USE OF EXCLOSURES IN STUDIES OF PREDATION BY SHOREBIRDS ON INTERTIDAL MUDFLATS

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ABSTRACT.—Exclosures have been valuable tools in elucidating the role of predation in community structure. These have often been used without proper controls for the effects of the exclosures, however, and have not been designed to test the effects of different groups of predators. Here, I describe how the effects of shorebird predation on invertebrate prey in an intertidal mudflat were separated from those of fish predation by the use of an exclosure with floating sides. Also, by comparing the changes in prey density and substrate composition in a control exclosure with two sides and a top to an open area, I show that the exclosures themselves had no significant effects on the prey or the substrate. *Received 20 October 1980, accepted 17 April 1981.*

LARGE mobile predators are potentially important as determinants of benthic community structure and density in intertidal mud- and sandflats. In my study areas these are birds, fish, and in one area crabs. Several studies (Hancock and Urquhart 1967, Goss-Custard 1977, Schneider 1978, Evans et al. 1979) have determined the effects of bird predation on intertidal invertebrates, but none has separated the effects of bird predators from those of other groups of predators. Exclosures have proven to be powerful tools in the investigation of community interactions in rocky intertidal areas (Connell 1975). Their application to soft-bottom intertidal and shallow subtidal habitats, however, has been less satisfactory (Virnstein 1978, Peterson 1979). The introduction of artifacts by the exclosures is apparently more important on soft-bottom than hard substrates. Sedimentation or erosion, shading of the substrate, the use of the exclosures as refuges by some predatory species, and the possible use of a common resource by several groups of predators are factors that have to be considered before one can determine the effects of predation by a particular group of organisms in this environment. Here, I report on a refinement of the exclosure methodology, the use of exclosures with floating sides, that allowed me to separate the effects of shorebirds from those of other types of predators on intertidal mudflats in southern California. I present data to demonstrate that these manipulations were effective in preventing predation in the ways that I planned.

The common species of shorebirds on mudflats in southern California are dowitchers (*Limnodromus griseus* and *L. scolopaceus*), Western Sandpipers (*Calidris mauri*), American Avocets (*Recurvirostra americana*), and Dunlin (*Calidris alpina*). These comprise what I call the surface-feeding guild of shorebirds, i.e. they feed on prey in the top few centimeters of the substrate. Four treatments were used to separate the effects of shorebird predation from those of fish predation. These were: (1) an open control area, where all predators could feed; (2) a rigid exclosure, which excluded both fish and birds from feeding on benthic invertebrates; (3) a floating exclosure, which prevented bird predation while allowing fish to feed in the area;

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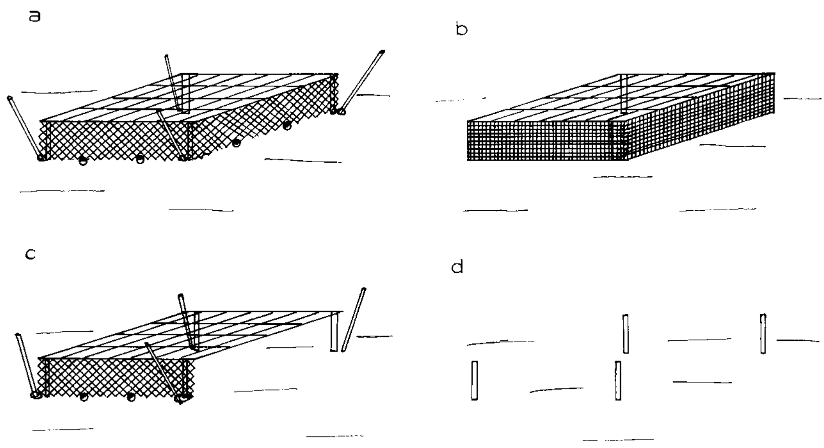

Fig. 1. A schematic drawing of the four types of treatments used in the experiment. The back two sides have not been filled in to retain clarity. (a) Floating bird exclosure with fish netting around all four sides. (b) Rigid exclosure to exclude both fish and birds with wire mesh around all four sides. (c) Control exclosure with fish netting around two sides. (d) Open area. See text for further explanation.

and (4) a control exclosure, a partial exclosure open on two sides that tested for the effects of the exclosure while allowing predators normal access.

Location and Methods

The experiments were done in two southern California lagoons, Upper Newport Bay (33°38'N, 117°53'W) and Mugu Lagoon (34°07'N, 119°07'W). Upper Newport Bay is approximately 55 km southeast of Los Angeles and has been described in a report by the California Department of Fish and Game (1970). Mugu Lagoon is approximately 65 km northwest of Los Angeles and has been the subject of several studies. The most relevant are Warme (1971), Peterson (1975), and California Department of Fish and Game (1976).

To separate the effects of bird predation from the effects of fish predation, two types of exclosures were used. An exclosure with sides that floated up when submerged prevented shorebirds, but not fish, from feeding in the area, and an exclosure with fixed rigid sides prevented both fish and birds from feeding in an area. The floating bird exclosure (Fig. 1a) was constructed of 5 × 10-cm steel mesh fencing on the top and 2.5-cm fish netting on the sides. The netting was guyed with a ring to a stake projecting out from each corner of the exclosure. Two plastic fishing floats on the bottom of each side of the netting caused the sides to float up during the high tide and fall back down when the tide was out. Guying each corner stretched the netting so that it would not catch on the top of the exclosure when it was floating. The rigid fish and bird exclosure (Fig. 1b) had the same type of top as above but had 1.3-cm mesh hardware cloth around the sides, thereby excluding large predators when the tide was in as well as out. The steel mesh on the top was large enough to allow adults of crabs (*Pachygrapsus crassipes* and *Hemigrapsus oregonensis*), which were common at Mugu Lagoon, to leave and enter the exclosures freely. Counts of the crabs found in the treatments were made at each sampling date to determine whether they were more abundant in any one of the treatments.

To make certain that the exclosure effects, independent of predation, were not altering the environment and affecting the densities and types of prey, a control exclosure, which mimicked the effect of the complete exclosures but allowed predators normal access, was used. The control exclosure (Fig. 1c) had the same fencing on the top as the complete exclosures, but only two sides had the fish netting with floats. The other two sides were left open so that predators would be able to enter under the exclosure. The open control, where all predators could feed, was marked only by stakes (Fig. 1d).

All exclosures were 1 m^2 in size and were stapled onto stakes so the tops remained approximately 25 cm above the substrate. The exclosures were checked at least every 10 days throughout the experiment and cleaned of debris and algae whenever necessary. Coverage by macroscopic algae (*Enteromorpha* sp. and *Ulva* sp.) occurred in the summer, and the exclosures sometimes had to be cleaned every 3–4 days.

TABLE 1. The number of shorebirds censused feeding under the control exclosure vs. the open control. *** = $P < 0.001$; n.s. = $P > 0.05$. Uncertainty is one standard deviation.

Shorebird species	Number of censuses present	Number in control exclosure	Number in open exclosure	Significance level
American Avocet	18	0 ± 0	5.8 ± 4.0	***
Dowitcher spp.	21	6.3 ± 5.7	6.7 ± 5.7	n.s.
Dunlin	6	4.7 ± 4.9	3.5 ± 5.8	n.s.
Western Sandpiper	13	8.9 ± 8.9	10.2 ± 9.8	n.s.

Four replicate sets of the four treatments were spread 1.5 m apart over a 40-m transect set parallel to the water so all exclosures would be at a similar tide level.

Samples were collected every 6 weeks from August 1976 to July 1977. Each exclosure was divided into 16 sections, and no section was sampled more than once. Two 100-cm^2 × 8-cm-deep cores were taken from each treatment in two sets of the exclosure treatments at each sampling date. These were divided into 0–2 and 2–8-cm sections. Only the 0–2-cm sections were considered in the experiments. This depth was chosen because it is the depth to which all the species of birds studied can penetrate. Dowitchers can feed deeper as well; 65–90% of prey density occurs in the top 2 cm, however, and the species composition does not change with depth. The sets of the exclosures from which samples were taken were alternated at each sampling to reduce the effect of the removal of the sediment from the exclosure on the prey species. The samples were sieved on a 0.5-mm mesh sieve, and what remained on the screen was preserved in a 5% formaldehyde solution. Samples were stained in a rose bengal/ethanol solution and sorted by species under a stereoscope.

A comparison of use by birds of the control exclosure and the open control was made by censusing the numbers of birds in the open areas and the control exclosures every half hour during half the tidal exposure. Censuses were made approximately every 10 days for the length of the experiment. The half of the tidal exposure censused was alternated each census. The numbers for the censuses in each day were summed. The numbers presented are for the muddy area in Upper Newport Bay, which was the area that had the largest number of birds. A two-way analysis of variance using time and treatment for the sums of each species as variables was used to determine significance.

To determine whether the exclosures had altered the sediment composition or if major changes in available food for the prey had occurred by an increase in organics, anlayses of sediment grain size and combustible organics were performed on each treatment at the beginning and the end of the experiment. For the sediment analyses, a 9-cm^2 × 1-cm-deep sample from each treatment was wet-sieved through a 0.062-mm mesh Tyler screen, and both the sieved portion and the portion retained on the screen were dried at 60°C and weighed. Changes in the percentage of sand, that portion retained by the sieve, were compared for the four treatments over time. Combustible organics were determined on a 9 cm^2 × 1 cm deep sample from each treatment. Worms were removed prior to this determination, the samples were dried at 60°C, weighed, ashed at 500°C for 24 h, and weighed again. Changes in the two weights give the amount of combustible organics. The changes in combustible organics were compared over time for the four treatments.

RESULTS

Observations at Mugu Lagoon showed that all species of fish except one large elasmobranch, the shovelnose guitarfish (*Rhinobatos productus*), freely swam in and out of the floating exclosures and the control exclosures when the tide was in. Shovelnose guitarfish occur only in the summer, when birds are absent, and were not found to feed on prey taken by the birds or on other predators that might compete with the birds. They therefore do not appear to be an important component of the system being considered here. Fish were never seen to swim in through the top of the rigid exclosure and were observed to change direction when they encountered it. Also, no fish were ever found caught in the exclosure once the tide fell. The observations were all made at Mugu Lagoon, because the water at Upper Newport

Bay was always too turbid. Because the same fish species are abundant at both locations (Quammen 1980), however, I expect that their behavior would be the same at Upper Newport Bay as at Mugu Lagoon.

The large mesh on top of the exclosures allowed crabs, another possible predator at Mugu Lagoon, easy access into and out of all the treatments. Observations made when the crabs were present showed that they could easily enter and leave the exclosures. The numbers of crabs found in each treatment at each sampling date were not significantly different, so that all treatments appear to have been equally affected by crab predation.

Except for the American Avocet, there were no significant differences in the number of birds feeding in the control exclosures compared to the open control (Table 1). Avocets are the largest bird of the species being considered and would have had to duck to enter the control exclosure. An exclosure tall enough for this species to walk under proved impossible to maintain.

Sedimentation was reduced by selecting areas where current movement, and therefore sediment movement, was low. Differential sedimentation or resuspension among treatments, as measured by the analyses of grain size and combustible organics at the beginning and at the end of the experiment, showed that no significant difference between treatments occurred over the time of the experiments. Also, the prey densities in 19 of 21 sets of samples were not significantly different in the control exclosures and the open controls. The effects of shading and sedimentation in the exclosures were not important factors affecting prey density. The exclosures, therefore, served their purpose of testing for the effects of predation by surface-feeding shorebirds and fish while minimizing the confounding effects that exclosures have been reported to have in other areas on soft-bottom substrates.

Discussion

In reviews on the use of exclosures on soft-bottom sediments, Virnstein (1978) and Peterson (1979) have pointed out several possible exclosure-related artifacts. Exclosures shade the substrate, which can cause changes in the abundance of the micro- and macro-algae, thereby affecting the food supply of the prey species. Exclosures may also reduce current flow, increasing the amount of sedimentation in the exclosure and possibly causing suffocation of larvae and suspension-feeding organisms or increasing the food supply of the deposit-feeding organisms. Strong currents may wash out holes around the stakes and thereby change the topography of the substrate within the exclosure (Hancock and Urquhart 1967). Exclosures may also provide refuges for some predatory species, especially crustaceans, from their predators, allowing abnormally high densities or unusually large individuals to occur in the exclosures (Young et al. 1976, Virnstein 1978). For these reasons, it is necessary to use a control that reproduces the effects of the exclosure but allows normal predation to occur and to have an assortment of treatments that separates the effects of the various predators. A design of an exclosure with floating sides has recently been reported by Bloom (1980). He shows that the sediment changes are minimized by using this type of exclosure. He does not report its application to predation studies or the outcome of an application, however, nor does he report the use of an exclosure control or an exclosure that worked to determine the effects of fish predation.

Only a few exclosure experiments on shorebirds have been reported; most lack adequate controls to allow unequivocal interpretation of the results. Bengston et al.

(1976) used exclosures to prevent predation by the Golden Plover (*Pluvialis apricaria*) on lumbricid worms in a hayfield in Iceland. The exclosures also prevented grazing and fertilization by manure, however, and the grass underneath the exclosures was twice as tall as outside. There were no controls for these effects. In a study of the causes of natural mortality in cockles (*Cardium edule*), Hancock and Urquhart (1967) used an exclosure to test the effect of predation by European Oystercatchers (*Haematopus ostralegus*). No control for the effect of the exclosure was used, although they did note that it collected weed and was hard to maintain in the winter storms, the time of year that the oystercatchers were present. They minimized the effects of sediment removal around the stakes by having stakes in both the open control and the experimental area and by sampling only in the center of the areas. To determine the effects of flounder predation, they used an exclosure without sides. Oystercatchers entered these exclosures, however, when the cockle density of the flat was low. Goss-Custard (1977) used exclosures to prevent waders from feeding on two bivalves and a polychaete. Movement by the bivalves prevented any effects from being detected. There was a measurable difference in the density of the polychaete inside and outside the exclosures at the end of the experiment. The exclosures were designed to permit fish and crabs to enter and leave by using string around the sides, but no report of how successful this was in keeping birds out or in letting the other predators in was given. A similar design did not keep birds from entering under the exclosures in my areas. Schneider (1978) used an exclosure to determine the impact of shorebird predation on a sandflat in Massachusetts. The effects of horseshoe crabs (*Limulus polyphemus*) and fish were not estimated independently of the effects of the birds and were assumed to be unimportant. This experiment did not use controls for the effects of the exclosures on the prey species nor for the effects of other groups of predators.

The method reported here provides a way to separate the effects of shorebird predation on benthic organisms from those of other marine predators that feed at high tide through the use of an exclosure with floating sides. This, along with the controls for the effects of the exclosures, allows for the experimental determination of the importance of shorebird predators and their effect on the intertidal community free from the artifacts caused by the exclosures and free of the confounding effects of other species. The results of these experiments are reported (Quammen MS) as part of a more general study considering the effects of crab and fish predation as well as bird predation. They show that shorebirds were seasonally important predators in the muddiest habitat but were not important predators on the mudflats with some sand, even though the potential prey were comparable in density and species composition when the birds were present. Crabs were found to be an important predator in the sandier mudflat, where they occur, on the same prey as were taken by the birds in the muddy habitat. The density of the crabs appears to be affected in turn by another shorebird, the Willet (*Catoptrophorus semipalmatus*), thus causing the density of the benthic prey in this habitat to be affected indirectly by bird predation.

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