

Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California

TODD J. BRAJE,^{1,6} JON M. ERLANDSON,^{2,3} TORBEN C. RICK,⁴ PAUL K. DAYTON,⁵ AND MARCO B. A. HATCH⁵

¹Humboldt State University, Department of Anthropology, Arcata, California 95521 USA

²University of Oregon, Department of Anthropology, Eugene, Oregon 97403-1218 USA

³University of Oregon, Museum of Natural and Cultural History, Eugene, Oregon 97403-1218 USA

⁴National Museum of Natural History, Smithsonian Institution, Department of Anthropology, Washington, D.C. 20013-7012 USA

⁵Scripps Institution of Oceanography, University of California–San Diego, La Jolla, California 92093-0227 USA

Abstract. Archaeological data from coastal shell middens provide a window into the structure of ancient marine ecosystems and the nature of human impacts on fisheries that often span millennia. For decades Channel Island archaeologists have studied Middle Holocene shell middens visually dominated by large and often whole shells of the red abalone (*Haliotis rufescens*). Here we use modern ecological data, historical accounts, commercial red abalone catch records, and zooarchaeological data to examine long-term spatial and temporal variation in the productivity of red abalone fisheries on the Northern Channel Islands, California (USA). Historical patterns of abundance, in which red abalone densities increase from east to west through the islands, extend deep into the Holocene. The correlation of historical and archaeological data argue for long-term spatial continuity in productive red abalone fisheries and a resilience of abalone populations despite dramatic ecological changes and intensive human predation spanning more than 8000 years. Archaeological, historical, and ecological data suggest that California kelp forests and red abalone populations are structured by a complex combination of top-down and bottom-up controls.

Key words: archaeology; Channel Islands, California, USA; coastal ecosystem; fishing; *Haliotis rufescens*; Holocene; kelp forests; marine ecology; middens; red abalone.

INTRODUCTION

Ecologists recognize the importance of understanding variation through time and space, but detailed ecological data rarely allow research on such broad scales. Many scholars also recognize the importance of understanding much longer timescales to more accurately evaluate “how humans have interacted with the rest of nature in the past” (Costanza et al. 2007:522), but a full understanding of modern ecological relationships often requires multidisciplinary study of contemporary and ancient human activities (Crumley 1994). As Pauly (1995, Pauly et al. 1998) and others (Jackson et al. 2001) demonstrated, deeper historical perspectives can be crucial to the effective management and restoration of marine ecosystems and fisheries, where modern perspectives on ecological relationships and abundance have been affected by “shifting baselines” caused by historical degradation (see also Dayton et al. 1998, Rick and Erlandson 2008).

Here we examine the human and natural history of southern California kelp forest habitats with the objective of integrating deep time into modern resource management. We synthesize archaeological data and

geological, oceanographic, and ecological literature to explore the resilience of local kelp forest ecosystems to natural and anthropogenic impacts through the Holocene. This includes emerging evidence for trophic cascades triggered by human hunting of sea otters, which appears to have released red abalone populations by 8000 to 7500 years ago, facilitating the development of an intensive fishery that lasted for at least 5000 years.

Trophic cascades involving sea otters, sea urchins, and kelp are well documented in the North Pacific. McLean (1962) demonstrated that sea otter predation on invertebrates (urchins and abalones in southern California waters) protected kelps from overgrazing by sea urchins. In the Aleutian Islands, Simenstad et al. (1978) documented a similar relationship through several millennia during periods when native hunting reduced otter populations, kelp forests apparently became rare, and sea urchins and other invertebrates became conspicuous in archaeological shell middens. When otter hunting was reduced, kelp forest fish became more common in shell middens, suggesting a recovery of local kelp habitats.

Although explored in numerous papers, such relationships are not universal. In southern California kelp forests, where sea otters have been functionally extinct since the early 1800s due to intensive hunting associated with the historic fur trade, food webs are more complex, other predators control urchin populations, and kelp

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⁶ E-mail: tjb50@humboldt.edu

forests appear to be more resilient and resistant to collapse (Foster and Schiel 1988, Tegner and Dayton 2000, Steneck et al. 2002).

In this paper, we use an 8000-year record of human predation on red abalones (*Haliotis rufescens*) to examine the resilience of southern California kelp ecosystems to natural and human disturbances. We utilize archaeological methods and data to explore spatial and temporal variation in the productivity of red abalone fisheries on California's Northern Channel Islands (Fig. 1). Our study compares modern, state-protected red abalone populations to the historical records of the last 150 years and an archaeological record spanning much of the Holocene. Despite major paleoenvironmental changes operating on a variety of scales, intensive human predation spanning several millennia, and dramatic ecological changes associated with historic ecosystem disruptions, there is evidence for considerable spatial continuity and ecological resilience of red abalone populations through the last 7500 years. Ultimately, the archaeological, historical, and modern records of red abalone distribution suggest a population structured by a complex combination of top-down and bottom-up controls.

ECOLOGICAL AND PALEOECOLOGICAL RECORDS

Haliotis rufescens is the largest abalone in the world, growing to lengths of ~30 cm. They live along the Pacific Coast of North America, in nearshore waters from Oregon to Baja California (California Fish and Game Commission 2001). Red abalone are relatively slow-growing herbivores that feed primarily on drift kelp, including detritus from the large and fast-growing giant and bull kelps (*Macrocystis pyrifera*, *Nereocystis luetkeana*) and various red algae. Red abalone live primarily in subtidal waters to depths of ~40 m, but they can be found in the low intertidal zone where local conditions allow. In southern California, they are generally restricted to cooler upwelling locations in mainland and Channel Island waters. Northern California and Oregon populations can be found from the intertidal to shallow subtidal depths (California Fish and Game Commission 2005). The distribution and abundance of red abalones are governed by numerous variables, including water temperature, food availability, rocky substrates, wave energy, predation, disease, and competition for food and space. Ideal temperatures range from 13° to 20°C, with spawning from April to July in northern latitudes where food resources are seasonal, but they spawn all year in southern California (California Fish and Game Commission 2001:91). Except for cryptic and/or other less accessible deeper water populations, red abalone larvae, juveniles, and adults are relatively susceptible to predation. As adults, their main predators are sea otters (*Enhydra lutris*) and humans (*Homo sapiens sapiens*), but juveniles are also preyed upon by sea stars, octopi, crabs, lobsters, and a

variety of fishes, including sheephead, cabezon, and bat rays (California Fish and Game Commission 2001:91).

The nearshore marine community surrounding the Northern Channel Islands is an upwelling community, surviving on cold nutrient-rich ocean water welling up from below the thermocline. For upwelling to bring nutrients into surface waters where kelps can utilize them requires a shallow thermocline. Climatic oscillations such as El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) change the thickness of the thermocline and directly affect nutrient regimes in Northern Channel Island waters. El Niño/Southern Oscillation events currently occur every three to seven years when the atmospheric pressure gradient changes between the high-pressure eastern equatorial Pacific and low-pressure western Pacific. El Niños occur during periods of lower-than-average pressure gradient between the eastern and western equatorial Pacific, when the thermocline deepens, resulting in less nutrients at the sea surface. For the Northern Channel Islands this is manifested as increased sea surface temperature (SST) and reduced nutrient levels, resulting in decreased kelp productivity and often reduced red abalone populations. La Niñas occur during times of greater-than-average pressure gradient between the western and eastern equatorial Pacific. La Niñas result in a shallow thermocline, decreased SST, and increased upwelling. The PDO is measured as the first principal component of the variations in SST north of 20°N in the Pacific Ocean. When the PDO is positive, mild El Niño-like conditions persist around the Northern Channel Islands for 15–30 years; when the PDO is negative, mild La Niña like conditions are experienced around the Northern Channel Islands for 15–30 years (see Masters 2006:74).

Several sources of environmental change identified in paleoecological records from the Santa Barbara Channel area may have affected red abalone distribution, abundance, and availability. These include postglacial sea level rise, especially prior to ~7000 years ago, and coastal erosion, which have changed the conformation and location of the coast, the nature of nearshore substrates, and the extent of kelp forests (Graham et al. 2003, Erlandson et al. 2005b, Kinlan et al. 2005). Dune building, droughts, ENSO events, and severe winter storms have also affected marine productivity and the structure of nearshore marine plant and animal communities. El Niño/Southern Oscillation events, in particular, can decrease upwelling in the Santa Barbara Channel, reducing marine productivity.

In 1982–1983, an El Niño event along the California Coast, associated with heavy winter storms, severely affected the marine ecosystem (Dayton and Tegner 1984a, Ambrose et al. 1993, Engle 1994). Widespread kelp die-offs probably significantly reduced shellfish populations that depended on kelp for cover and nutrients (Tegner et al. 2001). Deep-sea ocean cores (Kennett and Kennett 2000) and stable isotope analysis

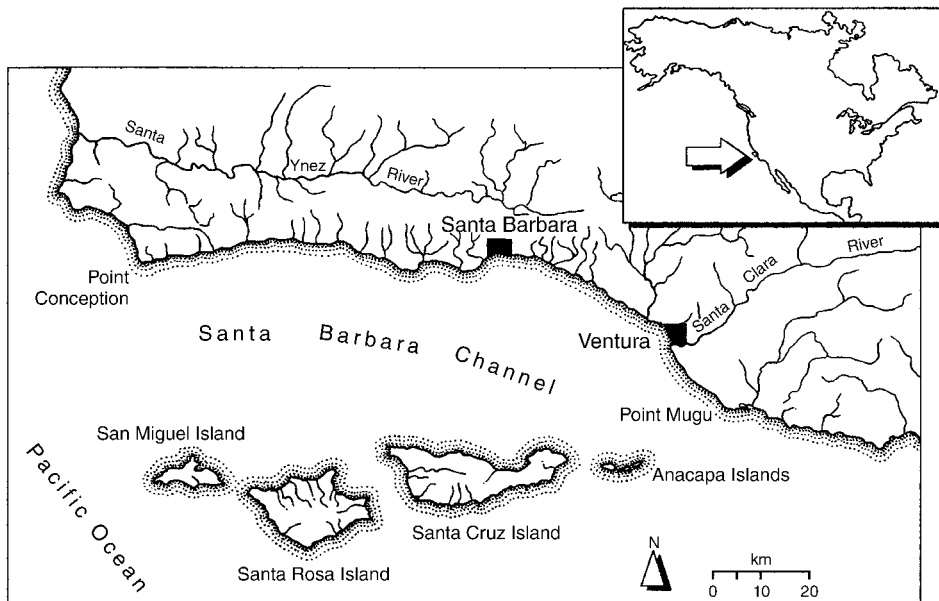


FIG. 1. The location of the Northern Channel Islands and the Santa Barbara Channel off the coast of California, USA.

of shellfish (Glassow et al. 1994, Kennett and Kennett 2000, Kennett 2005, Rick et al. 2006, Robbins 2007) have also documented periods of elevated SST and variability in ocean upwelling and regional marine productivity in prehistoric times.

During the late 1980s and 1990s, black abalones were devastated by withering foot syndrome (WFS) disease, which swept through California abalone populations, resulting in a wholesale collapse of the black abalone industry (Haaker et al. 1992). While subtidal populations of red abalone were also probably stressed by WFS and became more stressed as temperatures increased, serial overfishing was probably the primary cause of the collapse of red abalone populations in southern California (Karpov et al. 2000, Vilchis et al. 2005). Strict controls and restoration efforts regulate the abalone fishery today, but populations have not fully recovered, despite careful monitoring and a complete closure of the commercial and recreational harvest south of San Francisco Bay. Along the central California Coast, recovery of commercial abalone fisheries has been hampered by the demographic and geographic expansion of sea otter populations (Fanshawe et al. 2003), but off San Miguel Island, where no resident sea otter populations currently exist, the partial recovery of red abalone populations has led to increasing pressure to reopen commercial fishing on at least a limited basis.

HISTORICAL RECORDS

Beginning in the early 1800s, commercial hunting and trade driven by Russian, European, and American merchants resulted in the near extermination of sea otters (*Enhydra lutris*) from California waters (Ogden 1941). An important abalone predator, California sea

otters were completely eradicated from Channel Island waters by the late 1800s, surviving only as a small relict population along the rugged and remote Big Sur Coast. The other major predator of adult abalones, the relatively dense populations of Chumash people who occupied the islands for millennia prior to European contact, were decimated by diseases that may have been introduced as early as the 1540s by early Spanish explorers (Erlandson and Bartoy 1995). In AD 1769 the Spanish began an aggressive colonization campaign of Alta California, instituting a pastoral economy that accelerated the breakdown of traditional Chumash society. By approximately AD 1822 the last of the Island Chumash were removed to Spanish towns and missions on the mainland. With their two most effective predators removed from the Northern Channel Islands almost simultaneously, abalone and sea urchin populations exploded in the decades that followed. By the 1850s and 1860s, however, Chinese immigrants had established commercial abalone fishing camps in the San Francisco, Monterey, San Diego, and Baja California areas, focused primarily on harvesting abundant intertidal black abalone (*H. cracherodii*) stocks.

By the late 19th century, Chinese domination of the abalone harvest came to an end at the hands of harsh federal regulations directed at the Chinese community (Wilcox 1893, Braje and Erlandson 2007a, b). Japanese and Euro-American hardhat and (later) SCUBA divers took their place and expanded the industry to include subtidal species such as red, pink (*H. corrugata*), green (*H. fulgens*), and white abalone (*H. sorenseni*). Some of these early divers reported pavements of abalone sometimes five animals deep (but no sea urchin barrens), and early mapping surveys recorded very large kelp

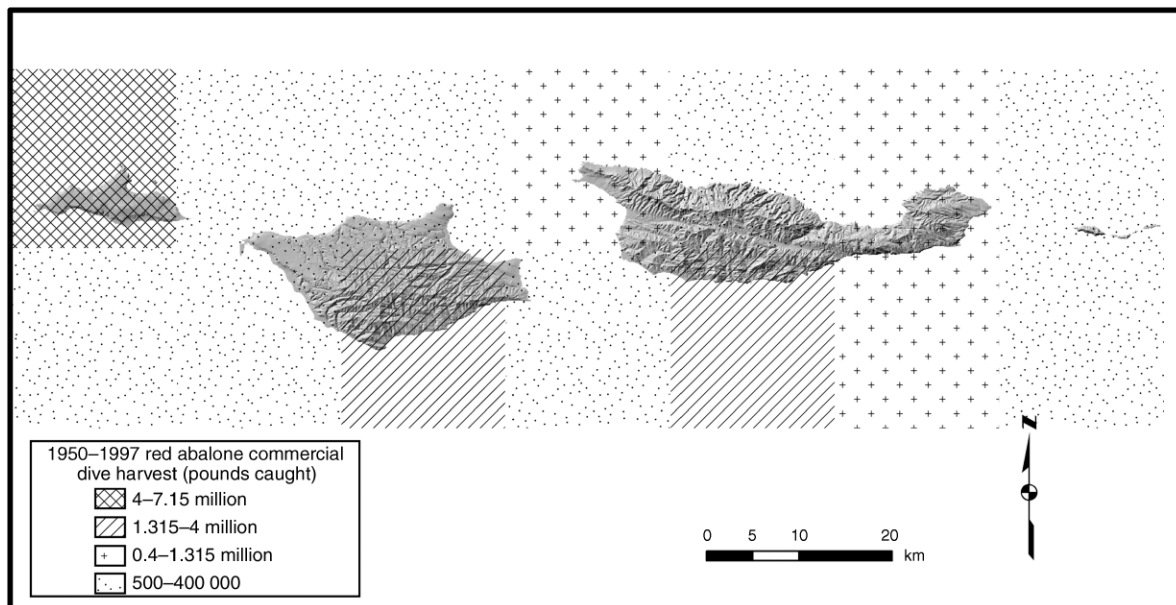


FIG. 2. Location map of historic commercial red abalone (*Haliotis rufescens*) harvest from the Northern Channel Islands from 1950 to 1997 (adapted from California Fish and Game Commission 2005: Appendix D). For conversion to SI units, 1 pound \approx 0.45 kg.

forests (North et al. 1993). Although regulated by government agencies, commercial abalone harvests along the California Coast survived several cycles of boom and bust due to over-harvesting, changing market forces, and environmental fluctuations until the industry's closure in 1997 (California Fish and Game Commission 2005:1-2, Rogers-Bennett et al. 2002:99-102).

As part of the California Department of Fish and Game's abalone recovery and management plan, historical data were compiled documenting the productivity of commercial and recreational dive harvests of red abalone for the Northern Channel Islands (Fig. 2) and the broader California Coast. The data presented in Fig. 2 are based on commercial landing records, and depict the level of red abalone harvest reported for each 6600-ha area of nearshore waters surrounding the Northern Channel Islands (see California Fish and Game Commission 2005: Table 6-1 and Appendix D). These data are relatively coarse-grained, not accounting for local environmental factors such as habitat type and length of coastline within each block, but they provide a general pattern of historic red abalone distribution and abundance that can be compared to archaeological records. As can be seen, the most productive areas recorded for commercial harvest of red abalone on the Channel Islands are centered on San Miguel Island. The waters surrounding the south shore of Santa Rosa and the south-central shore of Santa Cruz were the next most productive, followed by western and eastern Santa Cruz Island. The least productive areas seem to have been waters surrounding Anacapa Island, western Santa

Rosa, and north-central Santa Cruz. These modern distributions generally correlate well with marine SST, with cooler waters surrounding the westerly islands (e.g., San Miguel) and warmer waters to the east (see Schoenherr et al. 1999, Hobday and Tegner 2002).

Several management and restoration studies along the California Coast have incorporated historic commercial catch records to help establish baseline abalone abundances. Rogers-Bennett et al.'s (2002:98) survey, for example, found that some abalone species have "undergone a ten-fold decline" since 1950 and all species of abalone have experienced significant declines. While some resource managers and ecologists have recognized the need to establish restoration baselines that incorporate modern data and historic abundances, archaeological data can provide long-term ecological records prior to heavy historic fishing and other ecosystem disturbances.

ARCHAEOLOGICAL RECORDS

The earliest evidence for human exploitation of red abalone comes from eastern San Miguel Island, where terminal Pleistocene deposits at Daisy Cave (CA-SMI-261; Erlandson et al. 1996, Rick et al. 2001, Erlandson 2007) and the newly recorded Cardwell Bluffs (CA-SMI-678) site contain relatively high proportions of red abalone shell in middens dated between approximately 11 500 and 12 000 calendar years before present (cal yr BP). Even earlier evidence that humans fished for abalones may have been destroyed or submerged by rising postglacial sea levels. Despite such problems, more than 30 shell middens on Santa Cruz, Santa Rosa, and San Miguel islands have been dated between about



PLATE 1. Photograph of the dense red abalone midden component at CA-SMI-481 on northwest San Miguel Island, California, USA. Photo credit: T. J. Braje.

10 000 and 8000 cal yr BP, many of them associated with freshwater springs, caves, or tool-stone sources that drew early maritime peoples away from now-submerged coasts (Rick et al. 2005). Red abalone shells are rare or absent in these Early Holocene middens that contain intertidal mollusk assemblages dominated by California mussels (*Mytilus californianus*), black abalone, turban snails (*Tegula* spp.), owl limpets (*Lottia gigantea*), and other intertidal shellfish (see Erlandson et al. 1999, 2004, 2005a, Braje 2007a).

A major shift occurs between approximately 8000 and 7500 cal yr BP with the appearance of numerous Channel Island middens in which large red abalone shells make up a relatively high proportion of the shellfish assemblages (see Plate 1). The appearance of these red abalone middens and their subsequent disappearance at ~3300 years ago suggest either an increase in the availability of red abalone or a shift in human foraging behavior during the Middle Holocene. After about 3000 to 3500 years ago, red abalone shells (especially large individuals) are relatively rare in Channel Island middens, although this may be due, in part, to the increasing use of large shells for technological purposes such as bowls, fishhooks, and ornaments (Rick et al. 2005). The dominance of black abalone shells in archaeological sites related to the historic Chinese intertidal fishery supports the idea that red abalones on the Channel Islands were largely limited to the subtidal zone, at least in the mid- to late 19th century, much as they were until their recent decimation from commercial overfishing and disease.

Oceanographer Carl Hubbs and geologist/archaeologist Phil Orr conducted the first scientific investigations of Middle Holocene red abalone middens on the northwest coast of Santa Rosa Island. Hubbs (1967) and Orr (1968:97) believed the sites were related to episodes of cooler sea surface temperature during the Middle Holocene that allowed red abalones to migrate from subtidal to intertidal habitats and replace black abalone. Modern abalone distribution studies by Ault (1985) from the central California Coast and Piasias' (1978) SST curve from the Santa Barbara Basin seemed to support these conclusions and were used by Glassow (1993a) to corroborate Hubbs' and Orr's conclusions. Glassow (1993a, 2002, 2005, Glassow et al. 2009) suggested that human foraging for red abalones increased during the Middle Holocene when their intertidal location made them less costly to harvest.

Additional dating of red abalone middens and a more recent, trans-Holocene SST record developed from varved Santa Barbara Basin sediments (Kennett and Kennett 2000, Kennett 2005) suggest that the chronology of red abalone middens corresponds to a period when SSTs were dominated by relatively warm conditions. The Early and Middle Holocene reconstructions are drawn from 50-year running averages that may mask some shorter SST fluctuations. Such oscillations may have affected the availability of red abalone at scales currently undetectable with available climate records. Regardless, this complexity has spurred a reevaluation of earlier models and researchers have proposed alternative hypotheses such as human overexploitation

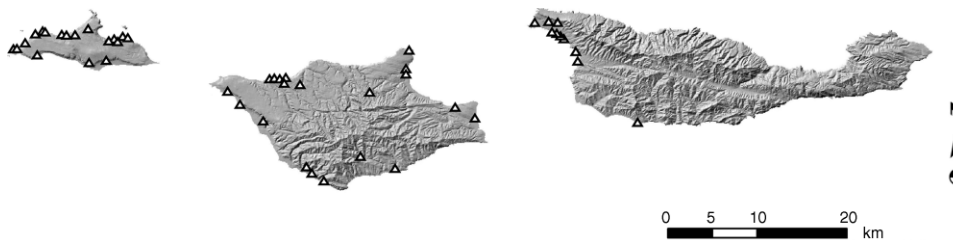


FIG. 3. Distribution map of all radiocarbon-dated Middle Holocene red abalone middens on the Northern Channel Islands.

(Salls 1992), subtidal diving (Sharp 2000), human depletion of sea otter populations (Erlandson et al. 2005b), reduced El Niño frequency (Kennett et al. 2007), or a combination of variables (Rick et al. 2006, Robbins 2007) to explain the abundance of Middle Holocene red abalone middens.

Erlandson et al. (2004, 2005b, 2008) argued that the florescence of San Miguel Island shell middens containing numerous large red abalone shells during the Middle Holocene could not have occurred without a reduction in the density of sea otters living in Channel Island waters (see also Tegner and Dayton 2000, Braje 2007b). A decline in sea otter density could have been caused by natural phenomena (e.g., Estes et al. 1998), but a cultural explanation seems more likely at present. Although there is only limited faunal evidence for sea otter hunting prior to 7500 years ago in San Miguel Island archaeological sites (Erlandson et al. 2004:66), for instance, recent documentation of sophisticated and widespread projectile point technologies dating between ~12 000 and 8400 years ago suggests that sea mammal hunting was an important component of the earliest maritime economies on the Channel Islands (Erlandson et al. 2005a, 2008, Braje 2007a, Glassow et al. 2009). Ecological data recorded as historical California sea otter populations have expanded their range support the notion that red abalone populations that are both abundant and accessible to human foragers are unlikely to coexist with substantial otter populations (McLean 1962).

HISTORICAL ECOLOGY: METHODS AND RESULTS

Historical ecology involves the synthesis of ecological, historical, and archaeological data to address issues related to documenting the structure of past ecosystems, identifying the impacts humans have had upon them, and determining those elements of modern ecosystems that might be anthropogenic in origin. Having reviewed the general ecology, history, and archaeology of red abalone populations on the Northern Channel Islands, we now examine red abalone middens on the islands, including spatial and temporal variation in their distribution and contents.

All the Northern Channel Islands have been extensively surveyed by archaeologists, with particularly thorough coverage around island perimeters. At least 48 Middle Holocene sites containing at least one well-

dated red abalone midden component have been identified (Fig. 3; see Kennett 2005, Rick et al. 2005, Braje 2007b): 18 (37.5%) on San Miguel Island, 20 (41.7%) on Santa Rosa, 10 (20.8%) on Santa Cruz, and none on Anacapa, the easternmost of the northern islands. A few red abalone middens have also been reported on San Nicolas Island and the central California mainland, but relatively little has been published on the contents or nature of these sites (see Glassow 1993a, b, Braje 2007b). The 10 Santa Cruz middens are clustered near the west end of the island, including one located at Punta Arena on the southwest coast (Glassow et al. 2009). The Santa Rosa Island middens are distributed more widely, with examples found around most of the island (Erlandson 1994:182–193, Kennett 2005, Rick et al. 2006, Braje et al. 2007). Red abalone middens have been identified around the entire periphery of San Miguel, where numerous red abalone components have yet to be dated.

The radiocarbon (^{14}C) dates available for red abalone components on the Northern Channel Islands are summarized in Table 1. The earliest examples date to ~8000 cal yr BP on northwest Santa Rosa, ~7300 cal yr BP on San Miguel, and ~7500 cal yr BP at Punta Arena on Santa Cruz. When broken into different time periods, 11 components date between 8000 and 7000 years (cal yr BP), 10 between 7000 and 6000, 18 between 6000 and 5000, eight between 5000 and 4000, and four between 4000 and 3000 years.

One problem in comparing Middle Holocene red abalone middens on the Channel Islands is the lack of clear definition for the site type. As we will show, the percentage of red abalone shell found in such sites varies widely and archaeologists working on Santa Cruz Island have defined red abalone middens differently than those working on other islands. Because the definition of what constitutes a red abalone midden has been vague (e.g., “a midden visually dominated by large red abalone shells”), we established a quantitative benchmark for excavated sites by defining a red abalone midden as a stratum or discrete lens that contains at least 5% red abalone shell by mass. Based on sites for which quantified data are available, 12 sites and 18 components meet these criteria: nine sites and 15 components on San Miguel, two sites and two components on Santa Rosa, but only one component and site on Santa Cruz (Fig. 4, Table 2). Our definition excludes at least four

TABLE 1. Radiocarbon-dated Middle Holocene red abalone (*Haliotis rufescens*) middens identified on the Northern Channel Islands, California, USA.

Site	One-sigma age range (cal yr BP)	Source
San Miguel Island		
SMI-87	4090–3830	Rick (2004)
SMI-138	3870–3660	Channel Islands ¹⁴ C database
SMI-153	4420–4230	Channel Islands ¹⁴ C database
SMI-161	5890–5760	L. Willis, T. C. Rick, and J. M. Erlandson, <i>unpublished manuscript</i>
SMI-161	4500–4300†	L. Willis, T. C. Rick, and J. M. Erlandson, <i>unpublished manuscript</i>
SMI-261	~3400‡	Vellanoweth et al. (2000)
SMI-261	6900–6400†	Erlandson et al. (1996:361)
SMI-350	7440–7360	Channel Islands ¹⁴ C database
SMI-388NW	7360–7230	Channel Islands ¹⁴ C database
SMI-396	5100–4500†	Braje et al. (2005)
SMI-470	4360–4110	Kennett (1998)
SMI-481	6160–5930	Vellanoweth et al. (2006)
SMI-492	5600–5400†	Walker and Snethkamp (1984)
SMI-504	3060–2860	Kennett (1998)
SMI-520	5920–5720	Channel Islands ¹⁴ C database
SMI-525	3240–3010	Kennett (1998)
SMI-528	5900–5720	Kennett (2005)
SMI-557	6600–6300†	Braje (2007b)
SMI-603	4500–3800†	Vellanoweth et al. (2000)
SMI-657	6200–6000†	Braje (2007a, b)
SMI-657	7060–6820	Braje (2007a, b)
SMI-685	7400–7240	Channel Islands ¹⁴ C database
Santa Rosa Island		
SRI-3	8000–7500†	Channel Islands ¹⁴ C database
SRI-4	4440–4280	Channel Islands ¹⁴ C database
SRI-5	8370–7340	Erlandson (1994)
SRI-6	8300–7400†	Erlandson (1994)
SRI-26	7940–7750	Erlandson (1994)
SRI-61	5560–5430	Channel Islands ¹⁴ C database
SRI-109	5790–5610	Kennett (2005)
SRI-147	5710–5570	Braje (2007b)
SRI-173	8360–7660	Channel Islands ¹⁴ C database
SRI-191	6100–5900†	Rick et al. (2006)
SRI-246	7610–7480	Kennett (1998)
SRI-247	6970–6785	Kennett (1998)
SRI-270	5770–5600	Kennett (1998)
SRI-287	5720–5560	Kennett (1998)
SRI-342	6100–5910	Kennett (1998)
SRI-344	6060–5910	Kennett (1998)
SRI-364	5700–5560	Channel Islands ¹⁴ C database
SRI-365	5900–5760	Channel Islands ¹⁴ C database
SRI-462	7060–6840	Kennett (1998)
SRI-590	4330–4140	Kennett (1998)
Santa Cruz Island		
SCRI-109	7600–4800†	Glassow (2005)
SCRI-236	5030–4715	Kennett (1998)
SCRI-333	5500–4400†	Wilcoxon (1993)
SCRI-424	5850–5580	Kennett (1998)
SCRI-426	5320–5020	Kennett (1998)
SCRI-427	6200–5500†	Glassow (2005)
SCRI-428	5900–3800†	Glassow (2005)
SCRI-429	7500–6300†	Glassow (2005)
SCRI-430	6060–5750	Kennett (1998)
SCRI-549	6870–5300†	Glassow (2005)

Note: All site references in the text include the “CA-” prefix.

† Denotes aggregated one-sigma ¹⁴C range (the interval from –1 SD to +1 SD around the mean) from multiple dates.

‡ Denotes approximate age based on bracketed ¹⁴C-dated strata.

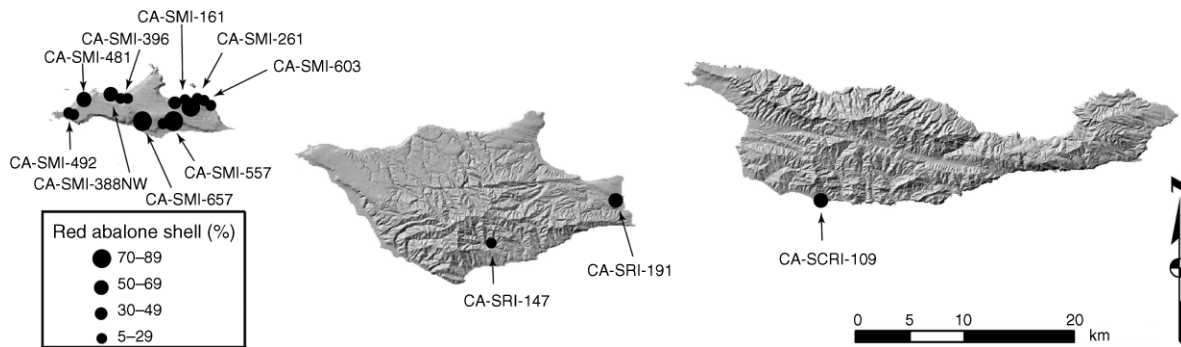


FIG. 4. Location map of Middle Holocene red abalone middens from the Northern Channel Islands, with quantified faunal data and the relative abundances of red abalone shell.

sites on western Santa Cruz Island identified by Glassow (2005) as red abalone middens, where excavated samples contain between 1% and 4% red abalone shell.

As with the number of red abalone middens on each island, the percentage of red abalone shell in Middle Holocene middens generally decreases from west to east, with the highest densities on San Miguel Island (range = 87.9–5.7%, with nine components containing >20% red abalone shell). More quantitative data are available from San Miguel Island than Santa Rosa and Santa Cruz (see Braje 2007b), but available data suggest that densities on Santa Cruz and eastern Santa Rosa are generally lower. Glassow (1993b, 2005) and Sharp (2000) investigated a series of sites with red abalone components on western and southern Santa Cruz, for example, and found only one stratum with >5% red abalone shell. Quantified data are available from just two Santa Rosa Island red abalone middens, with one containing some 67% of red abalone and the other ~28%. These values are closer to most San Miguel middens than Santa Cruz, supporting the west-east decrease in red abalone. Fig. 5 shows the temporal distribution of Middle Holocene red abalone middens that have been excavated by island. Excavated red abalone middens on San Miguel are distributed throughout the period from approximately 8000 to 3500 years ago, but red abalone middens on eastern Santa Rosa and Santa Cruz are generally found in a relatively narrow window between approximately 6100 and 5500 years ago. While San Miguel Island red abalone middens span intervals of warm and cold waters, many of the red abalone sites on western Santa Cruz and eastern Santa Rosa cluster during an interval of cooler SSTs and high marine productivity from 6300 to 5900 cal yr BP (Kennett 2005:147). However, there are some red abalone middens, especially on Santa Rosa, that have been dated outside of this interval (see Table 1), but the abundance of red abalone in these sites is unknown. The number of well-dated and excavated red abalone middens on Santa Rosa and Santa Cruz islands remains small, but the available data suggest that the cooler waters around San Miguel Island and

probably portions of Santa Rosa represent critical habitat for long-term sustainability of red abalone populations, with productive fisheries expanding to western Santa Cruz and some parts of Santa Rosa primarily during periods of colder SSTs (Fig. 5).

When compared to historic catch data, the Middle Holocene availability of red abalones generally corresponds with the most abundantly harvested historic populations. Waters surrounding San Miguel Island, southern Santa Rosa, and southern Santa Cruz generally had larger historic commercial dive harvests and archaeologists have identified Middle Holocene middens with dense concentrations of red abalone shell in these same areas. A series of similar red abalone middens are also known from the San Luis Obispo and San Simeon areas along the central California coast in areas of high historical harvests (Greenwood 1978; T. Joslin, *personal communication*), although too few quantitative data are currently available to allow a detailed discussion in this paper.

DISCUSSION, IMPLICATIONS, AND CONCLUSIONS

Debate about whether ecosystems are structured from the top-down (predator-driven) or the bottom-up (food- or resource-limited) has a long history in ecology (Hairston et al. 1960) with important implications for ecosystem management and restoration within national parks, marine sanctuaries, and other protected areas. Some studies suggest that many aquatic ecosystems are under top-down control, with effects on keystone predators cascading down to lower trophic levels, but others show that such communities are also influenced by bottom-up controls (Dayton and Tegner 1984b). Changing oceanographic factors (currents, upwelling, nutrients, and sedimentation rates, etc.) can result in variable populations at the bottom of food webs and lead to variation in apex trophic effects (Dayton and Tegner 1984b). Clearly, ecosystem-structuring processes are dynamic and influenced by both bottom-up and top-down factors (Tegner and Dayton 2000).

Archaeological data suggest that for at least 8000 years, despite heavy predation and major ecological

TABLE 2. Radiocarbon age and percentage of red abalone shell from Middle Holocene red abalone middens with quantified faunal data from the Northern Channel Islands.

Site	Provenance	Material†	Laboratory number	Measured ¹⁴ C age (yr BP)	Conventional ¹⁴ C age (yr BP)	Age range (cal yr BP)‡
San Miguel Island						
SMI-388NW	20 cm deep	<i>Hr</i>	Beta-194507	6570 ± 60	6980 ± 60	7360–7230
SMI-557	bulk sample 1	<i>Hr</i>	OS-44640	N/A	6310 ± 35	6580–6440
SMI-557	bulk sample 2	<i>Hr</i>	Beta-213143	5710 ± 60	6140 ± 60	6400–6265
SMI-657	bulk sample 1	<i>Hc</i>	Beta-217110	5460 ± 90	5900 ± 90	6190–5970
SMI-481	red abalone lens	<i>Hr</i>	Beta-145317	5430 ± 70	5870 ± 70	6160–5930
SMI-492	north profile, stratum 4	<i>Mc</i>	Beta-5807	4920 ± 80	5350 ± 80	5580–5420
SMI-492	strata 11 and 10	~5500
SMI-161	unit 3	<i>Hr</i>	OS-51581	...	5680 ± 45	5890–5760
SMI-161	unit 2	<i>Hr</i>	OS-51580	...	4520 ± 35	4500–4360
SMI-161	unit 1	<i>Hr</i>	OS-51579	...	4490 ± 35	4440–4290
SMI-396	southeast area	<i>Ms</i>	Beta-194509	4580 ± 50	4990 ± 50	5130–4900
SMI-396	northeast area	<i>Ms</i>	Beta-194508	4240 ± 70	4650 ± 70	4765–4490
SMI-603	stratum 3	<i>Ms</i>	Beta-115557	3830 ± 70	4270 ± 70	4280–3840
SMI-603	stratum 4	<i>Ms</i>	Beta-115558	4010 ± 70	4450 ± 70	4520–4070
SMI-261	stratum A	~3400
Santa Rosa Island						
SRI-191	red abalone midden	<i>Hr</i>	OS-46941	N/A	5870 ± 30	6110–5960
SRI-147	red abalone lens	<i>Hr</i>	Beta-87202	5060 ± 60	5500 ± 60	5710–5570
Santa Cruz Island						
SCRI-109	south unit, stratum 12	~6000

Notes: Measured and conventional ¹⁴C ages are reported as mean ± SD. Site references in the text include the “CA-” prefix.

† Key to abbreviations: *Hr*, *Haliotis rufescens*; *Hc*, *Haliotis cracherodii*; *Mc*, *Mytilus californianus*; *Ms*, marine shell.

‡ All dates were calibrated with Calib 5.0.2 (Stuiver and Reimer 2000, Stuiver et al. 2005) applying a ΔR of 225 ± 35 yr; ¹³C/¹²C were determined by the ¹⁴C laboratory or an average of +430 yr was applied; age ranges are at one sigma (the interval from –1 SD to +1 SD around the mean).

changes, similar bottom-up processes have facilitated geographic continuity in the distribution and abundance of red abalone populations around the Northern Channel Islands. For the islands and broader California Coast, however, key predators (e.g., sea otters and humans) have strongly influenced the abundance of red abalones in nearshore ecosystems. Archaeological, historical, and ecological data all suggest that Native American hunting and fishing had similar effects on keystone marine predators and nearshore communities as historical commercial fisheries (Tegner and Dayton 2000), providing important top-down controls and causing trophic cascades.

Although currently limited to San Miguel Island, evidence for Pleistocene abalone fishing on the Channel Islands shows that Paleocoastal peoples harvested red abalones on the Northern Channel Islands at least 11 500 to 12 000 years ago. In contrast, red abalones are rare or absent in island middens dated between approximately 10 000 and 8000 cal yr BP, which are typically dominated by California mussels and black abalones. This may be due to postglacial warming of SSTs after the cool Younger Dryas interval (Kennett and Ingram 1995), with warmer water intervals between approximately 10 000–9600 and 8200–7500 cal yr BP (Kennett 2005:64–65), leading to increases in the geographic range and abundance of intertidal black

abalone populations, especially in the western end of the archipelago.

Between approximately 8000 and 7300 years ago, red abalone shells of unprecedented size and abundance appear in Channel Island shell middens. Except for cooler intervals between approximately 6300–5900 and 3800–2900 cal yr BP, SSTs appear to have been relatively warm during this interval (Kennett 2005:65–66). These data suggest that the formation of Middle Holocene red abalone middens was not driven primarily by SST changes, as suggested by Hubbs (1967), Orr (1968), and Glassow (1993a), at least not for the Northern Channel Islands as a whole. On San Miguel Island, at the western end of the archipelago, there is little or no correlation between SST and the presence or absence of red abalone middens, the abundance of red abalone shell within these middens, or the size of whole red abalone shells.

Before 8000 years ago, Channel Islanders probably killed sea otters onshore or near the shore, probably releasing a few abalones and urchins that the people collected. But this “culling” would not much reduce the top-down control of subtidal populations of red abalone and sea urchins. Using modern ecological observations, historical accounts, and archaeological data, Erlandson et al. (2005b) speculated that by approximately 7500 years ago predation by growing numbers of Native

TABLE 2. Extended.

Red abalone shell (%)	Source
57.2	J. M. Erlandson, <i>unpublished data</i>
78.6	Braje (2007b)
25.8	Braje (2007b)
87.9	Braje (2007a, b)
67.9	Vellanoweth et al. (2006)
21.4	Walker and Snethkamp (1984)
17.2	Walker and Snethkamp (1984)
13.0	L. Willis, T. C. Rick, and J. M. Erlandson, <i>unpublished manuscript</i>
73.0	L. Willis, T. C. Rick, and J. M. Erlandson, <i>unpublished manuscript</i>
47.0	L. Willis, T. C. Rick, and J. M. Erlandson, <i>unpublished manuscript</i>
14.6	Braje et al. (2005)
5.7	Braje et al. (2005)
24.2	Vellanoweth et al. (2000)
19.5	Vellanoweth et al. (2000)
7.4	Vellanoweth et al. (2000)
67.2	Rick et al. (2006)
27.6	Braje et al. (2007b)
57.0	Sharp 2000

American hunters had depleted sea otters from local catchments to the point that they no longer controlled shellfish populations (see also Sharp 2000). Erlandson et al. (2005b:15–17) identified signatures of localized dense collections of urchins from deeply stratified shell midden deposits on San Miguel Island. This strongly suggests that prehistoric otter hunting released red abalones from predation, dramatically increasing their abundance and average size during the Middle Holocene.

Similar effects have been documented historically in California, British Columbia, and Alaska, in which removing or depleting sea otters allowed shellfish populations to explode (e.g., Estes and Duggins 1995, Steneck et al. 2002). Some historic cases were coupled with the rapid multiplication of sea urchins, deforestation of kelp forests, and the creation of urchin barrens (Simenstad et al. 1978, Steneck et al. 2002), a now well-known phenomenon. Historically, as California sea otter populations and ranges have expanded under federal and state protection, the opposite effects have also been well documented, with red abalone and sea urchin populations declining precipitously as otters enter new areas.

Nonetheless, the sea otter–sea urchin–kelp forest connections in southern California are much more complicated than in the Aleutians and the far northeast Pacific (see Steneck et al. 2002). The Northern Channel

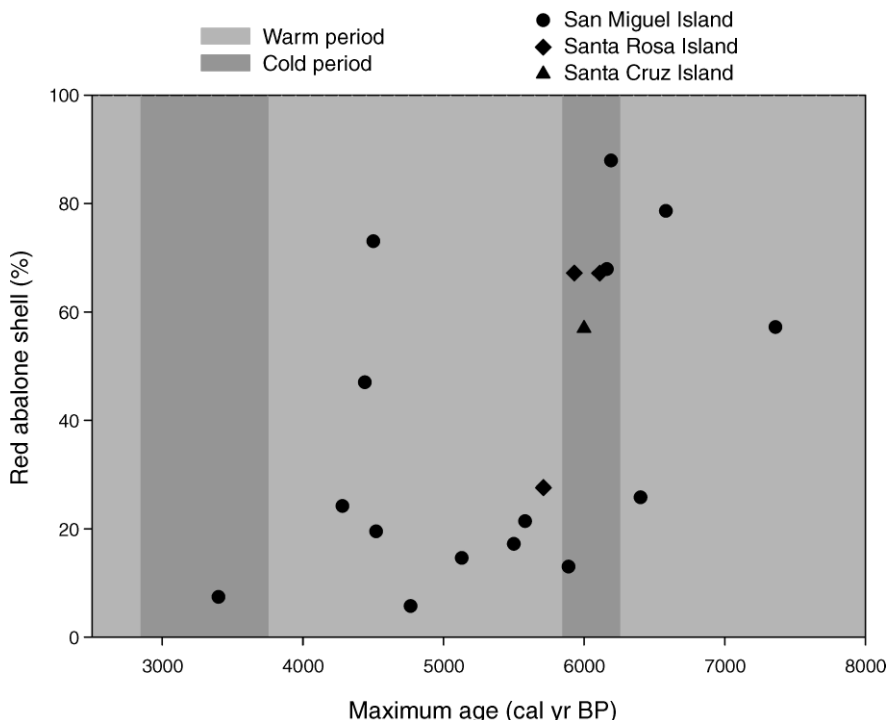


FIG. 5. Red abalone percentage from 19 dated shell midden components on the Northern Channel Islands: San Miguel ($n = 15$ middens), Santa Rosa ($n = 2$ middens), and Santa Cruz Island ($n = 1$ midden). For individual archaeological site listing see Table 2. Warm periods are represented as light gray sections, and cold periods (6300–5900 and 3800–2900 calibrated years before present), represented as dark gray sections, are taken from Kennett (2005). The disconnect between cold periods and red abalone abundance in shell middens suggests that red abalone were not solely controlled by temperature during the Middle Holocene.

Islands are near the northern limit of two important predators, the spiny lobster (*Panulirus interruptus*) and a labrid fish, the sheephead (*Semicossyphus pulcher*). The larger individuals of each consume sea urchins and are important predators because there is no escape in growth from the large predators (see Tegner and Dayton 2000). Furthermore, while sea urchins are clearly capable of creating barren grounds in California kelp forests (Harrold and Reed 1985), there is considerable evidence that abalones outcompete sea urchins for space (see Karpov et al. 2001). Finally, the ocean climate is tightly coupled with both kelp forest vigor and the recruitment and growth of red abalones (Tegner et al. 2001). Although possible evidence of small-scale urchin barrens and anthropogenic trophic cascades has been identified in San Miguel Island middens (Erlandson et al. 2005b), southern California kelp forest ecosystems appear to be relatively resilient and resistant to collapse.

Synthesizing modern knowledge, historical accounts, and archaeological records, we infer that early maritime peoples of the Channel Islands first significantly reduced sea otter populations as much as 8000–7500 years ago, after which otters lost their dominant role in structuring the abundance of nearshore populations of red abalones and sea urchins. The resulting trophic cascades may have included urchin barrens of limited extent, but humans, lobsters, and sheephead continued to consume urchins, and abalones actively competed with urchins for space. Although human foragers clearly preyed heavily on red abalones during the Middle Holocene, such predation was probably limited to the intertidal and relatively shallow nearshore waters accessible to free divers. Red abalones in deeper waters probably continued to be a source of larval production and recruitment that sustained abalone populations for millennia.

The persistence of Channel Island upwelling patterns and kelp forests may also help explain the resilience and spatial continuity of red abalone fisheries through the millennia. The consistent orientation (northwest-southeast) of island dunes of late Pleistocene and Holocene age suggests that the predominant pattern of strong northwesterly winds that drives upwelling and productivity in the Santa Barbara Channel area has operated for many millennia. Kinlan et al. (2005) argued that kelp forests around the Northern Channel Islands, apparently highly productive in the late Pleistocene and Early Holocene, were productive throughout the Holocene, although a surge in mid-Holocene dune building may signal a reduction of rocky reef and shoreline habitat suitable for abalones (Erlandson et al. 2005c). Viewed broadly, however, archaeological, historical, and ecological data suggest that similar top-down and bottom-up controls have operated on the Northern Channel Islands for much of the Holocene, with red abalone populations showing considerable resilience in the face of intensive predation and dynamic environmental conditions. Despite increasingly intensive human harvesting after approximately 8000–7500 cal yr BP, red

abalone stocks persisted from the Middle Holocene to historic times. The richest Middle Holocene and 20th century populations appear to have been concentrated around San Miguel Island, with densities decreasing to the east within the archipelago. The percentages of red abalone shell in the middens fall precipitously (Fig. 5) approximately 4000 years ago, possibly reflecting the partial replacement of rocky substrates by sand (Graham et al. 2003, Erlandson et al. 2005c) and an intensification of ENSOs along the southern California Coast (Masters 2006).

Since the emergency closure of the red abalone fishery in 1997 by the California Fish and Game Commission, debate has continued about the recovery and status of red abalone populations (Karpov et al. 2000). The commission recently identified San Miguel Island as a location where the population may be viable and rebounding. In December 2006, commercial divers proposed an experimental take around the island, despite resistance from many marine biologists, resource managers, and others. Historical ecological studies such as ours may be an effective mechanism to test management tools, evaluate the long-term structure and function of local ecological communities, and help mediate these debates.

Based on records of red abalone harvest over the last 8000 years on the Northern Channel Islands, for instance, we would expect substantial populations to recover around San Miguel Island first. Data from shell middens and historic catch records suggest that San Miguel waters have yielded the most productive red abalone fishery for millennia. The critical habitat around San Miguel Island has sustained red abalone populations for at least the last 8000 years, where the species appears to have been relatively resilient despite heavy fishing pressure in both prehistoric and historic times. From this deep historical perspective, the protection of this critical habitat and abalone population is crucial to the persistence of red abalones in Channel Islands waters, with early recovering populations an important source of larval production and recruitment that fuels the broader recovery of red abalone populations. The California Current sweeps down the central California Coast from the northwest, past San Miguel Island, and along the Northern Channel Island chain, potentially fueling the dispersal of abalone larval communities from San Miguel to Santa Rosa and Santa Cruz. A better test of the recovery of red abalones on the Northern Channel Islands, therefore, would be their rebound in areas where they have historically and prehistorically been available but less productive, such as the shores of Santa Cruz and eastern Santa Rosa.

It is increasingly apparent that many nearshore marine habitats have been fished with intensities sufficient to alter ecosystem structures for thousands of years (Jackson et al. 2001, Rick and Erlandson 2008). Using archaeological data to help decipher the deeper ecological histories of specific areas and fisheries can

provide valuable information about the structure of nearshore ecosystems in the distant past as well as the processes involved in the creation of the anthropogenic land- and seascapes so pervasive in today's "natural" world. Building effective management and restoration plans requires information about historic and ancient harvests and the establishment of reference points (baselines) that account for overfishing or other anthropogenic disturbances (Pauly 1995, Dayton et al. 1998, Pauly et al. 1998, Tegner and Dayton 2000, Jackson et al. 2001). For red abalone populations of the Northern Channel Islands, archaeological evidence for long-term spatial continuity and ecological resilience provides hope for the restoration of stable ecosystems and sustainable fisheries.

Our historical ecological analysis suggests that anthropogenic trophic cascades began some 8000–7500 years ago along the Santa Barbara Channel. Nonetheless, additional archaeological, historical, and ecological studies are necessary to confirm these complex relationships. Of utmost importance is a better understanding of the history of sea otter hunting by the Chumash and their ancestors. When did sea otter hunting begin, did otter hunting intensify with human population growth, and what were the effects on local shellfish communities? Additional data on the composition, distribution, and chronology of Middle Holocene red abalone middens are necessary. Was the formation of Middle Holocene red abalone middens on Santa Rosa and Santa Cruz islands controlled by SST? What are the mean sizes of red abalone shells through the Holocene (see Erlandson et al. 2008) and how do these compare to historic and modern measurements, both with and without sea otters in the system? Finally, additional research on the relationships between other important keystone species is necessary. How do the ecological associations between spiny lobsters, California sheepshead, sea urchins, sea otters, and humans evolve through time? All of these questions will be critical for helping us better understand the link between humans and marine ecosystems through the millennia.

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