: 1) barnacles (Balanus spp.); 2) mussels (Mytilus californianus); 3) ulvoids (a group of green algae); 4) Rhodomela larix (a bushy, red alga); and 5) sand (sand interwoven with algal filaments and overlying a sandstone substrate). All prey eaten were noted along with the foraging tactic to obtain it. All observations were made within a 2 mo period (February and March 1981).

The feeding behaviors were transcribed from the tapes and recorded as 15-second intervals (hereafter referred to as "bouts"). Observations from individual birds were separated. Only bouts in which the bird appeared actively to feed (at least three feeding attempts during the 15-second bout) were included in the analysis.

To examine interspecific differences, the data on feeding behavior were analyzed in the form of 2 x 2 contingency tables that compared the number of bouts of each species (columns) in which a specific behavior did and did not occur (rows). Each observer's results were analyzed separately. Significance was determined using Fisher's Exact Test of Independence (Sokal and Rohlf 1969).

RESULTS

Types of Prey Eaten

Surfbirds and Black Turnstones exhibited consistent differences in the types of prey selected and in the behaviors they used to obtain prey. Both the stomach (Model 1) and fecal (Model 2) classification models demonstrate that the Surfbird and Black Turnstone diet samples were dissimilar (Figure 2). Model 1 classified 34 of the 37 stomach samples correctly (overall certainty of correct classification = 87%). Similarly, Model 2 classified 94% of the 230 fecal samples examined correctly (overall certainty of correct classification = 98.9%). The necessary assumption of independence among the prey types in Model 2 was verified; only two of the 78 combinations possible yielded a probability significantly different from that expected with independent categories. Model 2 was also tested with a second set of fecal samples that were not used to build the model (Table 1). Model 2 correctly classified 39 of 40 fecal samples from the second set of fecal samples (overall average certainty of correct classification > 99%).

The two models were able to discriminate samples correctly because certain prey types were diagnostic of the two species of shorebirds (Figure 3). Mussels (Mytilus spp.) and gooseneck barnacles (Pollicipes polymerus) were the prey types most indicative of the Surfbird in both the stomach and fecal samples (Figure 4). The mussel Modiolus rectus was diagnostic of Surfbird stomach samples but not fecal samples. The prey types indicative of Black Turnstones (in both stomach and fecal

samples) were limpets (Collisella sp.), polychaetes (Nereis), isopods (Idotea wosnezenski and Gnomosphaeromum sp.), and gammaridean amphipods. Decapods were indicative of Black Turnstone fecal but not stomach samples, as none occurred in stomach samples of either species of shorebird.

Although several prey types were indicative of Surfbird or Black Turnstone samples, more than 75% of the predictive power of each model was due to three prey types (Figure 5). Mytilus and limpets were each responsible for more than 30% of the predictive power of Model 1, and Modiolus contributed 11% to the predictive power of the model. Mytilus was also responsible for most of the predictive power (43%) of Model 2. Amphipods and isopods were the next most important prey types used to predict fecal samples correctly (18% and 11%, respectively).

The results of the classification models indicate that Mytilus is a preferred prey type of the Surfbird and that limpets are preferred prey of the Black Turnstone. The comparison of prey selected by collected birds and prey abundance at the site of collection confirm this conclusion. Surfbirds took Mytilus at a higher frequency than predicted by its relative abundance ($P < 0.05$, Wilcoxon paired sign test; Figure 6); but they did not eat limpets even when they were abundant ($P < 0.01$). Differences between levels of abundance and consumption rates by Surfbirds did not consistently differ for Littorina and barnacles ($P > 0.20$).

Black Turnstones, in contrast, selected Mytilus less often than expected by its abundance ($P < 0.05$; Figure 6). Turnstones ate limpets in four of the six instances that they were available, but this

difference in limpet consumption and abundance was not statistically significant. This may have been due to small sample size, as limpet densities were low in the two cases that turnstones did not eat them.

Size of Prey Eaten

Diets of the Surfbird and Black Turnstone differed in types of prey selected but not in sizes of prey eaten, except with barnacles. The size of prey selected by a species did, however, depend on the prey type (Figure 7). Both species ate prey that were 1 to 16 mm in length; but the largest prey items eaten by Surfbirds were mussels (Mytilus or Modiolus) or barnacles, and the largest prey eaten by Black Turnstones were isopods, limpets, or barnacles (Figs. 7 and 8).

The barnacles eaten by Black Turnstones were significantly larger than those eaten by Surfbirds (Figure 8), regardless of whether size was represented by height or by basal width ($P < 0.01$ in both cases; Wilcoxon's Rank Test, Snedecor and Cochran 1980). The ability of turnstones to eat larger barnacles than do Surfbirds results from their consuming only the soft parts, whereas Surfbirds swallow barnacles intact.

Turnstones also selected a greater range of shapes of barnacles than did Surfbirds. The proportion of columnar (height > basal width) versus noncolumnar (basal width > height) barnacles was significantly different for the two species, in that Surfbirds ate a greater proportion of columnar barnacles ($P < 0.05$, 2 x 2 Chi-square Test).

Although the observed means for four of the prey types (Mytilus, Modiolus, Littorina, and Lacuna) were larger for Surfbirds than for Black Turnstones (Figure 7), a factorial design ANOVA indicated no significant interspecific differences compared to the among-individual differences ($P > 0.20$ for Modiolus, Mytilus, and Littorina; $P > 0.10$ for Lacuna). (The among-individual differences, however, were highly significant for all four prey types; $P < 0.001$).

Foraging Behavior

Data collected by the three observers confirm the initial hypothesis that the Surfbird and the Black Turnstone use different foraging tactics in the same microhabitat. On all five substrates Surfbirds used the tug behavior significantly more often than did Black Turnstones (Figure 9). Tugging was used most on barnacle, mussel, and Rhodomela substrates. In contrast, hammering was observed more often in Black Turnstones, although the interspecific differences were not as great as with tugging. The highest rates of hammering were observed on barnacle and mussel substrates. Turnstones used the push behavior much more often than did Surfbirds. Its use was associated with algal-dominated substrates, especially the dense bushy Rhodomela.

Rapid pecking was infrequently observed, but this foraging behavior was used by Surfbirds more often ($P < 0.01$, Wilcoxon's Signed Rank Test; Snedecor and Cochran 1980). Surfbirds primarily used the rapid pecking behavior when feeding on high densities of the small snails Littorina and Lacuna (C. Marsh, personal observation).

The analyses of the foraging behaviors assumed that variation among individual birds of the same species was not important. I tested this assumption by comparing the percentages of individuals of each species that were observed using a foraging behavior (see Appendix 2B). Similarity in the trends of the bout and individual data support the assumption that bout comparisons represent a valid test of interspecific differences in foraging behavior. Similar interspecific differences in behavior were recorded by both the individual and bout comparisons. Often the number of individuals observed was small. Consequently, the interspecific differences were less likely to be statistically significant. Only one discrepancy between the individual and bout results was noted. The proportions of the bouts containing tugs on the sand substrate were significantly different between the two species, but the proportions of individuals using tugs were approximately equal (0.05 vs. 0.06).

In some situations observers were able to identify the prey type a bird obtained by a specific feeding behavior (Table 2). The type of behavior used to eat barnacles was significantly different for the two species (Fisher's Exact Test, $P < 0.01$), with Surfbirds primarily using a tug tactic and Black Turnstones using a hammer tactic.

Morphometric Comparisons

Surfbirds were approximately 38% heavier than the Black Turnstones (Table 3), and in both species females were larger than males. The bill dimensions of the two species also differed in that the bill of the

Surfbird was longer and thicker at the base and at the tip (Table 3; Figure 1). Only the Surfbird exhibited sexual dimorphism in bill size; bills of females were longer and thicker than those of males (Table 3).

The stomach weight of Surfbirds comprised a greater proportion of the total weight than in Black Turnstones (5% vs. 3%; $P < 0.01$). This suggests that the Surfbird may be able to triturate larger prey. No significant differences in relative stomach weights was observed between males and females of either species.

DISCUSSION

Selection of Prey Types

Although the Surfbird and Black Turnstone commonly occur in the same feeding flocks, they have distinct foraging tactics and diets. Interspecific differences in the kinds of prey eaten appear to be a function of how the two species respond to attached prey and to clumps of macroalgae. Invertebrate prey of shorebirds in exposed microhabitats of wave-swept rocky shores survive by being strongly attached or by having a body shape with minimal resistance to wave action. Thus, a bird's choice of prey items is constrained by its ability to remove attached prey from the substrate. Surfbirds and Black Turnstones accomplish this by using one of two foraging tactics: 1) grasping a prey item and tugging it off the substrate, or 2) knocking it off the substrate or breaking through its outer plates (or shell) with a hammering motion. Small or poorly attached prey are removed from the substrate with a simple pecking motion.

Surfbirds used a tug behavior to eat Mytilus and gooseneck barnacles. Both of these prey have an upright profile and can be readily grasped (see Figure 10, F and G). Modiolus rectus >5 mm represent another columnar prey type. At Seal Rock Modiolus usually occurred in sand-filled recesses with only the posterior end of their shells exposed (C. Marsh, personal observation). Most acorn barnacles selected by Surfbirds appeared to be columnar in shape (Fig. 10E), and vulnerable to a tug foraging tactic.

Black Turnstones used the hammer tactic significantly more often than did Surfbirds. Limpets were abundant in their diet, but Mytilus and gooseneck barnacles were scarce. This correlation suggests that the hammer tactic, but not the tug tactic, is effective at exploiting prey with low body profiles. Chitons represent another potential prey with a low body profile (Figure 10, a). Only one turnstone sample contained a chiton. However, the general absence of small chitons as turnstone prey is probably due to their rarity in microhabitats accessible to short-billed shorebirds. Observations of turnstone predation on acorn barnacles indicated that turnstones used the hammer tactic to penetrate the barnacle's outer protective plates rather than removing the prey from the substrate. Because of the hammer tactic, turnstones appear able to exploit barnacles with a variety of shapes (e.g. Figure 10, C and E).

Differences in bill morphologies of the Surfbird and Black Turnstone are consistent with the proposed dichotomy of Surfbirds as "tuggers" and Black Turnstones as "hammerers." The bill of the Surfbird is larger and thicker with a slightly swollen tip (Jehl 1968, this study) suggesting that it is capable of grasping a prey item more firmly. The turnstone bill is more chisel-shaped as expected for a hammering tactic, and the tips of turnstone bills, but not Surfbird bills, were observed to be blunted by wear.

Connors' (1977) observations on Surfbird and Black Turnstone diets are consistent with the conclusions of this study. All seven Surfbird stomachs she examined contained mussels, and six of seven Black Turnstone stomachs contained limpets. In contrast only one Black

Turnstone stomach contained mussels, and only two Surfbird stomachs contained limpets. She also noted that only the Surfbird used a "pull" behavior.

The Surfbird and Black Turnstone employed different foraging tactics when hunting in algae-dominated patches. In clumps of algae Surfbirds used foraging tactics similar to those used in other patches, as well as occasionally using the push and rapid peck behaviors. Turnstones, however, reduced their hammer behavior and greatly increased their use of the push behavior, especially in dense beds of Rhodomela. The push or turn behavior is well-known in both species of turnstones (A. melanocephala and A. interpres; Bent 1929, Burton 1974, Connors 1977); but natural history accounts concerning the Surfbird (Bent 1929) make no mention of this behavior. Connors (1977) specifically states that during her field study she did not observe Surfbirds using a push behavior.

The types of invertebrate prey found in algal mats of Rhodomela larix differ from those in microhabitats that are not protected from direct wave action (C. Marsh, personal observation; C. D'Antonio 1983; Kozloff 1973). Small, mobile crustaceans (i.e., amphipods, isopods, and occasional decapods) and nereid polychaetes are usually restricted to the interior of algal clumps, but the coiled gastropods Littorina and Lacuna occur all over the algae. With the exception of the limpets, those prey taking refuge in algal clumps were also indicative of the turnstone diet. Through the use of the push behavior, turnstones appear to encounter different prey types from those in exposed microhabitats. The abundance of Lacuna in turnstone diets may result from turnstones

feeding in patches of Rhodomela more often than do Surfbirds (C. Marsh, personal observation).

This study implies that selection of exposed, poorly attached prey may be independent of bill morphology because prey selection is primarily a function of how firmly attached prey are removed from the substrate and whether a shorebird can exploit prey in algal mats. For example, either bill type should be capable of removing poorly attached prey such as limpets from algal fronds or mussels from filamentous algae. The coiled gastropods Littorina spp. and small Nucella spp. are examples of exposed, poorly attached prey (they rely on surface irregularities as protection from wave action); and these snails occurred with similar frequency in Surfbird and turnstone samples. Small individuals of the mussel Modiolus represent another type of poorly attached prey, as they usually occurred on the surface of sand-dominated patches. Fragments of small Modiolus regularly occurred in the fecal samples of both species, but no Modiolus from a turnstone stomach sample was >6 mm long (versus 16 mm for Surfbird). Jehl's observation of both species eating exposed grunion eggs (in Ricciuti 1978) provides evidence that both species may respond similarly to exposed, poorly attached prey. Also, Connors' observations of Surfbird predation on small crustaceans (Excirolana linguifrons and/or Emerita analoga) from sandy beaches suggest that this study recorded motile crustaceans as typical turnstone prey only because of their usual occurrence in algal mats. Thus, the similarity in diet of the Surfbird and Black Turnstone probably varies with the relative abundance of prey types that require specific foraging tactics (i.e., firmly attached prey

or prey in algal mats) versus the relative abundance of exposed, poorly attached prey that can be captured easily by either shorebird.

Selection of Prey Size

Several authors (Menge and Menge 1974, Hespenheide 1975, Strauch and Abele 1979) have pointed out the difficulty in distinguishing the relative importance of prey size versus prey types as cues to predators when the two prey variables are correlated. In this study, however, several prey types exhibited similar size ranges so that the relative importance of the two factors could be distinguished. In general, the two species consumed similar-sized prey, but of different types (compare Modiolus and isopods for Surfbirds and turnstones, respectively, in Figure 7). Surfbirds may be capable of swallowing larger shelled prey. I regularly found 10-15 mm long intact mussels or barnacles in Surfbird stomachs; but the largest shelled prey I recovered from a Black Turnstone was 9 mm in length. The larger prey items from turnstone stomachs were either eaten without their shell (i.e., barnacles or limpets) or were flexible (i.e., isopods). Surfbirds have disproportionately larger stomachs than Black Turnstones (this study, Connors 1977), suggesting that the digestive tract of the Surfbird is modified for consumption of larger shelled prey.

These results confirm the initial supposition that prey type is more important than prey size in understanding interspecific differences between the Surfbird and Black Turnstone.

Complementarity versus Competition

Two hypotheses have been proposed to explain resource partitioning between two co-existing species. The most commonly invoked hypothesis, interspecific competition, assumes that there has been strong genetic selection on one or both species to use resources other than those shared in common. Over evolutionary time such selective pressures result in two species that partition the available resources and therefore are able to coexist. An implicit assumption of this hypothesis (hereafter referred to as the "competition hypothesis") is that the two species had similar resource usage patterns before their ranges first overlapped.

The second hypothesis proposes that in some cases a resource spectrum exists that requires mutually exclusive feeding adaptations to exploit it (see Bloom 1981 for references). Consequently, the resource usage patterns of the two species will differ without the influence of interspecific competition. In other words, divergence results solely from intraspecific competition selecting individuals that increased the efficiency with which they captured and assimilated certain types of prey. Thus, this second hypothesis is referred to as the "energetic efficiency hypothesis."

These two hypotheses can not be tested directly because this would entail observations of population changes over evolutionary time. In some cases, however, inferences may be made by examining characteristics of a particular resource partitioning study. Bloom (1981) proposes three criteria, that if met, are sufficient to accept the energetic

efficiency hypothesis (Bloom's watershed effect) and reject the competition hypothesis. These criteria are "(1) a resource gradient requiring predator specializations must exist, (2) the predators must be demonstrably adapted to the extremes of the gradient, and (3) consumption of intermediate prey types must result in lower evolutionary fitness relative to consumption of prey from the appropriate gradient extreme."

Using Bloom's criteria, resource partitioning of attached prey by the Surfbird and Black Turnstone appears more consistent with the energetic efficiency hypothesis than with the competition hypothesis. First, a prey resource gradient exists which requires predator specializations. Prey with very flattened profiles (i.e., the highest attachment area to total biomass ratio; Figure 10, A, B) represent one extreme of the gradient; and prey with erect profiles (i.e., the lowest attachment area to total biomass ratio; Figure 10, F, G) represent the other extreme of the gradient.

Second, the predators appear morphologically adapted to the extremes of the gradient. The Surfbird and Black Turnstone appear specialized for exploiting the opposite extremes of the prey-shaped gradient because the foraging tactics of each species are effective at exploiting prey from only one end of the prey-shape gradient. The complementarity of Surfbird and Black Turnstone foraging behaviors seems a result of the shapes of their bills, and the constraints bill shape has on prey selection. A stout-shaped bill, such as the Surfbird's, appears to have greater gripping force at the tip of the bill compared to the chisel-shaped bill of the turnstone. Consequently, Surfbirds can more

effectively apply sufficient gripping force to remove columnar-shaped prey attached to the substrate than can turnstones. On the other hand, the stout-tipped bill of the Surfbird appears ineffective at grasping firmly attached prey with a low profile; but the chisel-shaped bill of the turnstone dislodges or breaks open these prey with a hammering motion. The latter foraging tactic is effective with thin-shelled columnar barnacles, but it is ineffective with the two columnar prey types with the lowest attachment area to total biomass ratio. These two prey, Pollicipes and Mytilus, are attached to the substrate by flexible tissue or proteinaceous threads, respectively. Such materials tend to stretch in response to a lateral blow rather than the shell of the prey breaking or becoming dislodged. Thus, the bill shapes of the two shorebirds appear adapted for mutually exclusive functions.

Because the first two criteria are met, interspecific competition in recent (ecological) time should not be a significant selective force. The possibility that past interspecific competition initiated the divergence of the two species can not be discounted, however, unless Bloom's third criterion is also verified. Testing the third criterion was not an initial objective of this study, but a tentative answer can be inferred from its results. Intermediate prey of the prey-shape gradient are considered to be those with a moderate ratio of attachment area to total biomass. These include coiled gastropods and certain shapes of barnacles. Both of these prey types were less preferred than mussels and limpets, the two extremes of the prey-shape gradient. Coiled gastropods are easily removed from the substrate, but individuals of the size preferred by birds (6-12 mm) are scarce (C. Marsh,

unpublished data). (Coiled gastropods above this size are immune to predation by either of these species.) Similarly, barnacles that are firmly attached must be taken by either a tug or a hammer foraging tactic, but small barnacles can be pulled off the substrate by either species. Are attached prey that are selected by both species on the average smaller than prey from the respective gradient extremes, and do they therefore provide less energy per prey item? To test if this interpretation is correct, one must present individuals of the two bird species with prey types from different parts of the resource gradient, and measure their feeding and assimilation rates.

Because this argument for the energetic efficiency hypothesis is a posteriori, this study cannot be considered a test of the two hypotheses. Nonetheless, it illustrates that ecologists first must examine the kinds of functional differences that exist between coexisting consumers before they apply niche theory models based on interspecific competition to resource partitioning studies. At a time when the usefulness of overlap indices is in question (e.g., Simberloff 1982), qualitative interpretations are a necessary first step before quantitative syntheses of resource utilization patterns are attempted.

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Table 1. Contents of the second set of fecal samples collected to test the fecal classification model. Values in Columns 1 and 2 represent the percent of fecal samples in which the prey type occurred. Column 3 represents the percentage that each prey type contributed to the classification of the samples. Only 1 of the 40 samples was misclassified by the model.

Prey Type	1) Surfbird	2) Black Turnstone	3) % Contribution to Classification
<u>Mytilus</u>	91%	6%	43
<u>Modiolus</u>	5%	0%	--
<u>Pollicipes</u>	5%	0%	1
<u>Balanus</u>	77%	50%	1
<u>Littorina</u>	95%	33%	3
<u>Lacuna</u>	18%	22%	1
<u>Thais</u>	23%	0%	2
<u>Collisella</u>	23%	78%	9
<u>Nereis</u>	17%	22%	1
Amphipods	<u>5%</u>	<u>83%</u>	31
N	22	18	

Table 2. The behaviors used by the two species to obtain the respective prey types. Most of the observations were made by Observer #2. Abbreviations are S.B. = Surfbird, B.T. = Black Turnstone.

BEHAVIOR	<u>PREY TYPES</u>					
	<u>Balanus*</u>		<u>Mytilus</u>		<u>Littorina</u>	
	S.B.	B.T.	S.B.	B.T.	S.B.	B.T.
Peck	23	9	4	0	6	19
Tug	44	1	6	0	0	0
Hammer	3	11	0	0	0	0

*The use of "tug" vs. "hammer" by the 2 species to obtain Balanus was significantly different ($p < .001$) as determined by Fisher's Exact Test of Independence.

Figure 1. Bill shapes of Surfbird and Black Turnstone. See Table 3 for morphometric data on bill dimensions.

Figure 1.

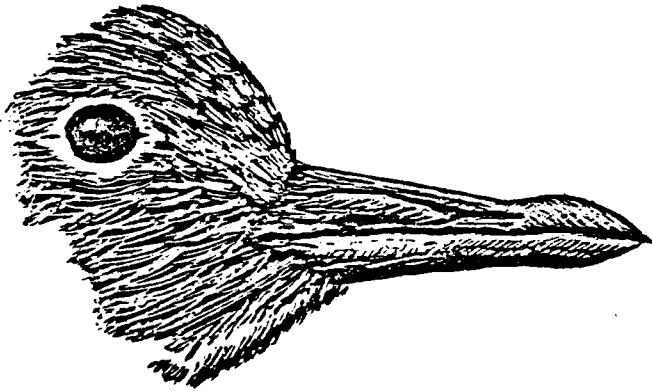
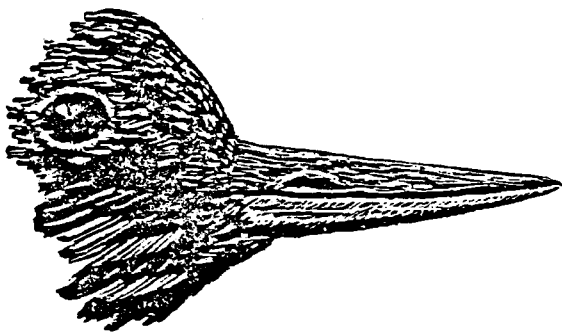
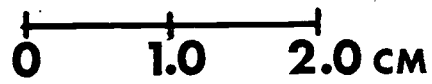
**Surfbird****Black Turnstone**

Figure 2. Frequency histograms of classifications of samples. The left-hand figure illustrates the classification of the stomach, the right-hand of the fecal samples. The central horizontal bar denotes equal probability of a sample being from either species.

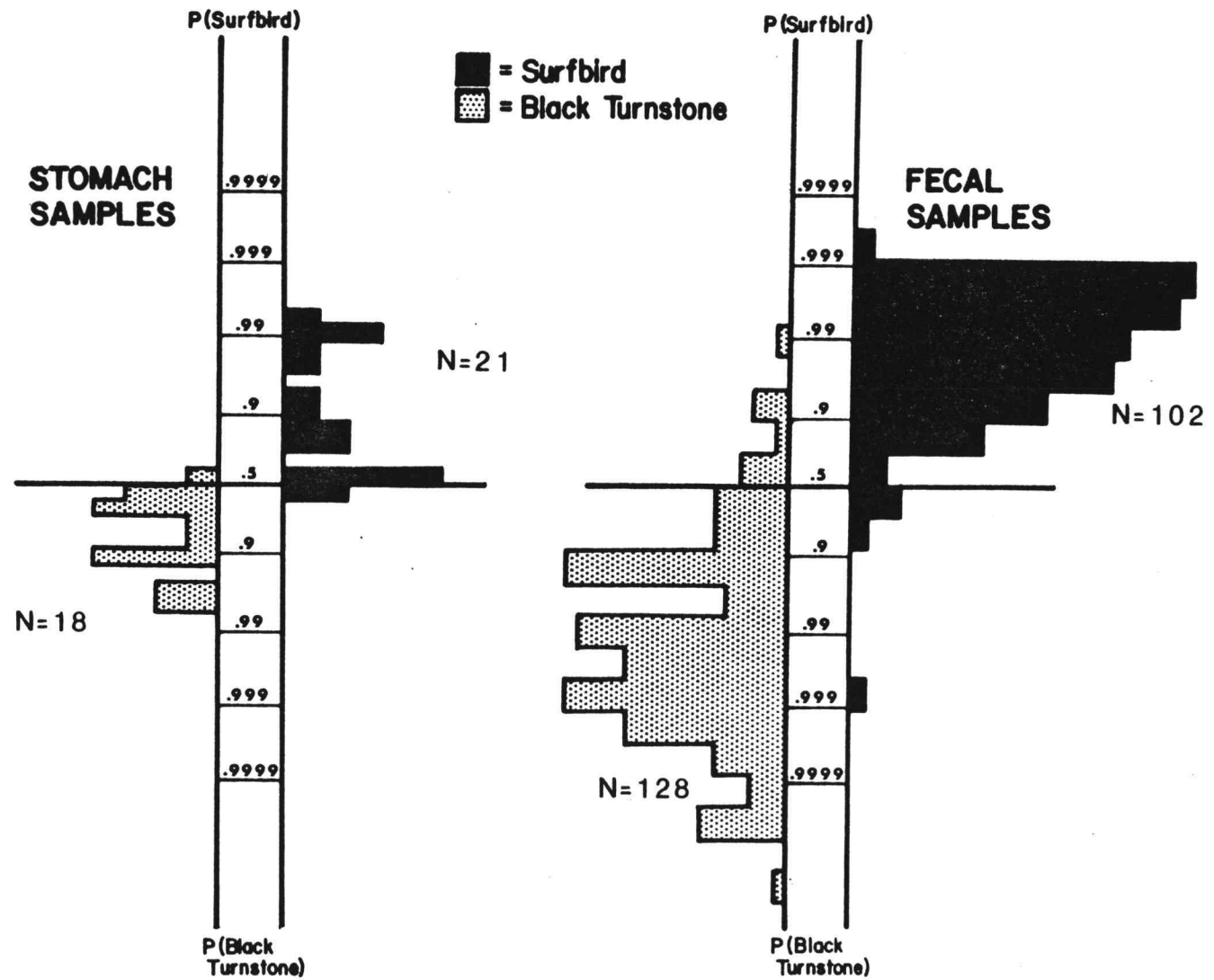


Figure 2.

Figure 3. Numerical frequency of occurrence of the common prey types. The left-hand scale represents the average percent (by number) of a stomach sample composed of the respective prey types. The right-hand scale represents the percent of the fecal samples in which the prey type occurred.

Figure 3.

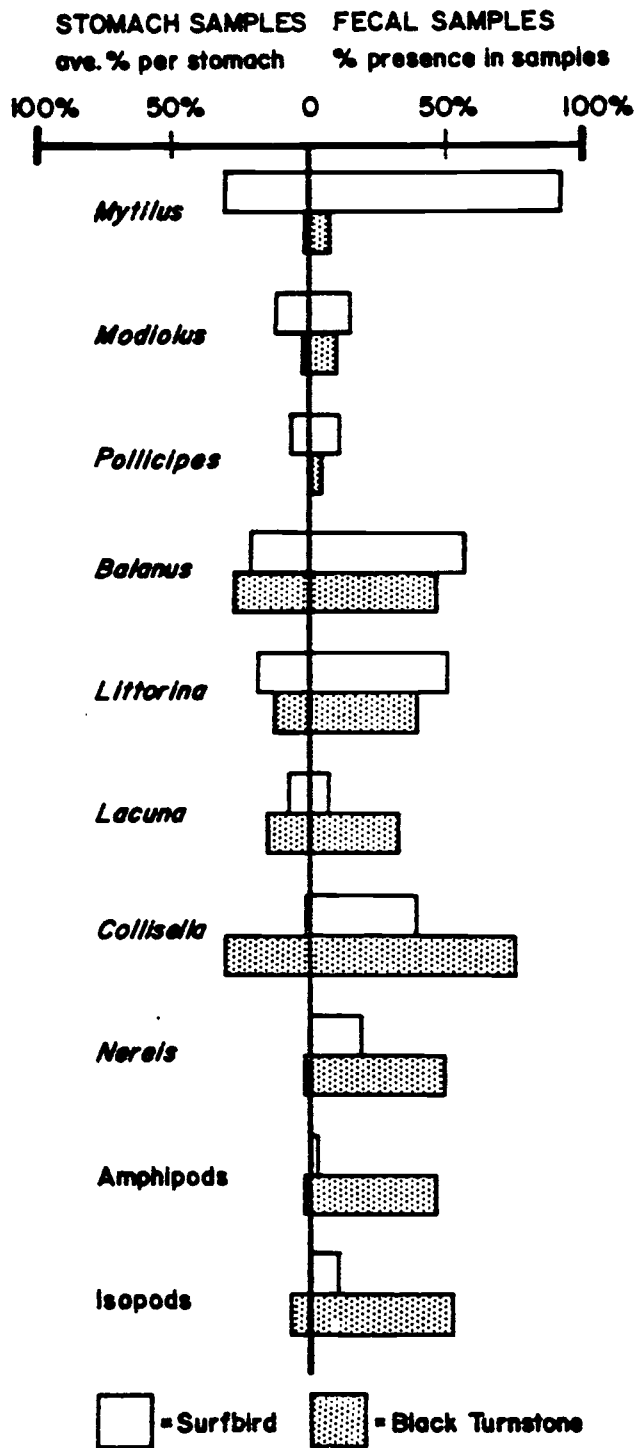


Figure 4. A ranking of prey types based on their contribution to the classification models as model factors. Ranking on the left-hand scale is based on the stomach samples (Model 1), and the right-hand scale shows ranking based on the fecal samples (Model 2).

Figure 4.

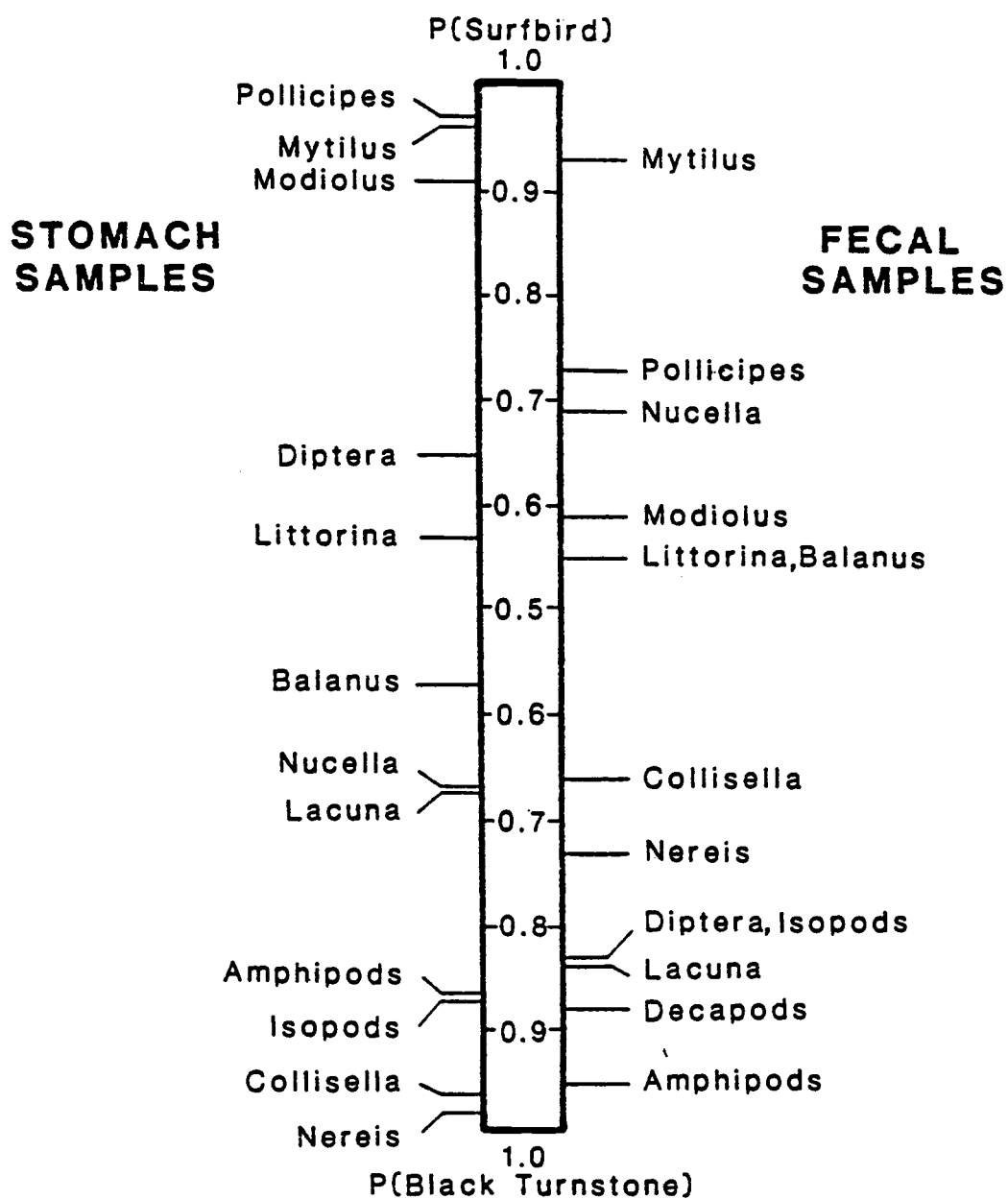


Figure 5. Percent contribution of prey types to the predictive power of the classification models (the dissimilarity indices).

Ranking on the left-hand scale is based on stomach samples (Model 1); ranking on the right-hand scale shows ranking based on fecal samples (Model 2). Prey types that contribute less than one percent are not included.

Figure 5.

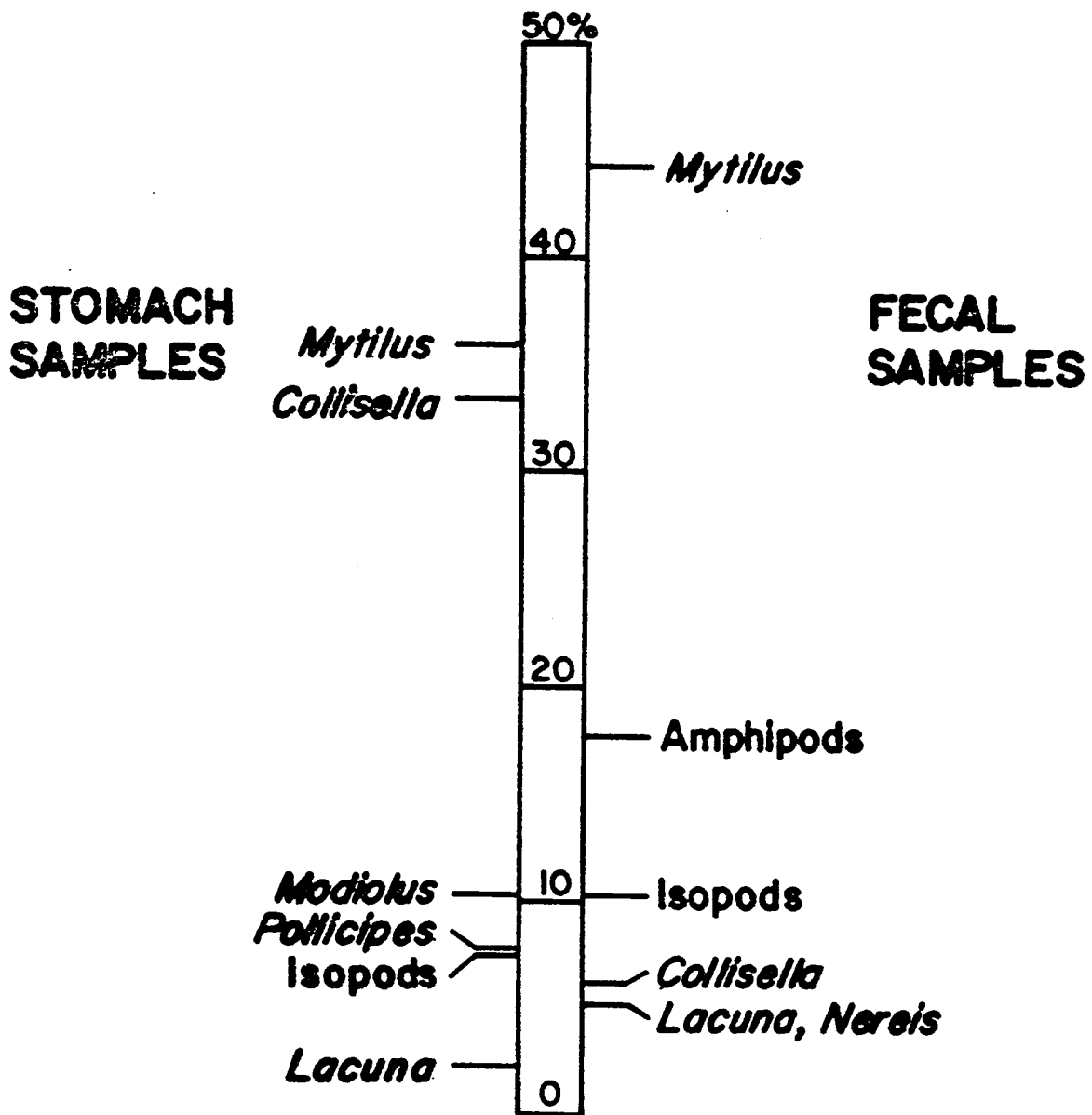


Figure 6. Prey preferences of Surfbird (solid circles) and Black Turnstone (open circles). Electivity index = $(r_i - p_i)/(r_i + P_i - 2r_iP_i)$, where r_i = proportion of prey type (by number) i in diet, and P_i = proportion of prey type i available in the environment (Jacobs 1974).

Figure 7. Lengths of common prey types. Thin solid lines represent prey sizes available at the study site. Lengths of prey from stomach samples of the 2 species illustrated by 'box-and-whisker' diagrams. The central vertical bar of each diagram denotes the mean, and the rectangular regions includes \pm one standard deviation. The horizontal line demarcates the observed range. The dashed line with the Collisella samples indicates the size of shells left by feeding turnstones, rather than shells that were taken from stomach samples.

Figure 7.

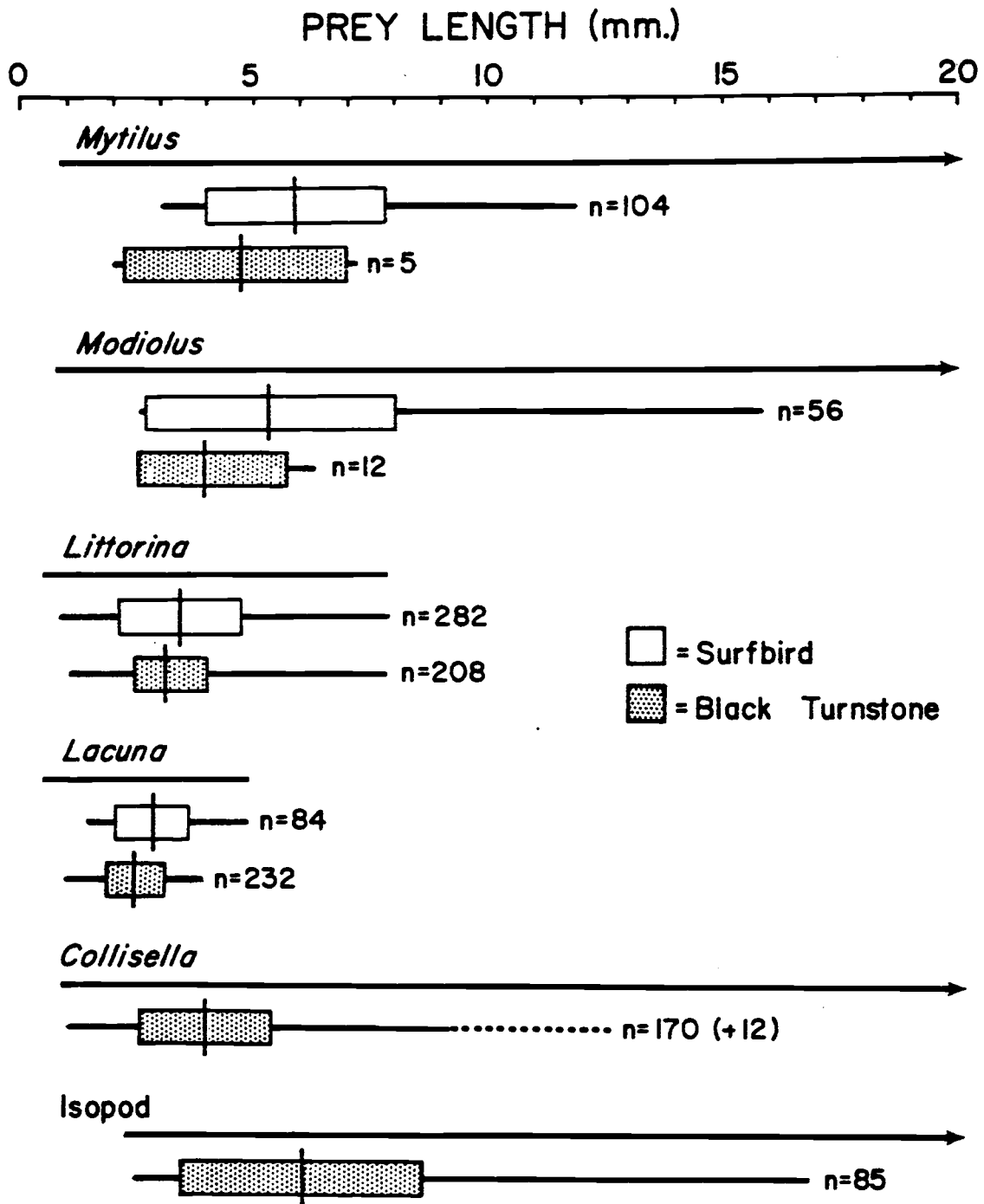


Figure 8. Dimensions of the barnacle Balanus glandula eaten by Surfbirds (solid circles) and Black Turnstones (open circles). The line defines the observed sizes of B. glandula present at the study site.

Figure 8.

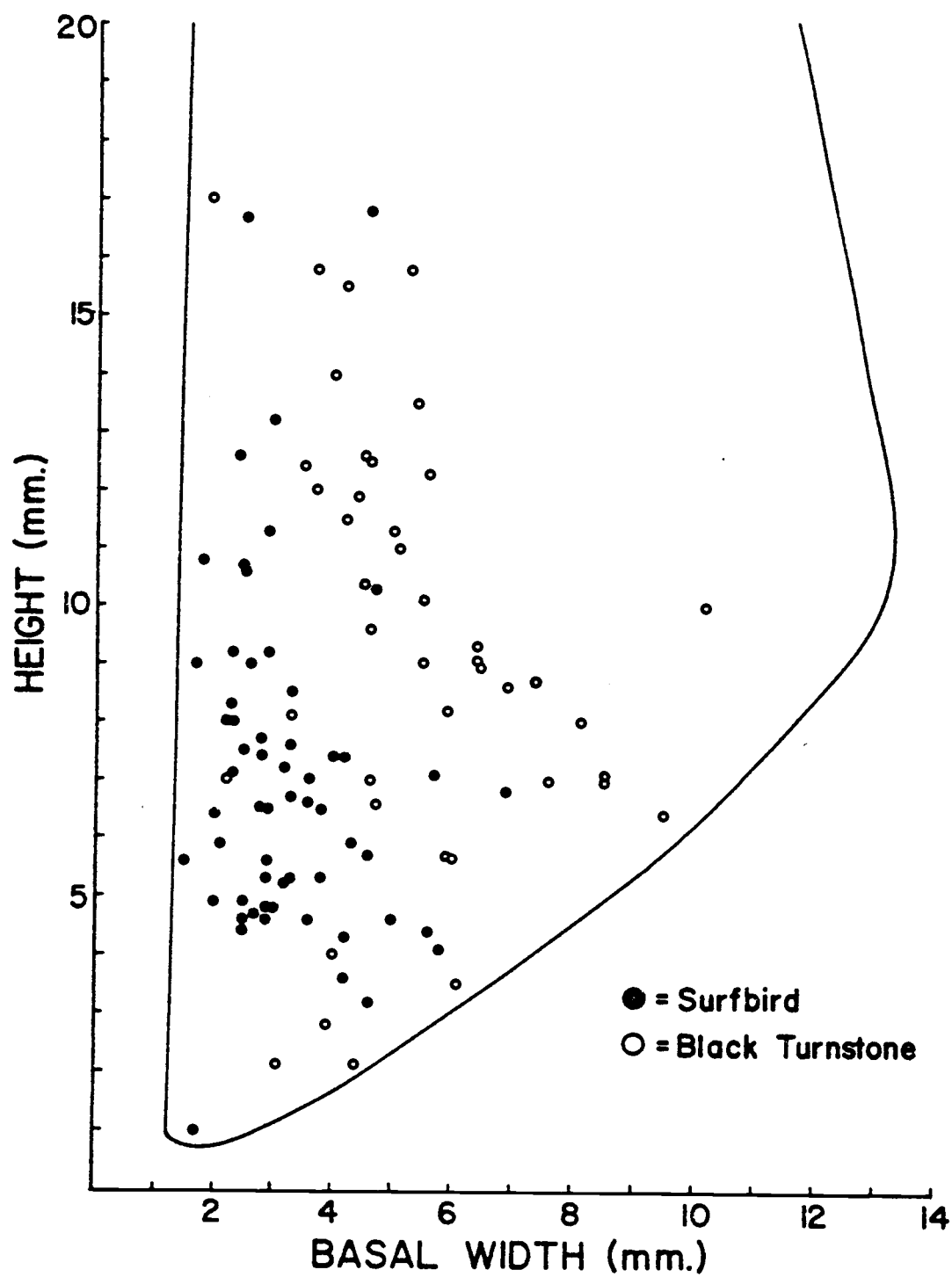


Figure 9. Relative occurrence of 4 foraging behaviors on 5 different substrates. Values represent the percent of 15-second intervals in which a behavior occurred. More than one behavior can occur during one bout. Vertical lines represent \pm S.D. based on data from three observers. The number above each bar-gram pair represents the number of observers for whom an interspecific difference in the proportion of bouts having that behavior was statistically significant.

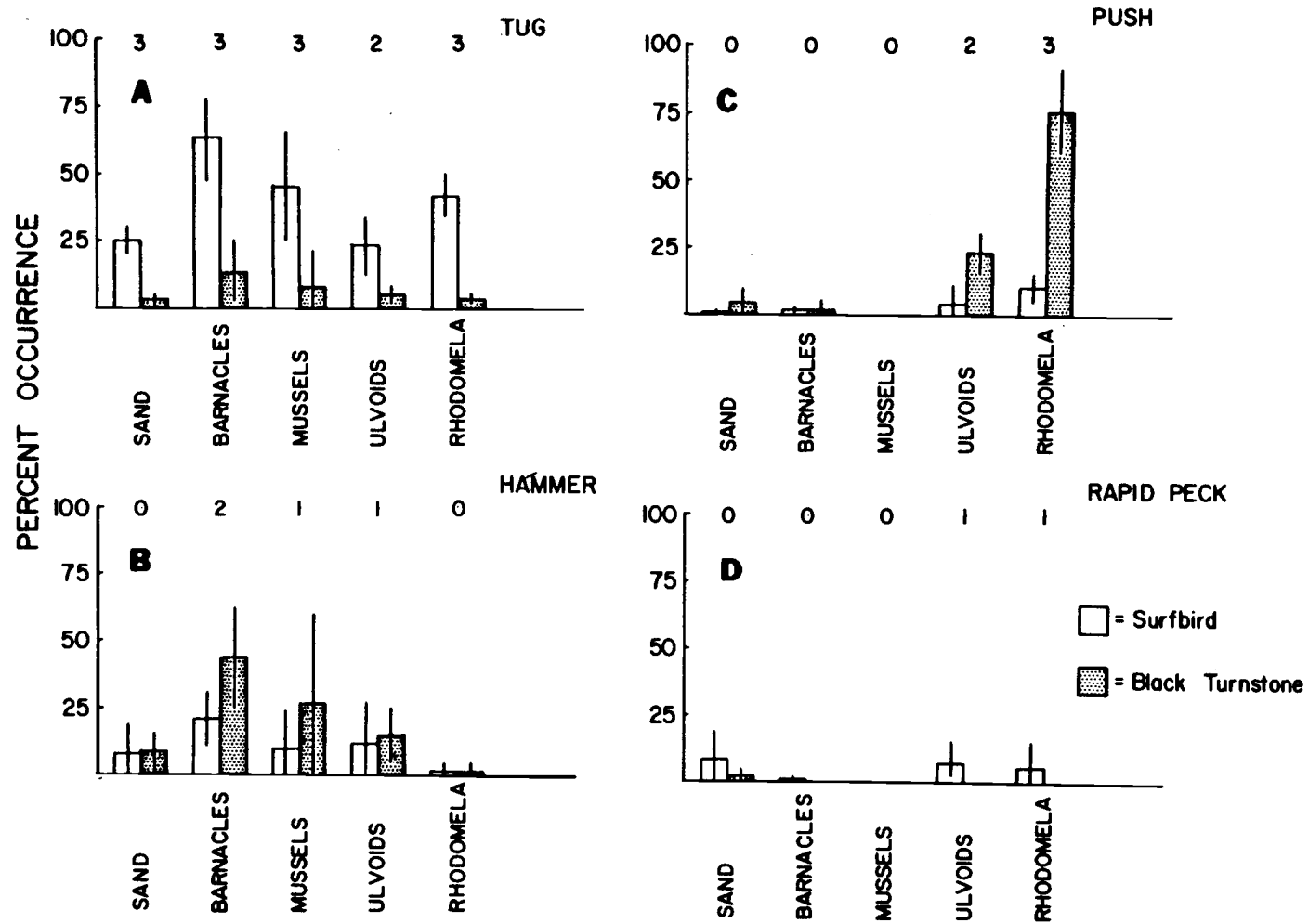


Figure 9.

Figure 10. Continuum of attached prey body shapes. A = chiton;
B = Collisella; C = B. glandula (short, wide morph);
D = Nucella (Thais) emarginata; E = B. glandula (tall,
columnar morph); F = Pollicipes polymerus; G = Mytilus.

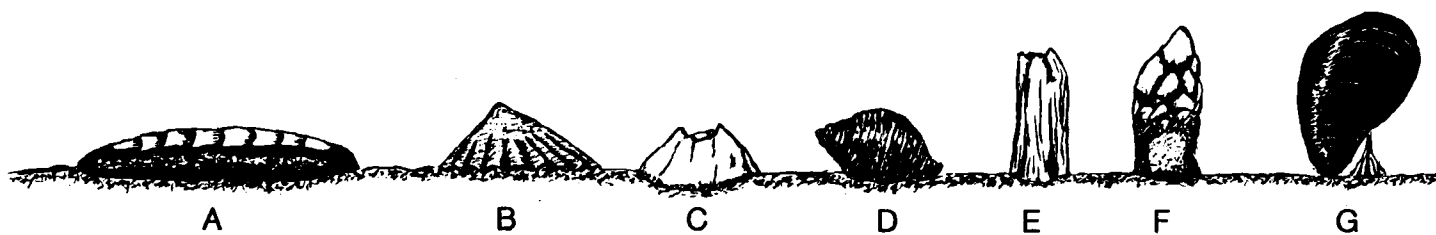


Figure 10.

Chapter III.

ROCKY INTERTIDAL COMMUNITY ORGANIZATION: THE IMPACT OF
AVIAN PREDATORS ON MUSSEL (MYTILUS SPP.) RECRUITMENT

ABSTRACT

In the Pacific Northwest, several shorebird species commonly feed on small mussels, Mytilus spp. Mussels are major prey items of Surfbirds (Aphriza virgata), gulls (Larus glaucescens and L. occidentalis), and Black Oystercatchers (Haematopus bachmani). The impact of such predation is potentially great, as mussels are the competitively dominant mid-intertidal space-occupiers in this community.

Bird exclusion cages tested the effect of these predators on rates of mussel recolonization in patches (50 x 50 cm clearings). Four of six exclosure experiments showed that birds had a significant effect on mussel recruitment. These experiments suggest that the impact of avian predators depends on substrate heterogeneity, mussel size and density, and the other types of mortality agents present. Highest mussel recruitment occurred in an experiment where invertebrate predators were naturally absent, and the substrate was fairly smooth. Exclosure effects on densities of larger mussels (11-30 mm in length) were more consistent than on smaller mussels (≤ 10 mm in length). A positive exclosure effect for smaller mussels was most often observed when densities were between 60 and 130 mussels/300 cm². Bird predation may have been insignificant above and below some thresholds.

In summary, birds have the greatest effect on density of recruiting mussels in patches with low spatial heterogeneity and few invertebrate predators; and hence, birds should be considered a significant mortality agent of recruiting mussels.

INTRODUCTION

The impact of bird predation on the density and distribution of invertebrate prey has long been of ecological interest. Most studies focused on whether birds decrease densities of forest insect pests (see Otvos 1979 for review), but recently the role of avian predators in marine communities has received increasing attention (O'Connor and Brown 1977, Schneider 1978, Quammen 1981, Evans et al. 1979, Zwarts and Drent 1981, Frank 1982). To date, however, only a few marine studies have examined the effect of avian predators in rocky intertidal communities (Feare 1967, Hartwick 1981, Frank 1982). In contrast, numerous studies on rocky shores have demonstrated that invertebrate predators can dramatically reduce the distribution and densities of other invertebrates (Paine 1966, 1974, Connell 1970, Menge 1976, 1978a, b).

Two main reasons may account for the lack of bird predation studies in rocky intertidal communities. First, most of the information about the role of invertebrate predators has been gained through the use of exclosures or by experimentally removing the predator. Application of similar techniques to avian studies is more difficult, requiring semi-permeable exclosures that exclude only birds. Second, to many, birds seem unimportant because birds usually occur at lower densities than invertebrate predators and some birds forage seasonally on rocky shores. Density, however, may be a poor indicator of predator intensity because birds have higher individual feeding rates than do invertebrates.

I studied the impact of avian predators on recruitment of mussels (Mytilus spp.) in an Oregon rocky intertidal community by using devices that excluded birds but not other molluscivores. I focused on mussels because 1) they are a major prey item of the birds, and 2) they are competitively dominant space-occupiers in the mid-intertidal zone in Washington and presumably throughout much of its range (Baja California to Alaska; Paine 1966, 1974). The dominance of midzone space by mussels is broken by storms or log battering, which form clearings in mussel beds (Dayton 1971, Paine and Levin 1981). Other sessile organisms invade these patches and coexist with Mytilus until the patch is closed by lateral movement or by recruitment (Paine and Levin 1981). Hence, by retarding mussel recruitment in patches, predators of Mytilus may delay local extinctions and contribute to persistence of subordinate competitors.

In this paper I first compare the patterns of usage of the study sites by the common mussel predators. Second, I present the experimental design of exclosures used to test the effects of avian predators and discuss its effectiveness. Third, I discuss the results of the six exclosure experiments. Finally, I consider how avian predators may affect the distribution of mussels on rocky shores.

Site Description.

Exclosure experiments were conducted at three sites on the outer Oregon coast: Boiler Bay (44°, 50.0'N), Yaquina Head (44°, 40.5'N), and Seal Rock (44°, 29.8'N). All three sites are partially protected, but

they still receive direct wave action during storms. The average tidal fluctuation is approximately 2.5 m with a semi-diurnal tidal cycle.

The slope, aspect, and type of substrate differed among the three sites (Table 3). The experiments at Boiler Bay (#4, #5, and #6) were located within the 3-5 m wide mussel bed in a semi-protected cove on a gently sloping mudstone substrate. Experiment #4 was located on harder mudstone than were Experiments #5 and #6.

The two experiments on the south side of Yaquina Head were on a horizontal bench of weathered basalt that is approximately 3 m wide. This site was often inaccessible during the fall and winter because it received direct waves from winter storms coming from the southwest.

The experiment at Seal Rock (#2) was located on the landward side of a large rock located 15 m offshore. The substrate was unweathered basalt with a highly irregular relief. Surface texture, however, was relatively smooth. The substrate was steep (approximately 30°-60° slope), but I observed birds traversing it with little difficulty. A general description of the Seal Rock area is given in Marsh (1984).

METHODS

The Experimental Design

The basic experimental design consisted of three treatments: a semi-permeable enclosure that excluded birds but not other mussel predators, a cage control, and an uncaged control. A set of the three treatments positioned near one another is referred to as a replicate. The two types of controls tested the effects of cage structure on settlement and survivorship of larval mussels. Birds were considered to have reduced mussel abundance if densities were greater in enclosures than in corresponding controls of the same replicate.

Two enclosure designs were employed. The most versatile design was used in five of six experiments (#2-#6): a dome-shaped frame enclosing an area of 2500 cm^2 was made of stainless steel bar ($1/4$ " in diameter) covered with polyethylene tubing (see Figure 11). Monofilament line (40 lb. test) spaced at 2 cm (sides) or 5 cm (top) intervals was sewn through the tubing of the eight arms of the cage. Cage controls were similar to enclosures but lacked the monofilament. The central 900 cm^2 was sampled. (Detailed instructions of enclosure construction will be supplied by the author upon request.) Cages were attached by drilling holes in the rock using a hammering drill powered by a portable electric generator (Honda Model 350). When attached to moderately hard rock, these cages withstood direct exposure to waves generated by 20-foot long ocean swells.

A different design was used in Experiment #1. Enclosures consisted of an angle-iron frame 30 x 50 cm x 15 cm tall. The lower crossbars at the narrow end were raised 6 cm to allow potential invertebrate predators access into the cage. Monofilament was strung at 2 cm intervals across the top and sides of enclosures, but not cage controls. This experiment also included a fourth treatment that was similar to the enclosure except for the monofilament on the top being spaced 15 cm apart to allow larger birds (gulls) to reach through the top of the cage. The presence of monofilament on the top was expected to discourage smaller birds from entering the cage.

All plots were originally covered with adult M. californianus beds that were one mussel deep. All Mytilus and other upright sessile organisms (Balanus spp. and Anthopleura spp.) were scraped from the plots, but no attempt was made to remove remaining byssal threads or barnacle scars. This procedure presumably mimicked the natural process of mussel removal. Clearings were made large enough to provide a 10 cm border around the census plot to reduce possible edge effects (see Suchanek 1978). Plots with the frame enclosures were slightly smaller than those with dome enclosures; the central area sampled was 800 cm² and the entire clearing was 2400 cm². Clearings for all except Experiments #3 and #6 were made in late February or early March when natural clearings commonly were created by winter storms. (Experiments #3 and #6 were initiated in early June and early May, respectively.)

The surface relief of the six experiments varied from smooth to highly irregular (see Table 3). Plots selected for experiments #1, #2, and #4 were relatively level and were without large crevices. In

Experiment #3 (at Seal Rock) the substrate was highly irregular with small water-filled recesses.

Experiment #6 had the smoothest substrate, and was in an area without mussel beds (but it was at a tidal level similar to the other experiments). Treatments were initiated in early May when the center 900 cm² of all plots were scraped with a putty knife.

Experiment #5 was specifically designed to test for interactions among substrate heterogeneity, Mytilus settlement patterns, and the effects of avian predators. I used non-toxic epoxy putty (Sea Goin' Pox Putty®) as the artificial substrate. One half of each artificial substrate plot (hereafter referred to as the "even substrate") was made smooth and then lightly tapped with a wire brush to simulate texturing similar to the mudstone surface of Experiment #4. The surface of the other half of each artificial substrate plot was made irregular with approximately a 5 cm difference between the depressions and raised areas. This irregular side was not textured with a wire brush and was meant to mimic conditions of unweathered basalt with moderate heterogeneity.

I measured both density and size distribution of mussels in each plot, except for Experiment #2 where I measured percent cover of mussels. In this experiment many mussels were not readily visible and thus could not be counted, because they were in crevices 5 to 15 cm underwater. In Experiments #1-#4 I censused mussel densities in 12 randomly chosen 25 cm² subsamples; in Experiments #5 and #6 I censused all of the plot because mussel densities were lower. I used the following size classes (as determined by length) to quantify the size

distribution of mussels: 2-5 mm, 6-10 mm, 11-20 mm, 21-30 mm, and >30 mm. I refer to Mytilus 2-10 mm as small mussels, and Mytilus >10 mm as large mussels. Almost all mussels in this study were in the first three size classes, and thus, with few exceptions, all large mussels were still <30 mm in length.

To be effective the enclosure had to exclude birds but allow easy access to all other important predators of mussels. Other molluscivores include seastars (Pisaster ochraceus and Leptasterias hexactis; Menge 1972), neogastropods (Nucella emarginata and N. canaliculata; Harger 1970), and fish (Rhacochilus vacca; Brett 1979). I observed that invertebrate predators easily moved in and out of enclosures, but the importance of fish at the study sites was not known at the onset of the study. Consequently, at high tide on 20 August 1980, 10 passes over the intertidal zone near Experiment #4 were made with a 14 m beach seine. Except for birds and fish, all other molluscivores could fit between the strands of the enclosures.

Enclosure artifacts were studied in two ways. First, cage controls tested the effects of the presence of a structure. This included observing if birds responded in a similar fashion to the uncaged and cage controls. Second, I correlated levels of mussel density with percent of algal cover in the plot because I observed that in three experiments the monofilament of the enclosures appeared to capture more drift algae than the frame of the cage control. The drift algae were only present during the month of August, but they could have caused an artificial caging effect by seeding enclosures with more algal spores/gametes than other plots. Other studies suggest that mussels

preferentially settle in certain algae (Dayton 1971, Paine 1974, Bayne 1976). Consequently, densities of larval mussels should be correlated with abundance of algae if this caging artifact occurred.

Statistical Analysis of Exclosure Experiments

Two methods of analysis were used to determine how birds affected Mytilus recruitment. These methods analyzed 1) densities at the conclusion of an experiment, and 2) the highest density reached in each plot. Parametric tests were not appropriate because variances of the replicates were not homogeneous even after transformations. Consequently, I used a nonparametric permutation test to examine the significance of observed treatment differences (Sokal and Rohlf 1969), and all tests were based on within-replicate comparisons. I calculated the probability that the number of exclosures observed having densities higher than their controls was due to chance alone. The null hypothesis assumes that the probability of the exclosure having the highest density is equal to $1/3$, given that there are two controls and one exclosure per replicate, and all plots have an equal chance of having the highest density. In three replicates of Experiment #1 the probability of an exclosure having the highest density was $1/2$, because these replicates had two types of both exclosures and controls.

The method of calculation differed between the two types of comparisons (final density versus highest density) with respect to their being subject to either a priori or a posteriori tests. I treated the comparisons of final densities as a priori, because I included this

comparison in the initial experimental design. Results of each experiment were tested separately, and all replicates in the experiment were treated as independent trials. For example, in an experiment with four replicates the probability that the highest density plot in all four replicates was an enclosure is $(1/3)^4$ or 0.012.

I treated the comparison of highest densities as a posteriori because I decided upon this comparison after examining the results. In this case, one third of the highest density plots are expected to be enclosures by chance alone. Therefore, the probability for the previous example would be $3 \times (1/3)^4$ or 0.037. When final densities and highest densities occurred on the same date, I treated the analysis as a priori.

Experiment #6 had too few replicates (three) for this method of analysis. Consequently, I used a Wilcoxon's Two Sample Rank Test to test if the three enclosure densities were significantly higher than the six control densities. Thus, I made no distinction between cage controls and uncaged controls, and between a priori and a posteriori tests.

Analysis of Density-related Responses

There was evidence that the density of mussels settling in the plots affected the outcome of an enclosure experiment. I examined this pattern by comparing the highest mussel densities that occurred in enclosures with those that occurred in controls. I analyzed enclosure experiments that represented similar microhabitats together. Consequently, I analyzed the enclosure experiments from Yaquina Head and

Boiler Bay separately, because the two sites differed with respect to patch availability (exposure time) and bird-use (see Results and Discussion). The experiment at Seal Rock was not used because percent cover, not density, of mussels was the abundance estimate.

The Boiler Bay analysis included Experiments #4 and #5, but not Experiment #6, because the former two experiments were set up in mussel beds had a moderately even substrate and were dominated by barnacles, but the latter was on a very even substrate with sparse barnacle cover. Presumably, it was easier for a bird to locate mussels in plots of the latter experiment.

I divided mussels into two size classes for this analysis: 2-10 mm and > 10 mm in length (few of the latter exceeded 30 mm). This choice of size classes was made because mussels \leq 10 mm appear to have different avian predators than have larger mussels (see Table 4).

Comparisons are based on the cumulative percent distribution of exclosure densities versus control densities. In other words, the data are expressed as the percent of plots of a treatment (exclosure or control) that had a density equal to or less than a given value.

Patterns of Habitat Use by Predators

I established permanent quadrats at Yaquina Head (17.5 m^2) and at Boiler Bay (20 m^2) to determine the relative frequency with which birds foraged in the mussel zones at the two sites. M. californianus occupied > 95% of the space in both quadrats. At each site I also established a second quadrat that extended from the upper edge of the mussel quadrat

to the upper edge of the intertidal zone. I recorded bird use of the high intertidal plot to determine if birds were feeding above the mussel bed when the mussel bed was submerged. The high intertidal quadrat at Yaquina Head was significantly smaller than at Boiler Bay (10m^2 versus 30m^2) because of its steeper slope.

Avian molluscivores at these sites were the Black Oystercatcher (Haematopus bachmani; see also Hartwick 1976), gulls (Western and Glaucous-winged, Larus occidentalis and L. glaucescens, respectively; Marsh and McCoy unpubl. data, . Irons 1982), and Surfbirds (Aphriza virgata, Marsh 1984; see Table 4). Other species of birds reported to prey on mussels, but not observed in the vicinity of the quadrats, are sea ducks (see Cottam 1932, Grosz and Yocum 1972) and crows (Zwarts and Drent 1981).

I measured bird activity on predetermined sampling dates by observing a site continuously for a low tide cycle. Bird activity was quantified by counting the number of actively foraging birds in a quadrat at one-minute intervals. I continued an observation period from the time the high intertidal plot was exposed until it was covered again. In a few cases I did not observe a site for a complete tide cycle because the tide began receding before it was sufficiently light to observe the birds. In all cases, however, observation periods were a minimum of four hours and a maximum of eight hours. Actual exposure times of the mussel bed quadrats could not be accurately determined because of intermittent waves covering the area during the ebb and flow of the tide. Consequently, I based inter-site comparisons on paired samples taken on the same tide (with the help of assistants) or on

subsequent days, and thus, had similar observation times. Data are expressed as number of foraging minutes per 10 m² of intertidal zone per low tide.

RESULTS AND DISCUSSION

PATTERNS OF HABITAT USE BY PREDATORS

Levels of bird use were low when measured for the mussel bed as a whole (Table 5). Patterns of activity appeared to be both temporally and spatially patchy.

Surfbirds were the most common avian molluscivore at both sites, but their occurrence in the quadrats was sporadic. For example, 85 percent of the Surfbird activity at Boiler Bay occurred only on one of twelve observation days. Similarly, 84 percent of their activity at Yaquina Head occurred on two of eight observation days. Other observations suggest that Surfbird foraging was localized within a quadrat as well. For example, one Surfbird fed for 10 minutes on small Mytilus in an area of approximately 250 cm². This is equivalent to 4,000 bird-minutes/10m² per tide cycle if extrapolated to the quadrat as a whole. Although the contagious nature of these data makes between-site comparisons tentative, Surfbird foraging activity seemed greater at Yaquina Head than Boiler Bay, both in terms of total time of activity and number of days Surfbirds were present.

Oystercatchers and gulls foraged infrequently and for only short periods in the mussel bed quadrats, despite their continual presence in the area (Table 5). At all three sites oystercatcher pairs were territorial year-around (C. Marsh, personal observation) rather than occurring in flocks as noted at other sites (Hartwick and Blaylock 1979, Frank 1982). Spacing of individuals because of territoriality may, in

part, account for the low usage per unit intertidal area by oystercatchers.

Larger numbers of gulls were observed foraging in the intertidal zone at Yaquina Head than at Boiler Bay. The maximum number of gulls seen feeding simultaneously in the intertidal zone of Boiler Bay was 10, as compared to 180 for Yaquina Head (and the intertidal area at Yaquina Head is smaller). This inter-site difference was reflected in the quadrat-use results. Gulls were observed in the Yaquina Head quadrat on three of the eight observation days, but no gulls were observed in 10 observation days at the Boiler Bay quadrat.

Predator activity was not quantified at Seal Rock, but repeated observations over a 3-year period indicated that almost twice as many Surfbirds wintered there compared to the other two sites. On several occasions large flocks (>50 individuals) of Surfbirds, as well as individual gulls and oystercatchers, were observed foraging in the vicinity of the exclosure experiment.

EFFECTIVENESS OF EXPERIMENTAL DESIGN

The validity of these results depends on the effectiveness of the experimental design. I only examined the effectiveness of the dome exclosure, as I used it in five of the six experiments. The dome apparatus was highly effective in preventing birds from reaching exclosure plots. Among 50+ observations of birds entering experimental plots, only two Black Turnstones (Arenaria melanocephala) were observed to enter exclosures; and in both instances the lower strands of

monofilament had been broken by recent storms. Otherwise birds made no effort to gain entry into an enclosure.

Cage controls were not totally effective because Surfbirds entered cage controls less often than uncaged controls (7 versus 24; $P < 0.05$; Fisher's Exact Test, Sokal and Rohlf 1969). Hence, comparisons of exclosures and cage controls are conservative estimates of bird predation intensity.

Neither differential algal settlement nor fish predation appeared to produce a caging artifact. Algal cover (predominantly Cryptosiphonia sp. and Ulva sp.) was greater in exclosures than in controls of Experiment #4 in September 1980 ($P = 0.04$; a priori Permutation Test), but not in February 1981 when small mussels reached their highest densities ($P = 0.54$, Table 6). Further, in September there was no correlation between the number of small mussels (< 5 mm in length) and algal cover in September ($r = 0.28$, $F = 0.08$; square-root transformation for densities and arcsin transformation for percent cover). In February these two variables were inversely correlated ($r = 0.79$, $F = 21.79^{**}$). Thus, any positive exclosure effect on mussel densities could not be attributed to differential algal abundance because there was no positive relationship between algal abundances and mussel densities. In all other experiments treatments and algal abundance were either not correlated (Experiments #2, #5, or #6) or algal cover was not seen (Experiments #1, and #3).

Seining in the mid-intertidal at high tide provided no evidence that fish large enough to be excluded by the exclosures foraged in the vicinity of the mussel zone at Boiler Bay or Yaquina Head. With few

exceptions, wave surge appeared too strong for benthic feeding in the mid and high intertidal zones of either study site. Calm seas did occur periodically in late summer, but only for a few days at a time. The seining attempt in August 1981 yielded a total of ten sculpin (Clinocottus embryum and C. globiceps), almost all of which were small enough to swim between the monofilament of the exclosures (lengths 23-92.5 mm, body heights excluding dorsal fins = 4.1-24.0 mm). None had molluscan prey in their stomachs. I tentatively conclude that large fish are unimportant mussel predators in mid and high intertidal areas.

RESULTS OF THE EXCLOSURE EXPERIMENTS

The exclosure experiments indicated that 1) birds significantly decreased densities of recruiting mussels in four of six experiments (Table 7), 2) the impact of bird predation varied among experiments and among replicates of an experiment, and 3) in many cases birds prevented mussel densities from reaching high levels but they did not affect final mussel densities.

Several factors were not controlled by the experimental design and may have contributed to the observed among-replicate variability. Temporal and spatial patterns of significant bird effects suggest that intensity of bird predation may be a function of the size and density of mussels, the heterogeneity of the substrate, and the presence of other mortality factors.

Size and Densities of Mussels

Birds decreased densities of both smaller (2-10 mm) and larger (11-30 mm) mussels, but they appeared to have a greater impact on larger mussels. Significant bird effects on small mussels (2-10 mm) occurred in two experiments. In all replicates of Experiment #1 (Yaquina Head), the highest density of 2-5 mm mussels in length occurred in an enclosure (Table 8). (In Experiment #1 no distinction was made in the results of the complete and small-bird frame enclosures because gulls did not visit the area during the experiment.) In Experiment #6 there was a significant enclosure effect for mussels 6-10 mm in length (Figure 12). Highest densities of large mussels (> 10 mm in length) were greater in enclosures than in the corresponding controls of Experiments #2, #4 and #16 (Figs. 13, 14, and 12, respectively). In Experiment #6 the final, as well as the highest, densities were in enclosures (Figure 12).

A greater number of replicates showed a positive enclosure effect for larger mussels than for small mussels (13 out of 17 versus 8 out of 21; $P = 0.02$, Fisher's Exact Test). (Experiment #1 was excluded from the summary of larger mussels, because it did not last long enough for mussels to grow to ≥ 10 mm). Gulls were assumed to be the major avian predator of larger Mytilus as almost all larger mussels were 11-30 mm in length (see Table 4).

Results from Boiler Bay suggest that birds may have responded to smaller mussels (≤ 10 mm in length) in a density-dependent fashion. Enclosures and controls had similar cumulative percent distributions at lower densities (< 60 mussels/300 cm²), but their cumulative percent

distributions diverged at higher densities (Figure 15). Fewer than 10% of the controls had densities greater than 75 mussels/300 cm², but 45% of the exclosures had densities higher than this (Figure 15A). The cumulative percentage of highest densities of larger mussels was also significantly different in exclosures and controls at Boiler Bay ($P < 0.05$, Wilcoxon's Two Sample Rank Test; Figure 15B), but it did not exhibit a density-dependent effect.

Results from the mussel bed experiments at Yaquina Head showed no evidence of a density-dependent effect. When the results of Experiments #1 and #2 were combined, the cumulative percent distributions of smaller mussels in exclosures and controls were not significantly different (Figure 16). The ineffectiveness of birds at Yaquina Head compared to Boiler Bay can not be explained by differences in intensity of bird predation because bird activity at Yaquina Head was \geq that at Boiler Bay. Substrate differences may have had some effect, but the significant exclosure effect in Experiment #1 indicates that substrate alone does not account for between-site differences. A striking difference between Yaquina Head and Boiler Bay experiments is that mussel densities were much higher at Yaquina Head (specifically in Experiment #2). Mussel densities may have been so high that bird predation was not sufficient to have a significant effect.

I hypothesize that birds have a significant effect on densities of smaller mussels only when densities are at intermediate levels. Low density plots may not be considered profitable patches (*sensu* Royama 1970); and consequently, birds did not forage in them. On the other

hand, recruitment rates of smaller mussels into plots (such as Experiment #2) may exceed predation rates by avian predators.

Because of this pattern of density-dependent predation intensity was deduced a posteriori, similar types of experiments should be replicated elsewhere to test the validity of the proposed pattern. Actual densities that are considered "intermediate" will depend on predator density and heterogeneity of the patch. Density-dependent effects on prey similar to that proposed here have been observed in woodpeckers (Picoides spp.; Knight 1958, Koplin 1972) and European Oystercatchers (H. ostralegus; Sutherland 1982).

Substrate Heterogeneity

Results from Experiments #3 and #6 were used to infer how substrate heterogeneity affected the impact of bird predation in a patch. A comparison of Experiment #3 (Table 9) with other experiments suggests that substrate heterogeneity may be important in determining if birds have a significant effect in a patch. The substrate of Experiment #3 (Seal Rock) was more irregular than in the other experiments. Despite high bird densities this experiment had no evidence of exclosure densities being higher than densities of the corresponding controls ($P = 0.44$; a priori Permutation Test). It appeared birds had little opportunity to reduce mussel densities because of the prevalence of microhabitats that were inaccessible to birds (i.e., water-filled crevices), or because many of the recruiting mussels were large

individuals (> 50 mm) that had invaded a plot laterally rather than settling from the plankton.

The attempt to test if moderate changes in substrate heterogeneity altered the intensity of bird predation did not yield conclusive results. Results from the experiment with artificial substrate (Experiment #5, Table 10) did not support this hypothesis. Only on the irregular substrate was there a suggestion that birds decreased mussel densities. In three of four replicates the irregular substrates of exclosures had higher densities of larger mussels (11-30 mm) than did their corresponding controls, but this pattern was not statistically significant (Table 7). In plots with even substrate, densities of larger mussels were very low, regardless of treatment. Because of low densities in this experiment, the degree to which intensity of bird predation changes with moderate increases in heterogeneity is still unclear.

Other Sources of Mussel Mortality

Although results of four of six exclosure experiments suggested that bird predation was a significant source of mussel mortality, other non-avian mortality agents also appeared important. Densities of large mussels decreased in exclosures, as well as controls, in a majority of the replicates that lasted 12 months or longer (10 out of 16 replicates). The seasonality of these decreases (usually in spring or summer) implicated increased activity of invertebrate predators or heat stress as the cause.

In some cases these other mortality factors appeared to act in a compensatory fashion with bird predation. In two of four replicates of Experiment #2 (Figure 13) and in two of five replicates of Experiment #4 (Figure 14), the highest density of larger mussels occurred initially in the enclosure; but subsequently, densities of larger mussels decreased in all treatments until final enclosure densities were not significantly different from those of the corresponding controls. In these replicates bird predation had only a temporary effect because another mortality source ultimately determined mussel densities.

In some cases invertebrate predators appeared to be a major mortality source. Of 135 dead Mytilus collected from experimental plots during late spring and early summer, 84% were drilled by Nucella emarginata. Nucella were regularly observed in many of the plots. The seastars Pisaster ochraceus and Leptasterias hexactis occurred in nearby mussel beds at low densities and may have removed mussels from the plots during high tide, but none were observed in the plots at low tide.

In Experiment #6 (Figure 12) physiological stress appeared to be a major mortality agent. No invertebrate predators were present, but mussel densities still decreased in both enclosures and controls between March and June. (Enclosure densities, however, still remained higher than control densities after this decrease.) The relative importance of physiological stress in the other experiments could not be quantified because small dead mussels that had not been drilled could have been killed by seastars as well as by physiological stress.

IMPACT OF BIRDS ON DISTRIBUTION OF MUSSELS

Other studies have shown that seastars (Paine 1966, 1974, 1980; Lubchenco and Menge 1978), crabs (Kitching et al. 1959, Peterson 1979), and predatory gastropods (Menge 1978a, Paine 1980) can restrict the distribution of mussels from lower intertidal areas. Birds have been recognized as important molluscivores in soft-sediment communities (O'Connor and Brown 1977, Zwarts and Drent 1979, Sutherland 1982; but see Hartwick and Blaylock 1979), but until now their importance on rocky shores has generally been ignored. This study provides evidence that birds reduce densities of juvenile mussels in the mid and upper intertidal zones of an Oregon rocky intertidal community. Bird predation appears to limit the distribution of mussels on flat, high intertidal benches (Experiment #6). However, the ability of birds to increase the time a patch in a mussel bed remains open is unclear.

Characteristics of the clearing and surrounding mussel bed may largely determine the rate of mussel re-establishment in a patch (Paine and Levin 1981). Clearings can be closed by lateral movement of adults at the perimeter of the clearing as well as by recruitment of juveniles. Rates of adult encroachment from the patch periphery are highest in mussel beds that are on a steep incline or are more than one individual deep. The size of a patch is also a primary determinant of the rate of clearing closure. Paine and Levin (1981) noted that only in patches $\geq 3500 \text{ cm}^2$ did larval recruitment of mussels increase the rate of patch recovery. Smaller patches ($100\text{--}3500 \text{ cm}^2$) were closed by peripheral recruitment of the surrounding mussel beds within one to

three years. Thus, only the dynamics of larger patches can be altered significantly by bird predation.

In clearings sufficiently large for mussel recruitment to be important, the relative impact of avian versus invertebrate predators needs to be tested. Microhabitat and mussel density must be recognized as important variables in such a comparison. The relative accessibility of mussels to birds and invertebrates varies spatially on a rocky shore. Mussels escape predation from invertebrate predators by occurring at a tidal height above which they can not feed (Paine 1966, 1974; Menge 1976) or in areas of strong wave action (Kitching et al. 1959, Menge 1978a, Peterson 1979). With these exceptions, invertebrate predators can reach mussels in a variety of microhabitats ranging from vertical walls to tide pools. In contrast, birds can only reach mussels that are regularly exposed at low tide and are outside crevices on relatively even substrate. Thus, only higher intertidal regions with appropriate substrate should experience heavy predation by birds, whereas in lower zones only invertebrates should have a significant impact.

Within microhabitats where both avian and invertebrate predators are common, the relative importance of avian versus invertebrate predators could be either compensatory or additive. The enclosure results indicate that in some cases the effect of bird predation is temporary because invertebrate predators compensate for the impact of birds. The density of mussels may in part determine when the respective predators will have the greatest impact. Invertebrates may be the major predators when mussel densities are low if birds treat such patches as being

unprofitable (*sensu* Royama 1970). In contrast, birds, with their high metabolism and feeding rates, have the potential of being more effective than invertebrates at depressing high mussel densities. In this case the effects of birds and invertebrates would be additive rather than compensatory because birds would be more effective predators at high mussel densities and invertebrates would be more effective predators at low mussel densities.

In summary, bird predation is proposed to contribute to the heterogeneity of the distribution of mussels by retarding establishment of juvenile mussels in certain types of patches. The impact of avian predators in a patch appears to be contingent on a suite of factors: the heterogeneity of the substrate, the size of a clearing, the other types of molluscivores present, as well as the density and recruitment rates of the mussels. Thus, the relative impact of predation by birds varies spatially depending on the permutation of intrinsic and extrinsic factors that characterize a particular patch.

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Table 3. Summary of pertinent information about six enclosure experiments. Also see Methods.

Site	Expt. #	# Replicates	Date	Date	Substrate description		Tidal Ht. (MLLW)
			Initiated	Completed	Type	Relief	
Yaquina Head	1	4	Mar. 1979	Sept. 1979	weathered basalt	even	+1.5 - +1.8 m
	2	4	Feb. 1980	Feb. 1982	weathered basalt	even	+1.7 m
Seal Rock	3	3	June 1979	May 1980	rugged basalt	very irregular	+2.0 m
Boiler Bay	4	5	Feb. 1980	Oct. 1981	hard mudstone	even	+1.4 - +1.7 m
	5	4	Feb. 1981	June 1982	artificial substrate	moderately irr- egular/even	+1.4 m
	6	3	Feb. 1982	June 1982	soft mudstone	very even	+1.4 m

Table 4. Sizes of Mytilus eaten by its common avian predators.

BIRD SPECIES	MUSSEL SPECIES ⁺	SIZE RANGE (N) ⁺⁺	REFERENCE (LOCATION)
Surfbird	cal. & ed.	2-10 mm (104)	Marsh 1984 (Oregon)
gulls (<u>Larus</u> sp.)	cal. & ed.	6-29 mm (19)	Marsh and McCoy, unpublished data (Oregon)
<u>L. glaucescens</u>	ed.	5-40 mm (?)	Irons 1982 (Alaska)
Black oyster- catcher	cal.	20-90 mm (2915)	Hartwick 1976 (B.C.)

⁺(cal. = M. californianus, ed. = M. edulis).

⁺⁺N = no. of mussels measured (no sample size was given by Irons).

Table 5. The relative amount of time mussel predators foraged in mussel beds at Boiler Bay and Yaquina Head on predetermined days. Amount of time expressed as no. bird minutes/10m² per low tide. BBay = Boiler Bay; YHd = Yaquina Head; stm = plots not exposed because of storm; / = plot not censused; * = birds visited high intertidal quadrat, but not mussel bed quadrat; ** = Peregrine Falcon (Falco peregrinus) present at the site.

dates	Surfbird		Gulls		Oystercatcher	
	BBay	YHd	BBay	YHd	BBay	YHd
<u>Late Summer</u>						
5-6 Aug.	0*	74.9	0	0	1.3	0
21-22 Aug.	17.5	23.4	0	0	0	0.6
3-4 Sept.	0	0**	0	0**	0.5	0**
17-18 Sept.	0	0	0	5.7	0	0
<u>Winter</u>						
31 Jan.	0	1.7	0*	30.9	0*	0
1 Feb.	1.0	61.1	0	1.2	0	0
7 Feb.	0	/	0	/	1.0	/
8 Feb.	2.0	0	0	0	0	0
21 Feb.	stm	stm	stm	stm	stm	stm
22 Feb.	0	/	0	/	0	/
<u>Spring</u>						
4 Apr.	0	0	0	0	0	0

Table 6. Algal abundance in Experiment 4 on two sampling dates following the presence of drift algae in Aug. 1980. Sept. 1980 is the first sampling date following the occurrence of the drift algae, and Feb. 1981 is when the highest densities of small Mytilus occurred. * denotes $P < 0.05$ that exclosures had higher algal cover than respective controls by chance alone. N.S. = no significant difference among treatments.

	Replicate Number				
	1	2	3	4	5
<u>Sept. 1980*</u>					
Exclosure	49	26	19	35	29
Cage Control	15	0	32	11	4
Uncaged Control	2	8	32	25	5
<u>Feb. 1981 (N.S.)</u>					
Exclosure	0	16	8	14	22
Cage Control	4	10	34	8	31
Uncaged Control	14	7	22	8	81

Table 7. A summary of statistical analyses (P values) of the experiments. Probabilities ≤ 0.05 are underlined. Experiment 3 is excluded because Mytilus abundance was quantified by percent cover rather than density. (No significant differences were observed in experiment #3). Results are presented in the form "a(b)"; where a = the level of significance for the comparison of final densities, and b = the level of significance for the highest densities (see Methods). In Experiment #1 highest density = final density so only "a" is given. In Experiment 5 "A" represents irregular substrate and "B" represents even substrate. In Experiment 6 only final densities were tested (see Methods).

Experiment	Size Class of <u>Mytilus</u>			
	(1) <5 mm	(2) 5-10 mm	(1+2) ≤ 10 mm	(3) >10 mm
1	<u>0.04</u>	0.13	<u>0.04</u>	<u>>0.2</u>
2	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)	0.10 (<u>0.04</u>)
4	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (0.12)	<u>>0.2</u> (0.12)	<u>0.04</u> (<u>0.01</u>)
5A	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)	0.07 (<u>>0.2</u>)
B	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)	<u>>0.2</u> (<u>>0.2</u>)
6	<u>>0.2</u>	<u><0.05</u>	<u>>0.2</u>	<u><0.05</u>

Table 8. Final mussel densities (no./300 cm²) in Experiment 1 (Sept. 1979). Experiment initiated in Mar. 1979. Exclosure' = small bird exclosure, see Methods. / = treatment absent.

Treatment	Size Classes of <u>Mytilus</u> (mm)											
	Repl. 1			Repl. 2			Repl. 3			Repl. 4		
	<5	5-10	>10	<5	5-10	>10	<5	5-10	>10	<5	5-10	>10
Exclosure	49	2	0	29	58	5	50	13	0	17	10	1
Exclosure'	88	5	0	87	12	5	0	21	0	/	/	/
Cage Control	3	0	0	28	22	8	0	23	0	3	6	3
Uncaged Control	47	5	0	11	1	0	37	6	1	0	0	0

Table 9. Percent cover of M. californianus in Experiment 3 at conclusion of experiment (May 1980). Experiment initiated in June 1979.

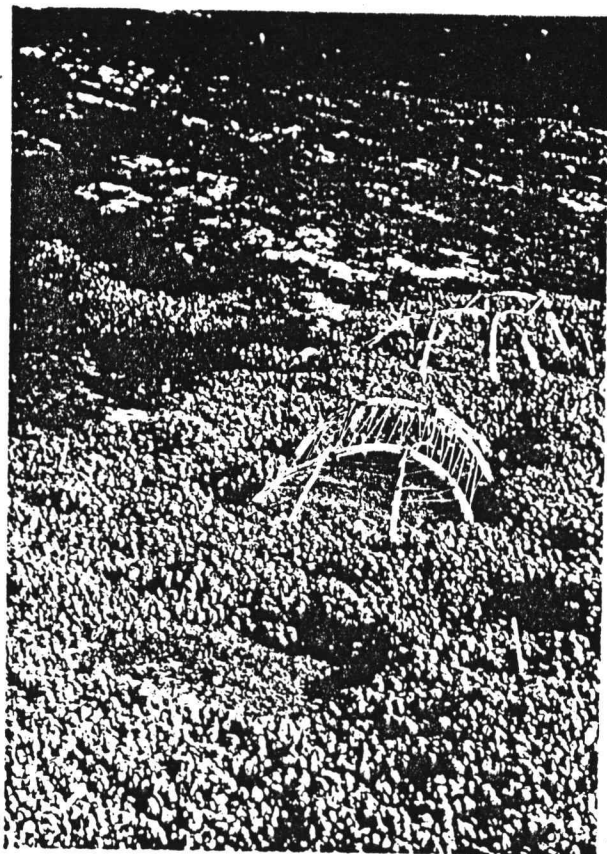
	Percent Cover of <u>M. californianus</u>		
	Repl. 1	Repl. 2	Repl. 3
Exclosure	15	12	5
Cage Control	27	2	2
Uncaged Control	5	22	1

Table 10. Densities of Mytilus in Experiment 5 (Boiler Bay; Feb. 1981-June 1982) on artificial substrate. Results presented as "a/b"; where a = density (no./450 cm²) on irregular side, and b = density on even side. The first set of data (A) represents densities in Feb. 1982, when the highest densities occurred. The second set of data (B) represents the final densities (June 1982) of the experiment.

Treatment	Repl. 1			Repl. 2			Repl. 3			Repl. 4		
	<5	5-10	>10	<5	5-10	>10	<5	5-10	>10	<5	5-10	>10
<u>A.</u>												
Exclosure	46/53	39/10	29/5	52/58	28/9	3/0	35/52	18/19	7/1	29/34	19/18	17/3
Cape Control	23/62	30/17	6/0	24/53	17/19	7/0	72/80	16/6	4/1	64/41	25/9	3/0
Clearing	49/32	22/9	0/0	60/132	29/9	21/2	47/105	20/8	3/0	48/40	16/3	6/2
<u>B.</u>												
Exclosure	14/13	30/10	24/2	25/16	6/15	1/1	14/35	5/4	2/0	14/78	15/12	5/0
Cage Control	6/8	18/12	1/3	11/34	22/39	20/5	47/54	11/5	0/0	79/17	8/0	0/0
Clearing	7/4	13/2	1/0	50/12	34/7	0/0	32/14	3/2	0/0	42/16	1/0	1/0

Figure 11. (A) Experiment 4 (Replicate 2) showing the enclosure (dome design), cage control, and uncaged control, respectively.
(B) Experiment 6 at Boiler Bay prior to the enclosures being strung. Note the absence of an established mussel bed.

A



B

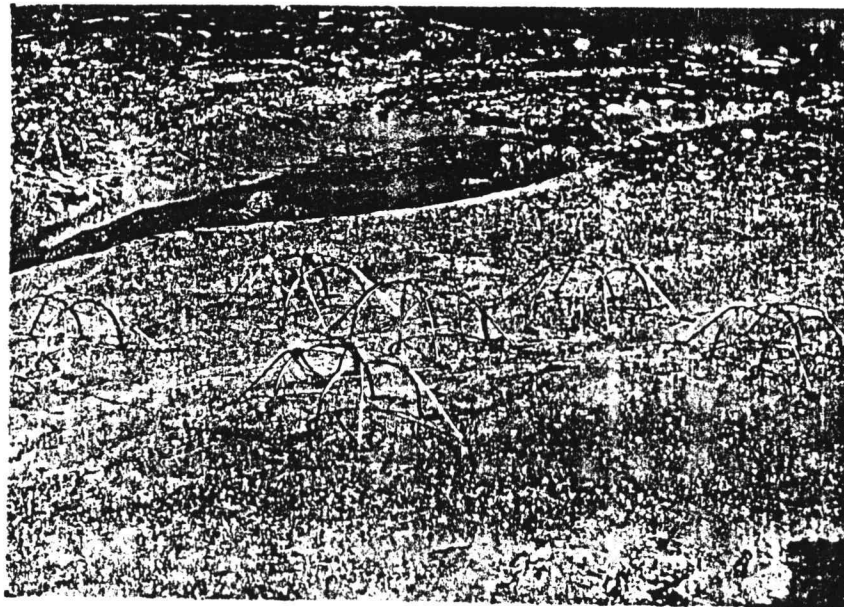


Figure 11.

Figure 12. The results of the three replicates of Experiment 6. Solid line (with triangle) denotes exclosure, dotted lines denote controls (closed circle = cage control, open circle = uncaged control). The density of each plot is denoted with the appropriate treatment symbol, and solid vertical lines connect the 3 replicates of a treatment for each censusing date. Lines between sampling dates connect median densities of the respective treatments. A single symbol for a treatment on a sampling date indicates that all three plots had the same density.

Figure 12.

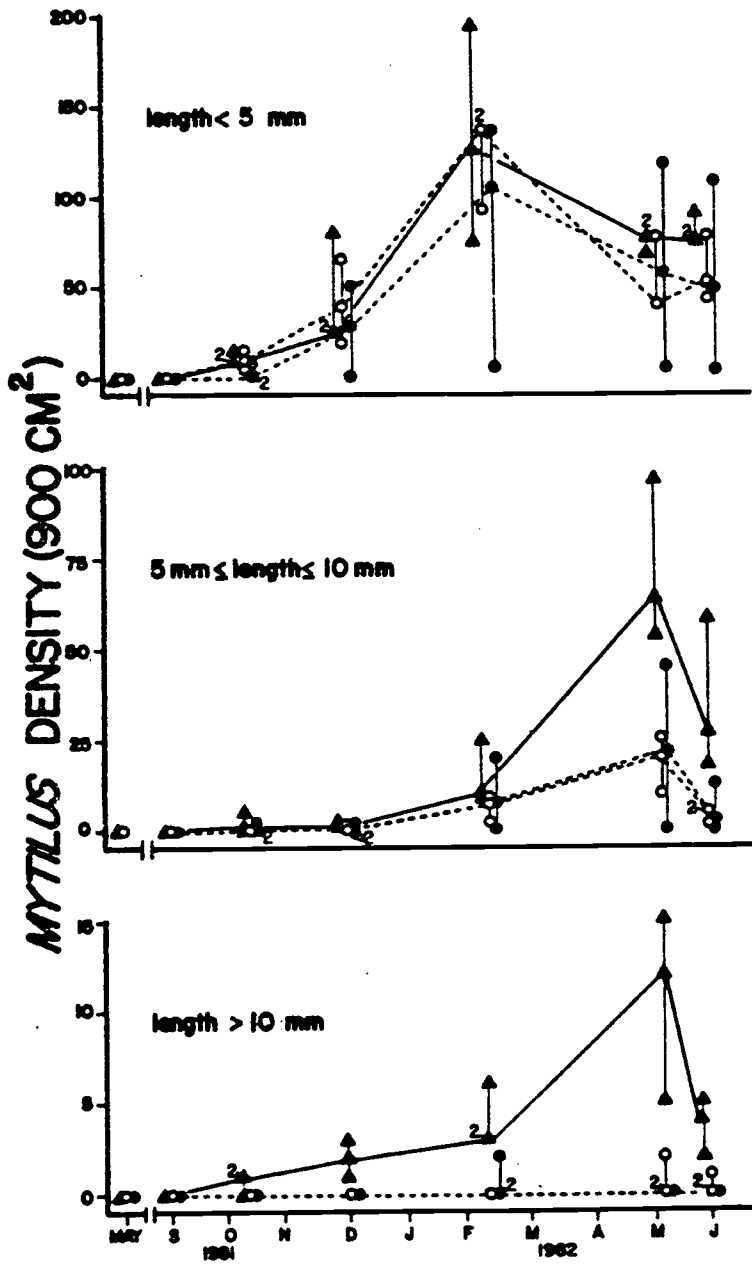


Figure 13. Mussel densities in 4 replicates of Experiment 2 (Yaquina Head). Shaded areas represent the season when Surfbirds are absent and gull activity in the upper intertidal is low. See legend to Fig. 2 for explanation of symbols.

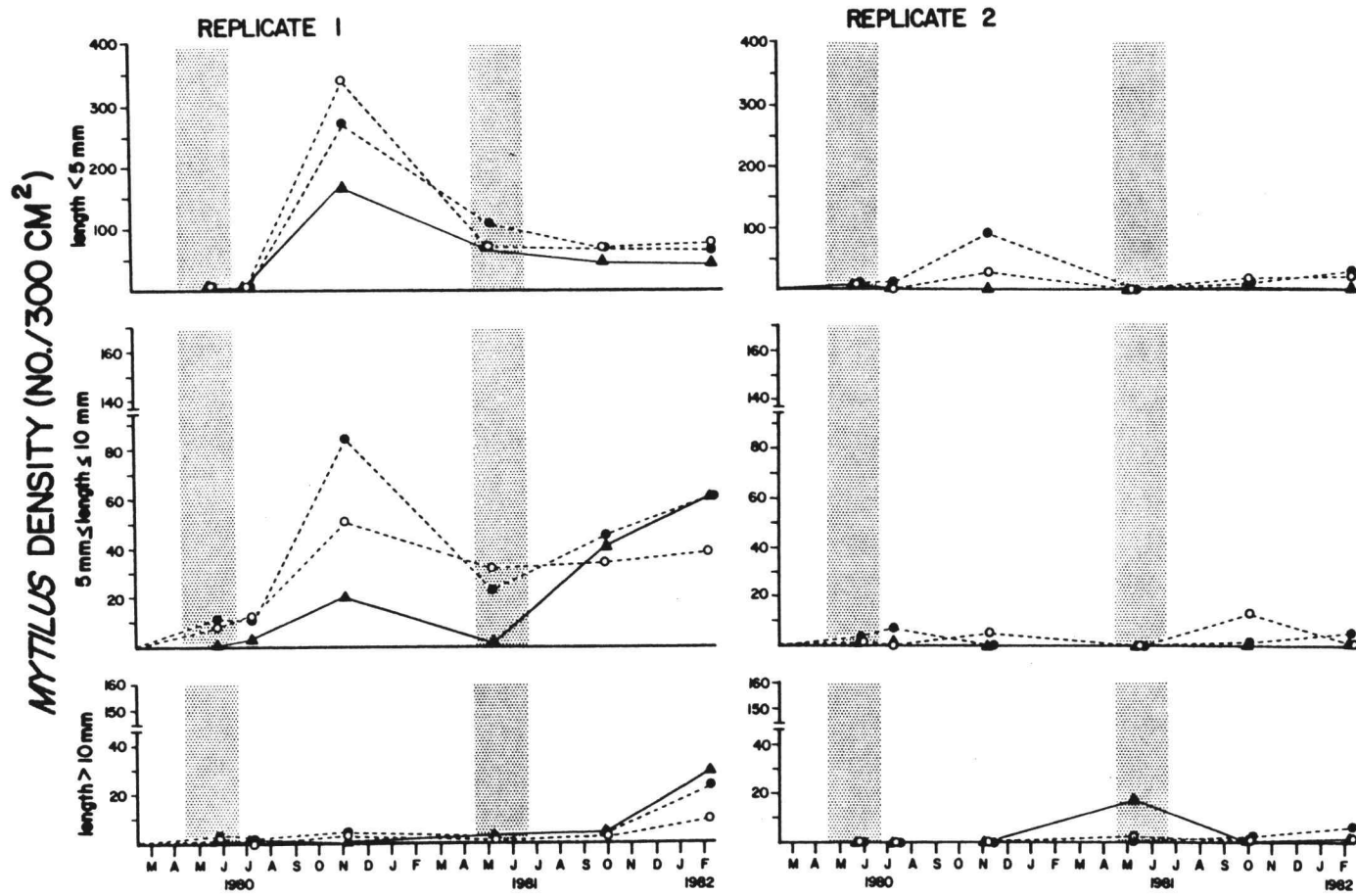


Figure 13. (Part 1)

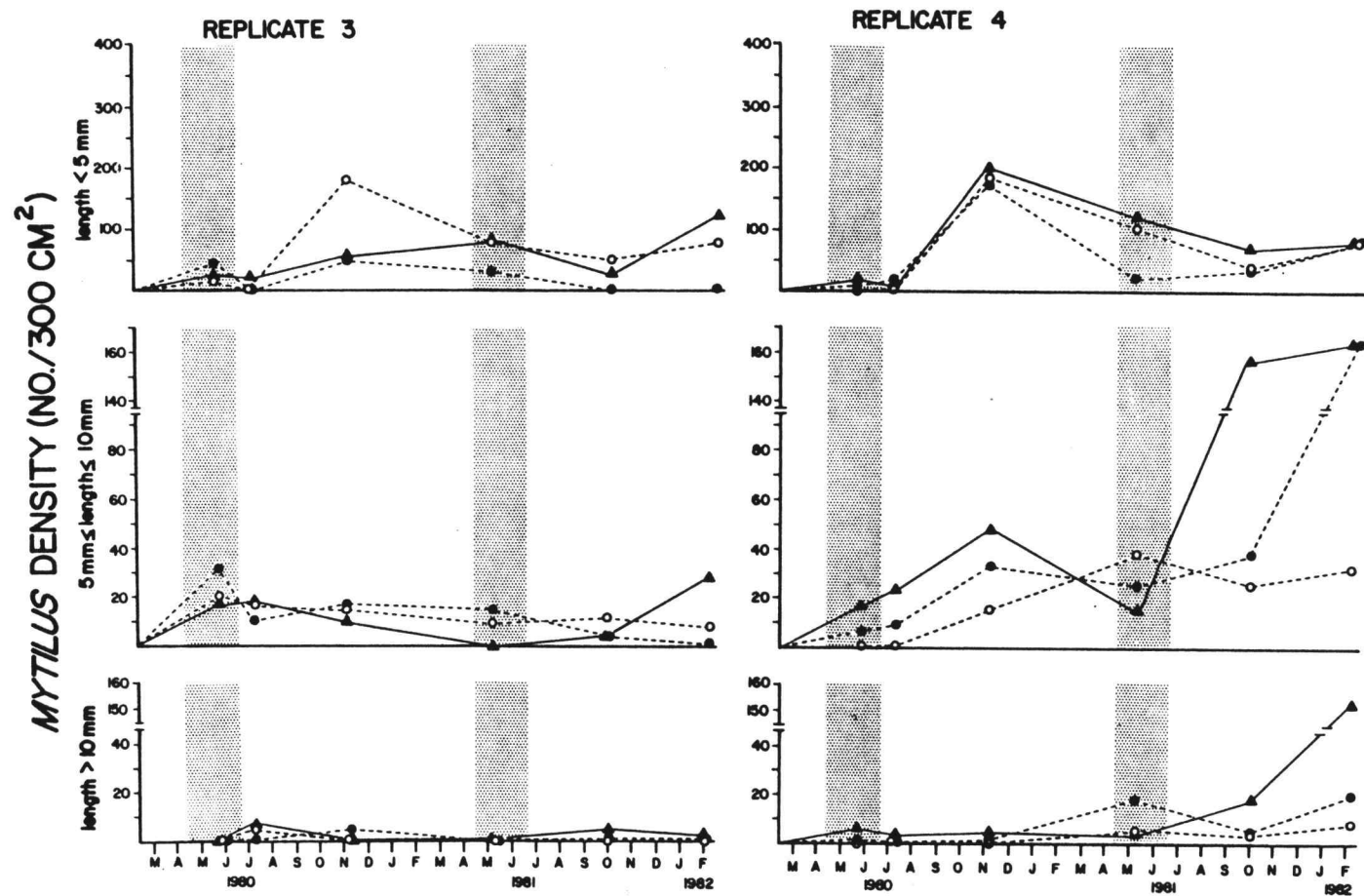


Figure 13. (Part 2)

Figure 14. Mussel densities in 5 replicates of Experiment 4 (Boiler Bay). For explanations of symbols and shading, see legends of Figs. 2 and 3, respectively.

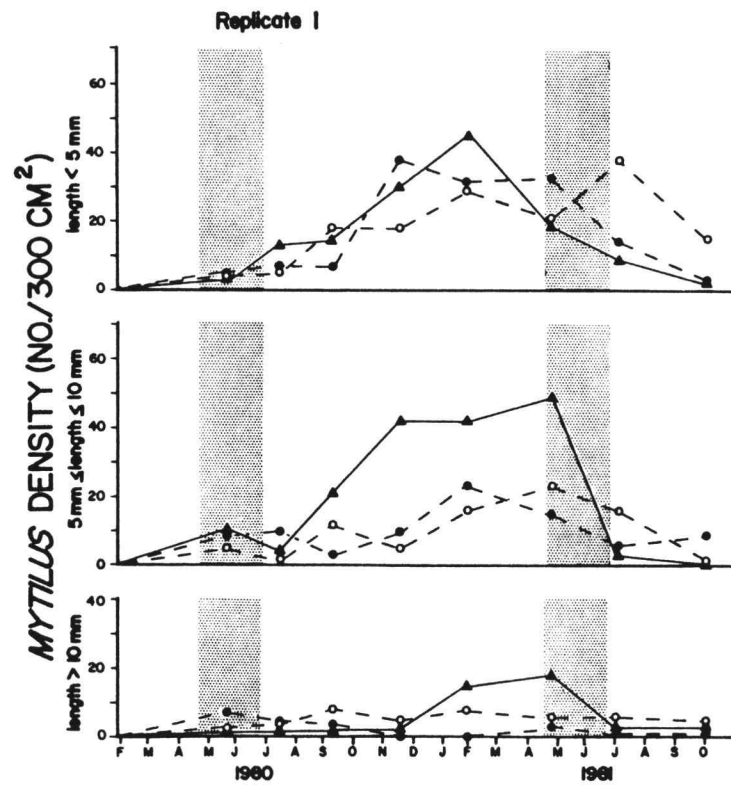


Figure 14. (Part 1)

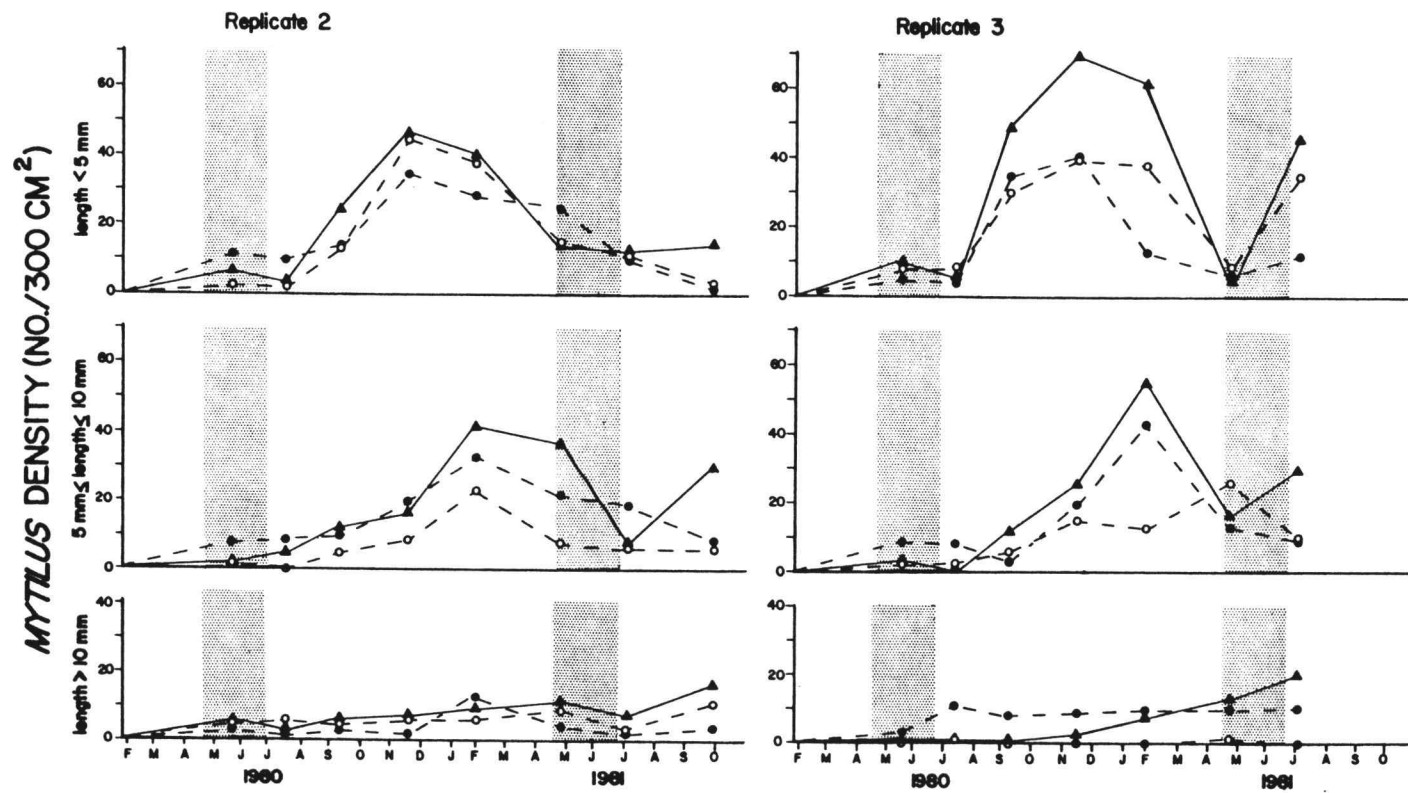


Figure 14. (Part 2)

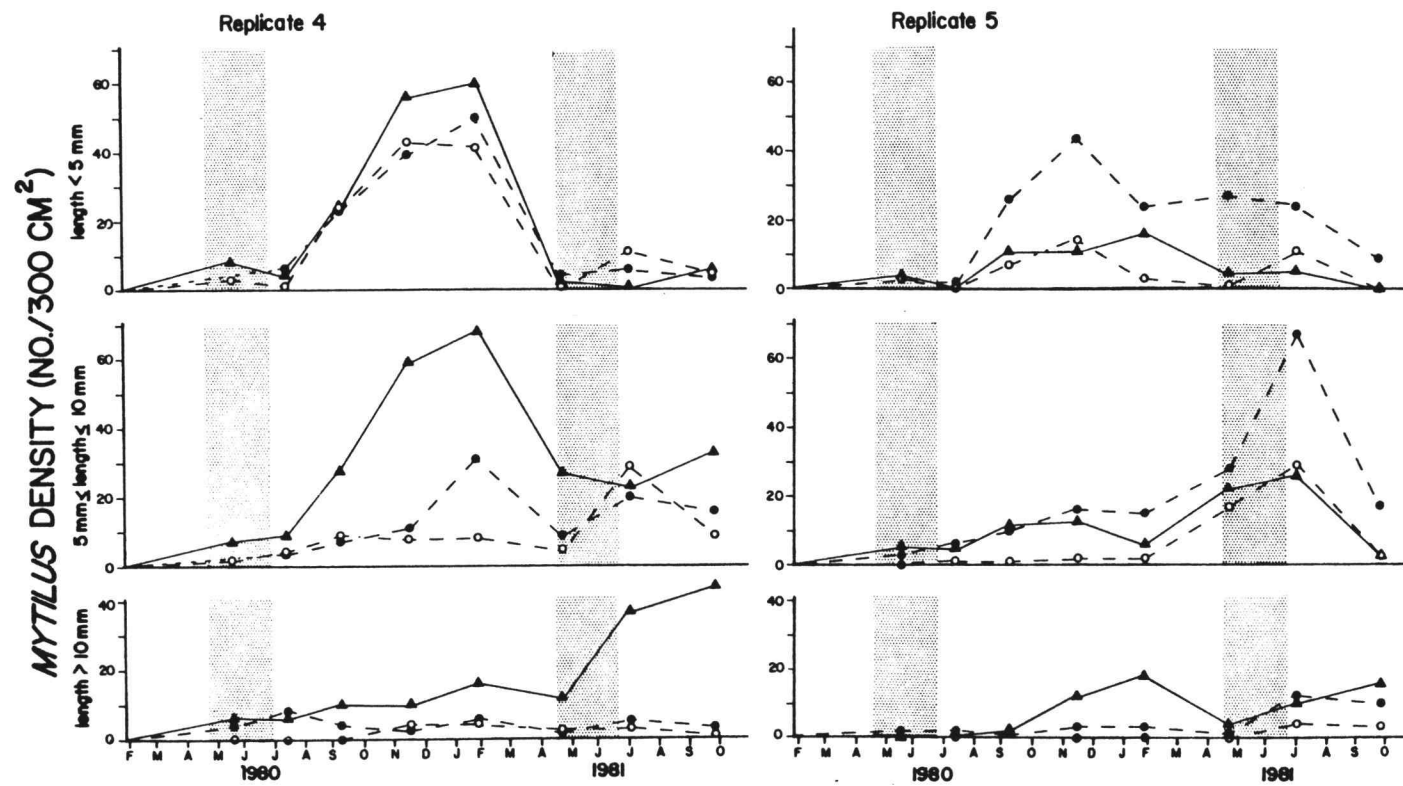


Figure 14. (Part 3)

Figure 15. The cumulative percentage of highest mussel densities in the Boiler Bay mussel bed experiments. The lines indicate the percentage of plots with densities \leq a given value. Highest densities of exclosures and controls are significantly different for both (A) small and (B) larger mussels ($P < 0.05$, Wilcoxon's Two Sample Rank Test).

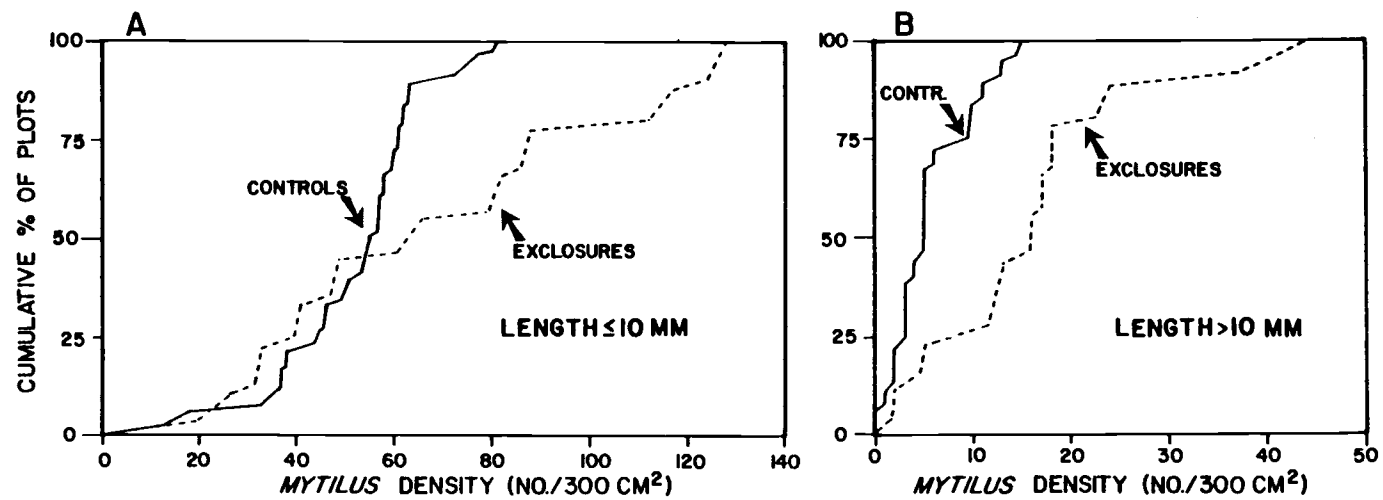


Figure 15.

Figure 16. The cumulative percentage of highest mussel densities in the Yaquina Head mussel bed experiments. See legend of Fig. 5 for explanation. Sample size of replicates with larger mussels is too small for cumulative percentage.

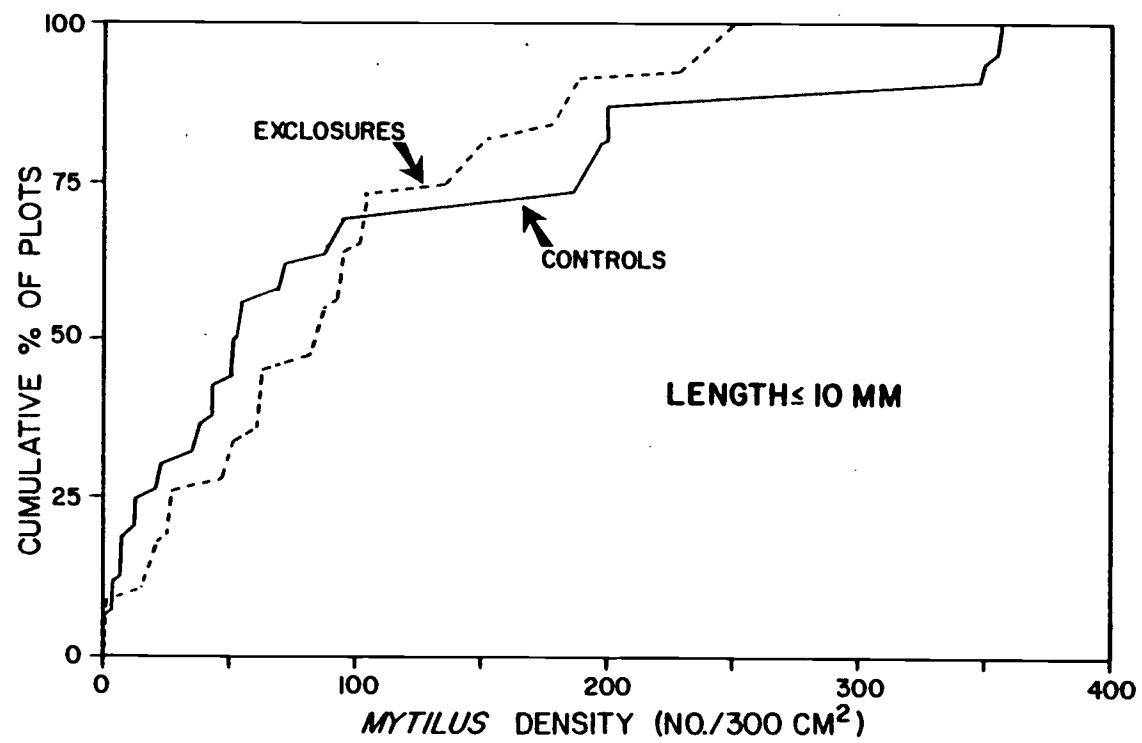


Figure 16.

Chapter IV.

IMPACT OF AVIAN PREDATORS ON HIGH INTERTIDAL LIMPET POPULATIONS

ABSTRACT

A series of exclosure experiments demonstrated that birds decreased densities of limpets (Collisella spp.) 5-10 mm in length, but not densities of smaller sized limpets. Larger limpets (> 10 mm in length) were rare on the flat portions of these upper intertidal mudstone benches. Experiments in which limpets were added to protected and unprotected plots indicated that bird predation varied seasonally; and that emigration, in addition to predation, may be responsible for the general absence of larger limpets in these microhabitats.

INTRODUCTION

Rocky intertidal communities are often characterized by distinct zones or patches of sessile organisms. Several studies have demonstrated that abrupt boundaries between two types of patches may be caused by the activity of consumers (see Carefoot 1977, Connell 1972, and Lubchenco and Gaines 1981 for references). The effect of consumers may be direct, as in the case of herbivores eating algae; or indirect as in the case of a predator significantly reducing the density of the herbivore allowing an increase in algal abundance (e.g. Estes et al. 1978).

Recently, Frank (1982) presented evidence that oystercatchers may alter local community structure by reducing the density and distribution of limpets, the primary herbivore of the upper intertidal region (see Cubit 1974). Other birds, however, also feed on limpets, but until now their impact on limpet densities has not been addressed.

The objective of this study was to determine if birds were responsible for the scarcity of limpets on flat mudstone shelves in the high intertidal zone. Specific goals were to 1) determine the sizes of limpets eaten by the birds known to be limpet predators, and 2) to determine by use of exclosures if limpet densities would increase in plots protected from birds. For much of the year these shelves are characterized by abundant growth of the ephemeral alga, Enteromorpha sp., except near crevices or on vertical slopes where limpets were abundant. Previous studies have shown that high densities of limpets can greatly reduce the amount of algal cover (Cubit 1974). The factors

causing low densities of limpets are less well-understood. Wolcott (1973) found no evidence of physiological stress in the limpets he studied. Based on my observations of foraging activities of shorebird flocks, I postulated that the absence of limpets from the horizontal surfaces was due to predation by birds, specifically oystercatchers (Haematopus bachmani; see Hartwick 1976, 1981, Frank 1982), Black Turnstones (Arenaria melanocephala; see Marsh 1984), and Glaucous-winged and Western Gulls (Larus glaucescens and L. occidentalis, respectively; see Irons 1982, C. Marsh and B. McCoy unpublished data).

METHODS

Study Site

Exclusion experiments, as well as most of the diet study, were conducted in Boiler Bay, Oregon (44°, 50.0'N). Flat mudstone benches characterize the south side of the bay, where the exclusion experiments were located. Tidal fluctuation in the bay is approximately 3 m, and the tidal heights of the exclusion experiments were +1.4 to +2.0 m (MLLW).

All of the limpets discarded by oystercatchers, as well as most of the limpets from gull pellets, were collected along the south side of Boiler Bay near the exclosure experiments. Black Turnstones were collected at another site (Seal Rock; see Marsh 1984) rather than disturbing birds at Boiler Bay while exclosure experiments were being conducted.

Sizes of Limpets eaten by Birds

Oystercatchers and gulls eat limpets from the low, as well as higher, intertidal zones; but in this study I only used measurements of limpets that are characteristic of the high and mid intertidal zones; i.e., Collisella digitalis, C. strigatella, and C. pelta (see Frank 1982). Oystercatchers eat limpets by dislodging them from the substrate with a blow of the bill to the edge of the shell, after which they consume only the soft body. To obtain information about sizes of

limpets selected by oystercatchers, I followed foraging oystercatchers and collected the discarded shells of consumed limpets. During summer 1981 I also collected shells of limpets that oystercatchers brought to a nest located adjacent to Exclosure Experiment #1 (see below). I recorded the sizes of limpets eaten by gulls by measuring the shells that were in regurgitated pellets from gull resting areas. Turnstones swallow small limpets whole, but they consume larger limpets (>10 mm) in a fashion similar to oystercatchers. Therefore, I recorded both the sizes of all limpets found in Black Turnstone stomachs and those left by foraging turnstones (see Marsh 1984).

Exclosure Experiments

I conducted two types of exclosure experiments to examine the effects of birds on flat intertidal benches. The design was the same for both experiments. A replicate consisted of three treatments: a bird exclosure that allowed invertebrates access to the protected plots, a cage control, and an uncaged control. The exclosure is described elsewhere (Marsh 1984), it consists of a wire frame that is strung with monofilament nylon and encloses an area of approximately 2500 cm² (Marsh 1984, see Figure 18). The cage control lacks the monofilament. Birds are considered to have reduced the densities of limpets if densities are greater in the exclosures than in the corresponding controls of the same replicate. The presence of a caging artifact is determined by comparing results from the cage control and uncaged control.

I set up one pair of experiments to determine if densities of limpets would increase in small plots protected from avian predators (hereafter referred to as exclusion experiments). Exclusion Experiment #1 was initiated in October 1980 and concluded in October 1981; Exclusion Experiment #2 was initiated in May 1981 when all barnacles were scraped from each plot and was concluded in June 1982. Both consisted of three replicates of each treatment, and the nine plots were arranged in a 3-by-3 Latin Square design (see Sokal and Rohlf 1969). The two experiments were located at a similar tidal height (+6.5 to +7.5 ft MLLW) on sandstone benches that were approximately 100 m apart. The substrate of Exclusion Experiment #2 was smoother than that of Exclusion Experiment #1.

With one exception the plots were censused once every eight weeks. All limpets in the center 900 cm^2 of the plot were counted and scored in one of four size classes: 1-4 mm in length, 5-10 mm in length, 11-20 mm in length, and >20 mm in length. Parametric statistical tests were inappropriate because of a lack of homogeneity of variances among the plot densities. The number of replicates, however, was also too low for nonparametric tests. Therefore, no statistical analysis was deemed appropriate for these experiments.

A second pair of experiments consisted of adding limpets 5-10 mm long to plots with one of the three treatments. These addition experiments were located on a flat, relatively smooth area of the sandstone bench where Exclusion Experiment #2 was located. This area of the shelf had few limpets, almost of which were <5 mm in length. In each plot I carved three 15 cm long grooves, approximately 1 cm deep,

that were 5 cm apart and were perpendicular to the direction of the incoming waves. Ten limpets 5-10 mm in length were added to each groove (yielding 30 limpets per plot) just before the area was inundated by high tide. Densities of limpets were censused immediately after the tide had receded, and the number of limpets remaining was used as the initial density for that plot. Rates of disappearance of the limpets were then followed over time. At the end of the first week and at the conclusion of the experiment, the numbers of limpets remaining in exclosures versus controls were compared using a Wilcoxon's Two Sample Test (Snedecor and Cochran 1980).

RESULTS AND DISCUSSION

Limpets of almost all sizes were eaten by at least one species of bird (Figure 17). Oystercatchers concentrated on larger limpets (9-37 mm), whereas Black Turnstones ate only small limpets (1-14 mm). A large size range of limpet shells appeared in gull pellets. Most smaller shells (≤ 5 mm) co-occurred with shells of the gooseneck barnacle, Pollicipes polymerus, suggesting that the limpets were consumed while the gulls were eating the barnacles. Some gull pellets consisted almost exclusively of C. digitalis (Marsh and McCoy, unpublished data). This implies that gulls either specialized on limpets for short periods of time, or they fed mainly on aggregations of limpets. The clumped distribution of C. digitalis is consistent with the latter explanation, but does not negate the first possibility.

The exclusion experiments revealed that birds affected limpet densities by preventing limpets from reaching a high density in a patch. In each row of the Exclusion Experiments #1 and #2 peak densities of larger limpets (5-10 mm in length) occurred in exclosures rather than in controls (Figures 18 and 19). At less than peak densities, controls often had more limpets than did the exclosures. Birds did not appear to have any effect on densities of smaller limpets (<5 mm in length). Limpets >10 mm rarely occurred in plots of either Experiment #1 or #2, and are not considered further.

Only in row #3 of Exclusion Experiment #1 did the highest control density exceed the highest density of the corresponding exclosure. The density of larger limpets in the uncaged control of Row #3 increased

dramatically during the early summer (May-July) when Black Turnstones were absent, but decreased again in September (two months after Black Turnstones had returned to Boiler Bay) until it was again less than that of the corresponding enclosure.

Although peak densities of larger limpets (5-10 mm) were higher in the three enclosures than in the six controls in Exclusion Experiment #2, they were consistently higher only in Row 3. At lower densities controls sometimes had higher densities than did the enclosures. In general, limpet densities were lower in Experiment #2 than in Experiment #1. In Experiment #2 densities of larger limpets never exceeded 6 individuals/900 cm², whereas they ranged from 15 to 82 individuals/900 cm² in Experiment #1. This density difference in the two experiments may in part explain why the enclosure effect was less in Experiment #2 than in Experiment #1. The substrate relief of Experiment #2 was noticeably more even than in Experiment #1, and this may have caused higher rates of emigration or mortality in the former.

The effect of bird predation appeared to be seasonal. In the exclusion experiments the greatest difference between the densities of larger limpets in enclosures and controls occurred in fall and winter when all three avian predators commonly foraged in the mid and upper intertidal zones. During fall and winter the intensity of bird predation in a plot also appeared to vary with time. The limpet addition experiments indicated that birds had a dramatic effect on limpet densities in October (Figure 20, Trial 1; $P < 0.05$, Wilcoxon's Two Sample Rank Test, Snedecor and Cochran 1980) but not in February (Figure 21, Trial 2; $P > 0.05$). Conclusions were the same after the

first week and at the conclusion of the experiment. The difference in the results of the two addition experiments appeared to be due to higher emigration rates and lower predation intensity in February. Control densities after three weeks were significantly higher in February than in October ($P < 0.05$, Wilcoxon's Two Sample Rank Test).

Major avian predators of 5-10 mm limpets appear to be Black Turnstones and gulls. The seasonal differences in the limpet addition experiments are consistent with my observations of Black Turnstone abundances. Flocks of turnstones were common at Boiler Bay through fall 1981 (during Trial 1 of the limpet addition experiment), but were absent during most of February and March 1982 (during Trial 2). They were not common again until the onset of northward migration in April (C. Marsh, personal observation). No apparent fluctuations in gull densities were observed from October to March.

Decreases in the densities of larger limpets in exclosures revealed that factors other than bird predation also influenced limpet densities on flat mudstone intertidal areas in Boiler Bay. Emigration was likely a major source of density fluctuations in the exclosures because some limpets > 5 mm do not remain in an area the size of the exclosures for over a month (see Frank 1965). At a study site 178 km south of Boiler Bay, Frank (1965) observed that individuals of Collisella (Acmaea) digitalis on a vertical substrate migrated upshore during the fall and winter, and moved downshore (but to a lesser extent) in the period May-July. Thus, the exclusion experiments of this study represent a conservative measure of the effects of bird predation, because

individual limpets were probably protected for only part of an experiment's duration.

Non-avian mortality factors did not appear to contribute to observed density fluctuations in the experimental plots. The seasonality of the decreases in limpet density indicated that wave action was probably not an important mortality agent. The roughest seas occurred from October to February when limpet densities were highest. Heat and desiccation stress may have caused density decreases observed in some plots during spring and summer, but I did not find any dehydrated limpets as Frank (1965) had.

These experiments indicate that in accessible microhabitats bird predation on small limpets may be seasonally important. Thus, when considered with the results of other studies (Frank 1982, Hartwick 1981), all sizes of limpets with the possible exception of the largest (> 35 mm) individuals are potentially vulnerable to bird predation. Relative predation intensity appears to be most intense for the moderate-sized individuals (5-30 mm in length). The results of the limpet addition experiments suggest that larger limpets may emigrate from or actively avoid microhabitats where the probability of bird predation is great. Thus, a major outcome of bird predation may be the expression of avoidance behaviors by limpets. This, in turn, restricts the types of microhabitats used by limpets. Such a proposal is difficult to test, however, because these microhabitats are often the same areas where the chance of desiccation or heat stress is also great.

In summary, this study provides evidence that bird predation must be considered a significant mortality factor of limpets, the major

herbivores of high rocky intertidal habitats. Further, future studies must recognize that the role of avian predators in a community will depend on such variables as substrate texture, abundance and distribution of crevices or other limpet refuges, and the accessibility of the shore to birds as determined by wave exposure and levels of human disturbance.

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Figure 17. Size distributions of limpets (Collisella) eaten by the common avian predators: Black Turnstone (solid line), Glaucous-winged and Western Gulls (dotted line), and Black Oystercatcher (dashed line).

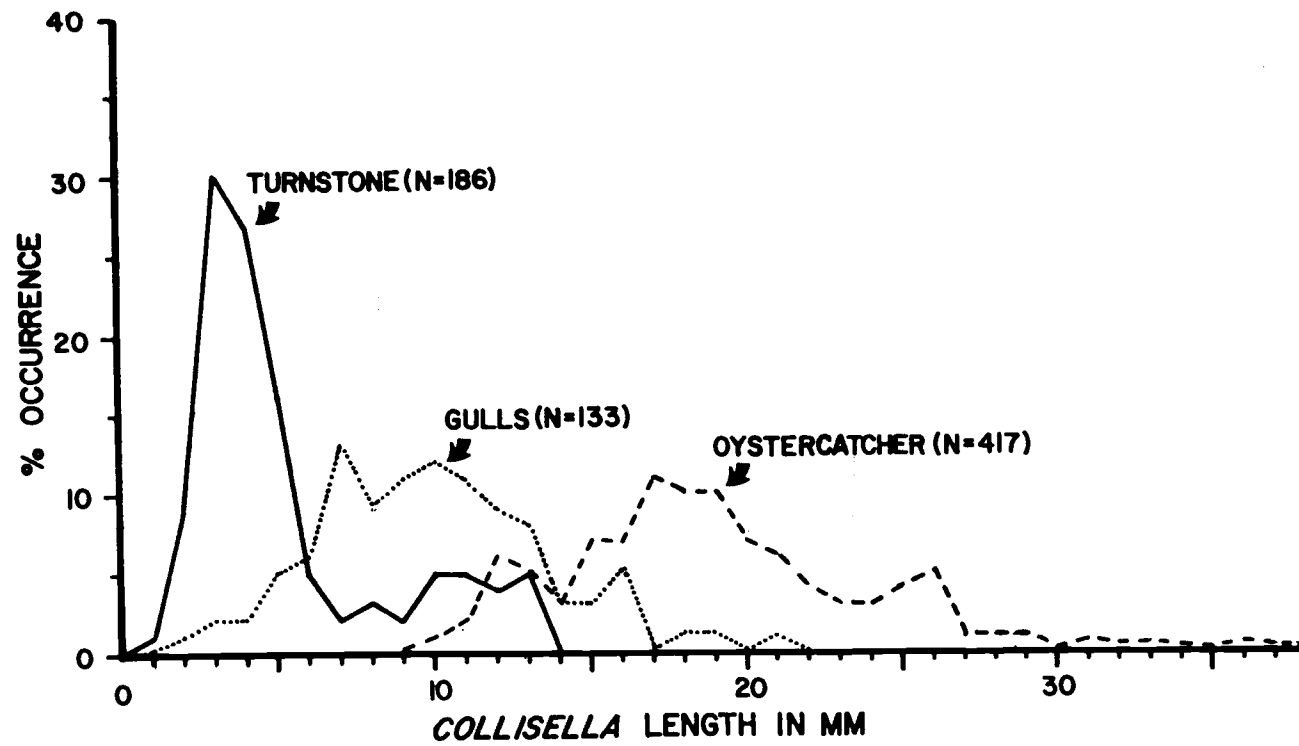


Figure 17.

Figure 18. Changes in densities of limpets (Collisella) in the three treatments of Exclusion Experiment #1. Results of each row of the Latin square design are presented separately; Row 1 is highest in the intertidal zone, and Row 3 is seaward (and hence the lowest of the three plots). Left-hand figures are for densities of limpets <5 mm, and right-hand figures are for densities of limpets 5-10 mm in length. Exclosures = solid line and triangles, cage controls = a dashed line and solid circle, and uncaged controls = a dashed line and open circle. Seasons when gulls and turnstones are absent in the high intertidal are shaded. Arrows with asterisks denote when exclosures were found missing and replaced.

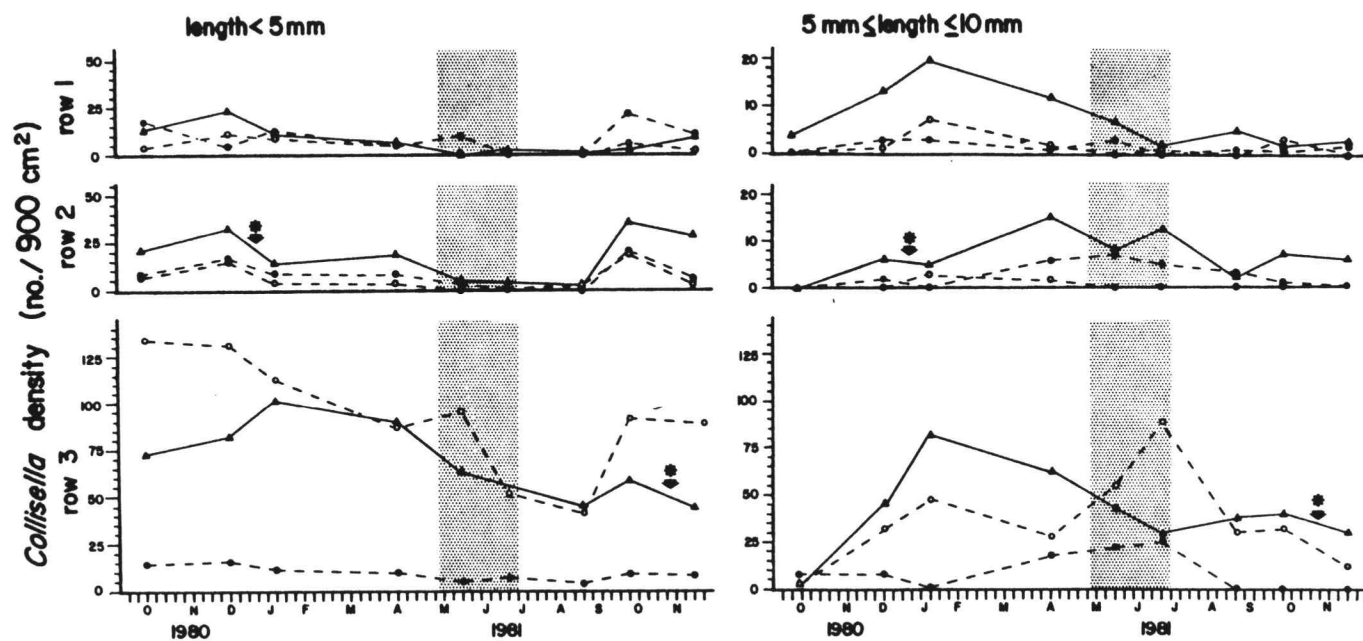


Figure 18.

Figure 19. Changes in the densities of limpets (Collisella) in the three treatments of Exclusion Experiment #2. See legend of Figure 2 for explanation.

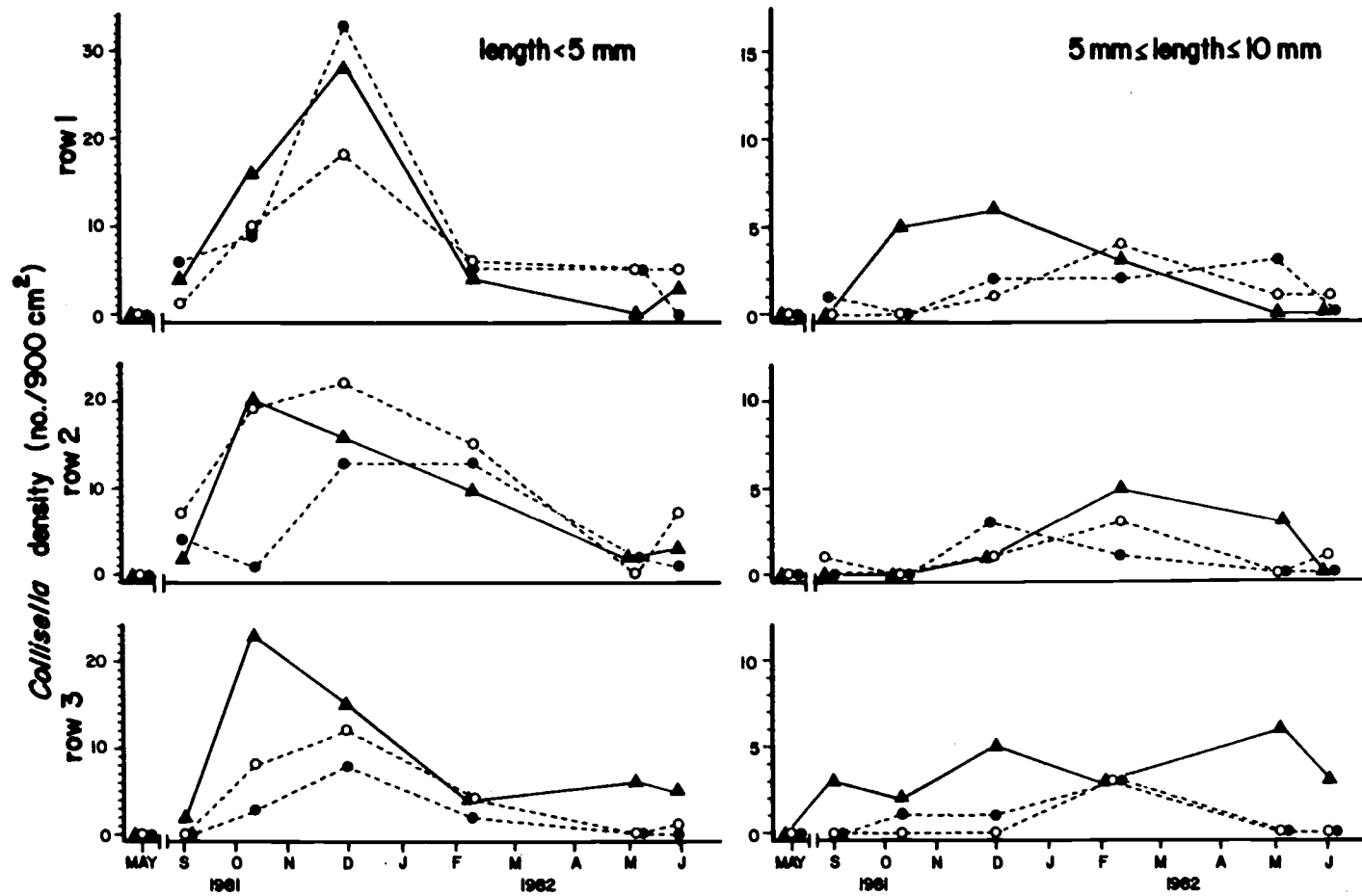


Figure 19.

Figure 20. Results of the limpet addition experiment #1. Symbols are the same as in Figures 18 and 19.

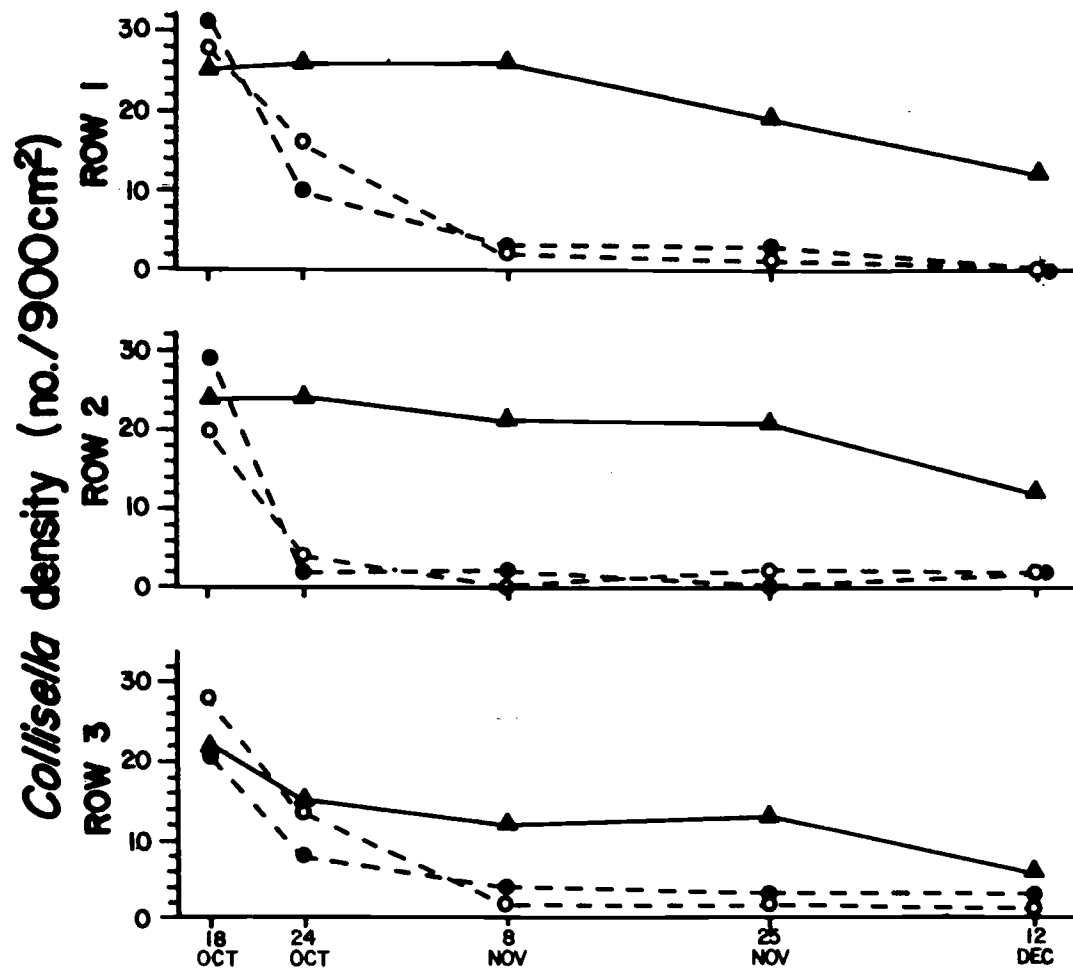


Figure 20.

Figure 21. Results of limpet addition experiment #2. Symbols are the same as in Figures 18 and 19.

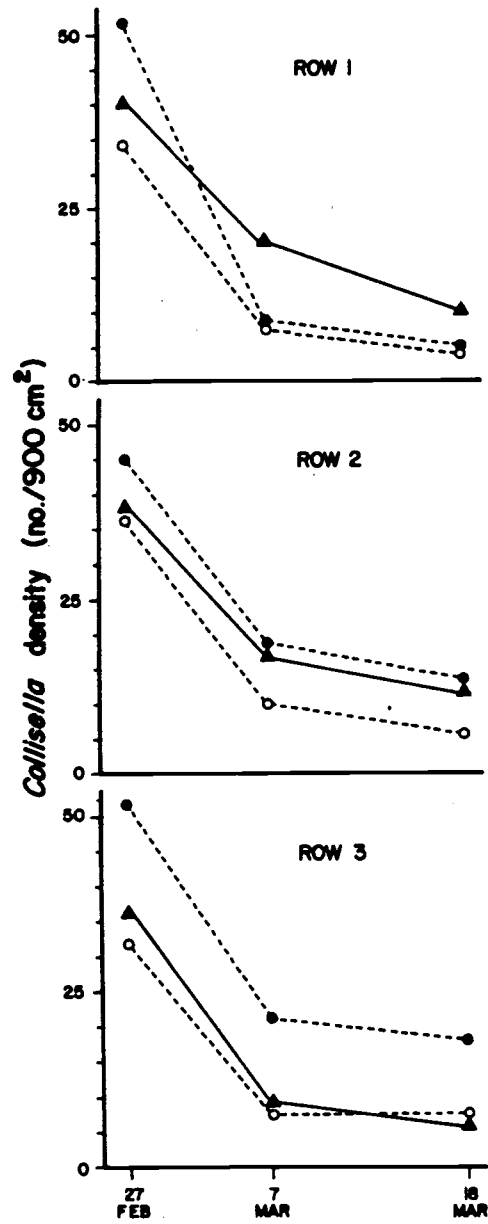


Figure 21.

Chapter V.

GENERAL CONCLUSIONS

The results of the enclosure experiments confirm the importance of bird predation as a significant mortality source for intertidal invertebrates. These experiments (Chapters III and IV), however, also illustrate how the magnitude of bird predation depends on characteristics of the birds, the prey, and the type of substrate.

A bird's access to intertidal invertebrates is limited in both time and space. The semi-diurnal tidal cycle restricts the availability of the mid and low intertidal zones, especially in fall and winter when storms are frequent and the lower low tides occur at night. In many areas the cracks and crevices in the intertidal substrate provides numerous refuges for invertebrates from their much larger-sized avian predators. Only the Black Oystercatcher with its long bill is capable of reaching prey in these refuges (see Hartwick 1976). Potential prey on vertical surfaces are usually safe from all avian predators (with the possible exception of an occasional gull that feeds on protected vertical walls by floating on an incoming or outgoing tide).

The actual availability of prey is also limited by a bird's ability to remove attached prey from the substrate (Chapter II). Some prey, such as limpets on algae, are vulnerable to all types of birds whereas other prey, such as large chitons and barnacles, appear to be immune to bird predation (C. Marsh, personal observation). As illustrated by prey selection by Surfbirds and Black Turnstones, some types of prey are more

vulnerable to one kind of foraging tactic. Thus, the probability that birds will significantly decrease the density of invertebrates in a patch depends on the type of prey as well as the accessibility of the patch to the birds.

Recruitment rates of prey into a patch also affects the likelihood that bird predation will decrease prey densities. Recruitment rates of prey into a patch, in turn, reflect periodicity of reproduction, mobility of prey, and the distance between the patch and the nearest prey refuge. High recruitment rates by prey will likely exceed predation rates by birds because observations on site usage by foraging birds (Chapter III) suggest that birds visit patches infrequently. Therefore, birds are most likely to depress densities of either sessile prey or prey with few refuges and low recruitment rates. For example, four of six exclusion experiments indicated that birds decreased densities of sessile mussels (Chapter III). On the other hand, limpets are moderately mobile; and consequently, the number of limpets that immigrate into a patch (after the visit of an avian predator) depends on both the distance from the patch to the nearest refuge for limpets, and the proportion of limpets in the area that occur in accessible versus inaccessible patches. The exclusion experiments indicated that birds significantly decreased limpet densities on flat, smooth benches where refuges were scarce (Chapter IV). Little or no bird effect on limpet densities should occur in patches adjacent to large areas inaccessible to birds.

In some patches bird predation is only one of several mortality sources acting on invertebrate populations. In addition to bird

predation, invertebrates succumb to predation by invertebrates (e.g. Paine 1966, Connell 1970), competition (Connell 1961) and heat and desiccation stress (Frank 1965). The relative importance of bird predation as a mortality source should depend on whether its effects are complementary or compensatory with other mortality factors (Chapter III). The effect of bird predation may be dramatic if it complements the effects of another mortality source. If, however, one of the other mortality sources dramatically decreases invertebrate prey densities, birds may not have the opportunity to have an effect.

In summary, I conclude that 1) bird predation can be a significant mortality source of certain intertidal invertebrates; and 2) the relative importance of bird predation depends on its interaction with a suite of other factors - notably prey mobility, prey density, substrate heterogeneity, and the presence of other mortality factors. Thus, future studies attempting to understand the role of bird predation in rocky shore communities must focus on the interaction of bird predation with these other variables, as well as the direct impact bird predation has on prey densities.

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APPENDICES

Appendix 1: Relative abundances of prey types infrequently eaten by Surfbirds (S.B.) and Black Turnstones (B.T.). Columns 1 and 2 represent the average percent of total prey items in stomach samples; Columns 3 and 4 represent the percent of fecal samples in which prey type occurred, N = no. prey items or fecal samples.

	<u>Stomach Samples</u>		<u>Fecal Samples</u>	
	<u>S.B.</u> (1)	<u>B.T.</u> (2)	<u>S.B.</u> (3)	<u>B.T.</u> (4)
Nemertea	tr	0	0	0
<u>Gastropoda:</u>				
Chitons	0	1	0	0
<u>Nucella</u>	<1	<1	11	5
<u>Crustacea:</u>				
Decapods	0	0	2	15
<u>Insecta:</u>				
diptera larvae	<1	<1	6	29
diptera adult	0	0	0	tr
Other	0	<1		
Unidentified	0	1		
N	1220	1970	102	128

Appendix 2: The frequencies of occurrence of the respective behaviors in the Surfbird and Black Turnstone. Results for each observer (1-3) and each of the 5 substrates are listed separately for both "bouts" and "individuals." S.B.=Surfbird; B.T.= Black Turnstone; * = $p < 0.05$, and **= $p < 0.01$ as determined by Fisher's Exact Test.

		<u>Tug</u>	<u>Hammer</u>	<u>Push</u>	<u>Rapid Peck</u>	<u>N</u>
A.						
<u>BOUTS</u>						
		<u>SB</u> <u>BT</u>	<u>SB</u> <u>BT</u>	<u>SB</u> <u>BT</u>	<u>SB</u> <u>BT</u>	<u>BS</u> <u>BT</u>
Sand	1	.23 .06 *	0 .06	.02 .10	.20 .06	60 50
	2	.22 .03	0 0	0 0	.06 0	36 67
	3	.32 .01	.21 .16	0 .01	0 0	28 67
Barnacles	1	.64 .26 **	.17 .55 *	.03 .0	0 0	88 107
	2	.78 .05	.15 .54 *	.01 0	0 0	106 92
	3	.48 .08 **	.33 .21	.02 .07	.02 0	60 75
Mussels	1	.70 .25 **	.05 .60 *	0 0	0 0	63 20
	2	.39 0 *	0 0	0 0	0 0	109 11
	3	.31 0 *	.25 .32	0 0	.03 0	36 19
Ulvoids	1	.35 .08 *	0 .07	.12 .26	.12 0 *	17 106
	2	.22 .03	.06 .26 *	0 .29 **	.12 0 *	50 31
	3	.13 .05	.29 .14	0 .13 **	.02 0	48 63
<u>Rhodomela</u>	1	.50 .08 *	0 0	.17 .84 *	0 0	6 77
	2	.33 .01 *	0 0	0 .86 **	.12 0 **	58 84
	3	.44 .15	.04 .04	0 .58 **	0 0	25 52
B.						
<u>INDIVIDUALS</u>						
Sand	1	.05 .06	0 .13	.05 .13	.32 .13	19 16
	2	.14 .08	0 0	0 0	.14 0	7 13
	3	.33 .04	.33 .30	0 .04	0 0	15 23
Barnacles	1	.85 .48 *	.33 .81 **	.11 0	0 0	27 27
	2	.81 .10 *	.30 .75 **	.04 0	0 0	27 20
	3	.73 .24 *	.59 .52	.05 .19	.05 0	22 21
Mussels	1	.81 .50	.06 .83 **	0 0	0 0	16 6
	2	.39 0	0 0	0 0	0 0	21 3
	3	.50 0	.42 .50	0 0	.08 0	12 8
Ulvoids	1	.83 .22	0 .09	.17 .57	.17 0	6 23
	2	.50 .17	.33 .33	0 1.0 *	.50 0	6 6
	3	.25 .05	.40 .23	0 .23	.05 0	20 22
<u>Rhodomela</u>	1	.33 .29	0 0	.33 .86	0 0	3 21
	2	.53 .04	0 0	0 .96 **	.20 0	15 26
	3	.73 .30	.09 .04	0 .70 **	0 0	11 23