

## ABALONES, SHELLS, AND SEA OTTERS: DYNAMICS OF PREY POPULATIONS IN CENTRAL CALIFORNIA<sup>1</sup>

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**Abstract.** Densities, sizes, and species composition of abalones, *Haliotis rufescens*, *H. walalensis*, and *H. kamtschatica*, remained stable from 1972 to 1981 within a sea otter habitat in central California. Almost all censused abalones were in crevices, with densities averaging 1.8 animals/10 m<sup>2</sup>. Live abalones and empty abalone shells resulting primarily from predation by sea otters averaged 7.5 and 9 cm in length, respectively. In contrast, out of the range of sea otters, live abalones were over twice as large and were numerous outside crevices (when protected from human predation). At our study site within their range, sea otters selected abalones larger than were proportionately available in crevices, and they broke many large shells with stone tools. An average of 55 freshly produced empty abalone shells, equivalent to ≈20% of the crevice population of live abalones, were found each month in our study area over a 12-mo period. Indirect calculations of feeding rates of sea otters also indicated a high production rate of abalones, as did observations of abalones in mapped crevices. The high production rates of abalones must result from high rates of juvenile recruitment and growth, and are indicative of a highly dynamic population, with a turnover time of 1-3 yr.

**Key words:** abalones; crevices; *Enhydra lutris*; *Haliotis* spp.; population dynamics; predator-prey interactions; production rates; refuge; sea otters.

### INTRODUCTION

Sea otters (*Enhydra lutris*) in central California prey on a wide variety of benthic invertebrates, especially abalones (*Haliotis* spp.), sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*), kelp crabs (*Pugettia producta*), rock crabs (*Cancer antennarius*), turban snails (*Tegula* spp.), octopus (*Octopus* spp.), and clams (*Tivela stultorum*, *Saxidomus nuttalli*, *Tressus nuttalli*; Ebert 1968, Vandevere 1969, Wild and Ames 1974, Loughlin 1977, Stephenson 1977, Costa 1978, Hines and Loughlin 1980). One of the reasons predator-prey interactions of sea otters and benthic invertebrates are of major interest is that sea urchins, a preferred prey item, have the potential for regulating algal populations of the kelp forest community (e.g., Estes and Palmisano 1974, Lawrence 1975, Estes et al. 1978, Simenstad et al. 1978, Pearse and Hines 1979, Duggins 1980). In addition, sea otters are known to have a profound impact on the abundance of other herbivores, especially abalones (Ebert 1968, Wild and Ames 1974). In the 1800s, sea otters were hunted for their fur, and the population was reduced nearly to extinction before laws protecting otters were enacted (Kenyon 1969). In central California, the sea otter population has expanded in numbers from a relict population of ≈50 animals off the Monterey County coast in 1911 to ≈2000 animals in 1978, with an enlarged range of ≈250 km from Santa Cruz County to San Luis

Obispo County (Fig. 1A; Wild and Ames 1974, E. Ebert, *personal communication*). Knowledge of predator-prey interactions of sea otters in California comes primarily from "before-and-after" studies as the sea otter population expanded into new areas. After initial depletion of the standing stocks of preferred types of prey (sea urchins and abalones), the diet of the sea otters appears to diversify (Wild and Ames 1974). However, very little is known about the details of these predator-prey interactions in areas within the established range of sea otters, where the predator and prey populations may have reached dynamic equilibrium.

Sea otters returned to Hopkins Marine Life Refuge, Pacific Grove, California, in the mid-1960s. The diet, energetics, and activity patterns of sea otters in this area have been studied by Loughlin (1977) and Costa (1978). These studies show that sea otters consume benthic invertebrates amounting to as much as 35% of their body mass per day and spend about one-third of their day foraging, primarily on snails, crabs, sea urchins, and abalones. Costa (1978) observed that 5% of the prey items taken by sea otters in Hopkins Marine Life Refuge were abalones and that sea otters obtained 21% of their energetic requirements by consuming an average of 10 abalones/d. In the subtidal zone, all large, accessible sea urchins and abalones have been consumed, and the distribution of these herbivores is restricted to crevices more or less inaccessible to sea otters (Lowry and Pearse 1973, Cooper et al. 1977). This restriction to crevices and the low densities of abalones reported by Lowry and Pearse (1973) and Cooper et al. (1977) are in contrast to conditions before sea otters became reestablished in the early 1960s, when the bottom was "... covered with urchins and

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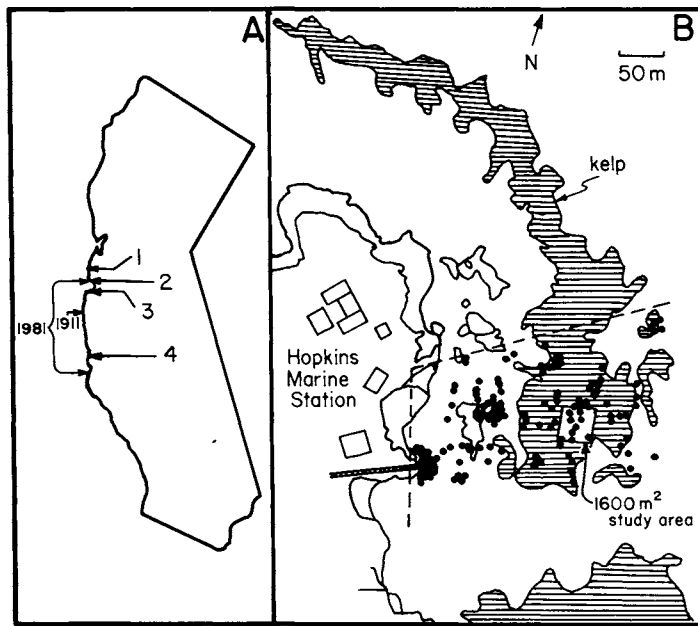


FIG. 1. (A) Locations of study sites in California: 1 = Año Nuevo Island; 2 = Point Santa Cruz; 3 = Hopkins Marine Life Refuge; 4 = Diablo Cove. The location of the relict population of sea otters is indicated by an arrow marked 1911; the present range of otters is within the brace marked 1981. (B) Hopkins Marine Life Refuge, Pacific Grove, California, drawn from an aerial photograph taken on 14 June 1978 by California Department of Fish and Game. Subtidal abalone populations were studied in the 1600-m<sup>2</sup> square in the middle of the kelp forest. Sea otters were counted in the entire area, excluding the kelp at the bottom of the map. Solid circles indicate locations of all foraging dives made by sea otters during one full day, four mornings, and three afternoons in August and September 1978. Dashed lines indicate field of view for observations of foraging dives.

abalones spaced only a few feet apart." (McLean 1962). The densities and size structures of the subtidal abalone populations appear to have been stable for the period from 1972 to 1976, indicating balanced recruitment and mortality rates for this period (Cooper et al. 1977).

Abalones are important prey to sea otters in central California because sea otters appear to prefer abalones as a food item rich in energy (Costa 1978), and because sea otters continue to take abalones in substantial numbers at Hopkins Marine Life Refuge even after nearly 20 yr of foraging on abalone populations restricted to crack refuges (Lowry and Pearse 1973, Cooper et al. 1977). As initially demonstrated by Gause's (1934) classic microcosm experiments on protozoan predator-prey interactions, the persistence of a preferred prey population under intense predation pressure may depend on the existence of a physical refuge; however, physical refuges from predation have been studied in only a limited number of natural systems (e.g., Connell 1961, 1970, Paine 1974, Virnstein 1979, Woodin 1981). The present study of abalones in crevice refuges provides evidence that these populations are highly productive and dynamic. Long-term data provide estimates of densities, species composition, and sizes of several abalone populations within and outside the range of California sea otters. The

dynamics of abalone populations in the study area at Hopkins Marine Life Refuge were determined by: (1) recruitment and loss of live abalones in mapped plots, and (2) the production of empty abalone shells. The species composition, size structure, and breakage characteristics of the empty shells are compared with the live populations as indicators of the sources of abalone mortality and of the selectivity of predators taking abalones. By comparing our long-term estimate of the average standing stock of abalones with our measurements of population dynamics and productivity, and with indirect calculations of feeding rates of sea otters, we conclude that abalones within a sea otter habitat have rapid recruitment, growth, and turnover rates.

#### MATERIALS AND METHODS

This study was done at Hopkins Marine Life Refuge (HMLR), Pacific Grove, California, where sport and commercial abalone fishing have been illegal since 1931 (Fig. 1B). The study site was part of a giant kelp (*Macrocystis pyrifera*) forest, and the bottom at 7–13 m was composed of granodiorite boulders, ridges, and outcrops interlaced with many crevices and sand-filled channels. A rich algal-invertebrate turf covered most of the hard substrate. Pearse and Lowry (1974) provide a further description of the study area and a species

list for the community. The site was the same location as that used in the studies of Lowry and Pearse (1973) and Cooper et al. (1977).

Populations of live abalones were sampled in four ways within a marked 1600-m<sup>2</sup> area (Fig. 1B). First, abalones were counted in at least 10 randomly placed 10-m<sup>2</sup> circular plots in October 1973, at about bimonthly intervals from September 1975 to December 1978, and in August 1981. Second, in June 1978, abalones were counted, and their shell lengths were measured in situ to the nearest 0.5 cm with calipers, in seven randomly selected 100-m<sup>2</sup> (5 × 20 m) swaths. The abalones in the study area were restricted to crevices, and distance in centimetres from the furthest recess to the opening of each crack inhabited by abalones was measured in the June 1978 samples. Third, detailed maps of abalones in 15 fixed plots (each ≈ 10–25 m<sup>2</sup>) were constructed in July 1978; plots were recensused in February 1979. The 15 plots were selected because of their high densities of abalones and large numbers of crevices. The mapped plots were visited periodically to observe movement of the abalones; some observations were made at night. In these three methods, abalones were sampled when visibility was good (at least 6 m), and during 1978 and 1981 an underwater light was used to look into cracks and under large boulders, but the habitat was not disturbed. Fourth, in August 1981, abalones were initially counted as described in the first method, and then plots were sampled destructively by collecting algae and holdfasts for examination on the surface and by turning over rocks and opening as many crevices as possible with pry bars.

All empty abalone shells and shell fragments were removed from the entire 1600-m<sup>2</sup> study area at about monthly intervals from November 1977 through December 1978. The area was partitioned into 16 swaths, each 5 × 20 m, using fixed markers and boundary lines, and we searched each swath systematically during each collection. We measured our collecting efficiency in August 1978 by scattering a representative sample of 100 numbered shells and shell fragments in the study area from the water surface 2 h before the routine collection. Eighty-three percent of these marked shells were retrieved in the August collection, and by the October 1978 sample, 96% of the marked shells had been found. Most of the items from the marked sample that were missed in August were small shell fragments. All shells from each monthly collection were identified to species, measured, and examined for fouling and breakage patterns. Although all shell fragments were collected and removed, only those with a body whorl were included for determination of production rates. Shells were categorized as "fresh" if the inner surface was shiny and free of fouling organisms. All other shells were categorized as "old," in the sense of time since death of the animal. Shell breakage was classified into three categories: unbroken shells, shells with the mid-

dle broken out of them, and shells with broken edges. Each shell was also examined for the presence of a drill hole produced by an octopus or for an acid-etched appearance indicative of partial digestion in a fish stomach.

Live abalones and fresh empty shells were measured at three other sites spanning the range of sea otters in California (Fig. 1). Measurements of live abalones were taken in August 1973 at Año Nuevo Island, San Mateo County, which was north of the range of sea otters. Fresh abalone shells were collected and measured at Point Santa Cruz, Santa Cruz County, during June, July, and September 1977, when the area was on the northern periphery of the range of sea otters and a small number of otters temporarily fed there. In July 1978, fresh abalone shells were collected and measured from Diablo Cove, San Luis Obispo County, which had been within the southern limit of sea otters for only ≈ 4 yr. Densities of live abalones were also measured at these three sites by counting animals in 10–12 randomly located 10 m<sup>2</sup> circular plots.

All sea otters within HMLR were counted from shore on most days from April 1976 through December 1978 at haphazard times from dawn to dusk, although most observations were at 0800–1000 and 1500–1800. Locations of foraging dives of sea otters near the study area were mapped to the nearest 2 m during one full day, four mornings, and three afternoons in August and September 1978.

## RESULTS

### *Long-term measurements of live abalones*

Densities of live abalones in crevices in the study site did not change significantly from 1973 to 1981 (ANOVA,  $P > .1$ ), although mean density per sampling period ranged an order of magnitude from 0.42 to 4.1 abalones/10 m<sup>2</sup> (Fig. 2). However, these erratic fluctuations may be in part artifacts of the random sampling design and the patchy distribution of abalones, rather than indicators of real major changes in the density of the population. The mean density ( $\pm 1$  SE) for this period was 1.8 ( $\pm 0.8$ ) individuals/10 m<sup>2</sup>, and this density is not significantly different from those found by Lowry and Pearse (1973) and Cooper et al. (1977;  $t$  tests,  $P > .05$ ; Table 1). The combined mean density of abalones for the period from 1972 to 1981 was 1.8 ( $\pm 0.25$ ) individuals/10 m<sup>2</sup> (Table 1). The species composition of the live abalone population had not changed significantly since 1972 ( $G$ -test,  $P > .1$ ) and averaged 68% *Haliotis rufescens* and 32% *H. walallensis* (Cooper et al. 1977, Lowry and Pearse 1973; Table 1). Live *H. kamtschatica* were observed very rarely in the study area, and not one was counted in the random samples of Cooper et al. (1977), Lowry and Pearse (1973), or June 1978 in the present study. Size frequency distributions of *H. rufescens* and *H. walallensis* were also constant from 1972–1978 (Coo-

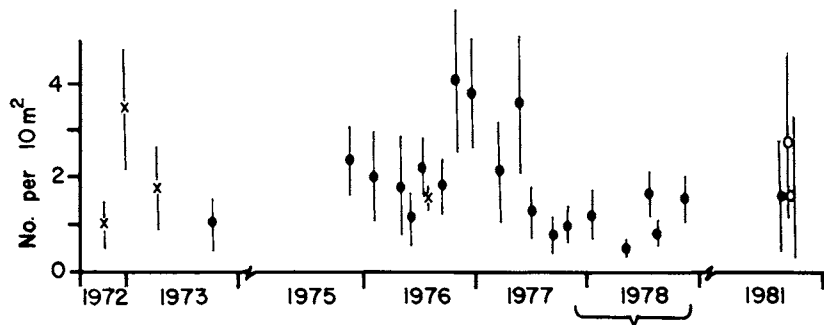


FIG. 2. Density of abalones within study site at Hopkins Marine Life Refuge. Means  $\pm$  2 standard errors are indicated. X's in 1972–1973 and 1976 indicate data from Lowry and Pearse (1973) and Cooper et al. (1977), respectively. Closed circles are data from routine sampling. Paired open circles in 1981 indicate the increase in density estimated by destructive sampling for small abalones under rocks. The brace under 1978 indicates the period shown in Fig. 6, when abalone shells were collected from the study area.

per et al. 1977, Lowry and Pearse 1973; Fig. 3C, Kolmogorov-Smirnov tests,  $P > .05$ ). These long-term data indicate that the populations of the two species have been stable, indicating relatively balanced recruitment and mortality rates since at least 1972 (see also discussion in Cooper et al. 1977). At an average density of 1.8 abalones/10 m<sup>2</sup>, the total population in the crevices of the 1600-m<sup>2</sup> study site was  $\approx$ 288 abalones (95% confidence interval: 208–368).

Very few small abalones were found in any of the long-term censuses or in the studies of Lowry and Pearse (1973) and Cooper et al. (1977). In 1981 we attempted to determine the location and abundance of small abalones by destructively sampling the habitat. Small abalones (<4.5 cm) had an extremely patchy distribution under rocks and boulders, and occasionally in shallow crevices. Small abalones were not found within algal holdfasts. Only a single large (10 cm) ab-

alone was found which would not have been counted with routine sampling. Destructive sampling for small abalones increased the density estimate of crevice-dwelling abalones from 1.8 to 2.8 individuals/10 m<sup>2</sup> (Fig. 2).

#### The crack refuge

*Haliotis rufescens* and *H. walallensis* larger than 4 cm were always found within cracks, and the rare *H. kamtschatkana* which were observed during the study were found on exposed, flat surfaces. Lowry and Pearse (1973) and Cooper et al. (1977) observed that *H. walallensis* inhabited shallower cracks than *H. rufescens*. However, *H. walallensis* does not grow as large as *H. rufescens* (Fig. 3C), and previous studies did not determine the relationship of abalone size to crack depth. Although large *H. rufescens* generally occurred in deeper cracks, smaller individuals of both species usu-

TABLE 1. Densities and species composition of live abalones in crevices and of fresh shells in the study site at Hopkins Marine Life Refuge. Data for live abalones from Lowry and Pearse (1973), Cooper et al. (1977), and the present study are not significantly different ( $t$  tests for densities;  $G$ -test for species composition,  $P > .1$ ) and were combined. The combined species composition for live abalones is significantly different from fresh shells ( $G$ -test,  $P < .005$ ) as a result of occurrence of *Haliotis kamtschatkana* shells, but the composition of *H. rufescens* and *H. walallensis* among the shells is not significantly different from the combined data for live abalones ( $G$ -test,  $P > .1$ ).

	Density (no. per 10 m <sup>2</sup> ) <i>Haliotis</i> spp. $\bar{x} \pm SE$	Species composition number (%)			Total
		<i>Haliotis</i> <i>rufescens</i>	<i>Haliotis</i> <i>walallensis</i>	<i>Haliotis</i> <i>kamtschat-</i> <i>kana</i>	
Live abalones					
Lowry and Pearse 1973	2.1 $\pm$ 0.05	56	25	0	81
Cooper et al. 1977	1.6 $\pm$ 0.41	84	51	0	135
This paper*	1.8 $\pm$ 0.8	82	30	0	112
Combined data	1.8 $\pm$ 0.25	222 (68%)	106 (32%)	0 (0%)	328
Fresh shells**					
		461 (69%)	178 (27%)	25 (4%)	664

\* Density 1973–1981; Species composition 1978.

\*\* Total collected, November 1977–December 1978.

TABLE 2. Numbers of abalones in 15 mapped plots in July 1978 (start) and in February 1979 (finish). Annual rates of survivorship, mortality, and recruitment relative to the total starting number of abalones were projected from this 6-mo period.

	<i>Haliotis rufescens</i>	<i>Haliotis walallensis</i>	Total no.	Projected annual rate (% of start)
Start	73	6	79	
Finish	81	9	90	
Survived	67	5	72	82
Lost	6	1	7	18
New	14	4	18	46

ally were found in shallower cracks, and there was no difference in depth of cracks inhabited by *H. rufescens* and *H. walallensis* of similar size (linear regression analysis of log crack depth vs. shell length, *t* tests of slopes and intercepts,  $P > .1$ ; Fig. 4). Therefore, we would expect that, for any given size-class of abalones, the ratio of *H. walallensis* to *H. rufescens* taken by sea otters would not differ from their proportions in the crevice population, unless some factor other than the crevice refuge differentially affects predation rates on the two species.

*Numbers of foraging sea otters in HMLR*

About one sea otter was present in HMLR on daily counts from April 1976 to November 1977, when this number increased markedly to a peak of  $\approx 20$  otters in January 1978 (Fig. 5). Most of this increase resulted from additional otters rafting in HMLR, but foraging elsewhere. However, the number of otters foraging also increased an order of magnitude during 1978. The mean number of sea otters in HMLR during 1978 was about six, with a mean of about one foraging otter per observation. Sea otters foraged over the entire area (Fig. 1), and obtained prey on  $\approx 40\%$  of the observed dives ( $N = 143$ ). The apparently low rate of obtaining prey mainly reflects a single foraging episode by one otter, which captured few prey (resulting in the cluster of nearshore points in the lower left of Fig. 1B). About 4% of the prey taken were abalones. The site where abalone populations were studied is  $\approx 3\%$  of the total area of HMLR where sea otters were counted. Assuming sea otters foraging throughout HMLR utilized the 1600-m<sup>2</sup> study plot in proportion to its area, the small study area would thus provide 3% of the prey for otters in HMLR. This assumption may be conservative because 7.7% of the mapped foraging dives occurred within the 1600-m<sup>2</sup> plot (Fig. 1B).

*Loss and recruitment of live abalones in mapped plots*

In July 1978 the 15 mapped plots contained 79 animals ( $\approx 27\%$  of the crevice population of 288 abalones in the study area), and 6 mo later 90 animals were present (Table 2). Frequent observations of the plots

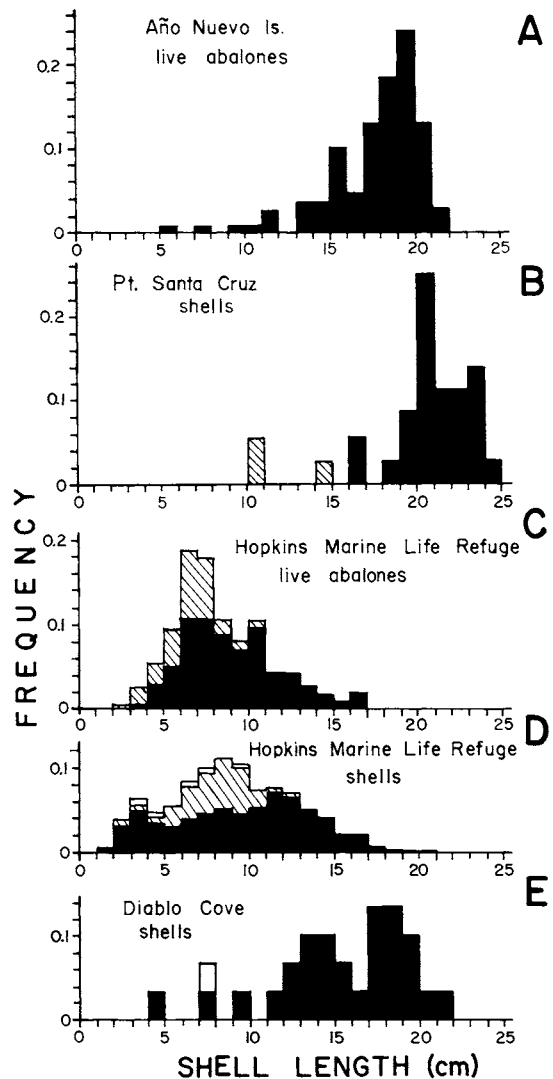


FIG. 3. Size-frequency distributions of empty abalone shells and live abalones along the north-south range of sea otters in central California. (A) Año Nuevo Island ( $N = 108$  live abalones; August 1973) was north of the range of otters. (B) Point Santa Cruz ( $N = 32$  shells; summer 1977) was on the northern periphery of the range and temporarily occupied by a small number of sea otters in 1977 when the shells were collected. (C) and (D) Hopkins Marine Life Refuge ( $N = 112$  live abalones;  $N = 635$  shells; 1978) was within the established range of otters for  $\approx 15$  yr. (E) Diablo Cove ( $N = 32$  shells; July 1978) was recently ( $\approx 4$  yr) within the southern limit of the distribution of otters. *Haliotis rufescens*: solid histograms, *H. walallensis*: hatched bars, and *H. kamtschakana*: open bars.

indicated that all the mapped abalones remained within their respective cracks, although many moved as much as 1 m back and forth within a crack and sometimes from one side of a crack to the other. Movement often appeared to be in positive response to the presence of drifting pieces of kelp, *Macrocystis pyrifera*. On occasion contact with the sea star *Pycnopodia he-*

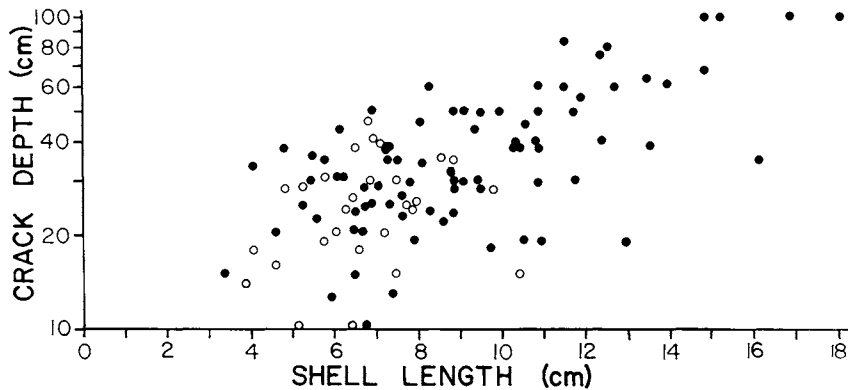


FIG. 4. Crack depth vs. shell length for *Haliotis walallensis* ( $\log y = 1.18 + 0.003X$ ; open circles) and *H. rufescens* ( $\log y = 1.14 + 0.004X$ ; solid circles) in June 1978.

*lianthoides* caused abalones to move rapidly 5–20 cm deeper into crevices. No obvious differences in behavior were seen at night. No abalone was observed to move out of a crevice or to move from one crack to another. Because of the restriction of abalones to cracks, the loss of abalones from the plots probably resulted from removal by predators rather than from migration out of mapped areas. The abalones in the mapped areas were not measured. However, field notes indicate that few "small" (<4 cm) abalones were found originally in the plots; most of the animals that disappeared were "medium" (4–9 cm) or "large" individuals (>9 cm), and most of the new abalones were medium sized. Based on the disappearance and appearance of animals in the plots for this period, the annual mortality rate was 18%, and the annual recruitment rate was 46% of the starting number of abalones (Table 2).

#### Production of empty abalone shells

Empty shells were plentiful in sand channels in the study area before November 1977, and it was easy to distinguish shiny, fresh shells from fouled, old shells. Our monthly removal of all empty shells from the study area depleted the population of old shells, until most of the shells collected were abalones that had died since the previous collection (Fig. 6). A total of over 2800 old and fresh empty shells was removed from the study area between November 1977 and December 1978. Of these, 664 were fresh shells, giving an average production of 55 empty shells/mo. The increase in total shells collected in January 1978 followed a period of storms, which uncovered many buried old shells. The increase in fresh shells for this same collection corresponded to the peak of sea otters present in HMLR (Fig. 5). Apart from the January 1978 collection, the

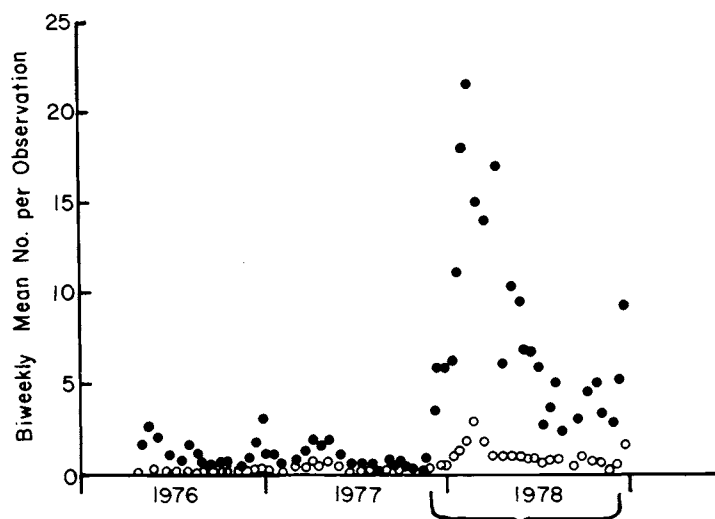


FIG. 5. Numbers on sea otters in Hopkins Marine Life Refuge. Biweekly mean numbers of sea otters in daily counts are plotted. Solid circles: all sea otters in the Refuge, including resting and foraging animals; open circles: foraging sea otters only. The brace under 1978 indicates the period shown in Fig. 6, when abalone shells were collected from the study area.

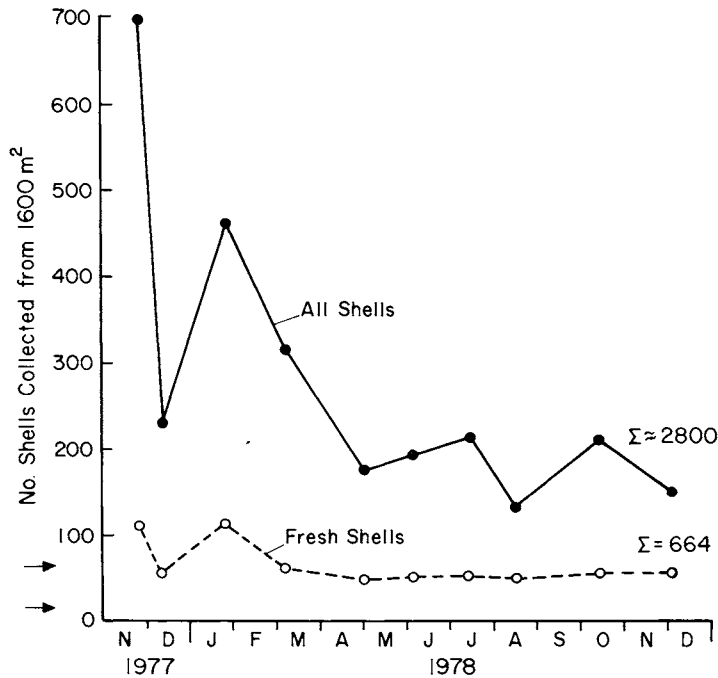


FIG. 6. Numbers of all abalone shells and fresh shells removed from the 1600-m<sup>2</sup> study site during repeated collections. Arrows on the ordinate indicate the number of shells per month predicted by the estimated feeding rates of six sea otters (top arrow) and of one sea otter (bottom arrow) in Hopkins Marine Life Refuge.

production rate of fresh empty shells was remarkably constant throughout 1978.

*Characteristics of empty abalone shells*

The species composition of fresh empty shells collected in the study area was significantly different from the combined measurements of the live populations (*G*-test,  $P < .005$ ; Table 1), mainly due to the presence of shells of *Haliotis kamtschatkana*. The proportions of *H. rufescens* and *H. walallensis* shells were not significantly different from their frequencies in the live population (*G*-test,  $P > .1$ ). The similar ratios of shells and live animals of *H. rufescens* and *H. walallensis* is in agreement with the expectation of equal vulnerability to otter predation based on utilization of the crack refuge (see "The crack refuge" above).

Mean sizes of fresh empty shells of *Haliotis walallensis* (8 cm) and *H. rufescens* (10 cm) were larger than mean sizes of the respective live abalones (6 and 8 cm; Kolomogorov-Smirnov tests of the size frequency distributions of the shells vs. the live abalones of each species,  $P < .05$ ; Fig. 3C, D), indicating differential mortality of large abalones. The fresh shells of *H. rufescens* also showed a peak at the 3-4 cm size-range; however, a peak at this size-range was not observed in the live population. The size frequency distribution of fresh shells collected from November 1977 through May 1978 (the first five collections) was not significantly different from that of fresh shells collect-

ed from June 1978 through December 1979 (the second five collections) for *H. rufescens*, *H. walallensis*, or for the two species combined (Kolomogorov-Smirnov tests,  $P > .10$ ).

There were three principal categories of shell damage noted on the fresh empty abalone shells collected at HMLR. Some shells (13%) had broken middles (Fig. 7A, Table 3) as a result of being hit with stones by sea otters (Cox 1962, Hall and Schaller 1964, Wild and Ames 1974); others (23%) exhibited broken edges, which were usually restricted to the anterior portion and which varied from a series of chips to the entire front portion of the shell being broken off (Fig. 7B, Table 3). A few shells (4%) showed an acid-etched appearance on their outer (dorsal) and inner surfaces (Fig. 7C), and this probably resulted from ingestion by the fish *Scorpaenichthys marmoratus* (O'Connell 1953, Cox 1962). Other shells (59%) were not damaged at all (Table 3). We found no shells with drill holes, indicative of predation by octopuses, as found by Tuttschulte (1976) in southern California.

The damage characteristics of fresh empty shells were significantly different among species (Table 3; *G*-test,  $P < .005$ ). Although <4% of all shells were acid etched, probably resulting from fish predation, *Haliotis kamtschatkana* shells had a significantly greater incidence of this type of damage than did shells of either *H. walallensis* or *H. rufescens* (*G*-test,  $P < .01$ ). The frequencies of acid-etched shells of *H. walallensis*

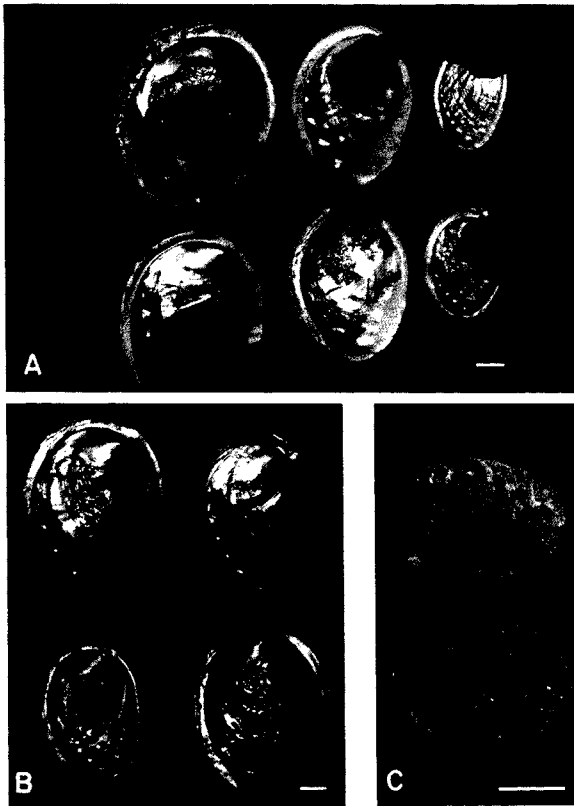


FIG. 7. Examples of damaged abalone shells collected in the study: (A) *Haliotis rufescens* shells (four shells on left), a *H. walallensis* shell (top right), and a *H. kamtschaticana* shell (bottom right) with broken middles characteristic of damage resulting from sea otters using stone tools; (B) three *Haliotis rufescens* shells and a *H. walallensis* shell (lower left) with broken edges, probably resulting from predation by sea otters; (C) dorsal view of an undamaged *Haliotis rufescens* shell (bottom) and an acid-etched shell of the same species (top), which probably has been ingested by a fish, *Scorpaenichthys marmoratus*. Scale lines = 2 cm.

and *H. rufescens* were not significantly different from each other ( $G$ -test,  $P > .5$ ). The occurrence of shells with broken middles, probably resulting from sea otter predation, differed significantly for each species, with *H. kamtschaticana* having the highest frequency and *H. walallensis* the lowest frequency of this damage ( $G$ -tests,  $P < .01$ ). Frequencies of shells with broken edges were significantly different for each species, with *H. rufescens* having the highest and *H. walallensis* the lowest incidences of edge damage ( $G$ -tests,  $P < .01$ ). Frequencies of shells with both broken edges and broken middles were low but differed significantly among the species, with *H. kamtschaticana* having the highest and *H. walallensis* having the lowest incidences ( $G$ -tests,  $P < .005$ ). The occurrence of shells with no apparent damage was also significantly different for each species, with *H. walallensis* having the highest and *H. kamtschaticana* having the lowest incidences of undamaged shells ( $G$ -tests,  $P < .005$ ).

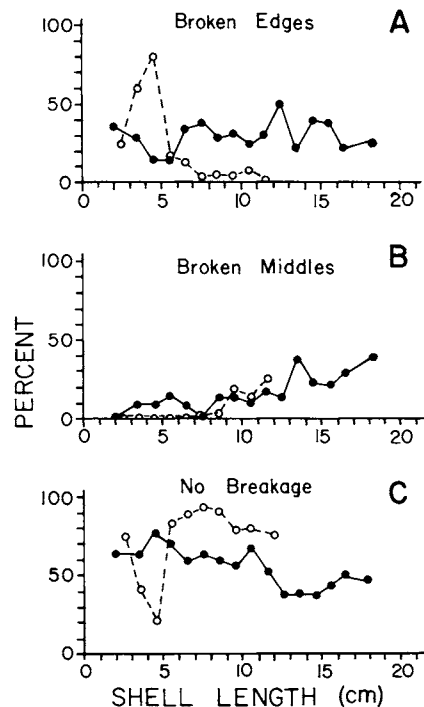


FIG. 8. Size-frequencies of shell damage for *Haliotis walallensis* (open circles) and *H. rufescens* (solid circles). (A) Shells with broken edges. (B) Shells with broken middles. (C) Undamaged shells.

The frequency of fresh empty shells with broken middles, probably resulting from sea otter predation, increased with increasing shell size to  $\approx 20\%$  for the largest *H. walallensis* and 20–40% for the largest *H. rufescens* (Fig. 8B). Too few *H. kamtschaticana* shells smaller than 7 cm ( $N = 12$ ) with those larger than 7 cm ( $N = 13$ ) showed that larger shells had a markedly higher frequency of broken middles than did smaller shells (38 vs. 8%). Edge damage could be caused by general wave action and abrasion after the animal died, and might be expected to be more prevalent in the thinner, more fragile shells of *H. walallensis*. However, except for 3–5 cm shells, few *H. walallensis* shells had broken edges, whereas  $\approx 30\%$  of *H. rufescens* shells of all sizes had broken edges (Fig. 8A). In addition, if wave action and abrasion were a major cause of edge damage, shells with broken middles would also be expected to have broken edges, but  $< 1\%$  of the shells had both broken middles and broken edges (Table 3). Cox (1962) reports an observation of a rock crab (*Cancer antennarius*) inflicting similar edge damage to an individual *H. rufescens*. However, the density of rock crabs is very low at HMLR (Hines 1982), and we have never observed rock crabs preying on large abalones held in laboratory tanks, even under starvation conditions. We believe



TABLE 3. Frequencies of shell damage for each species. For each species and for the combined species, numbers of fresh shells (with percentages in parentheses) are shown for category of shell damage. None = no apparent damage; middle, edge, and acid etch damage = damage categories illustrated in Fig. 7A, B, and C, respectively; both = shells with both middle and edge damage; total breakage = total number with middle, edge, and both types of damage.

Species	Broken part of shell				Total breakage	Acid etch	Σ
	None	Middle	Edge	Both			
<i>H. kamtschatkana</i>	8 (32%)	6 (24%)	5 (20%)	3 (12%)	14 (56%)	3 (12%)	25
<i>H. walallensis</i>	143 (80%)	14 (8%)	15 (8%)	0 (0%)	29 (16%)	6 (3%)	178
<i>H. rufescens</i>	240 (52%)	69 (15%)	134 (29%)	3 (<1%)	203 (44%)	15 (3%)	461
Σ	391 (59%)	89 (13%)	154 (23%)	6 (<1%)	243 (37%)	24 (<4%)	664

that sea otters caused the edge damage by either pounding the shell edges with a rock or prying at the edges with their teeth. One of us (A. H. Hines, *personal observation*) observed a captive sea otter in December 1980 at the Seattle Aquarium, Seattle, Washington, USA, attempting to remove an unknown object from the bottom by biting and prying with its teeth while pushing on the substrate from its forepaws. Acid-etched shells occurred only in the 2–7 cm size-range of all three species.

The frequency of unbroken *Haliotis rufescens* empty shells ranged from ≈60–70% in small-sized shells to ≈40% in the larger shells (Fig. 8C). Except among 3–5 cm shells, *H. walallensis* showed a higher frequency of 80–90% unbroken shells (Fig. 8C). The cause of mortality that resulted in these intact shells is uncertain, but some sea otters do not use stone tools and capture abalones with a sudden and/or strong pull, which does not cause shell damage (J. Ames, *personal communication*). Sea stars also may leave undamaged shells in the smaller size-range. However, during hundreds of observations of foraging in the study area by sea stars, including *Pycnopodia helianthoides*, *Pisaster giganteus*, *Pisaster brevispinus*, and *Orthasterias koehleri*, not one abalone was eaten (Harrold 1981, C. Harrold, *personal communication*).

#### Movement of empty abalone shells

Estimates of the production rate of empty abalone shells in the study area could be biased if there were a net transport of shells into or out of the study area by water movement, sea otters, and/or other means. We tested for possible shell movement in four ways: (1) by placing marked shells in the study area, (2) by observing edges of the study area for movement of shells from the surrounding uncollected area, (3) by observing the distribution of shells from intertidal black abalones (*Haliotis cracherodii*) along a transect from the intertidal zone to the outer edge of the kelp forest, and (4) by observing the foraging activity of sea otters in the vicinity. Marked shells placed in the center of the study area from August to October 1978 were dispersed only 2–3 m, and there was no net direction to the movement. Although there were no large storms to move shells long distances during this period, care-

ful observations of the edge of the collection area throughout the study did not reveal any obvious transport from the surrounding area of high shell density, even after major storms. However, large storms during winter 1977–1978 uncovered many buried shells (Fig. 5). In addition to subtidal abalones, sea otters regularly fed on *H. cracherodii*, and shells of this species could be transported into subtidal areas of the kelp forest by waves and currents or by sea otters. However, shells of *H. cracherodii* were only found in the intertidal and the very shallow (1 m) subtidal zones, and none of the more than 2800 shells collected in the study area was of *H. cracherodii*. Finally, foraging dives of sea otters were dispersed over the entire study area (Fig. 1). Although otters that captured abalones and crabs swam slowly on the surface for up to 20 m before dropping the remains of the prey, we did not observe any consistent direction in their movement. For all of these reasons, the estimates of empty shell production rate were probably not biased by net transport of shells into or out of the study area.

#### Abalone populations along the range of sea otters

The mean sizes of the abalones at HMLR were small when compared to those of other populations surveyed near the periphery of the range of sea otters (Fig. 1). At HMLR, mean sizes of live *Haliotis rufescens* and *H. walallensis* were 8 and 6 cm, respectively; mean sizes of empty shells of the two species were 10 and 8 cm, respectively. North of the range of sea otters, live *H. rufescens* at Año Nuevo Island averaged 18 cm in length in 1973 (Fig. 3A). Density of abalones at Año Nuevo was high at 9.08 individuals/10 m<sup>2</sup>, reflecting relatively low human fishing pressure as well as lack of predation by otters. Fresh empty shells collected at Point Santa Cruz averaged 21 cm in length, shortly after a small group of otters began feeding there in June 1977 (Fig. 3B). Density at Point Santa Cruz even before the arrival of otters was low at ≈0.1 individuals/individuals/10 m<sup>2</sup>, reflecting relatively high human fishing pressure. Near the southern limit of the range of sea otters, fresh empty abalone shells at Diablo Cove averaged 16 cm (Fig. 3E), with low density of live abalones of 0.4 individuals/10 m<sup>2</sup> in 1978. Sea

otters returned to Diablo Cove in 1974, and although abalone density was low after 4 yr of foraging, the size structure of the population in 1978 was still larger than that of the HMLR population.

## DISCUSSION

### *Stability*

Subtidal abalone populations in Hopkins Marine Life Refuge have been stable from 1972 to 1981, with relatively constant densities of 1.8 abalones/10 m<sup>2</sup>, constant species composition of about 2:1 *Haliotis rufescens* : *H. walallensis* and trace *H. kamtschatkana*, and constant size-frequency distributions (Lowry and Pearse 1973, Cooper et al. 1977; Figs. 2 and 3, Table 1). Populations with constant survivorship and birth rates exhibit stable age (size) distributions; conversely, stability of these abalone populations indicates constant survivorship and recruitment rates. The relatively constant production rate of fresh empty shells in 1978 (Fig. 6) is in agreement with this postulate of a constant mortality rate. Recruitment must have balanced mortality, and our data indicate rapid turnover of the crevice population, implying rapid growth and recruitment.

### *Turnover*

Turnover rates of the crevice population can be estimated by three different methods with the available data. First, published feeding rates of sea otters combined with our observations of the number of otters in the study area can provide an estimate of consumption of abalones by otters. An average sea otter in HMLR consumes  $\approx 10$  abalones/d (recalculated from Loughlin 1977, Costa 1978). The 1600-m<sup>2</sup> study area provides  $\approx 3\%$  of the prey for otters in HMLR, and thus would yield  $\approx 0.3$  abalone/d, or 110 abalones/yr for one otter. For the mean of six otters observed in HMLR in 1978, this would be 660 abalones/yr. This calculated impact of six otters is almost the same as the number of shells produced in 1978 (664 shells). Using our long-term estimate of a standing stock of 288 abalones in crevices, a single sea otter foraging in HMLR might produce an annual turnover of 38% of the abalones in crevices (110 abalones consumed/288 standing stock); six otters would produce a turnover of 229%/yr.

Apart from the indirect nature of the calculations, the biggest problem with this first estimate is the uncertainty of the number of otters actually feeding in the study area. Most of the sea otters counted in HMLR were not in fact feeding (Fig. 5). Loughlin (1977) found that otters in the area spent one-third of the 24-h day foraging, so only one-third of the otters at any given observation would be feeding. However, Loughlin (1977) also showed that the home ranges of otters foraging in the area averaged 56 ha, which is five times the 11-ha area of HMLR, and this would reduce the percentage (3%) of prey estimated to be obtained from

the 1600-m<sup>2</sup> study area. Because only one abalone consumed in the study site each day would result in  $>125\%$  annual turnover of the crevice population, an impractical number of hours would be required to observe directly the number of abalones taken by otters. Moreover, abalone turnover calculated from sea otter feeding rates would be an underestimate because it does not include other sources of mortality.

Second, turnover can be estimated from the dynamics of abalones in the mapped plots. In our short-term study, the 46% annual recruitment rate was much higher than the 18% annual loss rate (Table 2). However, loss and recruitment must be in balance over the long term in order to maintain the observed stability of the crevice populations. An average of the two rates indicates a long-term turnover of 32%/yr, which is close to the 38% turnover predicted from the feeding rate of one sea otter. However, although we never observed abalones moving out of or between cracks, we cannot be certain that the observed losses were mortalities, nor do we know the source of the recruits. Turnover might be underestimated as a result of undesigned losses being replaced by unobserved recruitment. The high annual survivorship (82%) of mapped abalones may be a result of the nonrandom selection of plots with many abalones and deep cracks: 27% of the population was mapped in 14% of the 1600-m<sup>2</sup> study site. These crevices may have provided optimal refuges from sea otter predation.

Third, the production rate of fresh empty shells clearly provides the best estimate of abalone mortality and turnover: 231%/yr (664 shells/288 standing stock). Uncollected shells and shells which fouled rapidly between collections would produce small errors of underestimation; net import or export of shells from the study area was minimal. Substantial error in the turnover rate estimated by this method could only come from an error in the original estimate of standing stock. The thousands of diving hours in the small study area logged by members of our research group convince us that we have not overlooked many larger abalones in crevices. However, most juvenile abalones smaller than  $\approx 5$  cm were located under boulders and within small spaces between rocks, sites which were not sampled by our nondestructive census. In 1981, when we did roll rocks and boulders, we found substantial numbers of small abalones 1–4 cm long. About 20% of the fresh empty shells collected in the study area were  $<5$  cm long and formed a size-mode which was clearly not sampled in the live population (Fig. 3).

To correct for our underestimation of the abundance of small abalones, the turnover estimated by empty shell production should be adjusted by also ignoring the 20% of fresh shells  $<5$  cm. Turnover of the crevice population of abalones ( $>5$  cm) would then be 184%/yr (530 shells/288 standing stock). Alternatively, we could correct our turnover calculations by incorporating an estimate of the small abalones into the standing

stock of all abalones. If we assume that small abalones have a much higher mortality rate than larger ones, and that a Deevey (1947) type III survivorship schedule applies to the population, we can infer from the shape of the size-frequency distribution of the live, crevice-dwelling population (Fig. 3) that the unsampled small animals amounted to  $\approx 150\%$  of the 288 larger abalones. The population would thus include  $\approx 432$  small animals for a total of  $\approx 720$  abalones, and the turnover would be  $92\%/yr$  ( $664$  shells/ $720$  abalones). Even though sea otters were mostly likely foraging only on larger abalones, which were probably censused accurately, annual turnover from calculated feeding rates of six sea otters would yield an estimate of  $92\%$  based on a standing stock of  $720$  abalones, which is the same as the turnover estimated from shell production. The  $32\%$  turnover estimated from mapped plots did not depend on the accuracy of the long-term standing stock, but this estimate may be low as a result of the sampling bias for abalones in the best refuge cracks. All these estimates indicate very high production and turnover rates; the subtidal abalone populations in HMLR must have been very dynamic but stable throughout most of the 1970s.

#### Growth

High production and turnover indicate a rapid growth rate. However, abalones are generally considered to be slow-growing, long-lived animals. *Haliotis discus* in Japan grows to  $10$  cm in  $\approx 5$  yr (Sakai 1962). *H. iris* in New Zealand takes  $4$ – $5$  yr to grow to  $5$  cm and  $10$ – $11$  yr to reach  $8$  cm (Sinclair 1963). Tagging studies of natural populations of *H. tuberculata* from the English Channel showed that this species grows to  $5$  cm in  $2$ – $3$  yr and to  $10$  cm in  $\approx 6$  yr (Forster 1967, Hayashi 1980). However, these three species attain a maximum size of only  $\approx 10$ – $12$  cm, less than half the potential maximum size of *H. rufescens* in the present study. *H. midae*, a South African species, grows up to  $20$  cm long, but size-frequency analysis indicated that it takes  $2$  yr to grow to  $5$  cm,  $7$  yr to  $10$  cm, and  $\approx 15$  yr to  $15$  cm (Newman 1968).

Most studies on growth rates of California abalones have been conducted on animals held in the laboratory or in cages in the field, and also suggest that abalones are relatively slow growing (Cox 1962, Leighton 1968, Tutschulte 1976, Paul et al. 1977). Laboratory studies on *Haliotis rufescens* indicate an average growth of  $3$  cm/yr, and a  $10$ -cm animal (which is larger than the average length of the population in HMLR crevices) would be  $\approx 3.3$  yr old (Leighton 1968). *H. kamtschatica* reaches  $3.5$  cm in  $\approx 1$  yr,  $7$  cm in  $3$  yr, and  $\approx 9$  cm in  $4$  yr (Paul et al. 1977). There are no published growth rates for *H. walallensis*. However, growth of several species of California abalones is highly variable in the laboratory, and it is generally well known that abalone growth rates are responsive to temperature, the quantity of fresh algal food, and water quality

(Leighton and Boolootian 1963, Leighton 1968, 1972, 1974, A. H. Hines and J. S. Pearse, *personal observation*). For example, Leighton (1968) observed growth of *H. rufescens* fed single-species algal diets, and measured growth of up to  $10$  cm in  $2$  yr. Because of the difficulties in tagging and retrieving marked abalones, the few growth measurements of uncaged California abalones in the field have been either for species with distinct year-class modes (e.g., *H. soreseni*) or for animals which were much larger, and therefore presumably much slower growing, than most of the animals in our study population (Tutschulte 1976). However, Leighton (1968) provides a unique description of growth of a cohort of *H. rufescens* in southern California. Within  $\approx 1.4$  yr after he detected  $0.5$ – $1$  cm long recruits under rocks, most of the abalones were  $\approx 4$  cm long, and  $1$  yr later (i.e.,  $\approx 2$  yr from recruitment), most were  $\approx 14$  cm long. These observations indicate that  $5$ – $15$  cm long *H. rufescens* (the size-range of most animals in HMLR crevices) are capable of growth of  $\approx 5$ – $10$  cm/yr in the field. Therefore, we propose that growth rates of natural populations of abalones in California are much faster than indicated by laboratory studies, and we hypothesize that animals of the size-range in the HMLR crevices grow fast enough to account for turnover rates of  $30$ – $100\%/yr$ .

#### Recruitment

In addition to growth rates, recruitment rates must be high to account for the abalone productivity we measured. *Haliotis rufescens* spawns year-round (Boolootian et al. 1962, Young and DeMartini 1970). The reproductive cycles of some other abalone species are distinctly seasonal (Tutschulte and Connell 1981), but the cycle for *H. walallensis* is unknown. However, the abundance and temporal pattern of occurrence of larvae and very small juveniles have not been measured for any natural abalone population. Tutschulte (1976) provides some field experimental evidence that in southern California the presence of small- and medium-sized animals somehow diminishes or prevents recruitment of *H. fulgens* and *H. corrugata*. Morse et al. (1979) suggest that settlement of *H. rufescens* larvae is induced by low ( $\approx 1$   $\mu\text{mol/L}$ ) concentrations of  $\gamma$ -aminobutyric acid (GABA) associated with crustose coralline algae, which are abundant all year in HMLR. Soon after settlement, negative phototaxis and/or geotaxis may induce movement down into small spaces between rocks and under boulders (A. H. Hines, *personal observation*). Very small abalones appear to feed on diatomaceous and bacterial films (Leighton 1972, 1974, D. Morse, *personal communication*, A. H. Hines, *personal observation*). However,  $1$ – $2$  cm long red abalones feed on macroalgae as well as on diatoms (A. H. Hines, *personal observation*). *H. rufescens* and *H. walallensis* larger than  $4$ – $5$  cm prefer and consume large quantities of drift kelp (*Macrocystis pyrifera*) (Leighton 1966, A. H. Hines, *personal observation*). We hy-

pothesize that subtidal abalones in HMLR recruit at a high rate under boulders and between rocks, and that they grow very fast. When they attain a size of  $\approx 5$  cm (after  $\approx 1$  yr in accordance with Leighton's [1968] field observations), they move out from this habitat and into crevices, where they can feed on abundant drift kelp brought to them by water motion. The observation that small *H. rufescens* switch their diet from diatom films to macroalgae as they grow, and our qualitative observations of 4–8 cm abalones recruiting into mapped cracks are consistent with this hypothesis. We believe that crevice-dwelling abalones continue to grow at a rate of up to 10 cm/yr, with larger abalones occurring in deeper crevices.

#### Mortality

Predation by sea otters was probably the major source of mortality for larger abalones in the study site. Roughly half the abalones in HMLR crevices were longer than 8 cm (Fig. 2), and 20–40% of fresh empty abalone shells above 8 cm had broken middles, known to result from sea otters using stone tools (Cox 1962, Wild and Ames 1974; Figs. 6 and 7). In addition, most large empty shells with broken edges and large undamaged shells probably resulted from sea otter predation. Mortality from predators that would have easy access to the crack refuge (e.g., sea stars, fish, and octopus) does not account for the high production of empty shells in the study site. Differences among abalone species in shell damage characteristics indicate that either: (1) otters use different techniques to capture each species, (2) the shells of each species have different susceptibility to damage, or (3) a combination of the two. However, because the species with the thinnest and most fragile shell (*Haliotis walallensis*) had the least breakage (Table 3), species differences in shell vulnerability may not have been the most important cause of the damage patterns. Perhaps species which cling more tenaciously to a substrate incur more shell damage before succumbing to sea otters, i.e., otters were able to remove *H. walallensis* without frequently resorting to damaging force. In any case, sea otters appear to have taken *H. rufescens* and *H. walallensis* in proportion to their occurrence in the population (Table 1), regardless of any potential differences in vulnerability of the two prey species.

Comparison of the size frequencies of empty shells and the live population (Fig. 3) indicates that otters selected abalones larger than were proportionately available in crevices. Because larger abalones occurred in deeper cracks (Fig. 4), perhaps the availability of these refuges from otter predation was limiting for larger abalones. Although abalone densities appear to have been constrained by sea otter predation, we can provide little evidence that the crevice refuges were a limiting resource for the HMLR populations. We often observed empty crevices which appeared to be suitable refuges, but factors such as crev-

ice orientation with respect to surge replenishing drift kelp, or potential competition for food with coexisting sea urchins (e.g., Shepherd 1973) are difficult to evaluate without further study. Resource partitioning is often a manifestation of competition (e.g., Diamond 1978), but *H. rufescens* and *H. walallensis* apparently did not partition crevices in the study site (Fig. 4). However, *H. kamtschatica* feeds primarily on diatoms and small algae (Cox 1962, Paul et al. 1977), which do not grow well in shaded crevices. Our rare observations of this species indicate that it occurred on exposed surfaces, where these food sources do grow, and this exposure to predators may account for its extremely low density.

Although we rarely observed large abalones outside of cracks (*Haliotis kamtschatica* only), they were often not at the bottom of their crevice residence, and they frequently moved within cracks in response to drift kelp food. Perhaps movement closer to the crevice opening in the normal course of abalone feeding resulted in increased vulnerability to sea otters. Because the frequency of abalones moving into more accessible portions of crevices may be relatively independent of predation pressure, increases in foraging activity of sea otters, as occurred in 1978 (Fig. 5), may not have had additional impact on prey populations that were already limited to minimal densities. Physical refuges in rocky intertidal zones are important features stabilizing populations of barnacles (Connell 1961, 1970) and mussels (Paine 1974), which are preyed upon by sea stars and neogastropods. Infaunal invertebrates obtain physical refuge from predatory fish, crabs, and horseshoe crabs by burrowing deeper into sediments (Virnstein 1979), by inhabiting areas of dense tube-forming polychaetes (Woodin 1979), or by inhabiting sea grass beds (Young et al. 1976, Orth 1977, Young and Young 1977, 1978). Epifaunal crustaceans also appear to obtain refuge from a variety of predators in sea grass beds (Nelson 1979, Coen et al. 1981). It is clear that the stability of the abalone population under intense predation pressure by sea otters depends both on high productivity and the crevice refuge.

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