Ecology, 67(3), 1986, pp. 771–786

ROCKY INTERTIDAL COMMUNITY ORGANIZATION: THE IMPACT OF AVIAN PREDATORS ON MUSSEL RECRUITMENT[1]

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Abstract. In the Pacific Northwest, mussels (*Mytilus* spp.) are major prey items of Surfbirds (*Aphriza virgata*), gulls (*Larus glaucescens* and *L. occidentalis*), and Black Oystercatchers (*Haematopus bachmani*). The impact of this predation is potentially great, as mussels are the competitively dominant members of the mid-intertidal community. I tested the effect of these predators on mussel recolonization of 50 × 50 cm clearings, using bird exclusion cages. Three of five exclosure experiments showed that birds significantly reduced recruitment of juvenile mussels (*M. californianus* and *M. edulis*) into clearings in established mussel beds. A sixth experiment indicated that birds were responsible for the absence of mussels from an area with smooth substrate lacking mussel beds. Here clumps of *Mytilus edulis* 10–20 mm in length became established in all exclosures, but not in any controls. These experiments indicate that the long-term impact of avian predators is greatest in patches where invertebrate predators are uncommon and larval settlement, rather than adult encroachment, is the major form of recruitment. The results of this and other studies suggest that avian predation increases the patchiness of a sedentary prey in heterogeneous habitats, but decreases patchiness where the habitat is sufficiently homogeneous that birds have access to all microhabitats.

Key words: Aphriza; *exclosures; gulls;* Larus; *mussels;* Mytilus; *Oregon; patchiness; predation; Surfbird.*

INTRODUCTION

Ecologists have long sought to understand the impact of avian predation on invertebrate populations (Tinbergen 1981). Most studies have considered predation on forest insect pests (see Otvos 1979 for review), but avian predation in marine communities has received increasing attention. Several studies have shown that birds significantly decrease densities of infaunal invertebrates (O'Connor and Brown 1977, Evans et al. 1979, Goss-Custard 1980, Schneider and Harrington 1981, Zwarts and Drent 1981, Quammen 1984), but few studies have examined avian predation on rocky intertidal species (Gibb 1956, Feare 1967, Hartwick 1981, Frank 1982). In contrast, several studies on rocky shores have shown that invertebrate predators can dramatically limit the distribution and limit the densities of other invertebrates (Paine 1966, 1974, Connell 1970, Dayton 1971, Menge 1976, 1978*a, b*).

This lack of knowledge about avian predation in rocky intertidal communities is due to two factors. First, invertebrate predation has usually been studied by excluding or by experimentally removing the predator. Application of this approach to birds is more difficult, requiring exclosures that exclude only birds. Second, many observers have considered birds to be unimportant because they are usually less abundant than invertebrate predators and are often present only seasonally. Density, however, is a poor indicator of predation intensity because birds have higher 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 cages that exclude birds but not other molluscivores. (I use "recruitment" to refer to survival of individuals to a length of 20 mm.) The exclosure experiments were designed to test whether avian predation significantly reduces mussel recruitment into open patches of the middle and upper rocky intertidal. I concentrated on mussels because juveniles are commonly preyed on by birds, and adults are dominant space-occupiers in the mid-intertidal zone in Washington, and presumably throughout much of their range (Baja California to Alaska; Paine 1974). Clearings in the mussel beds are created by log battering and heavy wave action (Dayton 1971, Paine and Levin 1981). By retarding mussel recruitment in these clearings, predators of mussels may delay local extinctions and permit the survival of competitive subordinates.

SITE DESCRIPTION

Exclosure experiments were conducted at three areas on the outer Oregon coast: Boiler Bay (44°50.0′ N), Yaquina Head (44°40.5′ N), and Seal Rock (44°29.8′ N). The sites used at each location were partially protected, but still received direct wave action during storms. The average tidal fluctuation was ≈2.5 m with a semi-diurnal tidal cycle.

The slope, aspect, and type of substrate differed among the three sites (Table 1). The experiments at Boiler Bay (numbers 4, 5, and 6) were located in a mussel bed 3–5 m wide on a gently sloping mudstone

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[1] Manuscript received 16 June 1983; revised 24 May 1985; accepted 29 May 1985.

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TABLE 1. *Characteristics of sites of exclosure experiments designed to test the impact of avian predation on mussel recruitment in rocky intertidal areas of the Oregon coast.*

Site	Expt. no.	No. replicates*	Date initiated	Date completed	Substrate description		Tidal ht. (MLLW) (m)
					Type	Relief	
Yaquina Head	1	4	Mar. 1979	Sep. 1979	weathered basalt	even	+1.5 to +1.8
	2	4	Feb. 1980	Feb. 1982	weathered basalt	even	+1.7
Seal Rock	3	3	June 1979	May 1980	rugged basalt	very irregular	+2.0
Boiler Bay	4	5	Feb. 1980	Oct. 1981	hard mudstone	even	+1.4 to +1.7
	5	4	Feb. 1981	June 1982	artificial substrate	moderately irregular/even	+1.4
	6	3	May 1981	June 1982	soft mudstone	very even	+1.4

* Each replicate consisted of a set of 3 treatments positioned within 1 m of each other: (1) a cage that excluded birds but not other mussel predators, (2) a cage control, and (3) an uncaged control.

substrate in a semi-protected cove. The two experiments on the south side of Yaquina Head (experiments 1 and 2) were on a horizontal bench of weathered basalt ≈3 m wide. This site was often inaccessible during fall and winter because it received direct waves from winter storms.

Experiment 3, at Seal Rock, was located on the landward side of a large rock 15 m offshore. The substrate was unweathered basalt with highly irregular relief but relatively smooth surface texture. The substrate was steep (≈30°–60° slope), but birds traversed it with little difficulty. This site is described in Marsh (1984).

METHODS

The experimental design

The experimental design consisted of three treatments: a cage that excluded birds but not other mussel predators, a cage control, and an uncaged control. A replicate refers to a set of these three treatments positioned within 1 m of each other, and an experiment consisted of three to five replicates in close proximity (Table 1). The two 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 exclosures than in corresponding controls of the same replicate.

Two exclosure designs were employed. The most versatile, used in five of six experiments (numbers 2–6), was a dome-shaped frame made of stainless steel bar (6.3 mm in diameter) covered with polyethylene tubing, which enclosed an area of 2500 cm^2 (Fig. 1). Monofilament line (18 kg test) was sewn at 2-cm (sides) or 5-cm (top) intervals through the tubing of the cage arms. Cage controls were similar, but lacked the monofilament. The central 900 cm^2 was sampled. Cages were attached by drilling holes in the rock. Once attached to moderately hard rock, these cages withstood direct waves generated by ocean swells 5–6 m high.

A different design was used in experiment 1. Exclosures consisted of an angle iron frame 30 × 50 × 15 cm tall. The lower crossbars at the narrow end were raised 6 cm to allow access by invertebrate predators. Monofilament was strung at 2-cm intervals across the

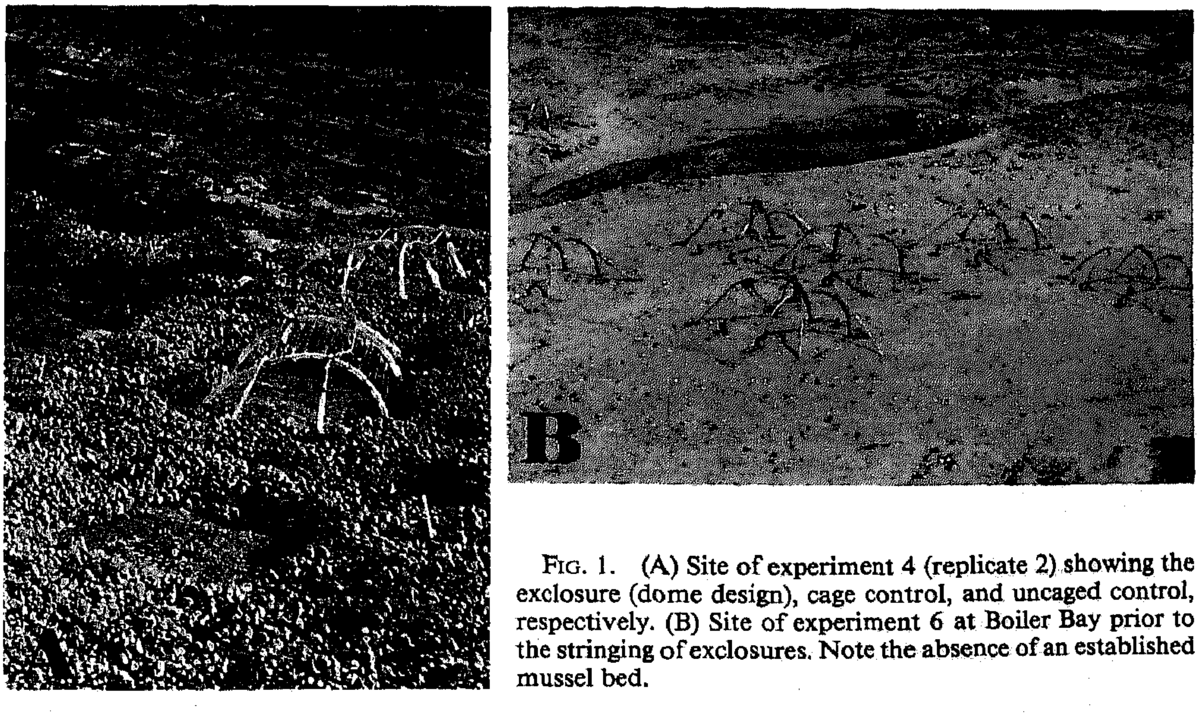

FIG. 1. (A) Site of experiment 4 (replicate 2) showing the exclosure (dome design), cage control, and uncaged control, respectively. (B) Site of experiment 6 at Boiler Bay prior to the stringing of exclosures. Note the absence of an established mussel bed.

top and sides of each exclosure, but not on cage controls. This experiment also included a fourth treatment in which the monofilament on the top was spaced at 15-cm intervals to allow 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. Plots in this experiment were slightly smaller than those with dome exclosures; the central area sampled was 800 cm² and the entire enclosed area was 2400 cm².

With the exception of those used in experiment 6, all plots were originally covered with adult *M. californianus* beds one mussel deep. All *M. californianus* and other upright sessile organisms (*Balanus* spp. and *Anthopleura* spp.) were scraped from the plots, but no attempt was made to remove the byssal threads or barnacle scars that remained. This procedure mimicked natural mussel removal. Clearings were large enough to provide a 10-cm border around the census plot to reduce possible edge effects (see Suchanek 1979).

The surface relief of the experimental sites varied from smooth to highly irregular (Table 1). Experiments 1, 2, and 4 were on relatively level plots that lacked large crevices. Experiment 3 (at Seal Rock) was on a highly irregular substrate with small water-filled recesses. Experiment 6 had the smoothest substrate, and lacked mussel beds (but was at a tidal level similar to that of the other experiments).

Experiment 5 was designed to test for interactions among substrate heterogeneity, *Mytilus* settlement patterns, and the effects of avian predators. I used nontoxic epoxy putty (Sea Goin' Poxy Putty) to create an artificial substrate. One half of each artificial substrate (hereafter referred to as the "even substrate") was smoothed and then lightly tapped with a wire brush to simulate the mudstone surface texture of experiment 4. On the other half of the plot I created an irregular surface with an approximate 5-cm difference between the depressions and raised areas. This irregular substrate was not textured, and mimicked unweathered basalt with moderate irregularity.

I recorded species, density, and size distribution of mussels in each plot, except that in experiment 3 I measured percent cover of mussels because at this site many mussels were in crevices 5–15 cm under water and could not be counted easily. In experiments 1, 2, and 4 I censused mussels in 12 randomly chosen 25-cm² subsamples; in experiments 5 and 6 I was able to census all mussels because densities were lower. I tallied mussels in the following length classes: 2–4 mm, 5–10 mm, 11–20 mm, 21–30 mm, and >30 mm. I refer to 2–10 mm mussels as small, 11–30 mm as medium, and those >30 mm as large. Mussels 2–4 mm long are referred to as "recently settled." Only mussels >10 mm in length were identified to species because smaller individuals cannot be identified accurately in the field (Suchanek 1979).

To be effective the exclosure had to exclude birds but allow easy access to all other important predators of mussels. Dogwhelks (*Nucella emarginata* and occasionally *N. canaliculata*) were the only invertebrate molluscivores I regularly observed in the mid- and upper intertidal zones (see Harger 1970). Small seastars (*Pisaster ochraceus* and *Leptasterias hexactis*) were occasionally found in mussel beds, and adults were common in the low intertidal zone (see Menge 1972). Dogwhelks moved in and out of exclosures easily, but I monitored their densities in all plots to determine if they occurred in all three treatments with similar frequency. Fish also prey on mussels (Brett 1979), and at the outset of this study the importance of fish was not known. Consequently, 10 passes were made with a 14-m beach seine over the intertidal zone near the site of experiment 4 at high tide on 20 August 1980. A second seining attempt in February 1981 was unsuccessful because of rough seas.

Exclosure artifacts were studied in two ways. First, I tested the effects of the cage control on avian foraging by observing whether birds responded in a similar fashion to the uncaged and caged controls. Second, I determined if the structures had an indirect effect on mussel abundance by altering patterns of algal settlement. Because mussels preferentially settle in the alga *Endocladia muricata* (Dayton 1971, Bayne 1976; see Paine 1974), densities of larval mussels should be correlated with the abundance of this alga if a caging artifact occurs.

Statistical analysis of exclosure experiments

Two analyses were used to determine how birds affected mussel recruitment. These methods analyzed (1) densities at the conclusion of an experiment, and (2) the peak 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 of treatment differences (Sokal and Rohlf 1969). All tests compared the density in the exclosure with the densities in the corresponding controls of the same replicate. I calculated the probability that the number of exclosures with densities higher than their controls was due to chance alone. Under the null hypothesis, the probability of the exclosure having the highest density is 0.33, given two controls and one exclosure per replicate (i.e., all three plots have an equal chance of showing the highest density). In three of the four replicates of experiment 1 the probability of an exclosure having the highest density was 0.50, because these replicates had two types of exclosures and two types of controls. In the fourth replicate the probability of an exclosure having the highest density was 0.33 because the small-bird exclosure disappeared early in the experiment.

The method of calculation of probabilities depended on whether the comparison was an a priori or an a posteriori test. I treated comparisons of final densities

TABLE 2. Size ranges of *Mytilus* eaten by its common avian predators.

Bird species	Mussel species*	Size range (mm)	(*N*)†	Reference (location)
Surfbird (*Aphriza virgata*)	*cal., ed.*	2–10	104	Marsh 1984 (Oregon)
gulls (*Larus* spp.)	*cal., ed.*	6–29	19	C. Marsh and B. McCoy, *personal observation* (Oregon)
L. glaucescens	*ed.*	5–40	?	Irons 1982 (Alaska)
Black Oystercatcher (*Haematopus bachmani*)	*cal.*	20–90	2915	Hartwick 1976 (British Columbia)

* *cal.* = *M. californianus*, *ed.* = *M. edulis.*

† Number of mussels measured (no sample size was given by Irons).

as a priori because they were specified in the initial experimental design. Results of each experiment were tested separately, the replicates representing independent trials. For example, in an experiment with four replicates the probability (under the null hypothesis) that in each of the four replicates the plot with the highest final density was an exclosure is $(0.33)^4$ or 0.012. I treated the comparisons of peak densities as a posteriori because I decided upon these comparisons after examining the results. In this case, one third of the plots with the highest peak density are expected to be exclosures by chance alone: with four replicates, $3 \times (0.33)^4$ or 0.037. When final densities and peak densities occurred on the same date, I treated the analysis as a priori.

Experiment 6 had too few replicates (three) for this analysis. Consequently, I used Wilcoxon's two-sample rank test (Snedecor and Cochran 1980) to test if the three exclosure densities were significantly higher than the six control densities.

Analysis of density-related responses

To examine if mussel density affected the outcome of an experiment, I combined data from all experiments at a site and compared the peak mussel densities in exclosures to those in controls. Experiments that had similar substrates and levels of bird activity were analyzed together: experiments 1 and 2 formed one group, and experiments 4 and 5 a second. The experiments from Yaquina Head and Boiler Bay were analyzed separately because the two sites differed in bird abundance, exposure time, and bird use (see Results). The Boiler Bay analysis included only experiments 4 and 5, which were set up in mussel beds that had a moderately even substrate dominated by barnacles. Experiment 6 was on a very even substrate with sparse barnacle cover, where birds could probably locate mussels much more easily. The experiment at Seal Rock was not used because percent cover, rather than density, of mussels was the abundance estimate.

I divided mussels into small (2–10 mm) and medium (11–30 mm) size classes for this analysis because Surfbirds (*Aphriza virgata*), the most common avian molluscivores at the study sites, eat only small mussels, whereas gulls (*Larus occidentalis* and *L. glaucescens*) and occasionally Black Oystercatchers prey on medium-sized mussels (Table 2). The data for large mussels (>30 mm) were not analyzed because large mussels were absent in the Boiler Bay and Yaquina Head experiments.

In these comparisons, the data were expressed as the percent of plots of a treatment (exclosure or control) that had a density equal to or less than a given density.

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 evaluate foraging by birds in mussel beds. *M. californianus* occupied >95% of the space in both quadrats. Avian molluscivores at these sites were Black Oystercatchers, Western Gulls, Glaucous-winged Gulls, and Surfbirds (Table 2). Other birds reported to prey on mussels, but not observed near the quadrats, are sea ducks (Cottam 1939, Grosz and Yocum 1972) and crows (Zwarts and Drent 1981).

I observed bird activity on predetermined sampling dates throughout a low tide cycle. The actively foraging birds in a quadrat were counted at 1-min intervals from the time the high intertidal plot was exposed until it was covered again. Usually, this period was 5–8 h. A few observation periods were slightly less than a complete tide cycle because the tide began receding before it was sufficiently light to observe the birds. Observation periods ranged from a minimum of 4 h to a maximum of 8 h. Actual exposure times of the quadrats could not be determined accurately because of frequent changes in water level caused by wave action during the ebb and flow of the tide. Consequently, I based intersite comparisons on paired samples, similar in observation times and ocean conditions, taken on the same tide (with the help of assistants) or on immediately subsequent days.

RESULTS

Patterns of habitat use by birds

The number of birds foraging on the mussel beds was usually very low, but patterns of activity were temporally and spatially patchy (Table 3). Surfbirds, which prefer small mussels (Marsh 1984), were the most common bird at both sites, but their presence in the quadrat was sporadic. For example, 85% of the

TABLE 3. Foraging time spent by avian predators in mussel beds at Boiler Bay and Yaquina Head.

Dates	Surfbird		Gulls		Oystercatcher	
	Boiler Bay	Yaquina Head	Boiler Bay	Yaquina Head	Boiler Bay	Yaquina Head
	Foraging time [bird − min$\cdot$(10 m^2)$^{-1}\cdot$(low tide period)$^{-1}$]					
Late summer						
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 Sep.	0	0†	0	0†	0.5	0†
17–18 Sep.	0	0	0	5.7	0	0
Winter						
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	/
Spring						
4 Apr.	0	0	0	0	0	0

* Birds visited high intertidal quadrat, but not mussel bed quadrat.

† Peregrine Falcon (*Falco peregrinus*) present at the site.

‡ / = plot not censused.

§ stm = plots not exposed because of storm.

Surfbird activity at Boiler Bay occurred on only 1 of 10 days. Similarly, 84% of Surfbird activity at Yaquina Head occurred on 2 of 8 days. Other observations suggest that Surfbird foraging was localized within a quadrat as well. For example, one Surfbird fed continuously for 10 min on small *Mytilus* in the Yaquina Head quadrat, but remained in an area of only 250 cm^2. Although the contagious nature of these data makes between-site comparisons tentative, Surfbird activity seemed greater at Yaquina Head than at Boiler Bay, both in total foraging time and in number of days Surfbirds were present.

Oystercatchers and gulls regularly foraged in the intertidal zones at both sites, but they visited the mussel bed quadrats only for short periods (Table 3). Pairs of oystercatchers maintained year-round territories at all three sites, rather than feeding in groups as noted at other sites (Hartwick and Blaylock 1979, Frank 1982). Territorial spacing of these pairs may, in part, have accounted for the low use per unit of intertidal area.

Fewer gulls were observed foraging in the intertidal zone at Boiler Bay than at Yaquina Head. The maximum number of gulls seen feeding simultaneously in the intertidal zone at Boiler Bay was 10, as compared to 180 at Yaquina Head (where the intertidal area is smaller). This intersite difference was reflected in the use of the quadrats by gulls. No gulls were observed in 10 d at the Boiler Bay quadrat, whereas they were observed in the Yaquina Head quadrat on three of eight days.

Predator activity was not quantified at Seal Rock, but repeated observations over 3 yr indicated that almost twice as many Surfbirds wintered there as at the other two sites. On several occasions large flocks (>50 individuals) of Surfbirds, as well as individual gulls and oystercatchers, foraged near the exclosures.

Effectiveness of experimental design

The dome apparatus, used in five of the six experiments, effectively prevented birds from entering exclosures. Among >50 observations of birds entering experimental plots, only two Black Turnstones (*Arenaria melanocephala*) were observed to enter exclosures; in both instances the lower strands of monofilament had been broken by recent storms. (Black Turnstones eat *Mytilus* infrequently; Marsh 1984.)

Cage controls, however, were not totally effective because Surfbirds entered them less often than uncaged controls (7 versus 24; $P < .05$, Fisher's exact test; Sokal and Rohlf 1969). Hence, comparisons of exclosures and cage controls are conservative estimates of avian predation.

Neither differential algal settlement nor fish predation appeared to produce a caging artifact. *Endocladia muricata*, the alga in which *Mytilus* larvae preferentially settle, was scarce in the plots ($\bar{X} = 1.7\%$ secondary cover, range = 0–14%), and never constituted more than 2% of the secondary cover in exclosure plots. Mussel abundance was not affected by other species of algae. In September 1981 algal cover per plot (predominantly *Cryptosiphonia* sp. and *Ulva* sp.) was greater in exclosures than in controls of experiment 4 ($P = .04$; a priori permutation test), but there was no correlation between the number of small mussels (<5 mm in length) and algal cover ($r = 0.28$, $F = 0.08$, square-root transformation for densities and arcsine transformation for percent cover). In February 1981, when small mussels reached their highest densities, exclosures and controls of experiment 4 did not differ consistently in algal cover ($P = .54$), but algal cover and density of small mussels were inversely correlated ($r = 0.79$, $F = 21.79$, $P < .01$), suggesting that the algae ac-

TABLE 4. Final mussel densities in the mussel size classes in each replicate of experiment 1, which was initiated in March 1979 and terminated in September 1979.

	Size classes (mm)											
	<5	5–10	11–30	<5	5–10	11–30	<5	5–10	11–30	<5	5–10	11–30
Treatment	Repl. 1			Repl. 2			Repl. 3			Repl. 4		
	Number of *Mytilus* per 300 cm^2											
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

* Exclosure' = small-bird exclosure.

† / = treatment absent.

tually may have inhibited mussel settlement. In all other experiments algal abundance was unrelated to treatment (experiments 2, 5, and 6) or algae were absent (experiments 1 and 3).

The exclosure design did not hinder access to experimental plots by dogwhelks, the only invertebrate molluscivore present in the plots. (Seastars from the nearby mussel beds might have removed mussels from the plots during high tide, but none was observed in the plots at low tide.) Rather, densities of dogwhelks were often higher in the exclosures. At Yaquina Head densities of dogwhelks were higher in the exclosures and cage controls than in the corresponding uncaged controls (Wilcoxon's signed rank test, $P = .016$ and .0006, respectively). At Boiler Bay dogwhelk densities were higher in the exclosures than in the corresponding cage controls ($P < .005$) but not in the uncaged controls ($P = .36$).

I found no evidence that fish too large to enter the exclosures foraged in the mussel zones at Boiler Bay or at Yaquina Head. Wave surge was usually too strong for benthic feeding in the mid- and high intertidal zones of both study sites. In late summer, seas were occasionally calm, but only for a few days at a time. The seining attempt in August 1981 yielded 10 sculpins (*Clinocottus embryum* and *C. globiceps*), almost all of which were small enough to enter the exclosures (lengths: 23.0–92.5 mm; body heights excluding dorsal fins: 4.1–24.0 mm). None had molluscan prey in its stomach. The small sizes of fish caught were not simply the result of a sampling bias, because the same procedure yielded large fish (lengths: 112–245 mm) from an adjacent intertidal surfgrass (*Phyllospadix* spp.) bed on the same day. Thus, I tentatively conclude that large fish are unimportant mussel predators in the mid- and high intertidal zones at my study sites.

Results of exclosure experiments

Experiment 1 (Yaquina Head) lasted only 6 mo; most mussels settling in these plots did not have sufficient time to exceed 6–9 mm in length. Nonetheless, the results indicate that birds significantly reduced mussel density (Table 4). Mussel densities varied greatly among replicates, but within each replicate the highest density (of all sizes combined) was in an exclosure. Some exclosures, however, had low mussel densities, indicating that low larval settlement and/or invertebrate predation caused the scarcity of mussels in these plots. The relative impact of gulls versus Surfbirds could not be determined because the variability within a treatment was at least as great as among treatments. Surfbirds were probably responsible for the observed predation because I did not observe gulls feeding in the mid-intertidal zone of this site after larval settlement occurred.

Birds also influenced densities of mussels in experiment 2 (Yaquina Head). Large mussels were absent, but in all four replicates the highest peak densities of medium-sized (11–30 mm) mussels were in exclosures (Fig. 2). In three of the four replicates, however, densities in exclosures decreased following the peaks until levels were comparable in exclosures and corresponding controls. In the remaining replicate the final density of medium-sized mussels in the exclosure was seven times greater than in either control. Densities of small (2–4 and 5–10 mm) mussels did not differ consistently between exclosures and the corresponding controls.

Birds had no measurable effect on mussel survivorship in experiment 3 at Seal Rock (Table 5). Unlike the situation in the other five experiments, large (>30 mm) mussels were present in several of the experimental plots at the conclusion of the experiment. The highly irregular substrate allowed large mussels to cascade into controls and exclosures from the surrounding mussel bed, and also created water-filled recesses in which large mussels became established. Mussels in these recesses were inaccessible to Surfbirds and, possibly, to gulls.

In experiment 4 (Boiler Bay), avian predation significantly decreased densities of medium-sized mussels (Fig. 3). The exclosures of all five replicates had higher peak densities than did their controls. In one replicate the final density of medium-sized mussels in the exclosure was ≈10 times greater than those in the caged and uncaged controls. In the other four replicates densities of medium-sized mussels in exclosures also declined at some time during the experiment, indicating that mortality agents other than birds also had a mea-

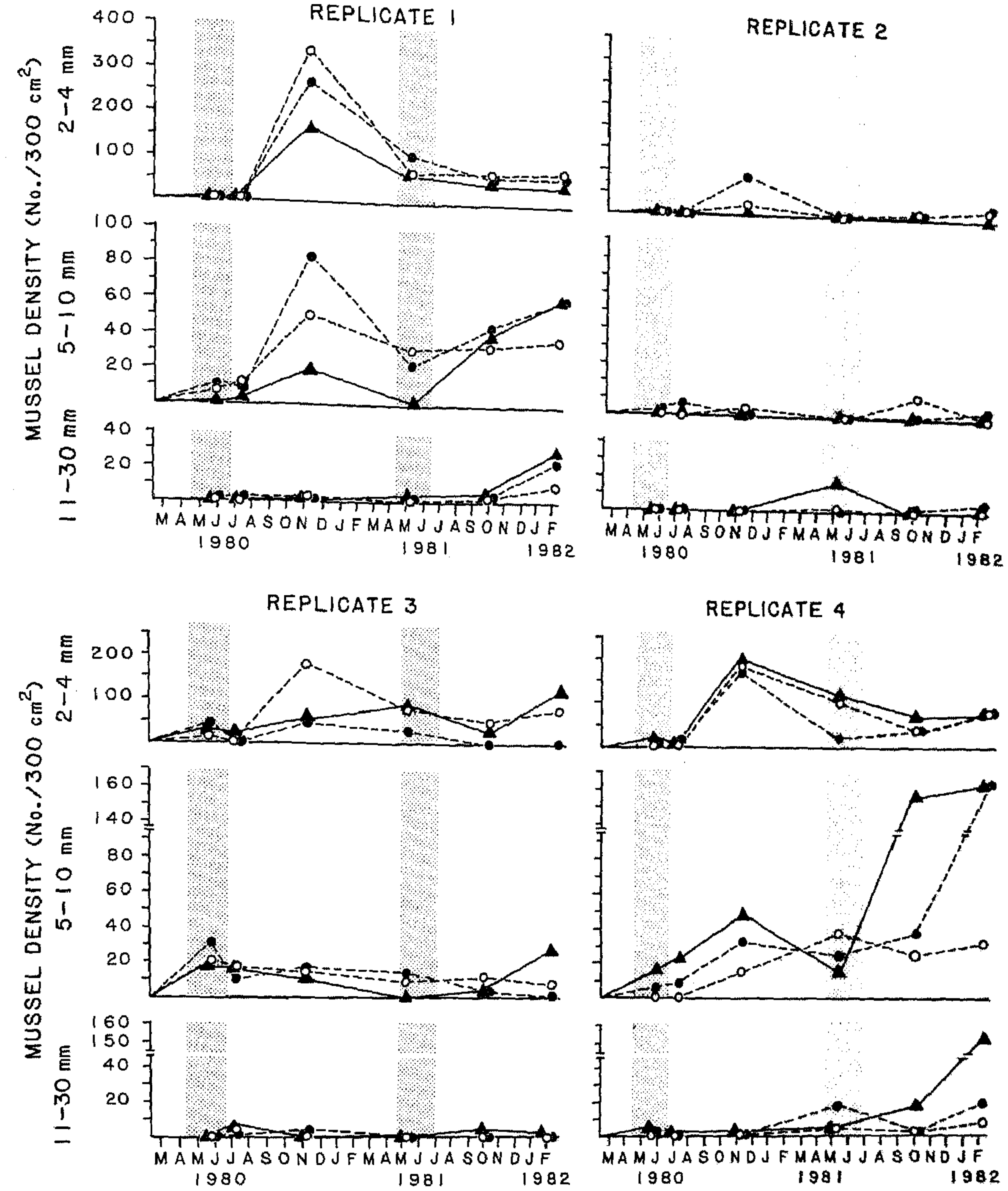

FIG. 2. Mussel densities in four replicates of experiment 2 (Yaquina Head). Shaded areas represent the season when Surfbirds are absent and gull activity in the upper intertidal is low. ▲——▲ exclosure, ●·····● cage control, O·····O uncaged control.

surable impact. As in experiments 1 and 2, large mussels were absent from the experimental plots.

Experiment 5 (Boiler Bay), with its artificial substrate, provided no conclusive evidence that avian predation was influenced by a moderate change in substrate relief (Table 6). Highest peak densities of medium-sized (11–30 mm) mussels occurred in the exclosure in three of four replicates (on the irregular, untextured substrate), but this difference was not statistically significant ($P = .29$). Densities of small mussels were higher on the even, textured surfaces than on the irregular smooth surfaces ($P = .05$, Binomial expansion; Snedecor and Cochran 1980), whereas me-

TABLE 5. Final percent cover of *M. californianus* in 900-cm^2 plots of experiment 3 at Seal Rock. Plots were cleared in June 1979 and percent cover was measured in May 1980.*

	Replicate		
Treatment	1	2	3
Exclosure	15	12	5
Cage control	27	2	2
Uncaged control	5	22	1

* The null hypothesis that the highest densities of mussels occur with equal probability in exclosures and controls was not rejected ($P = .44$, a priori permutation test).

dium-sized mussels were most abundant on the irregular, smooth surfaces. The scarcity of medium-sized mussels on the even, textured surface prevented comparisons of avian predation on the two substrates. The results indicate, however, that settlement of mussels was greater on the flat, textured substrate whereas survivorship was higher on the smooth substrate with irregular relief.

Birds had a dramatic effect on mussel densities in experiment 6 (Fig. 4). Peak and final densities of medium-sized mussels, as well as of mussels 5–10 mm in length, were higher in each of the three exclosures than any of the six controls. Although densities decreased in all plots during the late spring, exclosures were still the plots with highest densities at the end of the experiment. Densities of recently settled mussels did not

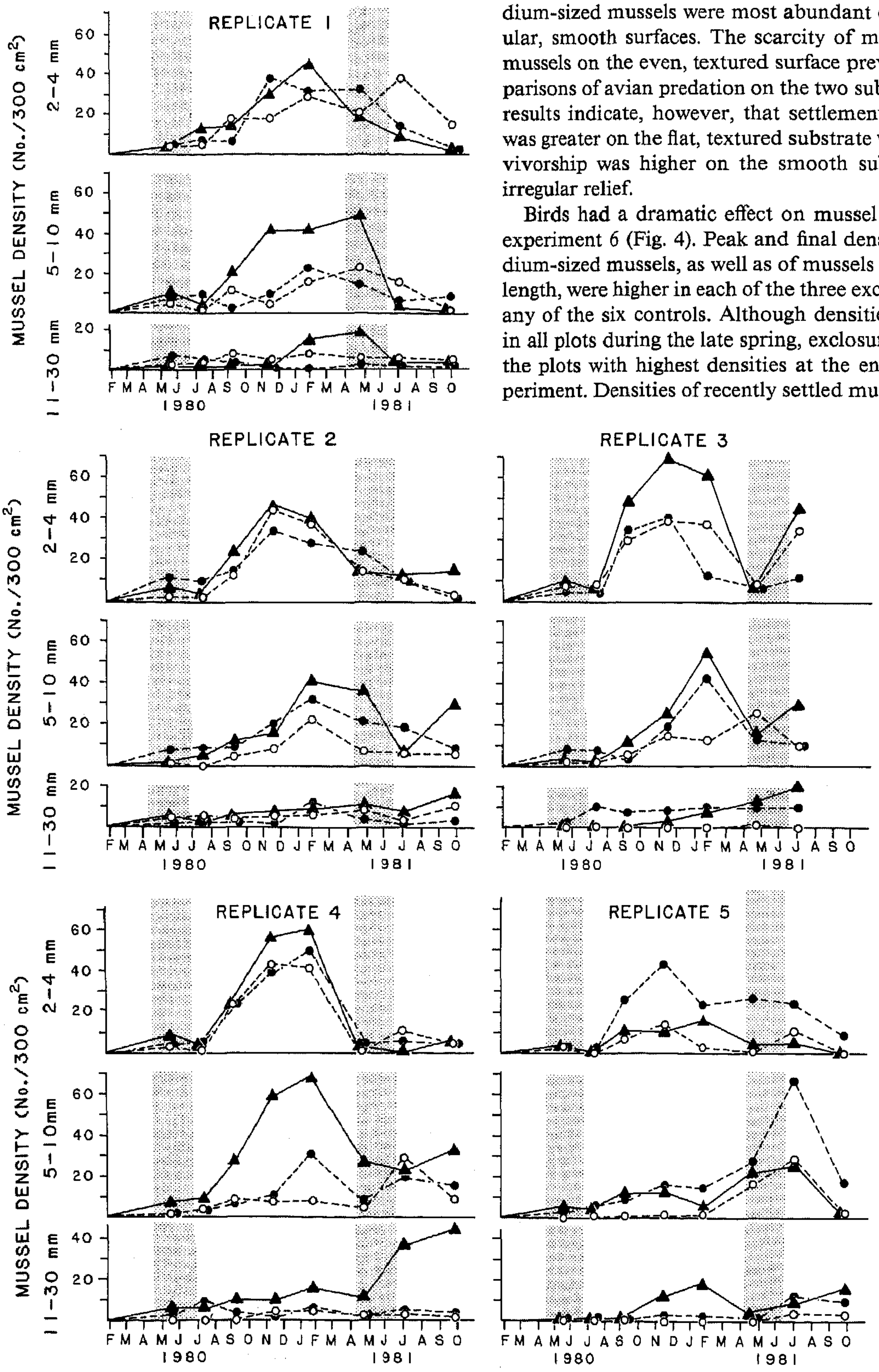

FIG. 3. Mussel densities in five replicates of experiment 4 (Boiler Bay). Use of symbols and lines as in Fig. 2.

differ consistently among treatments, indicating that the differences for medium-sized mussels were not the result of differential settlement.

Both *M. californianus* and *M. edulis* settled in the experimental plots, but their relative abundances differed in the various experiments. Experiment 3 was dominated by *M. californianus,* presumably because they had cascaded down from the adjacent mussel bed. In contrast, all medium-sized mussels in experiment 6 were *M. edulis.* Both species of *Mytilus* settled in experiments 2, 4, and 5, but the large increase observed in replicate 4 of experiment 2 (Fig. 2) was exclusively *M. edulis.*

Importance of invertebrate predators

Dogwhelks (*Nucella emarginata* and *N. canaliculata*) were at least partially responsible for the decreases in mussel densities in the exclosures of experiments 2 and 4. Of 135 dead *Mytilus* collected from these two experiments during late spring and early summer, 84% had been drilled by these gastropods. Dogwhelks occurred at higher densities and more often in the plots of experiment 2 (Yaquina Head) than in those of experiment 4 (Boiler Bay) ($P < .001$, Fisher's exact test; Fig. 5). The impact of dogwhelk predation was most dramatic in replicate 2 of experiment 2; almost none of the mussels settling in these plots survived until the next census date. Densities of medium-sized mussels in exclosures of experiment 4 at Boiler Bay increased significantly more often when dogwhelks were absent than when they were present ($P = .014$, Fisher's exact test).

DISCUSSION

Avian predation on Oregon mussel populations

Increased mussel densities in exclosures were not simply due to a caging artifact. The possibility that the monofilament barrier, rather than giving protection from birds, enhanced survivorship of medium-sized mussels in the exclosures is inconsistent with the results. More medium-sized mussels were often present in a control than in the corresponding exclosure when mussel densities were low. Only when mussel densities increased substantially were they consistently higher in exclosures than in controls. If the monofilament provided significant protection to medium-sized mussels from wave shock, densities of medium-sized mussels should have been higher in all exclosures. The exclosure experiments demonstrated that avian predators cause substantial mortality of small mussels on rocky shores. Birds significantly decreased recruitment in four of six experiments (Table 7).

When replicates showed significant avian predation, mussel densities changed in one of two ways. In some replicates the density of medium-sized mussels remained higher in exclosures than in controls (e.g., experiment 2: replicate 4 [Fig. 2]; experiment 4: replicate 4 [Fig. 3]; experiment 5: replicate 1 [Table 6]; and experiment 6: all replicates [Fig. 4]). In other cases, densities in exclosures were initially higher than in controls, but they subsequently decreased to levels similar to those in controls (experiment 2: replicate 2 [Fig. 2]; experiment 4: replicates 1 and 2 [Fig. 3]). Mortality in exclosures indicates that, in addition to avian predation, other variables (e.g., gastropod predation) also influenced mussel survivorship.

Birds can significantly decrease densities of mussels only in patches where larval settlement, rather than immigration of adults, is the major form of mussel recruitment. Paine and Levin (1981) noted that larval recruitment increased the rate of recovery only in patches >3500 cm^2. Smaller patches (100–3500 cm^2) were closed by recruitment from the surrounding mussel beds within 1–3 yr. Adult encroachment may also be more important than larval recruitment in mussel beds on steep surfaces, or in beds more than one individual deep (Paine and Levin 1981). Thus, birds should have the greatest impact in large natural clearings or in areas where mussel beds have been destroyed by overharvesting.

Densities of mussels sometimes declined dramatically within exclosures, indicating that mortality was also caused by factors other than birds. Dogwhelk predation and heat stress were probably important causes of mortality in the mid- and high intertidal zone at my study sites. In experiments 2 and 4 mussel densities increased only when dogwhelks were absent; most dead mussels had been drilled by these snails. Heat stress probably caused the decline in densities in the exclosures of experiment 6. Dogwhelks were absent at this site, and densities decreased between March and June, when tides were often low during midday.

The exclosure experiments suggested that substrate relief and mussel density also influenced avian predation. Substrate relief was recognized as a critical factor at the outset of the experiment because mussels on vertical walls or in crevices are unavailable to birds. Consequently, all experiments, with the exception of experiment 3, were located on substrates with little relief. Experiment 3 showed that irregular substrates are likely to be recolonized by expansion from surrounding mussel beds or by mussels settling in microhabitats inaccessible to birds.

The combined results of the Boiler Bay and Yaquina Head experiments suggest that the extent of avian predation on mussels is a function of mussel density. At Boiler Bay the replicates in which there was no evidence of avian predation on small mussels were those with the lowest densities. When the cumulative percentage of plots was graphed against peak density of small mussels, exclosure and control plots showed similar curves up to 60 mussels/300 cm^2 (Fig. 6A). At higher densities, however, the curves for exclosures and controls diverged. Forty-five percent of the exclosures, but only 10% of the controls, had peak densities >75

TABLE 6. Densities of *Mytilus* (no./450 cm^2) in each replicate of experiment 5 (Boiler Bay; February 1981 to June 1982) on artificial substrate. The "irregular" substrate had a smooth surface and ≈5 cm topographic relief; the "even" substrate was slightly textured.

	Size classes (mm)						
	<5	5–10	11–30	<5	5–10	11–30	<5
Treatment	Repl. 1			Repl. 2			Repl. 3
	(Density on irregular side)/(density on even side)						
Feb. 1982*							
Exclosure	46/53	39/10	29/5	52/58	28/9	3/0	35/52
Cage control	23/62	30/17	6/0	24/53	17/19	7/0	72/80
Clearing	49/32	22/9	0/0	60/132	29/9	21/2	47/105
June 1982†							
Exclosure	14/13	30/10	24/2	25/16	6/15	1/1	14/35
Cage control	6/8	18/12	1/3	11/34	22/39	20/5	47/54
Clearing	7/4	13/2	1/0	50/12	34/7	0/0	32/14

* Date of highest densities.
† Final densities.

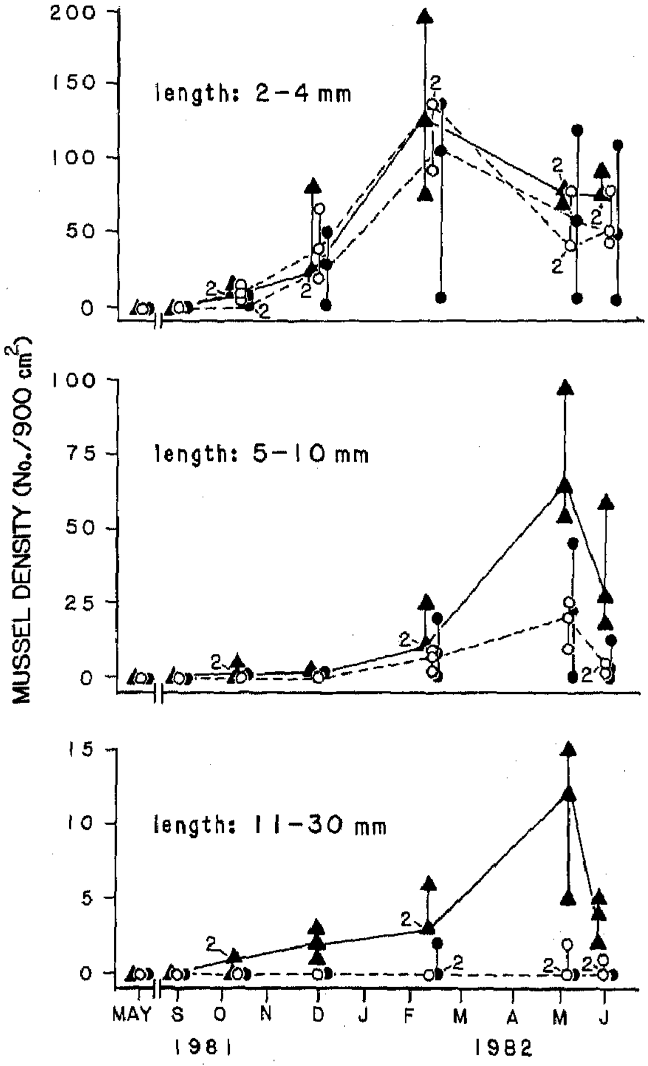

FIG. 4. Mussel densities in the three replicates of experiment 6. Use of symbols and lines as in Fig. 2. The density for each plot is denoted with the appropriate treatment symbol, and solid vertical lines connect the three replicates of a treatment for each censusing date. Lines between sampling dates connect median densities of the respective treatments. A single symbol for a treatment on a sampling date indicates that all three replicate plots had the same density.

mussels/300 cm^2. Birds did not appear to respond to densities of medium-sized mussels at Boiler Bay in a density-dependent fashion. The cumulative percentages of exclosure and control plots were consistently different ($P < .05$, Wilcoxon's two-sample rank test; Fig. 6B).

Results from the mussel bed experiments at Yaquina Head differed markedly from those at Boiler Bay in that the cumulative percentages of exclosure and control plots as a function of small mussel density did not differ significantly ($P > .50$, Wilcoxon's two-sample test; Fig. 7). Also, densities of small mussels were much higher in experiment 2 at Yaquina Head. Mussel densities may have been so high that avian predation was insignificant in spite of greater bird activity at Yaquina Head. Substrate differences may have had some effect, but the significant exclosure effect in experiment 1 indicates that substrate alone did not account for all between-site differences.

Because small mussels are eaten primarily by Surfbirds, I hypothesize that Surfbirds affect small mussels only at intermediate densities. Where avian predation was negligible, densities were either very low or very high. Clearings with low densities of small mussels may not be considered profitable patches (sensu Royama 1970) for foraging by individual Surfbirds, whereas in patches with high recruitment rates Surfbird predation may become insignificant. Actual densities that are "intermediate" depend on predator density and the algal cover in the patch. Similar patterns of density-dependent predation have been observed in woodpeckers (*Picoides* spp.; Knight 1958, Koplin 1972), parids (Otvos 1979, Solomon and Glen 1979), and European Oystercatchers (*Haematopus ostralegus*; Sutherland 1982). Nevertheless, other avian predators may still prevent large mussels from becomimg established. Gulls, and possibly oystercatchers, prey on medium-sized mussels. The scarcity of larger mussels on smooth surfaces outside exclosures may be due to the combined effects of predation by Surfbirds and gulls.

TABLE 6. Continued.

Size classes (mm)				
5–10	11–30	<5	5–10	11–30
Repl. 3		Repl. 4		
(Density on irregular side)/density on even side)				
18/19	7/1	29/34	19/18	17/3
16/6	4/1	64/41	25/9	3/0
20/8	3/0	48/40	16/3	6/2
5/4	2/0	14/78	15/12	5/0
11/5	0/0	79/17	8/0	0/0
3/2	0/0	42/16	1/0	1/0

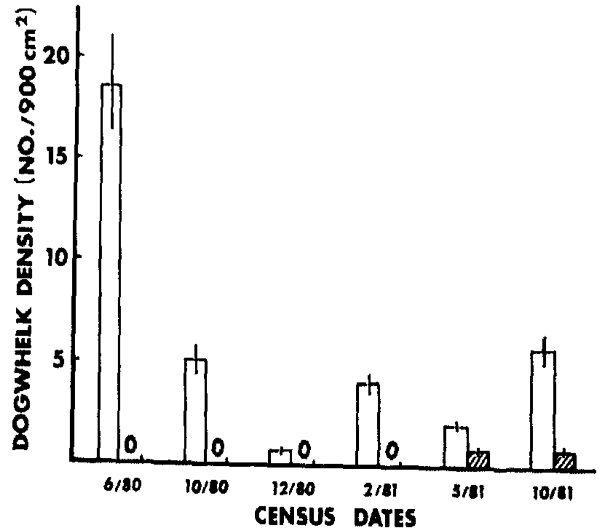

FIG. 5. Comparisons of densities (no./900 cm^2) of dogwhelks (*Nucella* spp.) in experiment 2 at Yaquina Head (□) and experiment 4 at Boiler Bay (▨). Vertical lines denote ±1 standard error.

Two species of mussels occupy rocky substrates in the Pacific Northwest. *M. edulis* is characteristic of high intertidal areas and large clearings, whereas juvenile *M. californianus* usually settle among the byssal threads of adult mussels (Suchanek 1978). Juvenile *M. edulis* should thus be more vulnerable to predation by birds than juvenile *M. californianus.* In this study, however, medium-sized individuals of both species often occurred together in clearings and in gull pellets (C. P. Marsh, *personal observation*). At present, evidence is insufficient to determine if avian predation is disproportionately greater on *M. edulis.*

These findings support the initial hypothesis that avian predation increases the time that clearings are available to organisms that are competitively inferior to *M. californianus* or *M. edulis.* In contrast, predation by birds on juvenile mussels does not alter the distribution of adult mussels on highly irregular surfaces or in small clearings within the mussel bed, because adult recruitment or invertebrate predation are more important in these microhabitats.

The impact of avian predators on intertidal communities

The immediate impact of avian predators on their prey is a function of three variables: (1) the proportion of prey that the predators remove from a patch per visit, (2) the frequency of visits to a patch, and (3) the recruitment rate of the prey into a patch. In turn, the proportion of prey removed from a patch depends on the prey's profitability (i.e., its energy content and ease of capture), its density (Lima 1984), and the abundance of more preferred prey (Royama 1970, Charnov 1976,

TABLE 7. A summary of *P* values from statistical analyses of mussel recruitment in exclosure experiments.*

	Size class of *Mytilus* (mm)							
	<5		5–10		≤10†		11–30	
	Density measured							
Experiment	Final	Peak	Final	Peak	Final	Peak	Final	Peak
1	0.04	0.04	0.13	0.13	0.04	0.04	≥0.2	≥0.2
2	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	0.10	0.04
3‡	NS		NS		NS		NS	
4	≥0.2	≥0.2	≥0.2	0.12	≥0.2	0.12	0.04	0.01
5A (irregular substrate)	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	0.07	≥0.2
5B (even substrate)	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2	≥0.2
6§	≥0.2		≥0.05		≥0.2		<0.05	

* Results of tests of the null hypothesis that the highest mussel density does not occur disproportionately more often in bird exclosures than in corresponding controls (nonparametric permutation test; Sokal and Rohlf 1969).

† Combination of the two smaller size classes.

‡ Mussel abundance in experiment 3 was measured as percent cover rather than by size class (NS = not significant at .05 level).

§ In experiment 6, only final densities were tested (see Methods: The Experimental Design).

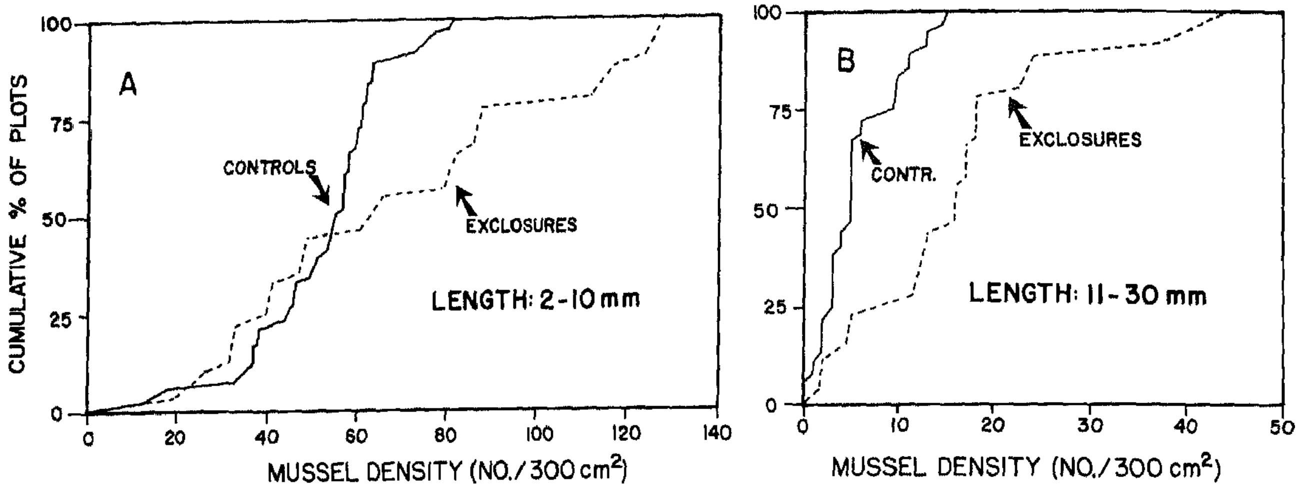

FIG. 6. The cumulative percentage of plots with peak mussel densities less than the indicated abscissa value, in the Boiler Bay mussel bed experiments. Peak densities of (A) small mussels and (B) medium-sized mussels in exclosure and control plots were significantly different; $P < .05$, Wilcoxon's two-sample rank test.

Goss-Custard 1977). Thus, prey densities decrease significantly only when predators consume a significant proportion of the prey (variable 1), and the immigration rates of prey (variable 3) are low compared to visitation rates of birds (variable 2). When avian predators exploit patches effectively and recruitment by prey is infrequent, the effects of birds will be long-term (e.g., Shachak et al. 1981).

Species that colonize empty patches slowly are most affected by avian predation. Most examples of significant avian predation in benthic communities involve sedentary invertebrates that either require >1 yr to mature or do not escape avian predation as adults (see Results: Patterns of Habitat Use by Birds; also O'Connor and Brown 1977, Goss-Custard 1980, Goss-Custard et al. 1981, Zwarts and Drent 1981, Frank 1982, Hulscher 1982, Suter 1982). For example, O'Connor and Brown (1977) observed that oystercatchers fed in different areas of an estuary in successive winters; apparently they depleted the abundance of large cockles (that require 3 yr to mature) before abandoning the area.

In contrast, avian predation appears to be insignificant (or only short-term) when the prey are hard to digest or when birds are present only part of the year and the prey's life cycle is a year or less. Short-lived prey may be unaffected by avian predation because (1) their small size attracts fewer species of birds and (2) their high reproductive rate quickly replaces the prey consumed. The densities of the small, thick-shelled molluscs *Gemma gemma* and *Ilyanassa obsoletus* were unaffected by avian predators in two exclosure experiments (Schneider 1978, Botton 1984), apparently because their high shell-to-tissue ratio reduced their digestibility or attractiveness. Short-lived invertebrates may also be affected less because avian predation is

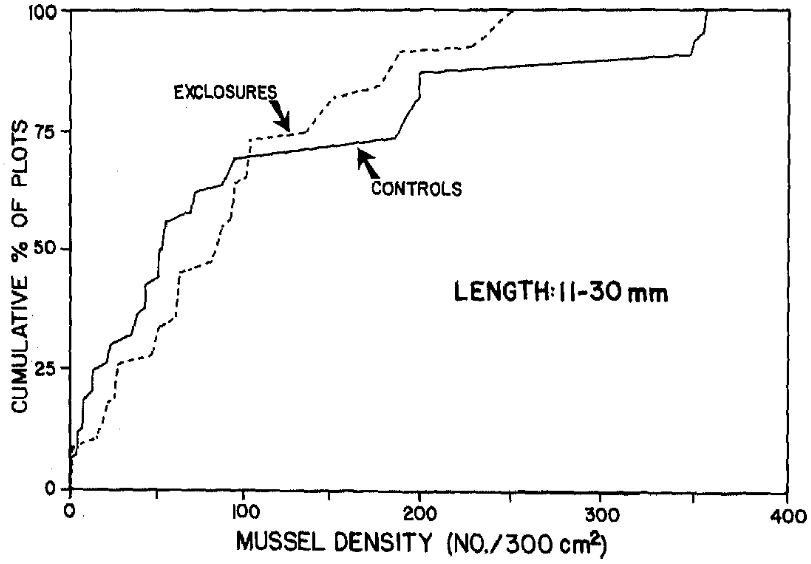

FIG. 7. The cumulative percentage of plots with peak mussel densities less than the indicated abscissa value, in the Yaquina Head mussel bed experiments. Sample sizes of replicates for medium-sized mussels were too small for inclusion of cumulative percentage data for that size class.

often only seasonal. Even within a single season birds observed during this study visited specific patches infrequently (see Table 3). Quammen (1984) demonstrated that summer recruitment of infauna repopulated controls that had previously been depleted by migratory birds. Similarly, Schneider and Harrington (1981) showed that migrating shorebirds caused only temporary declines of small macrofauna on the east coast of North America.

Some prey may not be affected by avian predation because much of the population is invulnerable to avian predators. In marine environments many potential prey occupy refugia created by large sessile macrofauna (C. P. Marsh, *personal observation*), live in deep burrows (Pienkowski 1981), or are difficult to capture (Kneib 1982).

Reducing the density or distribution of prey is only one aspect of an avian predator's role in a community. Reduction of the density of one prey species may affect other species if the prey is a competitively dominant space-occupier or a predator of such a species. Several studies have shown that predators in aquatic communities can control species composition and create zonation (Connell 1970, Dodson 1970, Sprules 1972, Paine 1974, Menge 1976). In addition, a predator's impact depends on the type of competitive interaction (Peterson 1979), the structural complexity of the habitat (Peterson 1979), the harshness of the environment (Menge and Sutherland 1976, Menge 1978*a*), and the presence of other mortality agents (Errington 1946). For birds, the prey type and habitat conditions influence how avian predators alter community organization.

Predation by birds appears to alter the spatial patchiness of sedentary invertebrates. The ability of birds to alter prey patchiness, however, also depends on the heterogeneity of the habitat and on the other predators present. When predators are substantially larger than their prey, heterogeneous surfaces such as clumps of algae or fissures in rocks provide refuges for prey. Consequently, modest quantitative changes in microtopography of the substrate may determine whether or not a large consumer can effectively locate and capture its prey (Gaines 1983, Lubchenco 1983). If the prey is also an important space-occupier, or preys on such a form, predation can transform quantitative differences in substrate relief between adjacent patches into substantial qualitative differences (Gaines 1983). Along the Oregon coast avian predation appears to create qualitative differences among patches that initially differ in substrate characteristics. For example, in this study birds prevented clumps of mussels from becoming established on smooth, exposed substrates in the high intertidal. Most crevices in this zone were inaccessible to the short-billed gulls and Surfbirds (C. P. Marsh, *personal observation*), and were filled by mussels. Similarly, Black Oystercatchers increased the heterogeneity of an Oregon rocky shore (186 km south of my study sites) by consuming limpets on the tops of, but not the sides of, boulders (Frank 1982). The removal of limpets creates a refuge for algal species that are eaten by these grazers; algae are abundant on the tops of boulders, but are scarce on the sides of boulders where limpets are abundant (Lubchenco and Cubit 1980).

Some soft-sediment habitats also exhibit heterogeneity that can influence the foraging effectiveness of birds so as to increase variability in prey density. Luckenbach (1984) inferred that shorebird predation caused infaunal densities to be higher among tall polychaete (*Diopatra cupra*) tubes than in the surrounding open areas. He observed that shorebirds commonly fed near clumps of *Diopatra* tubes but avoided feeding among the tubes. In a British estuary, Nicholls et al. (1981) noted that shorebirds avoided algal mats (*Enteromorpha* spp. and *Ulva* spp.) even though the mats contained more favored prey than did exposed sediments. Quammen (1982) showed that tactile-feeding shorebirds had difficulty distinguishing worms of small diameter from sediment particles of similar size. Thus, for a tactile feeder, sand and mud are structurally heterogeneous and simple substrates, respectively. Quammen (1982) also found that birds reduced infaunal densities seasonally in mud sediment but not in mud-sand sediment.

Avian predation increases patchiness only when the substrate is heterogeneous. In habitats devoid of relief or large-scale heterogeneity, avian predation may reduce, rather than increase, patchiness. For example, in the high intertidal zones of shores with relatively soft rocks (e.g., sandstone), clumps of mussels increase spatial heterogeneity. If avian predation prevents establishment of mussels on these surfaces, it eliminates many microhabitats for small macrofauna. Predation by birds may also reduce patchiness in soft-sediment habitats with little substrate heterogeneity. Patches with the highest prey densities often experience disproportionately high rates of predation (Goss-Custard 1980*a*, Hulscher 1982); such density-dependent predation can decrease the variability among patches. Schneider (1978) concluded that migratory shorebirds reduced variability in prey density in this manner. The density-dependent response by shorebirds may be moderated at high prey densities, however, by agonistic behavior (Goss-Custard 1980, Zwarts and Drent 1981). Nonetheless, high-density patches still experience greater predation pressure than do low-density patches.

The contribution of avian predation to patchiness also depends on the abundance, types, and distribution of other predators. A group of predators can reduce the distribution or density of its prey in three ways. (1) One predator may cause the observed reduction in prey distribution, thus being a "keystone predator" (Paine 1966). (2) Several predators together (a "multiple predator assemblage") may cause the observed reduction in prey distribution (Paine 1980). (3) The effects of different predators may be compensatory (or intercompensatory; sensu Errington 1946) so that the group can be termed a compensatory predator assemblage. Distinguishing among these alternatives is important for understanding the relative impacts of coexisting predators (e.g., Burnham and Anderson 1984).

Keystone predators can prevent the establishment of sessile prey individuals either by consuming all juveniles that settle in a patch, thereby acting as a bottleneck to maturation, or by consuming all sizes of adults so that the prey cannot escape predation by large size (Connell 1975). Oystercatchers represent the latter type of keystone predator because they eat all sizes of certain molluscs. Only exceptionally large limpets are immune to the Black Oystercatcher of the Pacific Northwest (Hartwick 1981, Frank 1982, Marsh 1984). Similarly, all adult cockles (*Macoma balthica*) are vulnerable to European Oystercatchers (O'Connor and Brown 1977, Hulscher 1982), which can thus effectively reduce their densities. Zwarts and Drent (1981) described a case in which gulls seemed to act as a keystone predator by preventing successful recruitment by *Mytilus edulis* on a Dutch mudflat. The appearance of large flocks of gulls coincided with the absence of successful mussel recruitment despite heavy spatfalls.

Evidence for compensatory predator assemblages containing birds comes from exclosure experiments in which both avian and nonavian predators can decrease the density of prey in the same patch (see Results: Importance of Invertebrate Predators; also Goss-Custard 1980). In these instances the removal of an avian predator may have an insignificant effect on the organization of a biotic community because of the compensatory effect of the other predator(s).

In contrast, a multiple predator assemblage can be effective because its members are active in different microhabitats or prey on different sizes of prey. The avian predator assemblage encountered in this study may prevent mussels from becoming established in exposed, high-intertidal patches because different species prey on different-sized individuals. Whether gulls can cause this effect in the absence of Surfbirds needs to be tested, however, before concluding that this is truly a multiple predator assemblage. My observations also suggest that the combined effects of birds and dogwhelks may prevent mussels from becoming established in large clearings in a mussel bed with exposed surfaces (where birds feed) and crevices (where dogwhelks feed). The action of such a predator assemblage could account for the slow recovery rates (or lack of recovery) noted in large areas cleared of mussels (Paine and Levin 1981).

ACKNOWLEDGMENTS

This research fulfilled part of the requirements for the Ph.D. degree, Department of Zoology, Oregon State University, Corvallis, Oregon. Numerous friends helped me during the course of this research. I am especially indebted to B. McCoy, W. Wakefield, and J. Choate for assistance with diet analyses; H. Batcheldor, S. Gaines, L. Johnson, R. Litts, B. Marsh, D. Strehlow, and T. Taylor for assistance with the exclosure experiments; and S. Bassett and T. Fitzgerald for assistance with making observations on bird usage of plots. I thank B. A. Menge, J. Lubchenco, P. W. Frank, R. T. Paine, G. W. Cox, J. A. Crawford, and an anonymous reviewer for their constructive criticisms on this manuscript. I also thank B. A. Menge and J. Lubchenco for their guidance and friendship, F. G. Ramsey and W. R. Rice for statistical counseling, S. Sargent for her typing skills, and the Depoe Bay Station of the United States Coast Guard for its rescue of the author. Financial aid was provided by the National Science Foundation (Predoctoral Dissertation Grant DEB8017449, OCE801902001 to B. A. Menge and J. Lubchenco), Frank Chapman Memorial Fund (American Museum of Natural History), Sigma Xi, the Department of Zoology at Oregon State University, and a faculty development grant from USC-Coastal Carolina College.

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