Prehistoric Predation on Black Abalone by Chumash Indians and Sea Otters

William J. Douros¹

Department of Biological Sciences

University of California

Santa Barbara, CA 93106

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Abstract - Present populations of black abalone (Haliotis cracherodii Leach) at Santa Cruz Island, California are presently dense, up to $90/m^2$. Examination of shell middens created by Chumash Indians suggests that such high present-day densities may have developed recently after the elimination of the black abalone's two cardinal predators: Chumash Indians and sea otters (Enhydra lutris). The size distribution of abalone in existing populations is skewed towards large individuals (>100 mm) whereas shells from midden populations are smaller (<80 mm). A difference in predation intensity may account for the disparity in population characteristics between historic populations and contemporary populations of black abalone. Intense intraspecific competition among black abalone, as well as certain behaviors, may be recent developments following reduction in predation intensity. If so, black abalone may be experiencing relatively new selection regimes.

Introduction

The degree to which predators affect their prey populations is an ecological question of considerable interest. Numerous studies have examined the constraining effect that predation may have on prey density and body size (see Gause 1934; Huffaker 1958; Connell 1961; Elson 1962; Paine 1974; Peterson 1979; Schmitt 1982, 1987). Other studies have shown that the prey may also limit predator densities (see Gause 1934). In this paper I consider the potential

¹Current Address: Energy Division, County of Santa Barbara Santa Barbara, CA 93101 influence two predators may have had on populations of the black abalone (*Haliotis cracherodii* Leach). Specifically, I explore whether abalone densities and body sizes may have shifted following changes in predation pressure.

The sea otter, Enhydra lutris, is a well known nearshore predator along the coast of California that can limit the distribution and abundance of one or several of its prey (Kenyon 1969; Wild & Ames 1974; Estes et al. 1981). In the subtidal region, sea otters can dramatically affect densities and microhabitat distribution of several abalone species (Ebert 1968; Wild & Ames 1974; Breen et al. 1982; Hines & Pearse 1982), including black abalone (Estes et al. 1981). Prehistoric man also preved upon black abalone and may have significantly impacted intertidal populations (Wilcoxon 1992). Both of these predators were active along the shores of the California Channel Islands including Santa Cruz Island.

Chumash Indians began inhabiting the Channel Islands around 7,500 years B.P. (Glassow 1980), but perhaps even as early as 37,000 B.P. (Orr 1968). Abalone and other shelled invertebrates were collected by Chumash as food, and shells were discarded into vast piles, termed middens. These often were located directly above the site where the animals were gathered, although some middens were on hilltops, several miles from shore (Wilcoxon 1992; Douros unpubl. obs.). The shell collection in middens represents a record of foraging by Chumash. By examining archaeological samples containing Haliotis cracherodii shells, I estimated the size structure of black abalone populations from thousands of years ago. Presently, high density populations of black abalone commonly occur at Santa Cruz Island, ranging in density from 80-100

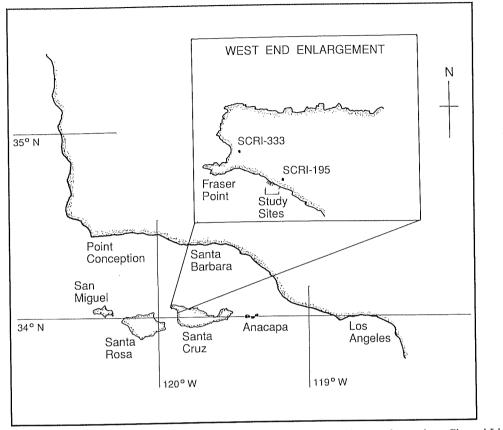


Figure 1. Map of study area. The general map is of the southern California area, showing the northern Channel Islands. The midden sites and study sites are indicated on the insert of the west end of Santa Cruz Island.

individuals/m²; subtidal populations are also extensive at Santa Cruz Island with maximum densities reaching approximately 30 individuals/m² in some areas. Differences between reconstructed prehistoric populations and contemporary intertidal populations of black abalone may indicate whether grossly different ecological constraints operated on the two populations.

In this paper, I present evidence that suggests predation by Chumash Indians and sea otters on Santa Cruz Island constrained populations of black abalone. The evidence supports the hypothesis that Chumash and sea otters together kept size distributions and population densities of black abalone at Santa Cruz Island far below the levels of contemporary populations.

Materials and Methods

Haliotis cracherodii shells from two midden sites at Santa Cruz Island (119°50'W, 34°00'N) were measured. The first site, SCRI-195, is located 1.5 km east of Fraser Point on the west end of Santa Cruz Island; the second, SCRI-333, is situated at the base of Fraser Point (Fig. 1). The sites provided information for the time period: 5,190 B.P. (SCRI-333) to near present (SCRI-195). At SCRI-333, the age of shells ranged from 5,190 years B.P. at the base of the midden to 3,500 years B.P. at the surface (Wilcoxon 1992). SCRI-195 shells ranged from 2,310 years B.P. at the bottom to historical contact, 280 years B.P., at the top (Glassow 1980). Temporal changes in the size distribution of the shells of consumed black abalone were estimated by examining the

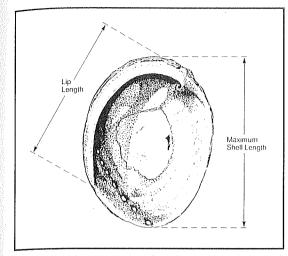


Figure 2. Measurements taken for midden shells and contemporary shells; whole shell measurement (maximum shell length) was taken where possible, lip length was measured for fractured shells.

archaeololgical remains of these middens. Whole shells as well as fragments and pieces of shells were collected by workers from the UCSB Anthropology Department, from June through September of 1981 and 1982 at SCRI-195 and August 1980 through October 1981 at SCRI-333. Boxes of shells from each midden were selected at random, and a total of 171 shells from each site were measured. The selection of shells complimented the distribution of shells within all strata of the archaeological site. Further, since all strata within the site were sampled for abalone shells by the originial collecting archaeologists, my measurements of these shells included the range of time the site was used for deposition of shells and thus represents a reasonable range of environmental conditions that affected the adjacent intertidal populations of abalone.

My goal was to measure or estimate the maximum shell length of individual black abalone at the tune of capture by the Chumash forager. Often however, the shell was fragmentary, with only the inner lip, the most robust portion of the shell, remaining. The lip length, measured linearly from the apex of the shell to where the lip blended into the shell proper was recorded, as was the maximum length of the shell when possible (Fig. 2). To estimate total length of shells represented by the lip only, I performed a regression analysis on whole shells to determine the relationship of lip length and maximum shell length. From this relationship, I calculated the maximum length of shells represented by only the lip portion.

I also measured 81 shells of contemporary black abalone collected from Santa Cruz Island to assess possible allometric changes between time periods. Only shells from sacrificed live animals or from recently deceased abalone found along the shore were used. An analysis of covariance was performed to test for allometric differences between shells from current and midden collections.

Lastly, extant, high density black abalone populations in the intertidal zone between - 2.0 ft and + 4.0 ft were surveyed by measuring the size of all black abalone within 10 random, 0.5 x 0.5 m quadrats (for details see Douros 1985). Four sites were sampled in this manner at the west end of Santa Cruz island, below the midden sites (Fig. 1). A Chi-square analysis was used to test whether the size distribution of midden shells was different from the size distribution of presently dense *Haliotis cracherodii* populations.

Results

The relationship between lip length and overall shell length for midden shells was fit well by the linear function: y = .838x - .323, $R^2 = .9985$ (units in mm; 'x' value represents maximum shell length, 'y' value represents lip length). This function was then used to predict the maximum length of fragmented shells. An analysis of covariance revealed no difference in the lip length to shell length ratio of midden and contemporary shells ($F_{1,185} = 1.09$, P = 0.297) (Fig. 3). Midden shells some 5,000 years old showed the same allometric relationship as contemporary shells.

The size distribution of shells from both midden sites, shown in Fig. 4, were not significantly different ($X^2 = 5.95$, df = 6, P > 0.10). Although based on only two historic

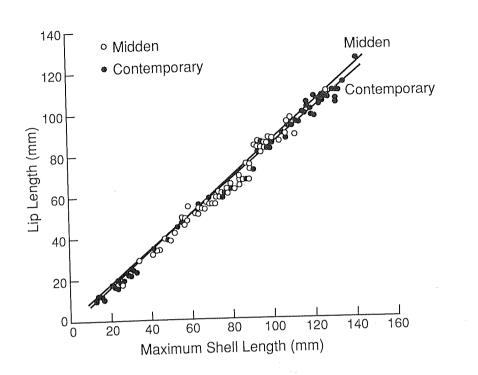


Figure 3. The relationship of lip length to maximum shell length for midden and contemporary shells. The slopes and intercepts of the lines are not significantly different, ANCOVA $F_{1,158} = 1.09$, P > 0.25.

dates, this result suggests that the sizes of shells in the two middens were similar for the two periods between 5,000 years ago and only two thousand years ago. The two midden sites were lumped together for subsequent analyses.

Comparison of the body size distributions of abalone shells in middens with contemporary populations shows marked differences (Fig. 5; X^2 = 307.6, df = 6, P < 0.0001). Large *Haliotis* cracherodii shells, virtually missing in the middens, were present in large numbers in extant populations. The average density of contemporary populations was 93 abalone/m² (ISE = 1.69, n = 4 sites); comparable density estimates for prehistoric populations are not available.

Discussion

The role of Chumash Indians in influencing black abalone populations in intertidal areas can be speculated from the archaeological shell record. Black abalone also were found in subtidal areas at Santa Cruz Island; however,

the subtidal zone was not a refuge from foraging as sea otters (*Endydra lutris*) were common at Santa Cruz Island and presumably, if consistent with contemporary sea otters, fed on black abalone. Thus, the effect of sea otter predation on prehistoric black abalone populations, based on an assessment of contemporary otter-abalone interactions, must be considered as well.

It is first important to note that examination of archaeological remains has proven to be an effective method for assessing prehistoric ecological parameters and conditions in many areas (Meighan 1959; Tartaglia 1976; Holbrook 1977; Wilcoxon 1992). For Santa Cruz Island populations of black abalone, the evidence that present day populations are now at relatively high densities is circumstantial. However, because there is no direct record of abalone densities when aboriginal man and sea otters were present, the archaeological record is the most relevant source of interpretive information.

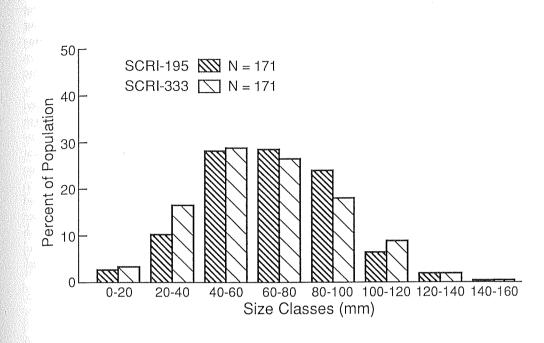
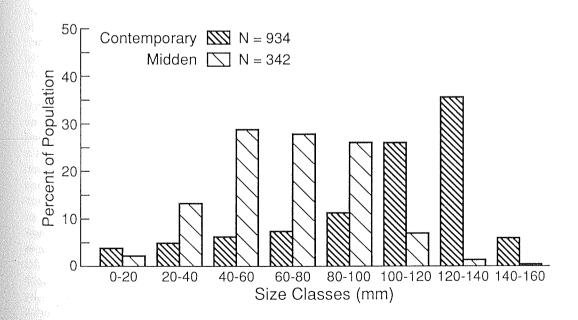
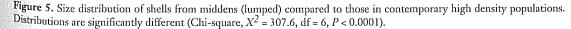


Figure 4. Size distribution of shells from two middens SCRI-333 (older) and SCRI-195 (younger). Distributions are not significantly different (Chi-square, $X^2 = 5.95$, df = 6, P > 0.10).





Predation by Chumash Indians: During the period from 5,200 B.P. to near present, the estimated 1,800-3,200 Chumash at Santa Cruz Island relied heavily upon intertidal populations of Mytilus californianus and Haliotis cracherodii collected from the intertidal zone (Glassow 1993). Abalone shells found in middens are quite probably exclusively from intertidal populations, as Chumash Indians at Santa Cruz Island probably were not diving for the abalone they collected (Glassow 1993). DiBartolomeo (1979) found that Pervuian Indians in South America, who commonly spend a great deal of time in the water showed extreme calcification in the ear canal, termed auditory exostoses, due to cold water in their ear canals. As part of a larger sampling, skulls examined from a cemetery at the base of Fraser Point on the west end of Santa Cruz showed little or no evidence of auditory exostoses, thereby supporting the theory that Chumash Indians only gathered abalone from land (Glassow 1993).

The intensity of predation by Chumash Indians on these species is reflected by the midden shell composition, and shows prehistoric black abalone populations strikingly different than present populations. The difference between midden and contemporary shell sizes may reflect one of the following four causes: 1) black abalone were smaller relative to present animals; 2) dis-proportionate postmortem loss of large abalone shells; 3) Chumash preferentially collected smaller black abalone, leaving larger adults on the rock; 4) Chumash preferentially selected the largest available size, and thereby eliminated the very large size classes.

The first interpretation seems unlikely since large black abalone in prehistoric populations as displayed in the archaeological record were present, albeit in low numbers. Further, prehistoric shells were nearly morphometrically identical to contemporary shells (Fig. 3), unlikely if prehistoric abalone were contemporary diminuitives. Both of these findings cast doubt on the hypothesis that prehistoric black abalone were a diminuitive race of present day animals. It is possible that growth rates of prehistoric abalone were lower than modern counterparts due to environmental factors. There is no information available to allow assessment of prehistoric food levels, and although prehistoric water temperature changes have been discussed (Glassow 1993), their effect on abalone growth is unclear. Clearly, if prehistoric populations suffered from lower growth rates than present populations, predation effects would have been even more pronounced since growth to reproductive size would have taken longer and ultimate number of offspring would have been greatly reduced. Therefore, assuming growth rates to be similar between prehistoric and contemporary populations is conservative with regards to determining predation effects.

Considering the second interpretation, disproportionate loss of large shells can be discounted by noting that the majority of abalone shells harvested are thought to have been deposited in the middens. Only a small fraction of abalone shells were used to make jewelry, unlike the shells of other invertebrates; and, although abalone shells had only moderate use as soup bowls, even these bowls were found in the middens and thus measured and counted (Wilcoxon 1992; Douros pers. obs.). Further, larger shells, more robust than small shells, would be expected to have been preserved in the middens better than smaller shells.

The third interpretation could be accurate if Indians did not select large black abalone because they could not remove them, could not consume them, or did not enjoy their taste. It is impossible to comment on Chumash taste; yet, it is important to note that large abalone apparently were prepared for consumption identically to small abalone, either dried or cooked (Wilcoxon 1992). Midden records show that Chumash foragers possessed tools such as wood and bone bars to pry abalone free (Orr 1968). Thus, it is doubtful that black abalone had a refuge from Chumash predation by growing large. Numerous large red abalone (Haliotis rufescens), including one 234 mm, and black abalone greater than 140 mm were found

in the midden samples, demonstrating that such large-sized animals could be harvested. Lastly, the population of Chumash on Santa Cruz Island may have been food limited (Wilcoxon 1992). Seemingly undesirable food items such as tiny mollusk shells, H. cracherodii, Olivella biplicata, Tegula sp., Mytilus sp. Crepidula sp. and Acmaea sp. and echinoderms, Strongylocentrotus sp. were very common in midden samples (Wilcoxon 1992; Douros unpubl. obs.). Although some small mollusk shells could have arrived from epibiontic passage, the large abundance of these coupled with food limitations of Chumash (Wilcoxon 1992) suggest that every edible invertebrate available was consumed. It therefore seems unlikely that large black abalone were available, but not collected.

The most parsimonious explanation then, is that large black abalone were not abundant because Chumash foragers continually selected the biggest animal they could find. Abalone may have had a low probability of avoiding predation and growing large. Common structural refuges, cracks and the undersides of boulders, are most suitable for small abalone (Hines & Pearse 1982; Douros 1985); intertidal individuals too large for such a refuge would have been highly susceptible to collection by Chumash foragers. Thus, midden shells may be an accurate reflection of the size-structure of prehistoric intertidal populations, which is skewed toward smaller abalone relative to modern day populations.

It is also conceivable that foraging by Chumash Indians was sufficient to reduce absolute densities of black abalone in the intertidal zone. Simply the presence in the middens of extremely small abalone shells (< 20 mm), and other small mollusk, echinoderm and arthropod shells, suggests that Chumash may have been harvesting and consuming all sizes of intertidal invertebrates encountered. A picture arises of Chumash foragers regularly patrolling intertidal areas at low tides, removing all abalone and other invertebrates observed, large and small.

Predation by Sea Otters: Available literature regarding predation on several abalone species was reviewed to determine the effect of sea otters on body size and population density of black abalone. Sea otters appear to forage by maximizing their energy intake per unit foraging time (Ostfeld 1982), and do so by consuming the largest available prey (Hines & Pearse 1982). Areas north of the current range of sea otters (e.g., Año Nuevo Island) have dense populations of large abalone, primarily red abalone (Haliotis rufescens), compared to areas presently occupied by sea otters (e.g., Hopkins Marine Refuge). Further, the body size of three abalone species selected by sea otters at newly colonized areas is markedly larger than at areas occupied by otters for years (Hines & Pearse 1982).

Sea otters can greatly reduce the density of subtidal black and red abalone populations (Estes et al. 1981), in part due to the strong preference for this food item. Nearly 25% of the diet of sea otters colonizing Pt. Buchon in 1973 was comprised of abalone (data from Wild & Ames 1974); two years later, abalone accounted for only 3% of the items harvested by this otter population (Estes et al. 1981). These data suggest several points. First, sea otters strongly prefer a number of abalone species over many other potential food items. Second, otters can radically alter the sizestructure of abalone populations by selecting the largest available animal. Finally, predation by otters can be sufficiently intense so as to reduce the abundance of abalone populations.

Sea otters were common at the northern Channel Islands until the early 1700's, (app. 3 otters/km²; Kenyon 1969). Based on the existing literature, sea otters do not appear to discriminate their foraging between abalone species, as at least four species have been shown to be affected by otter foraging. Thus, since there is little reason to believe that prehistoric otters foraged any differently from their present-day counterparts, it is conceivable that prehistoric sea otters had effects on abalone populations similar to those of modern otters, namely altering sizefrequencies of abalone toward smaller sizes and lowering abalone population densities. However, it is also likely that if prehistoric otters had such effects on black abalone, these would have been limited to the subtidal portion of the abalone population. Results reported by VanBlaricom (1993) suggest that sea otters in California rarely feed on intertidal mussels, even when that food, and other prey, are abundant there.

There are several reasons why subtidal predation by otters on black abalone may be important to intertidal populations of abalone. First, Haliotis cracherodii move between subtidal and intertidal habitats (Douros 1987), and thus can be subject to predation by sea otters. This may have the effect of reducing the number of black abalone in the intertidal zone by reducing the number of potential immigrants. Second, reduction in the body size and density of black abalone in subtidal areas could reduce the number of abalone larvae available to settle in either habitat by lowering the population's overall fecundity (Boolootian et al. 1962; Webber & Geise 1969; Tutschulte & Connell 1981).

Outcomes of Predation: Hines & Pearse (1982) describe areas with and without contemporary otter and human foraging pressure. In that study of subtidal populations of abalone, where both otters and humans preyed on abalone, only small abalone were found at extremely low densities (<1/10m²). Conversely, populations in areas free from both predators were more than an order of magnitude more dense (app. $10/10m^2$) and contained a sizeable fraction of larger individuals. Present populations at Santa Cruz Island, free from both predators average 93 abalone/m². Based on projections from contemporary studies, prehistoric populations having both predators, may have had densities one to two orders of magnitude lower.

Because Chumash exploited other food sources, some of which were costly in terms of time and energy such as fishing, it is unlikely that high or even moderate densities of black abalone were left unharvested in the intertidal zone. Again, the presence of numerous small mollusk, echinoderm, and arthropod shells in the middens demonstrates that black abalone densities may have been so low prehistorically that Chumash were willing to harvest and consume all sizes of intertidal invertebrates, regardless of their desireability or energetics as food.

A full discussion of community-level effects resulting from decreased black abalone population densities and body sizes would be beyond the scope of this paper. However, it should be noted that these effects could include changes in species distributions and abundances within intertidal areas at Santa Cruz Island. Reduction in competition for space and food, seen in contemporary populations of abalone (Douros 1985) and other invertebrate species (Connell 1961), could be reasonably expected within intertidal communities. The community structure seen today, relative domination by black abalone in surge channels and by Mytilus californianus in areas of higher relief (Douros 1985), is probably quite different than during prehistoric times of higher predation intensity.

Lastly, when the above arguments regarding present-day black abalone populations being more dense than prehistoric populations are considered, it becomes apparent that high levels of intraspecific competition currently observed (Douros 1985) may be a recent event. The relatively recent occurence of intraspecific competition may be driving new levels of selection within black abalone populations not experienced when prehistoric populations were subjected to predation by Chumash Indians and sea otters.

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The Occurrence of Red Abalone Shells in Northern Channel Island Archaeological Middens: Implications for Climatic Reconstruction

Michael A. Glassow Department of Anthropology, University of California, Santa Barbara, CA 93106

Abstract - Certain archaeological sites on the northern Channel Islands dating between *ca*. 4,500 and 7,500 B.P. contain unusually high frequencies of red abalone *(Haliotis rufescens)* shells. Assuming that aboriginal peoples living at these sites collected shellfish principally from the intertidal zone, the high frequency of red abalone shells may reflect a time when sea water temperatures were cooler than present, allowing red abalone to be the dominant abalone species in the intertidal zone.

Introduction

A spectacular feature of certain archaeological sites on the northern Channel Islands is the presence of midden deposits containing densely concentrated red abalone shells (Haliotis rufescens). In many cases, the shells are so dense as to form a continuous layer in which shells of other species are either absent or in minor quantities. In other cases, red abalone shells are a prominent constituent of a varied assemblage of shellfish remains. The red abalone middens are typically quite thin, no more than perhaps 25 cm thick, even at sites where red abalone is mixed with a number of other species. These middens are especially intriguing because today red abalone inhabit a subtidal zone around the northern Channel Islands and therefore are not obtainable in the intertidal zone in the substantial numbers implied by their dense concentrations in the middens. Instead, black abalone (Haliotis cracherodii) is the common intertidal species, and shells of this species often are found in considerable quantities in midden deposits which typically either overlie the strata

containing abundant red abalone shells or are in nearby sites. In the red abalone middens, black abalone shells are either absent or very rare, and when they do occur, they are frequently unusually small in size.

It is significant that most of the red abalone middens appear to represent relatively shortterm occupations and that in most of them red abalone shells occur in the hundreds, while in a few of them their numbers probably are in the thousands. These quantities, along with their relatively high proportional abundance in comparison to other shellfish species, imply that considerable numbers of red abalone could be obtained in one collection episode. In short, red abalone was abundant enough to have been a significant dietary staple to the prehistoric groups who created the red abalone middens.

As early as 1955, Hubbs (1955) postulated that the 7,000-year-old red abalone middens found by Orr on Santa Rosa Island are indicative of times during which sea water temperatures were cooler than today. Hubbs (1958, 1967) argued, in other words, that red abalone would flourish only if sea water temperatures were sufficiently cooler than today to cause red abalone to displace black abalone in the intertidal zone. Orr (1968:97) adopted Hubbs' position, arguing that the early phase of Santa Rosa Island's Dune Dweller Period, dating between about 6,800 and 7,500 B.P., was characterized by cooler than present sea water temperatures.

The implications of the red abalone middens are obvious. If indeed they reflect cooler sea water conditions, their occurrence can be used as a climatic indicator. Following Hubbs' logic, sea water temperatures would have to have been significantly cooler than is the case today for red abalone to be prevalent

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