

Dynamics and Distribution of Black Abalone Populations at San Nicolas Island, California

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Abstract — Dense populations of black abalones (*Haliotis cracherodii* Leach) were monitored in permanent intertidal plots at nine sites on San Nicolas Island from 1981 through 1990. Densities were essentially constant at all four sites along the north shore of the island throughout the study period. Densities at five sites along the south shore were more variable, possibly reflecting asynchronous variation in recruitment, mortality resulting from wave disturbance, and removal by people. Temporal variation of abalone densities apparently was not influenced by sea otters or abalone withering syndrome during this study. Abalones were strongly aggregated in space. Highest densities occurred in areas of irregular substrata, apparently as a result of preference for crevices and vertical faces. The locations of dense patches were persistent in time.

Introduction

The distribution, abundance, and dynamics of abalone populations typically are difficult to determine. Abalone populations most often occur in shallow nearshore waters, distributed in patches across large tracts of rocky substrata. Under such circumstances direct measurements of population size and variation are difficult, requiring costly, labor-intensive diving surveys of large areas (Tegner 1989). Black abalones (*Haliotis cracherodii* Leach) are a notable exception to the pattern because they occur primarily in rocky intertidal habitats (Cox 1962; Morris *et al.* 1980).

Black abalones occur along the western shore of North America from southern Oregon, USA, to Cabo San Lucas, Baja California Sur, Mexico

(Morris *et al.* 1980; Tegner 1989). In recent history they have been particularly abundant in the California Islands, especially San Miguel, Santa Rosa, Santa Cruz, San Nicolas, and San Clemente (Littler 1980; Kanter 1980; Douros 1985, 1987; Tissot 1990; United States National Park Service, unpubl. data).

Sea otters (*Enhydra lutris* [L.]) were reintroduced to San Nicolas Island in August 1987 as part of the recovery program for sea otters in California (United States Fish and Wildlife Service 1987; Rathbun *et al.* 1990). Sea otters apparently were abundant at the island prior to the unrestrained fur harvests of the 18th- and 19th-centuries (Ellison 1937; Ogden 1941), but have been locally extinct at San Nicolas during the 20th-century. At the time of this writing (August 1991) the success of the reintroduction program is promising but uncertain. Sea otters are widely known for their abilities as predators of abalones. Off central California, subtidal populations of abalones are confined largely to cryptic microhabitats which afford refuge from foraging sea otters (Lowry and Pearse 1973; Cooper *et al.* 1977; Pollard 1991). Established sea otter populations and commercially harvestable stocks of abalones are generally regarded as mutually exclusive in space (Estes & VanBlaricom 1985; Tegner 1989). Thus, the reintroduction of sea otters to San Nicolas Island likely will alter patterns of abundance and distribution in the four primarily subtidal species which occur at the Island: green abalone (*Haliotis fulgens* Philippi), pink abalone (*H. corrugata* Wood), red abalone (*H. rufescens* Swainson), and white abalone (*H. sorenseni* Bartsch). The possible effects of predation by sea otters on black abalone populations are more difficult to predict. Black abalones have remained relatively abundant in

some intertidal habitats in central California up to eight years after the return of sea otters to the area (Burge & Schultz 1973; Gotshall *et al.* 1984, 1986). Interest in the relationship of sea otters and black abalones is economic as well as academic; since 1980 the black abalone has been among the most important commercially-harvested species of abalone in California, in terms of landing weight. Between 1980 and 1983 San Nicolas Island was the source of 3-12% of the annual California harvest of black abalones (Table 1).

Since 1985 black abalone populations have declined significantly on at least six of the California Islands (Anacapa, San Clemente, San Miguel, Santa Barbara, Santa Cruz, and Santa Rosa Islands; Davis *et al.* in press; Haaker *et al.* in press; Tissot in press; United States National Park Service, unpubl. data). Mortality has approached 100% at some of the affected sites. Declines apparently have been caused by a disease condition known as withering syndrome (WS). The cause and dispersal mechanism of

WS are unknown. WS was first noted at Anacapa and Santa Barbara Islands, and has been seen most recently at San Clemente and San Miguel Islands (P. L. Haaker, D. O. Parker and G. E. Davis, pers. comm.). Thus, there is reason for concern that the dense populations of black abalones at San Nicolas Island might likewise be affected by WS.

In 1981 I began gathering data on temporal and spatial variation in dense populations of black abalones in the rocky intertidal zone at San Nicolas Island. Principal goals were: 1. To obtain a detailed record of variation over time in numbers of abalones in dense patches; 2. To determine the dimensions, environmental correlates, and temporal consistency of dense patches of abalones in the intertidal zone; 3. To measure the relationships among microhabitat type, growth rate, mobility, and survival of abalones in the intertidal zone. These goals were developed in order to contribute to improved understanding of abalone population dynamics, taking advantage of an unusually

Table 1. Commercial harvest of black abalone at San Nicolas Island, California, 1971-1983.

Year ¹	Total landings of black abalone from San Nicolas Island ² (10 ³ kg)	Total landings of black abalone in California ³ (10 ⁶ kg)	Percentage of statewide total from San Nicolas Island
1971	0.41	0.04	0.9
1972	2.91	0.41	0.7
1973	8.23	0.86 ⁴	1.0
1974	7.14	0.50 ⁴	1.4
1975	22.14	0.32	7.0
1976	11.86	0.18	6.5
1977	14.50	0.20	7.1
1978	4.18	0.20	2.0
1979	21.46	0.16	13.5
1980	26.77	0.23	11.8
1981	6.59	0.23 ⁴	2.9
1982	15.64	0.27 ⁴	5.7
1983	17.41	0.20 ⁴	8.5

¹ Following 1983, reporting procedures were changed such that total harvest at San Nicolas Island can no longer be determined from landing records.

² Source: California Department of Fish & Game, unpublished landings data for statistical blocks 813 814 and 858.

³ Source: California Department of Fish & Game, unpublished data.

⁴ During indicated years, total statewide landing weight of black abalone ranked first among commercially harvested abalone species.

accessible and abundant abalone population. In addition, this project was designed to provide a detailed quantitative record of the black abalone population at San Nicolas Island prior to the return of sea otters. Should a sea otter population be successfully established, continued study of the subject population of black abalones will contribute to an improved understanding of interactions of sea otters and abalones. Likewise, data on dynamics of black abalone populations at San Nicolas Island will be of value in understanding the causes, characteristics, and consequences of WS in the California Islands.

My specific purpose here is to review variation in abundance, patch characteristics, and patch persistence in dense populations of black abalones at San Nicolas Island during the period 1981 through 1990.

Methods

In 1981 I established nine study areas in rocky intertidal habitats at San Nicolas Island (Fig. 1). Sites were chosen following two surveys of the entire shoreline of the Island on foot during two series of low tides. The principal site selection criterion was the presence of dense patches of black abalones. At each site I established a number of permanent transect lines passing through dense abalone patches. Selection of locations for study sites, and of locations for transect lines within study sites, was not random, by design. My purpose was to monitor changes over time in dense aggregations of abalones, *not* to estimate mean densities of abalones on the Island.

Study areas included two to six permanent transects (most had five or six; Fig. 1), depending on size of the area and the number and size of abalone patches present. Transect

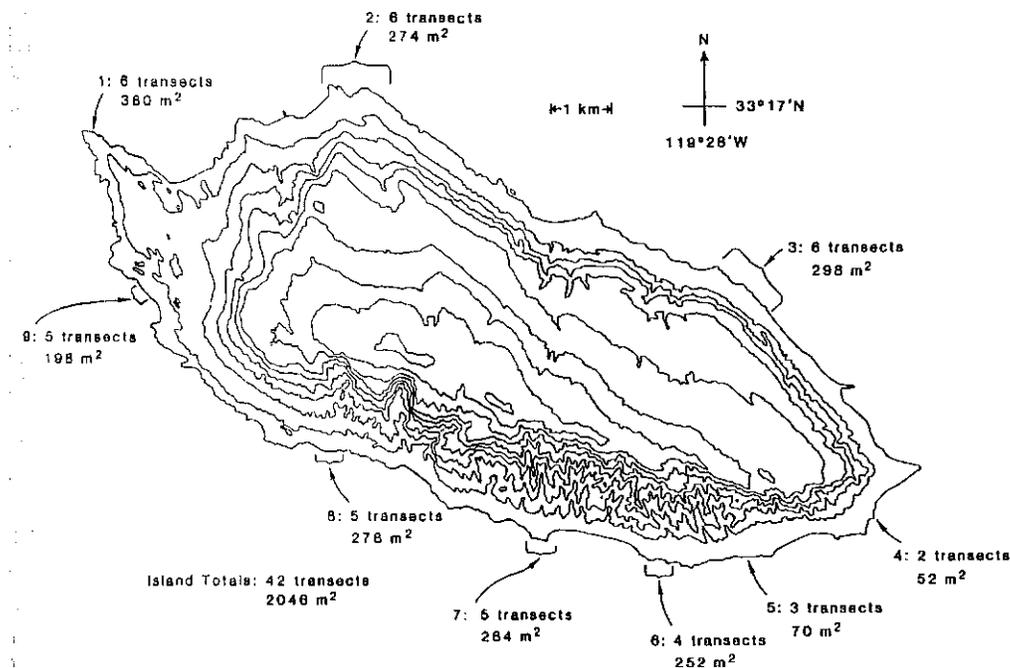


Figure 1. Location map of permanent study sites in the rocky intertidal at San Nicolas Island. Location, number of permanent transects, and total area within permanent transects are shown for each of the nine study sites around the island.

lines were defined by drilling holes in the rock substrata and permanently embedding stainless steel eyebolts in the holes with marine epoxy compound. Transects were prepared for collection of data by attaching a rope, marked at intervals of 1 m, to the eyebolts with snapshackles. Only the permanent eyebolts were left at the sites between visits. Transect length ranged from 7-40 m; most were between 20 - 30 m in length. Transect length was determined arbitrarily, based on the size of the study area and the local distribution of abalones.

Abalones were counted along transect lines by placing a 1 m² quadrat frame along each side of the line at 1 m intervals (Fig. 2). Each quadrat was surveyed for the total number of abalones, and for the number of abalones in each of three arbitrarily-defined categories of microhabitat: 1) open vertical (open, non-cryptic surface with an inclination of 45° or more above the horizontal); 2) open horizontal (open, non-cryptic surface with an inclination of less than 45° above the horizontal) and 3) cryptic (fully enclosed within cracks, crevices, or small caves). Each census produced a set of counts from an array of contiguous quadrats 2 m wide by x m long (x = transect length). A census cycle consisted of one complete census of all transects on the island.

Seven cycles were completed between 1981 and 1990.

Transects at site 1 were censused repetitively by the same observer on successive days in January 1986 to obtain an estimate of within-observer error in total abalone counts by transect. Transects at site 8 were censused repetitively by different observers (one experienced, one naive) on the same day in March 1988 to estimate error between observers. In all cases counts by transect differed by less than 1% among duplicate censuses.

To obtain size frequency data for abalones, one transect was selected at random for each study site, and a starting point along the selected transect was chosen at random. Moving in a randomly selected direction along the line, all reachable abalones encountered within 1 m of the line on either side were measured (maximum shell diameter) with calipers. Sampling continued until 100 animals had been measured. Abalones were chosen for measurement only if they could be reached with the calipers without removal from the substratum. Thus, this method was biased against abalones in cryptic microhabitats. A complete sample consisted of measurement of 100 abalones at each of the nine study sites during the course of one census cycle.

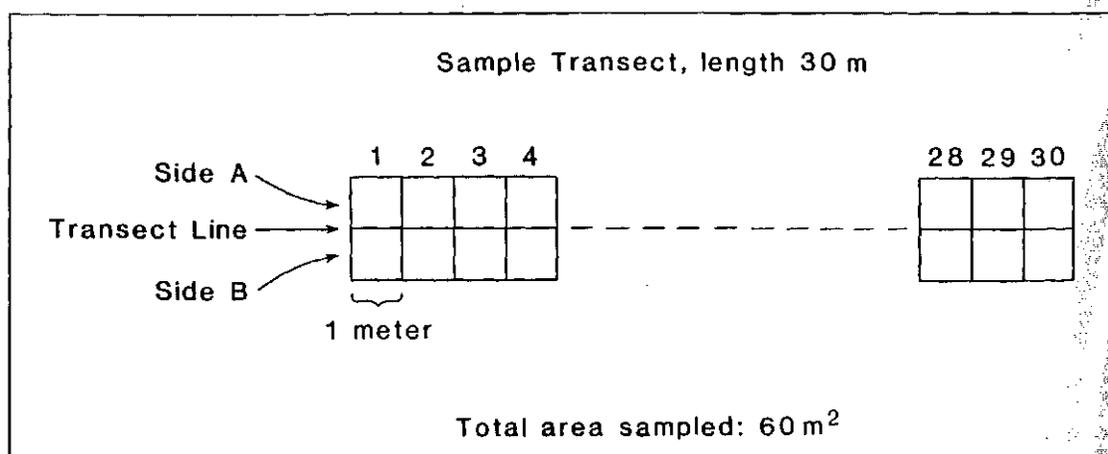


Figure 2. Example of configuration of a permanent transect used to census black abalones. The example shown is a transect 30 m in length; quadrat pairs 5-27 are deleted for brevity in the illustration. Quadrat size is one m².

Substratum characteristics were determined for all quadrats along all permanent transects in 1981 and 1982. After placement of the one m² quadrat frame, the percent cover of open vertical, open horizontal, and crevice microhabitat (defined above) were estimated visually and recorded. Substratum characteristics of quadrats were assumed to be constant over time, and were remeasured only in the event of obvious disturbance. Such disturbances, although sometimes spectacular in character, were rare and highly localized during the study period.

Dispersion in space was examined with Pielou's (1974) index of dispersion (I). For each study site, 50 quadrats were selected randomly from the total number censused. Selection was stratified among transects within each site, such that each transect was represented approximately according to its size. Only non-contiguous quadrats (quadrats with no common points, or those sharing only a corner point) were used for the dispersion analysis, in order to maximize independence of samples. Smaller numbers of quadrats were selected for the random samples at sites four and five because of the lesser overall size of these sites relative to other sites on the Island. The same set of randomly-chosen quadrats was used for computation of I values for each of the first five census cycles at each site. A critical significance level of 0.05 was determined *a priori* for all tests with the I statistic.

Results

Size frequency data (Fig. 3) indicated that most measurable abalones present on permanent transects were adults (minimum reported size for reproduction in black abalones is 45-60 mm maximum shell diameter; Boolootian *et al.* 1962; Webber & Giese 1969; Douros 1985). The pattern of size distribution is consistent with data for several abalone species (*e.g.*, Shepherd 1973), with juveniles typically confined primarily to cryptic locations, often well-separated from adults (and, therefore, under-sampled in this study),

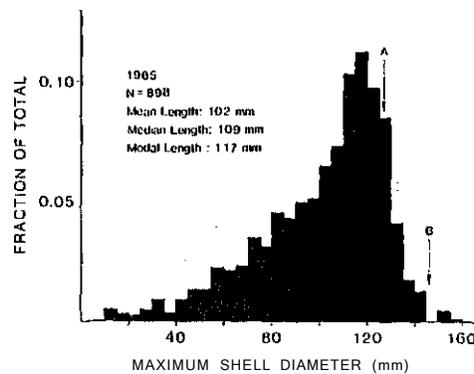


Figure 3. Size frequency data for black abalones sampled randomly from permanent transects in 1985. Approximately 100 abalone were measured at each of the nine permanent study sites. Arrow "A" indicates minimum size for recreational harvest (127 mm); arrow "B" the minimum for commercial harvest (146 mm).

to avoid predators. The 1985 data (Fig. 3) are typical of data from other years sampled. About 15% of abalones sampled were above the minimum legal size for sport harvest (127 mm), and less than 1% were above the minimum for commercial harvest (146 mm).

Densities of abalones per quadrat were high at all sites, and were in some cases extraordinarily high. For example, mean density at transect 3 (50 quadrats), site 7, was 37.8 abalones per quadrat in late winter 1982. In January 1987, 235 abalones were counted in one quadrat at site 7, transect 1. The island-wide mean density in permanent transects ranged from 12-14 abalones per quadrat during the study (2048 quadrats total). Actual areas of substratum within each quadrat may have been substantially greater than 1 m² because of irregularities in the rock. In cases where deep crevices opened into the quadrat, actual surface area within the quadrat may have been up to 3 or 4 m².

The pattern of temporal variation in abalone densities varied among locations (Fig. 4). Densities at sites along the north shore of the island did not vary substantially over the course of the study. Densities at sites along the south shore were more variable. Densities declined by approximately one-half at site 5 between

1982 and 1990, and by approximately one-third at site eight between 1985 and 1990 (Figure 4). Apparent increases occurred at site 6 between 1988 and 1990, and at site 9 between 1986 and 1990 (Fig. 4). Densities were most variable at site 7 (Fig. 4).

Black abalones were strikingly patchy in space on all permanent transects at the island; data from randomly-selected quadrats indicated significant aggregation at all locations in all years censused (Pielou's {1974} I , $p < 0.05$). Moreover, patches of abalones persisted at a given location over time, generally in areas where the availability of cryptic habitat or vertical surfaces is relatively high (examples in Fig. 5). For example, I used the data on

substratum characteristics to calculate expected values for microhabitat distribution of abalones along three permanent transects at site 1 in 1983 (Table 2), testing the hypothesis that microhabitat use is proportional to availability. Observed distributions during censuses departed significantly from expectation (Chi-square, $p < 0.005$; Table 2). The data indicated a particularly strong positive selection by black abalones for cryptic microhabitat, and a general avoidance of open horizontal substrata.

Sea otters occasionally have been observed feeding on black abalones at San Nicolas Island, primarily near site 9, and rarely near site 8. Black abalones appear to constitute less than 5% (by frequency of occurrence) of the

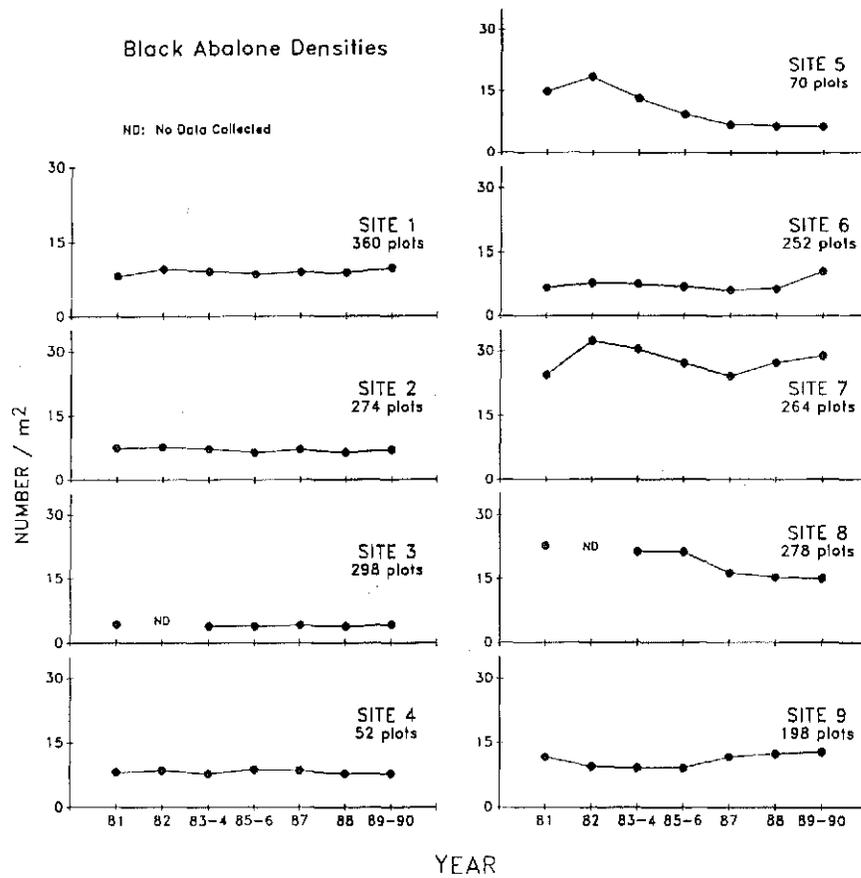


Figure 4. Temporal trends in censuses of intertidal black abalones in permanent transects, lumped by site.

diet of the sea otter population at the island (United States Fish and Wildlife Service, unpubl. data).

Black abalones afflicted with WS were not seen at any time during the study at San Nicolas Island.

Discussion

Black abalone populations sampled in this study were dominated by large individuals (110-130 mm maximum shell diameter), with a sharp truncation in the size distribution above 130 mm. The size distribution was consistent among years. I suggest that the observed distribution is a product of three primary factors: 1) low rates of recruitment in most

years at most sites (exception noted below); 2) low mortality rates of large individuals and 3) growth rates at or near zero in large individuals. Data collected at Santa Cruz (Wright 1975) and San Nicolas (VanBlaricom, study in progress) Islands were consistent with the latter two patterns. Growth rate (rate of increase in maximum shell diameter) was at or near zero for large black abalones at both Islands. Survival rate and longevity of large black abalones were high at San Nicolas Island. For example, 58 abalones were individually tagged as adults at site 1 in 1980. At least 10 tagged individuals remained alive in March 1988. Data on recruitment rates were not collected. However, frequent inspections throughout this study in deep crevices and

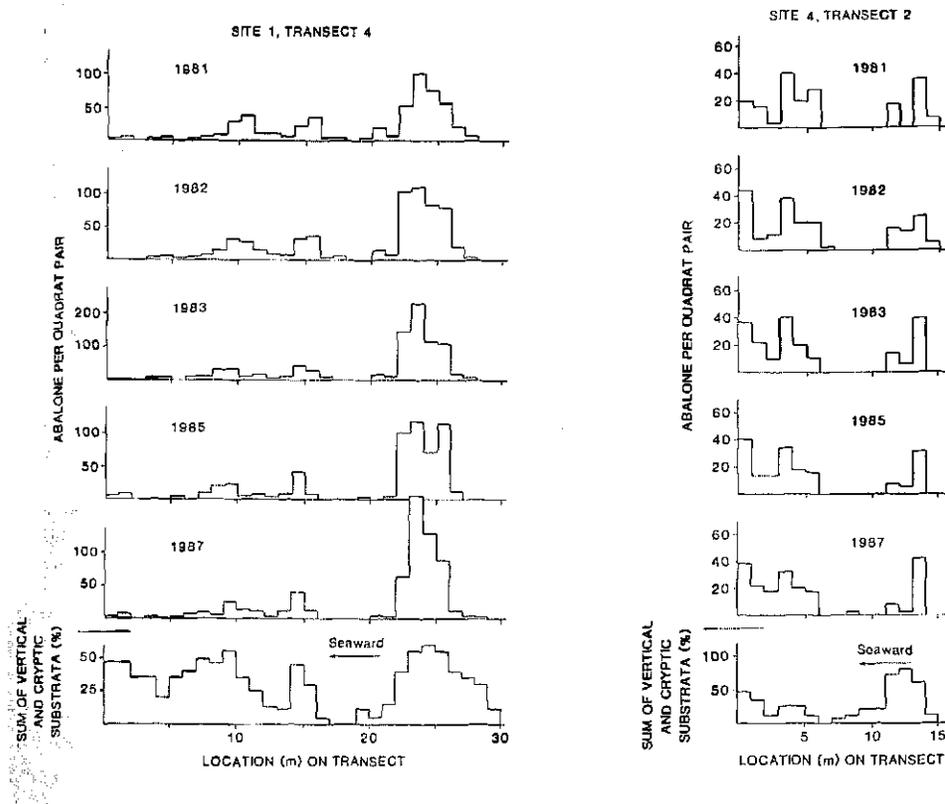


Figure 5. Examples of distribution of black abalones by quadrat pair along the length of a permanent transect line, over the course of five census cycles. For each example, the upper five plots show the distribution of abalones along the transect for each census. The bottom plot shows the distribution of microhabitat category (data are the sum of percent cryptic and percent open vertical rock surface in each quadrat pair; see text for definitions).

under boulders suggested typically low rates of recruitment (but see below) of black abalones at San Nicolas Island.

Human harvest may contribute to the truncated size distribution of black abalones at San Nicolas Island. Military personnel and civilian contractors stationed on the island remove black abalones on a recreational scale (minimum legal size for harvest is 127 mm). Commercial harvest of black abalones (minimum size 146 mm) at San Nicolas is in violation of U.S. Navy security regulations, but a significant commercial take has been tolerated through informal agreements for a number of years (see Table 1). My observations during this study suggested, however, that removal of black abalones by people is frequent only in certain easily accessible locations (additional discussion below), and likely has little influence on island-wide patterns of size distribution.

Patterns of temporal variation in black abalone numbers correlated well with physical characteristics of the study sites. South shore sites (especially 5 through 8) are exposed to the direct impact of incoming breaking waves. Remaining sites are somewhat protected from wave impact because a portion of the incoming wave energy is dispersed by offshore reefs and shoals. Observed declines at sites 5 and 7 coincided with a prolonged period of extreme wave events, thermal anomalies, and a

consequent reduction in algal food supply for abalones (Cane 1983; Earle *et al.* 1984; Seymour *et al.* 1984; Tegner & Dayton 1987). Declines at site 5 may have been exacerbated by the relatively frequent utilization of this site by island residents for recreational harvest of abalones. An obvious ecological correlate for the decline in abalone densities at site 8 was not observed.

Many small juvenile black abalones appeared in cryptic microhabitats at sites 6, 7, and 9, beginning in December 1985 and continuing, for several years. The timing of the initial appearance of the juveniles suggested a significant recruitment event in association with termination of the 1982-83 El Nino Southern Oscillation event (Cane 1983; Tegner & Dayton 1987). Subsequent increases in adult densities at the three sites may have resulted from entry of the "post El Nino" cohort of black abalones into local breeding populations. Based on these observations, it appears that maintenance of high densities of black abalones at sites regularly exposed to heavy wave impact requires the occurrence of anomalously high recruitment events at intervals less than the typical life span of individual abalones. Abalone populations at exposed sites should, therefore, generally show periods of decline punctuated by relatively rapid increases in numbers. Temporal patterns

Table 2. Utilization of microhabitat categories by black abalone at site 1 in 1983.

	Microhabitat Category ¹	No. abalone observed	No. abalone expected ²	Chi-square probability
Transect 1:	Open vertical	14	239	<0.005
	Open horizontal	7	240	
	Cryptic	596	138	
Transect 2:	Open vertical	99	39	<0.005
	Open horizontal	53	202	
	Cryptic	212	163	
Transect 3:	Open vertical	94	112	<0.005
	Open horizontal	115	354	
	Cryptic	319	62	

¹ Categories are defined in text.

² Expected values computed from distributions of substratum categories. Additional details in text.

of this type resemble those of *Haliotis laevigata* in South Australia (Shepherd 1990); alternating periods of strong recruitment and intensified predation by rays produce substantial oscillations in abalone numbers over multi-year periods. At more protected locations on San Nicolas Island, adult mortality rates apparently are sufficiently low that even low rates of recruitment are sufficient to maintain the adult population at relative constancy.

The distribution and frequency of consumption of black abalones by sea otters at San Nicolas Island were such that temporal variations in abalone stocks probably were not influenced by otters during the study.

Black abalones at San Nicolas Island are patchy in space, and patches are strongly persistent at a given location over time. Positions of patches correlate with the availability of cryptic and vertical substrata. The constancy of patch location and substratum character, and the substantial variation which can occur in other environmental correlates (wave exposure, food supply, predation) within and between years, suggest that substratum configuration determines patch location in black abalones. In dense patches, black abalones occupy most primary space on rock surfaces (Douros 1985, 1987; qualitative observations during the present study). Persistent patches of dominant organisms capable of resisting "invasion" by competitors can be principal factors in the structure and organization of other benthic marine communities (Dayton *et al.* 1984). To the extent that patch dominance by black abalones is verified by the appropriate experiments, substratum character is a primary contributor to the organization of the rocky intertidal community at San Nicolas Island. Sea otters could overshadow the importance of substratum character, but only to the extent that black abalones are taken from dense patches. Studies elsewhere indicate that patterns of intertidal foraging by sea otters may be difficult to predict (VanBlaricom 1988). The onset of WS likewise may influence patterns of

space utilization where black abalones would otherwise be abundant, but there is much to be learned before models connecting WS and use of intertidal space can be developed.

The strong affinity of black abalones for cryptic microhabitats may buffer the effects of sea otters as predators, even if black abalones are preferred prey. At least three factors will have a major influence on the eventual effect of sea otters on black abalone populations at San Nicolas Island, assuming that the sea otter population survives at the island: 1) The effectiveness of cryptic microhabitats in the intertidal zone as refugia for abalones from foraging sea otters; 2) the rate of utilization of the intertidal zone as a foraging habitat for sea otters, relative to rates for other habitats, such as kelp forests, also known to support sea otter foraging and 3) the degree of variation across time, space, and among individual sea otters (see VanBlaricom 1988; Riedman & Estes 1990) in the use of black abalones as prey by sea otters. Resilience of black abalone populations to predation by sea otters will be influenced largely by recruitment characteristics of the abalones. If larvae of black abalones disperse only short distances and are produced primarily by local stocks of adults (see Prince *et al.* 1987; 1988, McShane *et al.* 1988; Brown 1991) reproductive output and recruitment success of black abalones at the island will depend to a large degree on patterns of density and reproductive success of those abalone which survive in cryptic refugia, assuming that non-cryptic adults will be removed by sea otters. If, however, larvae of black abalones are long-distance dispersers which can be supplied by distant sources, recruitment success will be influenced significantly by large-scale oceanographic patterns (see Cowen 1985) as well as local reproductive success. Since dispersal and recruitment of black abalones are poorly understood, it remains difficult to predict the nature or extent of the effect of sea otters as predators on populations of black abalones at San Nicolas Island. Resolution of the above issues will also bear on the

development of strategies for restocking and management of black abalone populations under the influence of WS,

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