

Prey preference and seasonal predation by oystercatchers on limpets at San Nicolas Island, California, USA

David R. Lindberg¹, Kenneth I. Warheit², James A. Estes³

¹ Museum of Paleontology, University of California, Berkeley, California 94720, USA

² Department of Paleontology, University of California, Berkeley, California 94720, USA

³ U.S. Fish and Wildlife Service, Institute of Marine Sciences and Biology Board, University of California, Santa Cruz, California 95064, USA

ABSTRACT: We present data from 2 studies on San Nicolas Island, California, USA. First, we document changes in distribution and abundance of the Island's American black oystercatcher *Haematopus bachmani* population. As the oystercatcher population increased exponentially, the birds used more of the Island's rocky intertidal communities for feeding and roosting during winter and spring. Second, we document differential predation on members of a herbivorous limpet guild (primarily *Collisella* spp.) by a wintering flock that expanded into a previously unexploited portion of the island. For 4 of the 5 prey species (*Collisella digitalis*, *C. scabra*, *C. limatula*, *Lottia gigantea*) there was evidence for differential predation, either selection or avoidance, by the oystercatchers. However, no single causal mechanism explains the pattern for all 4 species. The combined phenomena of variation in oystercatcher distribution in space and time and differential predation on members of the patellacean limpet guild may have important implications for the ecology of rocky intertidal communities.

INTRODUCTION

Oystercatcher (Genus *Haematopus*) predation and its role in structuring intertidal communities has been increasingly studied during the past few years (O'Connor & Brown 1977, Castilla 1981, Frank 1982, Hockey & Branch 1984, Levings et al. 1986, Marsh 1987). These and other workers have qualitatively described and quantified interactions between birds and their invertebrate prey species. Prey species typically are important space occupiers (sessile bivalves) or herbivores (patellacean and siphonarian limpets) (Table 1), and the above studies have demonstrated or predicted the cascading effects of oystercatcher predation through other trophic levels in the intertidal community. The above studies and others in other habitats (Table 1) considered one or the other of 2 distributional groupings exhibited by foraging oystercatchers: flocks of numerous individuals (non-territorial) or breeding pairs (territorial) (Table 1).

During the non-breeding season, oystercatchers may form large foraging flocks. Wintering flocks of American black oystercatchers *Haematopus bachmani* may

contain as many as 90 birds (Hartwick & Blaylock 1979) and can exert an intense, but temporally sporadic, predatory effect on localized sections of rocky intertidal shoreline (Frank 1982; this paper). During the breeding season, the birds pair and defend territories in which they feed and raise their chicks (Legg 1954, Helbing 1977, Morrell et al. 1979). Predation effects within breeding territories are thought to be less intense than those caused by wintering flocks because bird densities are lower, but are more consistent because of the birds' constant presence. Thus, patterns of black oystercatcher predation can occur on widely differing temporal and spatial scales.

In this paper we present data from 2 studies on San Nicolas Island, Ventura County, California, USA (33° 16' N, 119° 30' W). The first study documents changes in distribution and abundance associated with an exponential increase in the Island's American black oystercatcher population. The second study documents differential predation on an herbivorous limpet guild over a 3 d period by a wintering flock of oystercatchers expanding into new habitat. Based on the combined data from these 2 studies, we suggest that American

Table 1. Summary of previous oystercatcher studies showing type of groupings of birds and prey species

Source	<i>Haematopus</i> sp.	Grouping	Molluscan prey
Drinnan 1957	<i>H. ostralegus</i>	Flock	Cockles
Drinnan 1958	<i>H. ostralegus</i>	Flock	Mussels
Norton-Griffiths 1967	<i>H. ostralegus</i>	Flock	Mussels
Feare 1971	<i>H. ostralegus</i>	Flock	Limpets
Thorson 1971	<i>H. ostralegus</i>	Flock	Cockles
Lewis & Bowman 1975	<i>H. ostralegus</i>	Flock	Limpets
Sutherland 1982a, b, c	<i>H. ostralegus</i>	Flock	Cockles
Goss-Custard et al. 1982a, b, 1984	<i>H. ostralegus</i>	Flock	Mussels
Levings et al. 1986	<i>H. ostralegus</i>	Pair	Limpets, snails
Webster 1941	<i>H. bachmani</i>	Pair	Mussels, limpets
Legg 1954	<i>H. bachmani</i>	Pair	Limpets
Hartwick 1976, 1978, 1981	<i>H. bachmani</i>	Pair	Mussels, limpets
Helbing 1977	<i>H. bachmani</i>	Pair	Mussels, limpets
Morrell et al. 1979	<i>H. bachmani</i>	Pair	Mussels, limpets
Frank 1982	<i>H. bachmani</i>	Flock	Limpets
Marsh 1987	<i>H. bachmani</i>	Flock	Limpets
Castilla 1981	<i>H. ater</i>	NA	Limpets, snails
Baker 1974	<i>H. ostralegus</i>	Flock	Cockles
Baker 1974	<i>H. unicolor</i>	NA	Limpets, chitons, mussels
Parry 1982	<i>H. fuliginosus</i>	Flock	Limpets, snails
Hockey & Branch 1984	<i>H. moquini</i>	Pair	Limpets

NA: not available

black oystercatchers can have a substantial impact on rocky intertidal communities, but that the impact varies because of differential predation among limpet species, and because of the seasonality, intensity and frequency of oystercatcher predation.

SPECIES, STUDY AREA AND METHODS

American black oystercatchers *Haematopus bachmani* are found on rocky shores on the northeastern Pacific Ocean from the western Aleutian Islands, Alaska (Ridgeway 1919) to central Baja California, Mexico (Kenyon 1949). The birds breed just above the upper limits of the intertidal zone, and except for the northern elements of the population, are non-migratory. Breeding territories are occupied and defended from May to September in California; in areas of high oystercatcher densities, territories may be occupied and defended for most of the year (Warheit unpubl. data). During autumn and winter, non-territorial birds form flocks. American black oystercatchers feed on various intertidal invertebrates, predominately mussels and gastropods. Between 40 and 50 % of the diet of adult birds consists of herbivorous molluscs – mainly limpets (Webster 1941, Hartwick 1976).

The distribution, abundance and recent history of oystercatchers on San Nicolas Island (Fig. 1) were assembled from published bird censuses and surveys, personal communications and, since late 1979, our own

observations. Data collected since 1979 include both occasional sightings of oystercatchers near permanent study sites, and since 1981, regular censuses conducted on foot at approximately 2 mo intervals, of all rocky shores around the western side of the Island between Thousand Springs and Dutch Harbor (Fig. 1).

The site of the predation event we describe was a 10 × 20 m intertidal sandstone bench on the southeastern coast of San Nicolas Island (Study Site 1 on Fig. 1). The bench is flat, sloping seaward at less than 5°. Thus, all invertebrates on the bench are accessible to oystercatchers except a few that are found in fissures in the substratum. The bench was divided into 5 zones that approximated species groupings from the high to low intertidal. Three permanent 0.25 m² quadrats were marked in each zone by 2 stainless steel bolts drilled and cemented into the substratum. All animals in the subplots were counted on 25 Feb 1984.

The site was visited by a wintering flock of oystercatchers on 26 Feb and again on 28 Feb 1984. Oystercatchers previously had not been seen in this area during 4 yr of bimonthly monitoring. Upon discovering foraging oystercatchers at the site on 26 Feb 1984, we collected all prey shells, and identified and measured them in the laboratory. On 27 Feb 1984 all remaining specimens of the gastropod limpet *Lottia gigantea* were removed from the bench and measured (as part of an ongoing manipulative experiment unrelated to our oystercatcher work). Photographs were taken of each quadrat on 28 Feb 1984 after the second

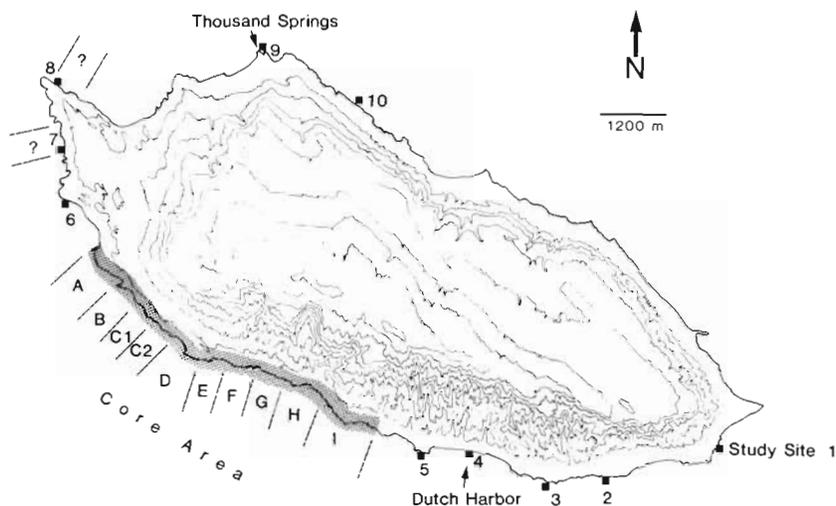


Fig. 1 San Nicolas Island, California, USA. (■) Rocky intertidal localities where black oystercatchers were observed (1979 to 1984). A to I: approximate boundaries of black oystercatcher breeding territories within core area (stippled); ?: possible new breeding territories; 1 to 10: permanent intertidal study sites. Contour interval = 15 m

visit by the oystercatchers. Predation rates were based on the number of shells present on the bench, the number of birds observed in the area and the maximum exposure time for the bench based on its tidal height.

All limpet species preyed on by the oystercatchers are important components of rocky intertidal communities between southern Baja California, Mexico and northern California (Abbott & Haderlie 1980, Carlton 1981, and references therein). *Collisella digitalis* and *C. scabra* are abundant in the high intertidal zone and affect algal cover (Castenholz 1961, Dayton 1971, Stimson & Black 1975, Sousa 1984); *C. digitalis* clusters at low tide (Millard 1968) while *C. scabra* returns to specific home sites (Hewatt 1940). *Collisella limatula* and *C. pelta* are mid-intertidal zone species, and like the high intertidal species, are important grazers on a variety of algae (Craig 1968, Eaton 1968). *Lottia gigantea* is a territorial species (Stimson 1970, 1973) and exerts an exceptionally strong influence on rocky intertidal community structure at San Nicolas Island (Lindberg et al. 1984, Lindberg & Estes unpubl. data).

RESULTS

The number of American black oystercatchers on San Nicolas Island per kilometer of rocky intertidal habitat, compared to the other northern Channel Islands, has been remarkably low (Warheit et al. 1984), probably for many years. The shorebird counts of L. Jones (1974 to 1978; pers. comm.) and Sowls et al. (1980) list fewer than 5 oystercatchers on the island. However, in 1981, the number of oystercatchers began to increase rapidly (Fig. 2). Moreover, they began to form wintering flocks that were seen in areas well outside what we will subsequently call the 'core area', which

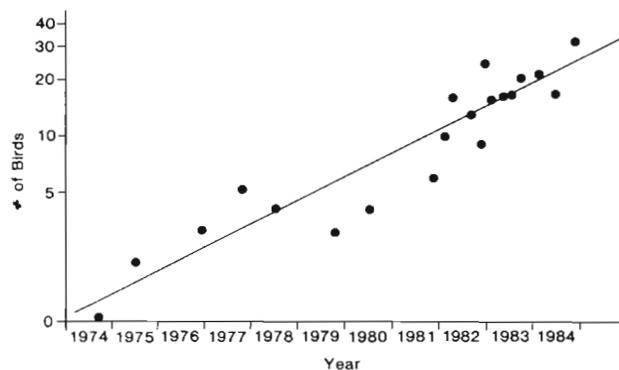


Fig. 2. *Haematopus bachmani*. Numbers of American black oystercatchers on San Nicolas Island, California, between 1974 and 1984. $r = 0.9365$

contains most of the breeding territories (Fig. 1); human disturbance in this area is minimal because of the lack of roads into this portion of the island.

The first flock was sighted west of the core area during winter of 1981. In 1982, flocks were seen at sites west of the core area more frequently than at sites to the east (Fig. 3). In 1983, flocks were observed both east and west of the core area at all times of the year except during the breeding season (Fig. 3). For the first 9 mo of 1984, flock sightings were more frequent than ever before and, for the first time, continued into the breeding season (Fig. 3). The occurrence of flocks during the breeding season may mark the saturation of the core area with breeding territories and the subsequent exclusion of non-breeding birds from the area.

During 1981 through 1984, wintering flocks were recorded at 10 sites shown on Fig. 1 at different frequencies. Oystercatchers were seen at half of the sites 5 times or more, while they were seen at 4 of the sites only once (Fig. 4).

Besides the increasing frequency of wintering flocks

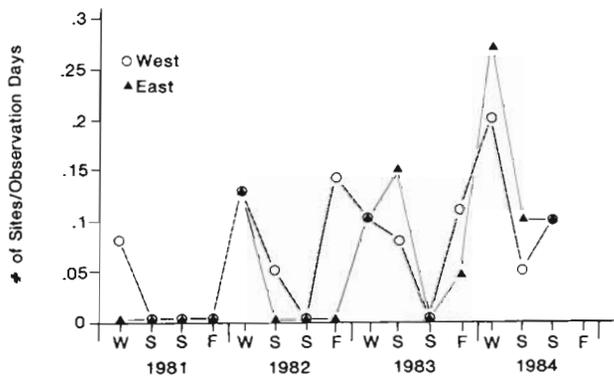


Fig. 3. *Haematopus bachmani*. Seasonal occurrence of black oystercatcher flocks at rocky intertidal localities on either side of the breeding core area (corrected for the number of observation days per season). East: Study Sites 1 to 5; west: Study Sites 6 to 10 on Fig. 1

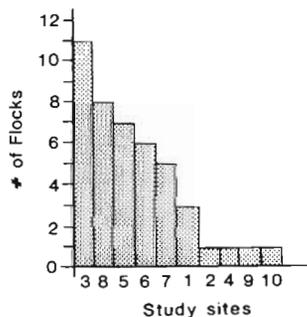


Fig. 4. *Haematopus bachmani*. Number of sightings of oystercatcher flocks at 10 rocky intertidal localities on San Nicolas Island, California, USA (1979 to 1984)

on the island, the number of birds per flock also increased. In 1981 the largest flock observed consisted of only 6 birds ($\bar{x} = 3.0 \pm 1.7$ SD, $n = 4$); by 1984 flocks of up to 15 birds were observed ($\bar{x} = 5.2 \pm 3.7$ SD, $n = 10$). While this latter number is comparable to flocks observed by Frank (1982) on rocky shores in Oregon, it is far smaller than the 20 to 30 bird wintering flocks that occur on Southeast Farallon Island, San Francisco County, California, USA (Morrell et al. 1979).

Thus, oystercatcher populations on San Nicolas Island were low for most of the 1970's (0 to 4 birds). By the mid- to late 1970's, the population began increasing. As population size increased, flocks visited more rocky intertidal sites, and new breeding sites were established at the west end of the Island (Fig. 1). Current numbers (as of December 1986) include 12 to 15 breeding pairs and wintering flocks of up to 15 birds.

The distribution, densities, and estimates of population sizes for limpet species at our study site the day before the first predation event are presented in Fig. 5 and Table 2. The low density of *Lottia gigantea* on the bench was not natural. As part of an ongoing manipulative experiment, this bench has been periodi-

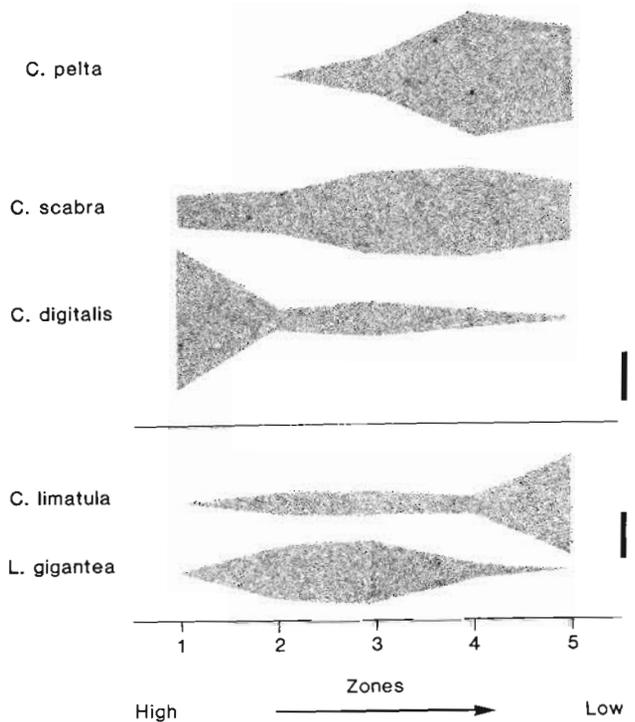


Fig. 5. Mean densities of patellacean limpet species on bench 24 h before predation event. Upper scale bar = 80 limpets m^{-2} ; lower scale bar = 1 limpet m^{-2}

Table 2. *Haematopus bachmani*. Summary of American black oystercatcher predation of intertidal patellacean limpets (*Collisella* spp. and *Lottia gigantea*) on 10 m \times 20 m rock bench at San Nicolas Island, California, USA, in 1984

Prey species	Est. pop. size, 25 Feb*	Rel. abund. on bench (%)	No. eaten		% population eaten		Rel. abund in diet		Total no. of limpets removed	Mean size (mm)
			26 Feb	28 Feb	26 Feb	28 Feb	26 Feb %	28 Feb %		
<i>C. digitalis</i>	13280	26.31	208	61	1.56	0.46	54.37	61.61	269	14.16 \pm 1.87
<i>C. scabra</i>	19360	38.37	2	0	0.01	0.00	0.52	0.00	2	17.03 \pm 0.25
<i>C. pelta</i>	17440	34.56	148	37	0.84	0.21	38.94	37.37	185	15.45 \pm 2.77
<i>C. limatula</i>	320	0.63	18	0	5.62	0.00	4.73	0.00	18	20.53 \pm 2.52
<i>L. gigantea</i>	56	0.11	4	1	7.14	1.92	1.05	1.01	5	26.20 \pm 7.12
Totals	50456		380	99					479	

Nos. for *L. gigantea* are results of complete censuses and are not estimates

cally (6 times annually) cleared of *L. gigantea* since June 1980. Thus, the *L. gigantea* present in February 1984 had been previously overlooked, recruited or immigrated to the bench since the last clearing in October 1983, and the size frequency distribution of the population was therefore strongly skewed towards smaller size classes (\bar{x} = about 19 mm).

On 26 Feb 1984 at 1230 h, 3 oystercatchers were seen flying away from the study site. On arrival at the site, 3 more birds were seen. Empty limpet shells were found littering the study site. Because of an unusual combination of low tides (-0.1 m) and the absence of ocean swells, the bench was not awash and shells were found at all tidal heights. Based on the height of the upper portion of the bench ($+0.6$ m to $+0.3$ m) and the tidal curve for 26 Feb 1984, the birds would have had a maximum of 2.7 h in which to feed at the higher levels of the bench. If all 6 birds fed for the entire 2.7 h, the approximate average feeding rate would be 0.39 limpets min^{-1} per bird. We did not observe oystercatchers at the study site on 28 Feb. However, we infer they fed because the sea was calm and the bench was dry and littered with empty shells. The time available for foraging was almost identical to that of 26 Feb based on the tidal curve and our arrival time at the site.

Because we had sampled the fixed quadrats on the bench on 25 Feb, we were able to quantify limpet reductions from the 26 and 28 Feb predation events (Table 2). Based on our shell collections, a minimum of 479 limpets were removed from the bench during the 2 events. Most of the empty shells were found in Zones 2 and 3. Prey ranged in shell length from 9.25 mm to 35.3 mm; *Collisella digitalis* was the most common prey item and *C. scabra* was the rarest.

There was no difference in relative abundance of limpet species eaten between 26 and 28 Feb (2×5 contingency table; $\chi^2_4 = 5.690$, $p = 0.223$) (Table 2). Overall, the prey frequency consumed by oystercatchers was significantly different from the frequency distribution of limpet species on the bench (χ^2 goodness of fit; $\chi^2_4 = 95.29$, $p < 0.0001$; all species pooled for 26 and 28 Feb). Except for *Collisella pelta* (χ^2 goodness of fit; $\chi^2_1 = 0.789$, $p > 0.10$), the number of each species eaten was not related to that species' relative abundance on the bench before the predation event on either day. The data presented in Table 2 indicate that *Lottia gigantea* (χ^2 goodness of fit; $\chi^2_1 = 16.31$, $p < 0.005$), *C. limatula* (χ^2 goodness of fit; $\chi^2_1 = 27.28$, $p < 0.005$), and *C. digitalis* (χ^2 goodness of fit; $\chi^2_1 = 79.01$, $p < 0.005$) were taken at frequencies much higher than expected, while *C. scabra* (χ^2 goodness of fit; $\chi^2_1 = 76.00$, $p < 0.005$) was taken at frequencies much lower than expected.

Lottia gigantea, the rarest but largest limpet species, sustained a larger percentage loss of its population

than all the other limpet species combined (Table 2). Moreover, mostly large *L. gigantea* were taken; the mean length of the study site population of *L. gigantea* was $19.3 \text{ mm} \pm 6.3 \text{ SD}$ ($n = 56$), while the mean length of the eaten specimens was $26.2 \text{ mm} \pm 7.12 \text{ SD}$ ($n = 5$) (Mann-Whitney U, $p < 0.05$). If the data in Table 2 for *L. gigantea* are recalculated to reflect the population reduction of those size classes subject to predation (i.e. >18.0 mm long), the total decline would be 17.0 % rather than 7.14 %.

Collisella digitalis had the smallest mean size of any limpet species, was the third most abundant, and yet accounted for over 50 % of the limpets eaten (Table 2). While this pattern appears enigmatic compared to the selection exhibited by the birds for the large limpets *Lottia gigantea* and *C. limatula*, it is interpretable if physical and behavioral factors are also considered. *C. digitalis* is most abundant in the upper zones (Fig. 5), and the upper zones provide the birds the longest exposure time in which to feed. Moreover, because *Digitalis* aggregates at low tide (Millard 1968, Willoughby 1973), locating one limpet may be equivalent to locating many (Fig. 6A).

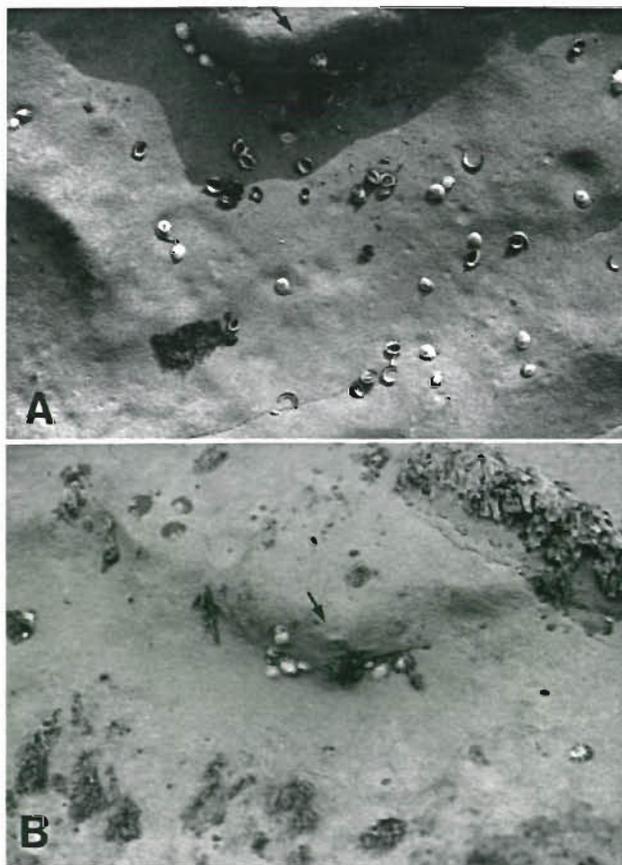


Fig. 6. *Collisella digitalis*. (A) Shells *in situ* after concentrated predation on an aggregation of individuals clustered along a small ridge (arrow) on the bench. (B) The same area 178 d later

Although *Collisella scabra* was the most abundant limpet species on the bench and the third largest in mean size, it was least selected by the oystercatchers. Only 2 individuals were eaten. Oystercatchers have more difficulty dislodging *C. scabra* from the substratum (i.e. greater handling time) than the other limpet species (Warheit pers. obs.). *C. scabra* is the only limpet species in the study area that forms a complex home depression, and because of this, the shell margin is placed below the substratum. This behavior restricts access to the shell margin by oystercatchers and other predators (Lindberg & Dwyer 1983, Kunz & Connor 1986), and we believe that oystercatchers avoid *C. scabra* for this reason.

DISCUSSION

Our results suggest that varying distributions of foraging oystercatchers in time and space, coupled with the birds' differential foraging on species of patellacean limpets, could be an important mechanism for producing patchy mosaics of species in rocky intertidal landscapes (Paine & Levin 1981). Moreover, because the interactions between oystercatchers and limpets occur on widely varying scales of space (from islands to an individual limpet's home range or cluster) and time (from season to a single low tide cycle), any patterns produced by oystercatcher foraging might vary greatly both within and between habitats, and thus be difficult to recognize or predict (see also Marsh 1987).

A wintering flock can remove significant numbers of invertebrates from the community during a single tidal cycle. At San Nicolas Island, a minimum of 380 limpets were removed from the community in less than 2.7 h. The estimated average feeding rate of 0.39 limpets min^{-1} per bird favorably compares with the 0.37 limpets min^{-1} per bird average feeding rate that Warheit (unpubl. data) has observed on Southeast Farallon Island, California and the 0.35 limpets min^{-1} per bird average feeding rate Frank (1982) observed for flocks in Oregon. However, Frank also observed individual day feeding rates as high as 0.97 limpets min^{-1} per bird. Using values from the San Nicolas predation event and feeding rate data from above, we estimate that a flock of 10 birds could remove between 599 and 1571 limpets during each low tide foraging period ($2.7 \text{ h} \times 10 \text{ birds} \times 0.37 \text{ limpets min}^{-1}$ per bird and $0.97 \text{ limpets min}^{-1}$ per bird); this form of oystercatcher predation would be primarily limited to the 7 mo non-breeding season. In comparison, an average of only 224 limpets d^{-1} would be eaten by adults and a single chick between hatching and fledging (a 36 to 45 d period) (value calculated from Helbing 1977, p. 122 and Hart-

wick 1976, Fig. 2; Warheit unpubl. data). Thus, seasonal differences in the behavior of American black oystercatchers could create substantial differences in predation pressure between sites visited only by wintering flocks and those sites used as breeding territories.

Black oystercatcher predation alters population densities of interacting species within a habitat because of the birds' differential predation on certain members of the patellacean limpet guild. For 4 of the 5 prey species (*Collisella digitalis*, *C. scabra*, *C. limatula*, *Lottia gigantea*), there is evidence for either selection or avoidance by oystercatchers. However, no single causal mechanism explains the pattern. For *C. scabra* homing behavior and the formation of a home depression appears to increase handling time to such an extent that this large and abundant species is avoided or consumed less successfully. For *C. pelta*, the lack of homing and aggregating behaviors, combined with its lower intertidal distribution and therefore shorter exposure time, probably results in this species being of intermediate rank. For *C. digitalis*, high abundance in the area with the longest exposure time, combined with its aggregating behavior, may result in this smallest species being most common in the oystercatcher's diet. Harrold (1982) has reported similar behavioral roles in selection hierarchies by sea stars for kelp forest snails.

Past studies have also demonstrated that black oystercatchers can substantially reduce numbers of patellacean limpets (Hartwick 1981, Frank 1982, Hockey & Branch 1984, Marsh 1987). Several of these studies showed that the birds' removal of limpets enhances algal growth, especially that of early successional species (Frank 1982, Hockey & Branch 1984). These results are not surprising because the removal of limpets from experimental plots leads to increased algal growth (Lodge 1948, Dayton 1971, Sousa 1979, 1984, Branch 1981 and references therein, Lubchenco & Gaines 1981 and references therein, Underwood & Jernakoff 1981, Robles 1982, Cubit 1984). However, the phenomena of selective predation on members of the patellacean limpet guild and variation in oystercatcher distribution in space and time have implications for the ecology of rocky intertidal communities that extend beyond trophic interactions.

Oystercatcher predation influences species interactions in rocky intertidal communities by selectively removing certain species from the community or patch. One of the most marked changes that we observed following the oystercatcher predation at Site 1 was the replacement of *Collisella digitalis* by *C. scabra* as the most abundant species in the mid-intertidal of the bench (Estes & Lindberg in press). This change was exemplified by events that occurred along a small ridge that projected slightly above the bench surface. This

surface had been dominated by aggregations of *C. digitalis* since the beginning of our study in February 1980. On 26 Feb 1984, this microhabitat was the site of concentrated predation and more than 50 % of the *C. digitalis* were removed, whereas no *C. scabra* were taken (Fig. 6A). Between March and June, perhaps due to further depredations by oystercatchers, all but one *C. digitalis* disappeared, and *C. scabra*, which initially made up less than 5 % of the limpet assemblage, dominated the patch by comprising 90 % of the individuals (Fig. 6B). Although it is not known whether the subsequent reduction of *C. digitalis* in the patch after the predation event (March to June) resulted from additional visits by wintering flocks, from interactions between *C. digitalis* and *C. scabra* (Haven 1971, 1973), or from some other disturbance, the selective removal of *C. digitalis* by oystercatchers marked the beginning of a complete change in species composition in the patch. Moreover, because *C. scabra* actively defends its home depression (Lindberg pers. obs.), the probability of *C. digitalis* regaining its numerical dominance in this patch without some future disturbance to *C. scabra* is probably low.

The removal of *Lottia gigantea* from rocky intertidal communities by oystercatchers has special implications for rocky intertidal community dynamics. *L. gigantea* is a territorial limpet (Galbraith 1965, Wright 1982) and individuals maintain territories free of most macroalgae and other invertebrate species (Stimson 1970, 1973). Because of its territorial behavior, the consequences of removing *L. gigantea* from the rocky intertidal community are disproportionately large in comparison with the removal of an equal biomass of non-territorial limpet species (Estes & Lindberg in press, Lindberg & Estes unpubl. data).

The seasonality of limpet removal by oystercatchers can also affect recruitment patterns and thereby influence subsequent interactions of species in an area. Lowering the density of adult limpets, particularly larger individuals and territorial species, can substantially increase survival of newly-recruited limpets (Stimson & Black 1975, Branch 1981, Lindberg & Estes unpubl. data). All limpet species discussed herein spawn in the late winter or early spring (Fritchman 1962). At this same time, wintering flocks of oystercatchers are selectively removing larger individuals and territorial limpet species from the habitat into which the larvae will settle. Moreover, because some sites will be visited by flocks numerous times while other sites will be visited only once or not at all, different recruitment patterns could result along a coastline experiencing the same physical regime. Ultimately, these different recruitment patterns could influence community structure. This scenario has the same outcome as one proposed by Underwood & Denley (1984,

p. 178) who argued that the 'vagaries of larval settlement' contribute substantially to species composition, and therefore the type and intensity of interactions in a community. In our scenario, the vagaries of patch availability caused by oystercatcher predation further enhance and complicate larval settlement patterns.

Acknowledgements. We thank G. Branch, P. Frank, S. Levings, W. Sousa and 3 anonymous reviewers for comments on the manuscript; T. Hahn, T. Pearce and B. Roth for assistance in the field; and L. Jones and G. VanBlaricom for access to their field notes and other unpublished information. We are grateful to the U.S. Navy Pacific Missile Test Center, Pt. Mugu, California, and especially to R. Dow, for access to San Nicolas Island. This work was supported by the U.S. Fish and Wildlife Service.

LITERATURE CITED

- Abbott, D. P., Haderlie, E. C. (1980). Prosobranchia: marine snails. In: Morris, R. H., Abbott, D. P., Haderlie, E. C. (ed.) Intertidal invertebrates of California. Stanford Univ. Press, Stanford, p. 230-307
- Baker, A. J. (1974). Prey-specific feeding methods of New Zealand oystercatchers. *Notornis* 21: 219-233
- Branch, G. M. (1981). The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanogr. mar. Biol. A. Rev.* 19: 235-380
- Carlton, J. T. (1981). Bibliography of Pacific coast Acmaeidae. In: Lindberg, D. R. *Acmaeidae: Gastropoda, Mollusca*. Boxwood Press, Pacific Grove, p. 106-119
- Castenholz, R. W. (1961). The effects of grazing on marine littoral diatom populations. *Ecology* 42: 783-794
- Castilla, J. C. (1981). Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II. Depredadores de alto nivel trófico. *Medio Ambiente* 5: 190-215
- Craig, P. C. (1968). The activity pattern and food habits of the limpet *Acmaea pelta*. *Veliger* 11 (Suppl.): 13-19
- Cubit, J. D. (1984). Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65: 1904-1917
- Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389
- Drinnan, R. E. (1957). The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*). *J. Anim. Ecol.* 26: 441-469
- Drinnan, R. E. (1958). The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. *Fishery Invest., Lond., Ser. II:* 1-15
- Eaton, C. M. (1968). The activity and food of the file limpet, *Acmaea limatula*. *Veliger* 11 (Suppl.): 5-12
- Estes, J. A., Lindberg, D. R. (in press). Multi-causal disturbances and the non-equilibrium structure of a rocky intertidal community at San Nicolas Island, California. *Proceedings 3rd California Islands Symposium, Santa Barbara Mus. Nat. Hist., Santa Barbara*
- Feare, C. J. (1971). Predation of limpets and dogwells by oystercatchers. *Bird Stud.* 18: 121-129
- Frank, P. W. (1982). Effects of winter feeding on limpets by black oystercatchers, *Haematopus bachmani*. *Ecology* 63 (5): 1352-1362

- Fritchman, H. K., III (1962). A study of the reproductive cycle in the California Acmaeidae (Gastropoda). Part IV Veliger 4: 134-139
- Galbraith, R. T. (1965). Homing behavior in the limpets *Acmaea digitalis* and *Lottia gigantea*. Am. Midl. Nat. 74: 245-246
- Goss-Custard, J. D., le V dit Durell, S. E. A., McGroarty, S., Reading, C. J. (1982a). Use of mussel *Mytilus edulis* beds by oystercatchers *Haematopus ostralegus* according to age and population size. J. Anim. Ecol. 51: 543-554
- Goss-Custard, J. D., le V dit Durell, S. E. A., Ens, B. J. (1982b). Individual differences in aggressiveness and food stealing among wintering oystercatchers *Haematopus ostralegus* L. Anim. Behav. 30: 917-928
- Goss-Custard, J. D., Clarke, R. T., le V dit Durell, S. E. A. (1984). Rate of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe Estuary. J. Anim. Ecol. 53: 233-245
- Harrold, C. (1982). Escape responses and prey availability in a kelp forest predator-prey system. Am. Nat. 119: 132-135
- Hartwick, E. B. (1976). Foraging strategy of the black oyster catcher (*Haematopus bachmani* Audubon). Can. J. Zool. 54: 142-155
- Hartwick, E. B. (1978). Some observations on foraging by black oystercatchers (*Haematopus bachmani* Audubon). Syesis 11: 55-60
- Hartwick, E. B. (1981). Size gradients and shell polymorphism in limpets with consideration of the role of predation. Veliger 23: 254-264
- Hartwick, E. B., Blaylock, W. (1979). Winter ecology of a black oystercatcher population. Stud. Avian Biol. 2: 207-215
- Haven, S. B. (1971). Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis*. Veliger 13: 231-248
- Haven, S. B. (1973). Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. Ecology 54: 143-151
- Helbing, G. L. (1977). Maintenance activities of the black oystercatcher, *Haematopus bachmani* Audubon, in northern California. M.Sc. thesis, Humboldt State Univ., Arcadia
- Hewatt, W. G. (1940). Observations on the homing limpet, *Acmaea scabra* Gould. Am. Midl. Nat. 24: 205-208
- Hockey, P. A. R., Branch, G. M. (1984). Oystercatchers and limpets: impact and implications. A preliminary assessment. Ardea 72: 199-206
- Kenyon, K. W. (1949). Observations on behavior and populations of oystercatchers in lower California. Condor 51: 193-199
- Kunz, C., Connor, V. M. (1986). Roles of the home scar of *Collisella scabra* (Gould). Veliger 29: 25-30
- Legg, K. (1954). Nesting and feeding of the black oystercatcher near Monterey, California. Condor 56: 359-360
- Levings, S. C., Garrity, S. D., Ashkenas, L. R. (1986). Feeding rates and prey selection of oystercatchers in the Pearl Islands of Panama. Biotropica 18: 62-71
- Lewis, J. R., Bowman, R. S. (1975). Local habitat-induced variations in the population dynamics of *Patella vulgata* L. J. exp. mar. Biol. Ecol. 17: 165-203
- Lindberg, D. R., Dwyer, K. R. (1983). The topography, formation and role of the home depression of *Collisella scabra* (Gould). Veliger 25: 229-234
- Lindberg, D. R., Estes, J. A., Warheit, K. I. (1984). Intertidal community structure in central and southern California: the interaction between human disturbance, bird predation and limpet territoriality. Am. Malacol. Bull. 2: 80
- Lodge, S. M. (1948). Algal growth in the absence of *Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man. Proc. Liverpool biol. Soc. 56: 78-83
- Lubchenco, J., Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. Ann. Rev. Ecol. Syst. 12: 405-437
- Marsh, C. P. (1987). Impact of avian predators on high intertidal limpet populations. J. exp. mar. Biol. Ecol. 104: 185-201
- Millard, C. S. (1968). The clustering behavior of *Acmaea digitalis*. Veliger 11 (Suppl.): 45-51
- Morrell, S. H., Huber, H. R., Lewis, T. J., Ainley, D. G. (1979). Feeding ecology of black oystercatchers on South Farallon Island, California. Stud. Avian Biol. 2: 185-186
- Norton-Griffiths, M. (1967). Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. Ibis 109: 412-424
- O'Connor, R. J., Brown, R. A. (1977). Prey depletion and foraging strategy in the oystercatcher *Haematopus ostralegus*. Oecologia (Berl.) 27: 75-92
- Paine, R. T., Levin, S. A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51: 145-178
- Parry, G. D. (1982). The evolution of the life histories of four species of intertidal limpets. Ecol. Monogr. 52: 65-91
- Ridgeway, R. (1919). The birds of North and Middle America. U.S. Nat. Mus. 50 (No. 8): 1-852
- Robles, C. (1982). Disturbance and predation in an assemblage of herbivorous Diptera and algae on rocky shores. Oecologia (Berl.) 54: 23-31
- Sousa, W. P. (1979). Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227-254
- Sousa, W. P. (1984). The role of disturbance in natural communities. Ann. Rev. Ecol. Syst. 15: 353-391
- Sowls, A. L., DeGange, A. R., Nelson, T. W., Lester, G. S. (1980). Catalog of California Seabird colonies. U.S. Dept. Interior, Fish and Wildlife Service, Biol. Prog. FWS/OBS 37/80
- Stimson, J. (1970). Territorial behavior of the owl limpet *Lottia gigantea*. Ecology 51: 113-118
- Stimson, J. (1973). The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). Ecology 54: 1020-1030
- Stimson, J., Black, R. (1975). Field experiments on population regulation in intertidal limpets of the genus *Acmaea*. Oecologia (Berl.) 18: 111-120
- Sutherland, W. J. (1982a). Do oystercatchers select the most profitable cockles? Anim. Behav. 30: 857-861
- Sutherland, W. J. (1982b). Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. I. The cockle population. J. Anim. Ecol. 51: 481-489
- Sutherland, W. J. (1982c). Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. J. Anim. Ecol. 51: 491-500
- Thorson, G. (1971). Life in the sea. McGraw-Hill, New York
- Underwood, A. J., Denley, E. J. (1984). Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D. R., Jr., Simberloff, D., Abele, L. G., Thistle, A. B. (ed.) Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton, p. 151-197
- Underwood, A. J., Jernakoff, P. (1981). Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia (Berl.) 48: 221-233

-
- Warheit, K. I., Lindberg, D. R., Boekelheide, R. J. (1984). Pinniped disturbance lowers reproductive success of black oystercatcher *Haematopus bachmani* (Aves). Mar Ecol. Prog. Ser. 17: 101–104
- Webster, J. D. (1941). Feeding habits of the black oystercatcher. Condor 43: 175–180
- Willoughby, J. W. (1973). A field study on the clustering and movement behavior of the limpet *Acmaea digitalis*. Veliger 15: 223–230
- Wright, W. G. (1982). Ritualized behavior in a territorial limpet. J. exp. mar. Biol. Ecol. 60: 245–251

This article was submitted to the editor; it was accepted for printing on May 4, 1987