# LATE QUATERNARY CHANGES IN THE SIZE AND SHAPE OF THE CALIFORNIA CHANNEL ISLANDS: IMPLICATIONS FOR MARINE SUBSIDIES TO TERRESTRIAL COMMUNITIES

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ABSTRACT-Studies of glacial-interglacial variability in the configuration of California's Channel Islands have focused on shifts in island area and isolation, rather than changes in the size of adjacent marine reefs that represent an important source of production to island food webs. We present reconstructions of sea-level driven variability in the geomorphology of California's Channel Islands and the size of offshore reefs since the Last Glacial Maximum (~18,500 radiocarbon years before present [RYBP]). Our data document gradual decreases in size and increases in isolation of all California Islands since the glacial period. Changes in the area of nearshore reefs capable of supporting productive kelp forest ecosystems were more complex, and generally decoupled from patterns of change in island size. For most of the current interglacial, the northern Channel Islands were surrounded by a substantially larger area of productive reef than occurs today. Reduction in reef area to present levels occurred over two relatively short periods in the terminal Pleistocene (ca. 16,000–14,000 RYBP) and the middle to late Holocene (ca. 4,000–2,000 RYBP). In contrast, southern island reefs contracted to less than half the size of northern reefs by 12,000 RYBP and changed little over the Holocene. These results suggest that even as islands grew smaller and more isolated, the availability of marine productivity to land-based communities on the California Islands decreased from the early Holocene to the present, a decrease that was most rapid and substantial in the northern islands. Because these geomorphological changes would not have directly affected the pelagic marine ecosystem further offshore, our work implies a redistribution of marine productivity since the Last Glacial Maximum. Such variations in nearshore marine resource distribution may help explain both spatial and temporal variability in Native American communities along the southern California coast during the Holocene.

Keywords: California Channel Islands, climate change, coastal geomorphology, Holocene communities, paleoecology, trophic subsidies

#### INTRODUCTION

At the interface between two ecosystems that differ in productivity, spatial subsidies of organic matter and nutrients can have a strong influence on the diversity, trophic structure, productivity, and persistence of communities in the poorer environment (Polis and Hurd 1996, Barrett et al. 2003). On arid islands and coastlines adjacent to productive marine upwelling regions, marine resources subsidize terrestrial ecosystems, leading to enhanced diversity, productivity, and/or abundance of organisms per unit area, as well as increased food web complexity (Polis and Hurd 1996, Anderson and Polis 1998, Sanchez-Pinero and Polis 2000, Anderson and Wait 2001, Barrett et al. 2003). The relative importance of marine inputs on islands and coastlines is a function of terrestrial productivity, marine productivity, and the rate of flow of productivity across the land-sea interface (Polis and Hurd 1996). Terrestrial productivity is closely related to available land area and average annual precipitation (Lieth 1978), whereas productivity on nearshore marine reefs (i.e., ridges of rock in shallow water) depends on the availability of nutrients, light, and in the case of macroalgae, appropriate attached substrate. Essentially, the rate of flow of organic subsidies

across the marine-terrestrial interface is related to the edge area of the interface (perimeter:area ratio) and the ability of organisms to actively acquire and move resources across the boundary (Polis and Hurd 1996). Mobile land-based organisms capable of foraging in both marine and terrestrial environments can be expected to exhibit a strong response to marine resource availability when the terrestrial ecosystem they inhabit is relatively unproductive.

Humans are capable of integrating resource use across the marine-terrestrial interface to a greater extent than most terrestrial organisms. Therefore, the persistence and dynamics of human populations inhabiting coastal margins may be strongly influenced bv marine resource availability, especially in areas of low terrestrial productivity. Predicted shifts in the relative magnitude of marine inputs over time may shed light on changes in terrestrial ecosystem dynamics and provide a context for cultural change in coastal human settlements.

The semi-arid California Channel Islands (mean annual precipitation = 280-480 mm; Daly and Taylor 1998) are surrounded by shallow rocky reefs that support highly productive macroalgal assemblages dominated by the giant kelp, Macrocystis pyrifera. Kelp forests provide food and complex three-dimensional habitat structure for a wide variety of associated organisms and support diverse communities of fishes and invertebrates (Graham 2004). Many kelp forest species are important fisheries today (Leet et al. 2001), and are known to have been important for subsistence of coastal human communities throughout much of the Holocene (ca. 11,000 radiocarbon years before present [RYBP]-Present; Steneck et al. 2002). At decadal time-scales, the distribution of kelp corresponds closely to the distribution of rocky substrates in shallow waters receiving an adequate fraction of surface light, generally less than 25-28 m in depth (North 1994). Thus, kelp forests are located immediately adjacent to islands and coastlines, extending from the coast to several kilometers offshore, and their total productivity is dependent on the areal extent of shallow reef (Graham et al. 2003).

At millennial time scales, the sizes of reefs and islands are not static. Fluctuations in global eustatic sea-level occurring as a result of glacialinterglacial cycles interact with physiography to generate changes in coastal geomorphology (Kennett 1981, Graham et al. 2003). Because bathymetric profiles and the time course of sealevel change are highly non-linear, temporal changes in island and reef size are complex and may be decoupled from one another. The relative influence of marine subsidies, and consequently the diversity, productivity, and dynamics of terrestrial ecosystems in the southern California region, may be strongly affected by these variations. high-resolution Here we use bathymetric profiles and a region-specific time series of sea-level change to reconstruct late Quaternary variability in the geomorphology of the California Channel Islands and size of offshore reefs since the Last Glacial Maximum (~18,500 RYBP). This is the first study to examine joint changes in island and reef area in this region, and expands significantly on past reconstructions of paleo-coastlines (e.g., Johnson 1983, Porcasi et al. 1999). Implications of change in the configuration of islands and reefs are considered for the terrestrial ecosystem as a whole, as well as cultural changes over the past 11,000 years.

### **METHODS**

To estimate late Quaternary changes in the size and shape of California Channel Islands and reefs, we combined millennial-scale paleo-sea-level estimates from the Santa Monica Basin with a digital bathymetry profile for the Southern California Bight. Sea-level estimates (Fig. 1) were



Figure 1. Late Quaternary sea-level change in southern California (Santa Monica Basin). [Reproduced, with permission, from Graham et al. 2003 and Nardin et al. 1981].

taken from Nardin et al. (1981), and were based on radiocarbon dates, sedimentologic analysis, and high-resolution seismic stratigraphic analysis of late Quaternary sediment deposits. Our estimates span the past 18,500 radiocarbon years in 500-year intervals, from the Last Glacial Maximum (LGM) to the modern day (defined, by convention, as AD 1950). A digital bathymetric map was developed by interpolating United States National Ocean Service (NOS) Hydrographic Survey depth soundings conducted over 80 years (AD 1920-2000) onto a 1-m resolution grid, and contouring the resulting grid at 1-m intervals. Although the density of soundings declines offshore over deep basins, depth survey data were sufficiently dense in nearshore areas to warrant interpolation at the chosen resolution. Contours derived from USGS 30-m resolution digital elevation models were merged with the NOS-derived digital bathymetric



Figure 2. Configuration of islands and reefs in the Southern California Bight, (A) at present, and (B) at the Last Glacial Maximum approximately 18,500 RYBP. Black shading shows distribution of shallow reefs, i.e., 0–25 m depth contours. Dashed lines in (A) indicate Northern and Southern island groups.

contours to depict topography above present-day sea-level. All geospatial analyses were performed using ArcView GIS 3.2 and ArcGIS 8.2 (Environmental Systems Research Institute, Redlands, CA).

Paleo-coastlines were reconstructed bv adjusting the zero datum (mean sea-level) relative to modern sea-level on the basis of each paleo sealevel estimate (Figs. 1, 2A-B). This resulted in predictions of island area and shoreline perimeter for all eight modern-day Channel Islands at 500year intervals (see below for a discussion of the assumptions inherent in this method). Further analyses were carried out using total area and total perimeter estimates for the northern (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) and southern (Santa Barbara, San Nicolas, San Clemente, Santa Catalina) Channel Island groups. Groups were defined on the basis of proximity, similarities in bathymetry profiles, and geology. Observed patterns generally hold for all islands within an island group. For comparison to the islands, a "zone of coastal influence" was defined for the mainland that extended from 5-30 km inland from the regional coastline (defined as the coast between 32.5 and 34.5°N latitude), and the area and perimeter of the coastally-influenced terrestrial habitat was calculated at each time point. The coastal zone was defined primarily to assess anthropological implications of sea-level change, and the range of widths (5-30 km) was chosen on the basis of human movement abilities, human settlement and subsistence patterns in this region, and the presence of mountain barriers within 30 km of the coast along most of the region of interest (see Jones 1991).

To reconstruct the distribution of subtidal reefs capable of supporting giant kelp habitat, we drew on more than 50 years of field studies on this ecologically and commercially important species. Factors limiting the distribution of giant kelp include competition, grazing, storm disturbance, sedimentation, nutrients, temperature, light, and substrate availability (e.g., Neushul 1962, Anderson and North 1969, Dayton 1985, Deysher and Dean 1986, Graham 1997). In general, however, the long-term distribution of kelp (i.e., averaged over years to decades) is constrained by two critical factors: bottom irradiance and the availability of hard substrate (Dayton 1985, North

1994, B. Kinlan and M. Graham unpubl. data). Digital maps of kelp canopy cover show that when hard substrate is available, the lower limit of kelp forest distribution occurs near the 25-m isobath (North et al. 1993; Fig. 3A), where irradiance is reduced to approximately 1% of surface values (Anderson and North 1969). Because island watersheds are small, little sediment is transported by streams to the open coast and most subtidal substrates are rocky (Kennett 1981). Thus, the area of submerged land between 0- and 25-m depth contours may be a reasonable predictor of the areal extent of kelp forests. We used multi-year composite maps of kelp canopy cover derived from infrared aerial photography to test this assumption in present-day kelp forests at the Channel Islands. For all eight islands, including San Miguel and Santa Barbara (Fig. 3B-C), we found >80% concordance between the area of reef predicted from the 0-25-m isobaths and the actual observed extent of kelp forest canopies. We therefore use reef area between 0 and 25 m as a proxy for kelp forest size. Because the areal extent of kelp canopy is significantly correlated with canopy biomass in kelp forests of the Southern California Bight (B. Kinlan unpubl. data), this measure also serves as a first order proxy for kelp forest productivity.

The central assumption of the methodology we apply here is that of "ecological uniformitarianism." We assume that the same processes that govern the distribution and dynamics of kelp forests today have operated similarly in the past. We also assume that bathymetric profiles have not been changed so radically by geomorphological processes such as sediment deposition and erosion as to render the modern bathymetric profile unrepresentative of past physiography. While neither assumption is likely to hold perfectly, we believe this method places bounds on late Quaternary changes in reef and island size and allows examination of large fluctuations in these parameters.

# RESULTS

Reconstructions of paleo-topography and bathymetry show that coastal regions of the Southern California Bight were radically different at the LGM than they are today (Fig. 2A-B, Table 1). As shown in previous studies (e.g., Johnson



Figure 3. Prediction of giant kelp (*Macrocystis pyrifera*) distribution from bathymetric contours. (A) Infrared aerial photograph showing the distribution of giant kelp and the 25-m depth contour at Otter Point, CA (36°38'9" N, 21°55'39" W) in July 1987; [image courtesy of the Monterey Bay Aquarium]. (B) Predicted distribution of giant kelp based on the present 0–25-m depth contours (gray shading) and the composite of observed distributions of giant kelp in annual aerial infrared surveys from 1978–1989 (hatched area) on San Miguel Island. (C) Same as (B), but for Santa Barbara Island. [Kelp cover data courtesy of D. Glantz (ISP Alginates, Inc., San Diego, CA) and the Channel Islands National Marine Sanctuary].

1983, Porcasi et al. 1999, Graham et al. 2003), all the modern Channel Islands were substantially larger and less isolated from each other and from the mainland at the LGM. The northern islands coalesced to form a single large island, called Santarosae, which did not begin breaking up until the Bolling-Allerod interstadial approximately 14,500 RYBP. The southern islands, in contrast, remained separate and more isolated throughout the glacial-interglacial cycle (Porcasi et al. 1999, Graham et al. 2003). A number of now-submerged islets and islands were also exposed at that time. Qualitatively, shifts in the distribution of shallow reefs surrounding islands were complex (Fig. 2B), highlighting the need for a quantitative comparison of changes in island vs. reef area.

Quantitative analysis of reconstructed topography shows that island area decreased monotonically since the LGM, with a brief interruption correlated with the Younger Dryas cool period ca. 12,000-11,000 RYBP (Fig. 4A). The most rapid decrease in island area occurred from 18,500-10,500 RYBP, after which area decreased much more gradually. The largest Holocene drop in island area (~15%) occurred over a period of about 1,500 years, ca. 5,000-3,500 RYBP. Changes in the northern and southern island groups paralleled each other, but the total area of the northern islands was consistently 30-60% larger than the southern islands. The total area of the California Channel Islands approached that of the coastally-influenced mainland at the LGM, depending on the assumed width of the coastal zone (dashed lines in Fig. 4A), but rapidly became

1–2 orders of magnitude smaller than the mainland in the transition to the interglacial period.

The perimeter: area (P:A) ratio of islands changed in accordance with their size; as islands became smaller, their P:A ratio grew as expected from simple geometric principles (Figure 4B). Local variability in the P:A ratio may be attributed to changes in the tortuosity of the coastline as different geologic formations were exposed (e.g., fluctuations ca. 12,000 and 3,500 RYBP). However, these were minor and short-lived compared to the size-driven changes in P:A ratio. Thus, P:A ratio increased rapidly from 18,500-10,500 RYBP, and gradually thereafter, with the largest Holocene increase occurring rapidly ca. 5.000–3.500 RYBP. Due to their smaller size. P:A ratio was consistently higher in the southern islands, with the P:A ratio rising rapidly above that of the mainland coastal zone after the LGM.

In contrast to the relatively simple, monotonic changes in island areas and perimeter:area ratios, reef areas exhibited more complex temporal patterns of change independent of variation in the size of adjacent islands, and decoupled in northern vs. southern island groups (Fig. 5). Reef area was remarkably similar in the northern islands, southern islands, and the southern California

Table 1. Estimated areal extent of the California Channel Islands and adjacent shallow reefs (0-25 m depth) since the last glaciation<sup>a</sup>.

	Present		10,000 RYBP <sup>b</sup> (Holocene peak)		16,500 RYBP <sup>b</sup> (Post-glacial peak)	
Island or island group	Island area (km <sup>2</sup> )	Reef area (km <sup>2</sup> )	Island area (km <sup>2</sup> )	Reef area (km <sup>2</sup> )	Island area (km <sup>2</sup> )	Reef area (km <sup>2</sup> )
Northern	495.47	246.72	643.81	332.94	1,422.00	599.60
San Miguel Island	37.55	39.40				
Santa Rosa Island	208.93	140.90	635.62 <sup>c</sup>	324.25 <sup>c</sup>	1,422.00 <sup>c</sup>	599.60 <sup>c</sup>
Santa Cruz Island	245.80	59.02				
Anacapa Island	3.18	7.39	8.19	8.69		
Southern	386.41	123.35	456.98	142.06	877.80	403.94
Santa Barbara Island	2.25	8.46	6.71	9.42	34.73	28.98
San Nicolas Island	54.18	59.50	79.01	82.81	332.44	225.71
San Clemente Island	140.74	33.43	167.10	29.98	244.23	70.45
Santa Catalina Island	189.25	21.96	204.15	19.85	266.41	78.80
All	881.88	370.07	1,100.79	475.01	2,299.81	1,003.54

<sup>a</sup> Islands completely submerged in the present day are not included.

<sup>b</sup> Radiocarbon years before present.

<sup>c</sup> Islands coalesced to form Santarosae.

mainland at the LGM, and increased by 250-350% in all three regions during the early post-glacial period. However, as sea-level continued to rise, the trajectories rapidly diverged. Mainland reefs continued a gradual increase to a plateau ca. 10,000 RYBP, and remained essentially constant during the Holocene. Reef area at the northern islands peaked ca. 16,500 RYBP, and decreased sharply (48%) from about 16,000–14,000 RYBP. Northern reef area remained stable through the late to middle Holocene, at which point it underwent a rapid, substantial (25%) decline to its present level between about 4,000 and 2,000 RYBP. In contrast, southern reef size peaked sooner than in the north (ca. 17,000 RYBP), contracted by 70% over the period from 16,500-12,000 RYBP, and remained low (less than half the size of northern reefs and one-eighth the size of mainland reefs) and constant over much of the Holocene, with one period of slight decline (~8%) coincident with the larger decline in northern reefs. The difference between northern and southern island groups can be attributed to the steeper and more uniform bathymetry of the southern island group.

Our assumption that all areas in the shallow photic zone (0-25 m) represent rocky reefs capable of supporting kelp forest ecosystems was validated using modern data on kelp distribution at the Channel Islands (Fig. 3). A similar comparison between predicted 0-25 m reef area and the modern distribution of kelp forests on the southern California mainland yields far different results (Fig. 6). Although the 0-25 m bathymetric contours constrain the distribution of giant kelp, kelp forests are patchy in their occurrence and occupy only 15-30% of the predicted region. We know from extensive subtidal surveys in this region that the primary driver of this pattern is burial of rocky substrates by sediment (e.g., Pierson 1987). Along the modern-day southern California mainland, coastal watersheds export coarse sediments that are transported along the coast in littoral cells (Kennett 1981), blanketing many areas of the hard substrate required by giant kelp. Geomorphological and archaeological evidence indicates that the abundance of sediment in shallow areas of the mainland coast is a relatively recent phenomenon associated with the last stages of sea-level rise prior to the current high



Figure 4. Late Quaternary changes in (A) areal extent, and (B) perimeter: area ratios of the California Channel Islands. Data are based on the total area and perimeter of northern and southern island groups (see Fig. 2) and were estimated from a bathymetric profile and paleo-sea-level curve as described in text. Dashed lines show corresponding areal extent and perimeter: area ratios for the southern California mainland, assuming a coastal zone width of 5–30 km, as indicated. The approximate period of human occupation is shown (Erlandson 1997).

sea-level stand, occurring about 6,000–3,000 RYBP (Kennett 1981, Masters and Gallegos 1997, Graham et al. 2004), although some coastal areas with deep sediment deposits probably remained buried throughout the glacial cycle. Thus, the decline in shallow reef area at the northern Channel Islands in the late to middle Holocene seems to have coincided with a shift on the mainland from a rocky-reef dominated system to a mixed reef/softbottom patchwork, suggesting a regional decline in the distribution of giant kelp forests.

## DISCUSSION

Some caution is necessary in interpreting the variations in reef and island area described here, as we have based our reconstructions on a modern-day bathymetric profile and a regional sea-level curve for the Santa Monica Basin derived from geological and sedimentological proxies. Although this is not an uncommon approach (e.g., Johnson 1983, Porcasi et al. 1999), erosional and depositional processes have surely modified the bathymetric profile over the late Quaternary (Kennett 1981) and there are uncertainties inherent in the estimation of paleo-sea-level from proxies (Nardin et al. 1981). The Nardin et al. (1981) sea-level curve shares the essential features of many global eustatic sea-level reconstructions, including the Bolling-Allerod interstadial ca. 14,500 RYBP and the Younger Dryas cooling ca. 11,000 RYBP (Fleming et al. 1998). However, eustatic curves suggest a gradual rise of sea-level during the Holocene, occurring continuously from 10,000-2,000 RYBP, rather than the rapid rise from 5,000-2,500 RYBP seen in the Nardin et al. curve. This deviation could be due to local geological processes, or an artefact of the Nardin et al. curve. Caution is therefore necessary in assigning the precise timing of the Holocene shift in reef area. We focus here on evaluating



Figure 5. Late Quaternary change in the areal extent of shallow (0–25 m) reefs adjacent to islands in the Southern California Bight. Data are based on the total area of reefs in northern and southern island groups (see Fig. 2) and were estimated from a bathymetric profile and paleo-sea-level curve. Dashed line shows corresponding areal extent of reefs adjacent to the southern California mainland. The approximate period of human occupation is shown (Erlandson 1997).

implications of the approximate timing of major changes in island and reef configuration that occurred since the peak of the last glaciation.

Three results in particular underscore the likely importance of marine resource subsidies to landbased communities on the California Channel Islands, including humans. First, the above-water area of the Channel Islands decreased markedly from the LGM to the present, rapidly at first and then more gradually during the Holocene. Under a constant precipitation regime (discussed below) this would correspond to lower total terrestrial productivity (Lieth 1978). Second, the relative size of the land-sea interface at the islands (i.e., perimeter: area ratio) increased rapidly from the LGM and was consistently two to three times higher than for the mainland. The formation of numerous mainland estuaries-many of which have now disappeared—during the rapid sea-level rise of the terminal Pleistocene and early Holocene (Erlandson 1994, Graham et al. 2003) may reduce these disparities somewhat, but the differences are still likely to have been substantial. Third, the area of shallow reefs capable of supporting highly productive kelp forests was equal to or greater than the total area of exposed land at the northern (but not southern) Channel Islands for much of the current interglacial. Thus, although reef-based marine resources were important for mainland terrestrial communities, their impact was likely to have been proportionally far greater on the islands than on the mainland.

We focused our analysis on changes in the area of substrates capable of supporting marine and terrestrial primary production. A number of other factors not addressed here are likely to have influenced variation in the per-unit-area productivity of marine and terrestrial habitats over the late Quaternary. The single greatest factor controlling regional primary productivity in terrestrial ecosystems is mean annual precipitation (Lieth 1978, Polis and Hurd 1996). Marine primary productivity, on the other hand, is influenced principally by rates of upwelling of cold, nutrientrich deep water, intensity of downwelling irradiance, and, in the case of attached macroalgae, availability of hard substrate. Evidence of glacialinterglacial changes in the paleoclimate of the Southern California Bight is limited and often difficult to reconcile (e.g., Jones et al. 1999, Kennett



Figure 6. Predicted distribution of giant kelp on a portion of the southern California mainland, based on the present 0–25 m depth contours. The observed distribution of giant kelp in annual aerial infrared surveys from 1967–1999 represents a composite of kelp occurrence in all years. [Kelp cover data shown by permission of L. Deysher and Southern California Edison].

and Kennett 2000, Muhs et al. 2002), but several generalizations are possible. Evidence from coastal southern California suggests a damper climate during the transitional and early interglacial period, with semi-arid conditions established by about 8,000 years ago (Masters and Gallegos 1997). Paleoceanographic proxies provide evidence of cooler sea surface temperatures in the Santa Barbara Channel at the LGM and early post-glacial, with warmer sea surface temperatures established by the early Holocene ca. 10,000 RYBP (Kennett and Ingram 1995). Finally, regional evidence from the northeastern Pacific, including the transitional region near Pt. Conception, points to decreased upwelling and marine productivity during cool stadial periods and increased productivity during warm interstadials (Kirst et al. 1999, Herbert et al. 2001, Hendy et al. 2004). In general, these results suggest that elevated marine productivity and reduced terrestrial productivity (per unit area) prevailed at the Channel Islands since the early Holocene. If true, this would have enhanced the already large differential between marine (high) and terrestrial (low) productivity at the northern Channel Islands.

Our reconstructions of island and reef area are not a direct record of changes in total regional productivity, but very large fluctuations in productivity per unit area would need to occur to erase the signal of changing reef and island area on production. Moreover, at any particular point in time, assuming no systematic differences in climate change among regions (north, south, and mainland), changes in precipitation and upwelling should not affect relative regional differences in productivity associated with differences in land/ reef area. Disparities between the islands and mainland in sediment dispersal and deposition, however, could result in significant deviations from the predicted amount of rocky reef at the mainland (Fig. 6; Graham et al. 2003, Rick et al. 2005). Modern kelp forest distributions indicate that most of the predicted reef area at the Channel Islands supports kelp forests at least some of the time over decadal scales (Fig. 3B-C), suggesting that rocky substrates dominate at the islands. In contrast, since sea-level rise began to plateau ca. 6,000-4,000 RYBP the mainland coastal margin has experienced greater sediment deposition and transitioned to a patchwork of reef- and sandy bottom-dwelling organisms (Masters and Gallegos 1997). Compared to today, except for the southern Channel Islands where reef area has consistently been small, we conclude that reef-based primary productivity is likely to have been substantially greater across the entire Southern California Bight after emergence from the last ice age, and prior to the late to middle Holocene. A major reduction in reef productivity appears to have occurred during the middle Holocene, from about 6,000-2,000 RYBP.

It is important to note that we have addressed only the benthic component of marine primary productivity (i.e., marine plants that are anchored to the bottom). A second component of marine primary productivity, which has no terrestrial analogue, derives from drifting planktonic microalgae (phytoplankton) in the pelagic realm. These organisms respond to changes in upwelling, irradiance, and circulation patterns (especially vertical mixing), but not to the availability of hard substrate. Thus, changes in the pelagic component of marine productivity have no direct connection to the reconstructions of reef area we present here. Pelagic primary productivity can fuel nearshore secondary productivity directly by providing food for filter feeding invertebrates. It also indirectly seabirds, supports populations of fishes. invertebrates and marine mammals that drive inputs to terrestrial communities through carcass drift, harvest, food droppings, and guano (Polis and Hurd 1996). In general, however, full utilization of increased pelagic productivity by terrestrial organisms requires active movement and foraging extending farther offshore than the kelp beds that reach within meters of the coast. Thus, our results may imply a redistribution of marine productivity both spatially and among species since the last ice age, and in particular, a marked shift in the relative distribution of these resources near the end of the middle Holocene.

Non-human terrestrial communities may have been impacted greatly by changes in the balance of marine and terrestrial productivity over the past 18,500 years. Effects on these communities were probably most dramatic at the LGM and during the transitional period, leading up to the Bolling-Allerod interstadial ca. 14,500 RYBP. This is where the largest changes in both island size and reef area occurred, correlated with major changes in the isolation of islands from each other and the mainland, which in the extreme case manifested as the break-up of the four northern Channel Islands. Diversity, species-area relationships, trophic structure, and productivity of terrestrial ecosystems may have been strongly influenced by all of these processes (Polis and Hurd 1996, Anderson and Wait 2001, Barrett et al. 2003), and represent rich grounds for future research. For example, the extent to which an island's history (e.g., its past land and reef area) and context (e.g., the size of adjacent reefs and the rate of flow of materials across the interface) influence patterns of species diversity and community structure at any given point in time is unknown.

However, it is unlikely that the mainland or islands of southern California were occupied by humans during the glacial maximum or early transitional period (Erlandson 1994). The best available evidence suggests that humans colonized the southern California mainland during the terminal Pleistocene about 11,000  $\pm$  500 RYBP (Erlandson 1997, Erlandson 2001). The northern islands appear to have been colonized by about 11,000–10,500 RYBP, and the southern islands by

about 8,500-6,000 RYBP (but perhaps earlier, as some of these islands have seen less archaeological research; Erlandson 1994, Raab 1997, Erlandson 2001). Thus, the principal changes experienced by Holocene peoples include gradually decreasing island size, increasing isolation (Fig. 4A), and a redistribution of marine productivity at some point during the middle Holocene (Fig. 5). For the southern Channel Islands, smaller total island area, greater isolation from the mainland, and much smaller fringing reefs may help explain their later colonization and smaller human populations (Jones 1991, Erlandson 1994, Arnold et al. 1997, Raab 1997). The higher productivity of rocky reef, kelp forest, nearshore, and intertidal habitats may also help explain the much larger number of early shell middens identified on the northern Channel Islands. Island and mainland peoples of the southern California coast also appear to have undergone major cultural shifts during the last 4,000 years, including increased cultural complexity, an elaboration of maritime technologies, intensified marine fishing, and increases in craft specialization, trade, disease, and violence (e.g., Lambert 1993, Arnold et al. 1997, Glassow 1997, Jones et al. 1999, Kennett and Kennett 2000, Erlandson and Rick 2002, Glassow 2005). These changes are best documented for the last 2,000 years, but significant cultural shifts may have occurred earlier. Emerging archaeological evidence may shed light on the degree of correspondence between mid- to late Holocene cultural change and the redistribution of marine productivity hypothesized in our study. On the northern Channel Islands, marked reductions in the extent of shallow rocky reef and kelp forest habitats-as well as the intertidal productivity they support-may have contributed to resource stress and economic diversification and intensification documented for late Holocene peoples. Finally, the greater reliance of mainland human settlements on terrestrial resources (Jones 1991, Erlandson 1994) is consistent with our finding that marine subsidies are likely to be proportionally more important on the islands than on the mainland. Such results are in keeping not only with anthropological evidence, but with comparisons of the ecology of terrestrial communities on small, arid islands vs. continents (Polis and Hurd 1996).

As with many studies attempting to integrate archaeological findings with environmental

records, the relatively coarse temporal resolution of our environmental data makes it difficult to infer specific connections between cultural events and climate changes. However, we hope that the data presented here may offer a context for Holocene shifts in the subsistence, organization, and population dynamics of human communities along the southern California coast, as well as a framework for evaluating the shifting ecology of natural communities in the California coastal zone. Around the arid California Channel Islands, in particular, our analysis of the dynamics of rocky reef and kelp forest communities through time should add another dimension to discussions about the relationships between millennial-scale fluctuations in marine productivity and the development of maritime cultures in the region.

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### REFERENCES

Anderson, E.K. and W.J. North. 1969. Light requirements of juvenile and microscopic stages of giant kelp, *Macrocystis*. Proceedings of the International Seaweed Symposium 6:3–15.

- Anderson, W.B. and G.A. Polis. 1998. Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. Oikos 81:75–80.
- Anderson, W.B. and D.A. Wait. 2001. Subsidized island biogeography hypothesis: another new twist on an old theory. Ecology Letters 4:289– 291.
- Arnold, J.E., R.H. Colten and S. Pletka. 1997. Contexts of cultural change in insular California. American Antiquity 62:300–318.
- Barrett, K., D.A. Wait and W.B. Anderson. 2003. Small island biogeography in the Gulf of California: lizards, the subsidized island biogeography hypothesis, and the small island effect. Journal of Biogeography 30:1575– 1581.
- Daly, C. and G. Taylor. 1998. California Average Monthly or Annual Precipitation, 1961–90.Water and Climate Center of the Natural Resources Conservation Service, Portland, OR.
- Dayton, P.K. 1985. The ecology of kelp communities. Annual Review of Ecology and Systematics 16:215–245.
- Deysher, L. and T.A. Dean. 1986. Interactive effects of light and temperature on sporophyte production in the giant kelp *Macrocystis pyrifera*. Marine Biology 93:17–20.
- Erlandson, J.M. 1994. Early Hunter-Gatherers of the California Coast. Plenum, New York, NY, 336 pp.
- Erlandson, J.M. 1997. The Middle Holocene along the California coast. Pages 1–10. *In*: Erlandson, J.M. and M.A. Glassow (eds.), Archaeology of the California Coast During the Middle Holocene. University of California, Los Angeles Press, Los Angeles, CA.
- Erlandson, J.M. 2001. The archaeology of aquatic adaptations: paradigms for a new millennium. Journal of Archaeological Research 9:287–349.
- Erlandson, J.M. and T.C. Rick. 2002. Late Holocene cultural developments along the Santa Barbara Coast. Pages 166–182. *In*: Erlandson, J.M. and T.L. Jones (eds.); Catalysts to Complexity: The Late Holocene on the California Coast. Cotsen Institute of Archaeology, University of California, Los Angeles.
- Fleming, K., P. Johnston, D. Zwartz, Y. Yokoyama, K. Lambeck and J. Chappell. 1998. Refining the

eustatic sea-level curve since the Last Glacial Maximum using far- and intermediate-field sites. Earth and Planetary Science Letters 163:327–342.

- Glassow, M.A. 1997. Middle Holocene cultural development in the central Santa Barbara Channel region. Pages 73–90. *In*: Erlandson, J.M. and M.A. Glassow (eds.), Archaeology of the California Coast During the Middle Holocene. University of California, Los Angeles Press, Los Angeles, CA.
- Glassow, M.A. 2005. Variation in marine fauna utilization by Middle Holocene occupants of Santa Cruz Island. Pages 23–34. *In*: Garcelon, D.K. and C.A. Schwemm (eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01, Institute for Wildlife Studies, Arcata, CA.
- Graham, M.H. 1997. Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* (L.)
  C.A. Agardh, along the Monterey Peninsula, central California, USA. Journal of Experimental Marine Biology and Ecology 218:127–149.
- Graham, M.H. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems 7:341–357.
- Graham, M.H., P.K. Dayton and J.M. Erlandson. 2003. Ice ages and ecological transitions on temperate coasts. Trends in Ecology and Evolution 18:33–40.
- Hendy, I.L., T.F. Pedersen, J.P. Kennett and R. Tada. 2004. Intermittent existence of a southern California upwelling cell during submillennial climate change of the last 60 kyr. Paleoceanography 19:PA3007, doi:10.1029/ 2003PA000965.
- Herbert, T.D., J.D. Schuffert, D. Andreasen, L. Heusser, M. Lyle, A. Mix, A.C. Ravelo, L.D. Stott and J.C. Herguera. 2001. Collapse of the California Current during glacial maxima linked to climate change on land. Science 293:71–76.
- Johnson, D.L. 1983. The California Continental Borderland: landbridges, watergaps and biotic dispersals. Pages 481–527. *In*: Masters, P.M. and N.C. Fleming (eds.), Quaternary Coastlines and Marine Archaeology: Towards

the Prehistory of Land Bridges and Continental Shelves. Academic Press, New York, NY.

- Jones, T.L. 1991. Marine resource value and the priority of coastal settlement: a California perspective. American Antiquity 56:419–443.
- Jones, T.L., G.M. Brown, L.M. Raab, J.L. McVickar, W.G. Spaulding, D.J. Kennett, A. York and P.L. Walker. 1999. Environmental imperatives reconsidered: demographic crises in Western North America during the Medieval Climate Anomaly. Current Anthropology 40:137–169.
- Kennett, J.P. 1981. Marine Geology. Prentice-Hall, New York, NY, 813 pp.
- Kennett, J.P. and B.L. Ingram. 1995. Paleoclmatic evolution of Santa Barbara Basin during the last 20 k.y.: marine evidence from Hole 893A. Proc. Ocean Drilling Prog. Scientific Results (Part 2) 146:309–325.
- Kennett, D.J. and J.P. Kennett. 2000. Competitive and cooperative responses to climatic instability in coastal southern California. American Antiquity 65:379–395.
- Kirst, G.J., R.R. Schneider, P.J. Muller, I. von Storch and G. Wefer. 1999. Late Quaternary temperature variability in the Benguela Current derived from alkenones. Quaternary Research 52:92–103.
- Lambert, P.M. 1993. Health in prehistoric populations of the Santa Barbara Channel Islands. American Antiquity 58:509–522.
- Leet, W.S., C.M. Dewees, R. Klingbeil and E.J. Johnson. 2001. California's living marine resources: a status report. State of California Resources Agency and Fish and Game, Sacramento, CA.
- Lieth, H. 1978. Primary productivity in ecosystems: comparative analysis of global patterns. Pages 300–321. *In*: Lieth, H. (ed.), Patterns of primary production in the biosphere. Dowden, Hutchinson & Ross, Stroudsburg, PA.
- Masters, P.M. and D.R. Gallegos. 1997. Environmental change and coastal adaptations in San Diego County during the Middle Holocene. Pages 11–22. *In*: Erlandson, J.M. and M.A. Glassow (eds.), Archaeology of the California Coast During the Middle Holocene. University of California Los Angeles Press, Los Angeles, CA.

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- Muhs, D.R., K.R. Simmons, G.L. Kennedy and T.K. Rockwell. 2002. The last interglacial period on the Pacific Coast of North America: timing and paleoclimate. Geological Society of America Bulletin 114:569–592.
- Nardin, T.R., R.H. Osborn, D.J. Bottjer and R.C.J. Scheidemann. 1981. Holocene sea-level curves for Santa Monica shelf, California continental borderland. Science 213:331–333.
- Neushul, M. 1962. Studies on the giant kelp, *Macrocystis*. II. Reproduction. American Journal of Botany 50:354–359.
- North, W.J. 1994. Review of *Macrocystis* biology. Pages 447–527. *In*: Akatsuka, I. (ed.), Biology of Economic Algae. Academic Publishing, The Hague, The Netherlands.
- North, W.J., D.E. James and L.G. Jones. 1993. History of kelp beds (*Macrocystis*) in Orange and San Diego Counties, California. Hydrobiologia 260/261:277–283.
- Pierson, L.J. 1987. Archaeological resource study: Morro Bay to Mexican border: final report. MMS 87–0025. United States Department of the Interior Minerals Management Service, Washington, DC.
- Polis, G.A. and S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. The American Naturalist 147:396–423.

- Porcasi, P., J.F. Porcasi and C. O'Neill. 1999. Early Holocene coastlines of the California Bight: the Channel Islands as first visited by humans. Pacific Coast Archaeological Society Quarterly 35:1–24.
- Raab, L.M. 1997. The southern Channel Islands during the Middle Holocene. Pages 23–34. *In*: Erlandson, J.M. and M.A. Glassow (eds.), Archaeology of the California Coast During the Middle Holocene. University of California Los Angeles Press, Los Angeles, CA.
- Rick, T.C., D.J. Kennett and J.M. Erlandson. 2005.
  Archaeology and paleoecology of the abalone rocks paleoestuary, Santa Rosa Island, California. Pages 55–64. *In*: Garcelon, D.K. and C.A. Schwemm (eds.), Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01, Institute for Wildlife Studies, Arcata, CA.

Institute for Wildlife Studies, Arcata, CA.

- Sanchez-Pinero, F. and G.A. Polis. 2000. Bottomup dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology 81:3117–3132.
- Steneck, R.S., M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes and M.J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29:436–459.