

Post-glacial redistribution and shifts in productivity of giant kelp forests

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Quaternary glacial–interglacial cycles create lasting biogeographic, demographic and genetic effects on ecosystems, yet the ecological effects of ice ages on benthic marine communities are unknown. We analysed long-term datasets to develop a niche-based model of southern Californian giant kelp (*Macrocystis pyrifera*) forest distribution as a function of oceanography and geomorphology, and synthesized paleoceanographic records to show that late-Quaternary climate change likely drove high millennial variability in the distribution and productivity of this foundation species. Our predictions suggest that kelp forest biomass increased up to threefold from the glacial maximum to the mid-Holocene, then rapidly declined by 40–70% to present levels. The peak in kelp forest productivity would have coincided with the earliest coastal archaeological sites in the New World. Similar late-Quaternary changes in kelp forest distribution and productivity likely occurred in coastal upwelling systems along active continental margins worldwide, which would have resulted in complex shifts in the relative productivity of terrestrial and marine components of coastal ecosystems.

Keywords: paleoecology; giant kelp; *Macrocystis pyrifera*; productivity; holocene; temperate reefs

1. INTRODUCTION

During glacial–interglacial transitions, the distribution of habitat-forming terrestrial plants responds directly to changes in glaciation, global air temperatures, aridity and atmospheric concentrations of CO₂, especially at temperate and boreal latitudes (Hewitt 2000; Davis & Shaw 2001; Walter & Eperson 2001). For example, at temperate latitudes in North America, the most recent post-glacial warming resulted in an expansion of oak (*Quercus*) at the expense of spruce (*Picea*), generating much of the contemporary population genetic and community structure of terrestrial forest ecosystems (Davis & Shaw 2001). Effects of the glacial–interglacial transition on genetic and community structure of these ecosystems have been cross-validated using fossil-pollen records (see examples in Davis & Shaw 2001). Owing to the lack of paleo-records of the distribution, abundance and productivity of kelps and other marine algae (Graham *et al.* 2003), such an historical perspective is conspicuously absent for temperate benthic marine systems (but see Fraser *et al.* (2009) for recent genetic study of ice age biogeography of a sub-Antarctic kelp).

Temperate kelp forests represent some of the most productive and diverse ecosystems on the planet (Mann 1973; Dayton 1985), owing primarily to the provision of energy and complex habitat by the kelps themselves. Spatial and temporal variability in kelp distribution and abundance can cause variability in the productivity and diversity of kelp-associated communities, with cascading effects on nearby ecosystems and human economies

(Dayton 1985). The role of kelps as foundation species is especially apparent along the northeast Pacific coastal margin where diverse kelp forests dominate near shore marine systems (Graham 2004). In the Southern California Bight, present-day populations of the canopy-forming giant kelp *Macrocystis pyrifera* are the largest in the world, supporting more than 275 common species of macroscopic algae and animals (Graham 2004). Some of the most extensive and detailed evidence for human reliance on kelp forests comes from southern California, where Native American shell middens dating to the early Holocene have been discovered on the mainland and offshore islands (Erlandson 2002; Erlandson *et al.* 2005). Giant kelp is widely distributed along the offshore islands and mainland of this region, which encompasses the area from Pt. Conception, CA to the US-Mexico border, bounded seaward by the outer edge of the continental slope. Despite the relatively high diversity and productivity of the contemporary southern California giant kelp system, however, recent studies indicate late-Quaternary fluctuations in population structure of kelp-associated species (Bernardi 2000). Archaeological evidence from southern California also suggests that human interactions with kelp forests varied greatly over the Holocene (Erlandson *et al.* 2005), with possible consequences for economic diversification, trade, conflict, disease and other fundamental cultural changes (Erlandson 2002). Finally, the detailed paleoceanographic record that has emerged from the varved sediments of the Santa Barbara Basin (Kennett & Ingram 1995) reveals a history of dramatic late-Quaternary changes in ocean dynamics and productivity in this region. The Southern California Bight thus offers a rich context of ecological, genetic, archeological and paleo-climatic information in

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129 which responses of kelp forest ecosystems to millennial
130 climate forcing can be examined and interpreted.

131 In this paper, we reconstruct millennial-scale variabil-
132 ity in the distribution and productivity of southern
133 California giant kelp forests since the last glacial maxi-
134 mum (LGM). Kelps (Class Phaeophyceae, Order
135 Laminariales) do not readily fossilize, limiting the appli-
136 cation of traditional paleoecological approaches for
137 reconstruction of giant kelp distributions. Instead, we
138 use niche-based reconstructions that link known environ-
139 mental constraints of present-day giant kelp forest
140 distribution and productivity (reviewed in Graham *et al.*
141 2007) with paleoceanographic records of spatio-temporal
142 variability in key environmental parameters; our implicit
143 (and untestable) assumption is that the response of
144 giant kelp to environmental forcing (i.e. ecophysiology)
145 has remained relatively constant over the last 20 000
146 years. Using this integrative approach, we show that gla-
147 ciation may cause variability in kelp forest distribution,
148 abundance and connectivity over a range of spatial
149 scales (tens to hundreds of kilometres) in the Southern
150 California Bight, and estimate the magnitude and
151 timing of this millennial variability. We discuss the
152 impacts of major changes in kelp forest distribution in
153 relation to associated communities, including early
154 maritime peopled.

157 2. MATERIAL AND METHODS

158 We aimed to reconstruct the past dynamics of southern
159 California kelp forests based upon our understanding of
160 their present-day distribution, dynamics and responses to
161 environmental variation (figure 1). Although kelp forests
162 are highly dynamic at small scales (<10 km), their spatial
163 and temporal distribution at regional-to-global scales is
164 known to be limited by a suite of environmental factors
165 (Foster & Schiel 1985; Broitman & Kinlan 2006; Reed
166 *et al.* 2008). The availability of rocky substrates within
167 areas of sufficient irradiance and nutrients is the primary
168 constraint on the distribution and productivity of present-
169 day giant kelp (*Macrocystis pyrifera*) populations. In southern
170 California, high irradiance requirements for sexual reproduc-
171 tion generally restrict giant kelp populations to depths
172 <25 m, where giant kelp is the competitive dominant
173 throughout its range (Foster & Schiel 1985). Peak
174 giant kelp productivity occurs during seasonal upwelling
175 (Zimmerman & Robertson 1985), when local wind forcing
176 brings deep, nutrient-rich water to the surface. Grazing by
177 sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus*)
178 can also locally limit giant kelp distribution in California
179 (Behrens & Lafferty 2004), although not in the company of
180 the primary urchin predator, sea otters (*Enhydra lutris*),
181 which were present in the region prior to extirpation by
182 Europeans in the 1700s (Kenyon 1969; VanBlaricom 1988);
183 sea otter and sea urchin remains have been continuously
184 observed in southern California archaeological records from
185 9800 to 220 calendar years before present (Erlandson *et al.*
186 2005). Thus, at least until the regional loss of sea otters, the
187 most important requirement for reconstructing paleo-kelp
188 forest distribution is a temporal sequence of maps that detail
189 past distributions of rocky substrate, located at depths <25 m.

190 The complex physiography of the Southern California
191 Bight is caused by a variety of processes involved with the
192 transformation of a subduction zone into the contemporary

193 San Andreas strike-slip fault system, approximately 40 Myr
194 BP. Geological events episodically modify bathymetric fea-
195 tures over short geological time scales (decades to
196 millennia); however, typical rates of these vertical motions
197 (uplift and subsidence) are small relative to that of the
198 most recent sea level transgression (Graham *et al.* 2003).
199 Therefore, millennial-scale variability in the availability of
200 rocky substrates within 25 m depth can be approximated by
201 superimposing temporal changes in sea level on a present-
202 day high-resolution bathymetric map. We used extensive
203 depth sounding surveys from the United States National
204 Ocean Service (NOS) Hydrographic Survey (1920–2000)
205 to produce such a map for the Southern California Bight
206 (1 m vertical resolution, 100 m horizontal resolution grid,
207 1 m depth contours). Although the density of soundings
208 declined offshore over deep basins, depth survey data were suf-
209 ficiently dense in near-shore areas to warrant interpolation at
210 the chosen resolution. All geospatial analyses were performed
211 using ArcView GIS 3.2 and ArcGIS 8.2 (Environmental
212 Systems Research Institute, Redlands, CA, USA).

213 To estimate changes in available giant kelp habitat as a
214 function of variable sea level, the 0 m datum of the map
215 was sequentially adjusted to reflect changes in sea level
216 since the LGM (approx. 21 500 calendar years before pre-
217 sent (cal. yr BP)) and areas between 0 and 25 m depth
218 were estimated for each 500-year interval. The best available
219 relative sea level curve for the southern California region was
220 a synthesis from several sea level records (Masters 2006); the
221 Masters (2006) sea level curve was digitized and linearly
222 interpolated to extract sea levels at 500 cal. yr intervals
223 from the LGM to present. Published ¹⁴C dates were cali-
224 brated to calendar years according to Stuvier *et al.* (1993),
225 Ingram & Southon (1996) and Hughen *et al.* (2004). The
226 result was a digital reconstruction of late-Quaternary changes
227 in the available giant kelp habitat (forest area) for island and
228 mainland regions in the Southern California Bight. To high-
229 light scale- and location-dependence of kelp forest response
230 to sea level rise, we also discriminated among different
231 regional island groups owing to differences in geomorphol-
232 ogy: a northern island group ‘Santarosae’ consisted of four
233 islands (San Miguel, Santa Rosa, Santa Cruz and Anacapa)
234 that were contiguous during the LGM, whereas a ‘southern’
235 island group consisted of four islands (San Nicolas, Santa
236 Barbara, Santa Catalina and San Clemente) that were separ-
237 ated from all other islands and from each other by deep water
238 throughout the last glacial–interglacial cycle. To validate use
239 of the 0–25 m depth band as potential kelp habitat, we deter-
240 mined kelp forest occupancy by analysing the contemporary
241 fraction of 0–25 m forest area inhabited by giant kelp using
242 high-resolution infrared aerial surveys conducted by the
243 California Department of Fish and Game, Southern California
244 Edison (data provided by L. Deysher, T. Dean and
245 W. North), and ISP Alginates, Inc. (data provided by
246 D. Glantz and the Santa Barbara Coastal LTER). Surveys
247 occurred quarterly between 1968 and 2002 from Newport
248 Beach, CA to the US-Mexico border (32.5° N to 33.6° N,
249 approx. 200 km of coast) and less frequently over the entire
250 region. Infrared aerial photos and digital infrared images
251 were georeferenced using ArcGIS 8.2, a landmask was
252 applied and kelp canopies were classified by a standard vege-
253 tative index (Tucker 1979). This process allowed for the
254 production of digital maps of kelp canopy distribution at
255 approximately 2 m spatial resolution with a positional accu-
256 racy of approximately 2–10 m. Using a subset of surveys

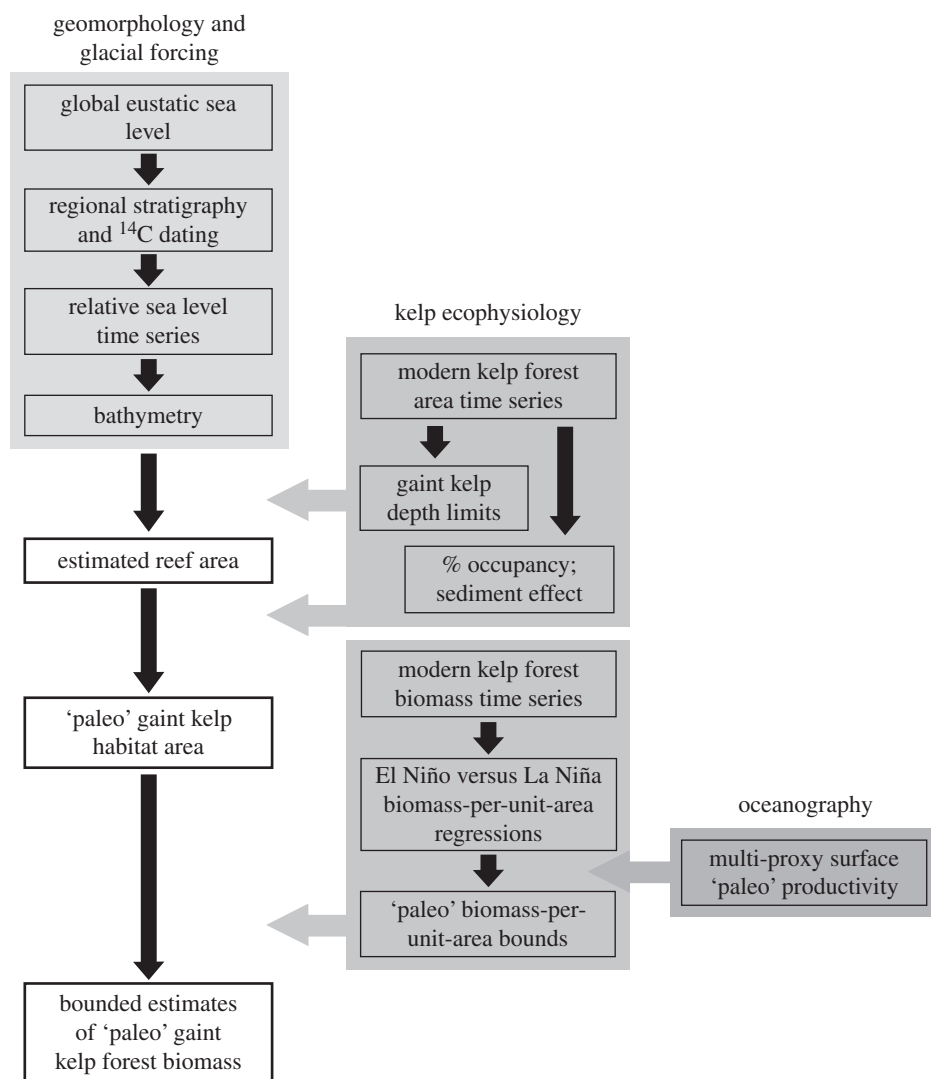


Figure 1. Primary methodological steps in the reconstruction of 'paleo' forest areas, giant kelp habitat areas and giant kelp forest biomass. Shaded boxes indicate key geomorphological, ecophysiological and oceanographic inputs used in reconstructions.

conducted over most or all of our study region (1977, 1978, 1989, 1999 and 2002–2005), we estimated kelp forest area occupancy as the fraction of predicted forest area (i.e. the 0–25 m depth band) in which kelp canopy was observed in at least one aerial survey (i.e. potential kelp habitat).

In addition to the areal extent of kelp populations, kelp forest productivity depends primarily on the biomass density of kelp canopies (Reed *et al.* 2008), nutrient flux to surface waters (Zimmerman & Robertson 1985) and incident solar irradiance. High-frequency oceanographic warming and cooling events (i.e. El Niño or La Niña) alter nutrient availability and can strongly and rapidly influence near-shore kelp biomass and productivity (Tegner *et al.* 1997; Dayton *et al.* 1999); as such, these events may provide a conservative analogue for the response of kelp systems to glacial–interglacial shifts in oceanographic productivity potential. Thus, to estimate variation in kelp biomass owing to fluctuations in area-specific productivity, we combined historical time series (1968–1999) from visual and infrared photographic surveys of (i) peak annual kelp forest canopy area and (ii) peak annual biomass in southern California to develop regressions describing the relationship between canopy area and standing crop (biomass) during different ENSO states (normal, El

Niño and La Niña). Annual canopy survey methods were the same as described in the previous paragraph. For each year, the highest kelp canopy surface area was determined for each administrative kelp bed unit designated by the California Department of Fish and Game, to estimate *peak annual kelp forest canopy area*. ISP Alginates, Inc., a kelp harvesting company in San Diego, CA, surveyed kelp canopy biomass in the same administrative bed units on a monthly basis since 1958. Trained observers made visual determinations of biomass of the kelp surface canopy (defined as 0 to approx. 1 m depth) from fixed-wing aircraft, which were subsequently calibrated to harvest records. Surveys have been carried out continuously using the same methods since 1958; thus the 1968–2002 data were based on 10 years of initial calibration and method development from 1958–1968 (D. Glantz, ISP Alginates, Inc., personal communication). Diver surveys of whole-water-column kelp forest biomass in southern California subsequently confirmed that canopy biomass correlates well with both whole-forest biomass and annual net primary productivity (Reed *et al.* 2009). From this record, we selected biomass estimates corresponding to the peak annual kelp forest canopy area for each administrative bed unit to give the

385 *peak annual biomass.* We then classified each year from 1968
 386 to 1999 as 'El Niño', 'La Niña' or 'Normal' based on the
 387 multivariate Southern Oscillation Index (SOI, Pacific Fish-
 388 eries Environmental Laboratory, [http://www.pfeg.noaa.gov/
 389 products/PFEL/](http://www.pfeg.noaa.gov/products/PFEL/)). We applied a 3-year moving-average filter
 390 to monthly values of this index to remove variation at fre-
 391 quencies higher than the ENSO period (approx. 4–7
 392 years), and values were further averaged within each year to
 393 match the resolution of the canopy area data. El Niño years
 394 were operationally defined as years in which the smoothed,
 395 averaged SOI was < -1.5 , La Niña years as $\text{SOI} > 1.5$ and
 396 Normal years as $-1.5 \leq \text{SOI} \leq 1.5$. Both variables were
 397 square root-transformed for normality and linearity and
 398 regressed using a fixed intercept at (0,0). The regression statis-
 399 tics for canopy biomass in kilogram wet mass and canopy
 400 area in square-metre were: La Niña $\sqrt{\text{canopy biomass}} =$
 401 $1.52010 \sqrt{\text{canopy area}}$, $p < 0.0001$, $r^2 = 0.635$; Normal
 402 $\sqrt{\text{canopy biomass}} = 0.99269 \sqrt{\text{canopy area}}$, $p < 0.0001$,
 403 $r^2 = 0.603$, El Niño $\sqrt{\text{canopy biomass}} = 0.69908 \sqrt{\text{canopy}}$
 404 area , $p < 0.0001$, $r^2 = 0.302$.

405 In addition to biomass, the area-specific productivity of
 406 giant kelp strongly depends on the availability of nutrients,
 407 particularly nitrate, in shallow surface waters. In present-
 408 day southern California waters, nitrate concentration exhibits
 409 a strong, consistent relationship with sea temperature
 410 (Zimmerman & Robertson 1985; Dayton *et al.* 1999), and
 411 is correlated with the upwelling of cold sub-thermocline
 412 water driven by coastal winds. However, over millennial
 413 time scales, the supply of nutrients to surface waters also
 414 depends on the source of upwelled water. If source water
 415 below the photic zone is nutrient-depleted, surface waters
 416 may be low in nutrients even during the physical process of
 417 coastal upwelling. Thus, to estimate late-Quaternary changes
 418 in giant kelp productivity potential we chose proxies for three
 419 environmental variables (sea surface temperature (SST),
 420 presence of nutrient-rich sub-photoc water ($\delta^{15}\text{N}$) and sur-
 421 face water productivity ($\%C_{\text{org}}$) from the varved sediments
 422 of the Santa Barbara Basin, one of the best-known regional
 423 records of late-Quaternary climate change (Kennett &
 424 Ingram 1995). Data from two well-studied sediment cores
 425 in the Santa Barbara Channel region, Hole 1017E and
 426 Hole JPC76, were used to reconstruct periods of low or
 427 high productivity potential since the LGM (SST, Friddell
 428 **Q1** *et al.* 2003; Hendy *et al.* 2004; $\delta^{15}\text{N}$, Hendy *et al.* 2004;
 429 $\%C_{\text{org}}$, Hendy *et al.* 2002). These proxies provided indepen-
 430 dent measures of relative changes in temperature, nutrient
 431 delivery and productivity, three processes that are highly
 432 coupled are daily to decadal scales but may be decoupled
 433 at centennial to millennial and longer time scales. It should
 434 be noted that, owing to incomplete burn-down, the most
 435 recent 10 000 cal. yr BP of the $\%C_{\text{org}}$ record should be con-
 436 sidered an upper bound (Hendy *et al.* 2002). To approximate
 437 subsequent variation in kelp productivity, we applied (i) the
 438 normal-condition canopy biomass-area regression equation
 439 to the reconstructed time series of giant kelp forest areas to
 440 predict expected kelp forest canopy biomass; and (ii) either
 441 the El Niño- or La Niña-condition regression equations to
 442 predict the lower or upper limits of canopy biomass during
 443 the low and high-productivity periods, respectively. That
 444 is, we bound our predictions with the assumption that
 445 millennial-scale conditions favourable to kelp productivity
 446 are similar to modern-day La Niña conditions, whereas
 447 unproductive conditions are similar to modern-day El Niño
 448 conditions.

3. RESULTS

449 Predicted forest area in the Southern California Bight 450
 451 varied dramatically over the late Quaternary period. 452
 453 Unexpectedly, there were striking differences in the mag- 454
 455 nitude and timing of peaks in the predicted forested area 456
 457 both among islands and between islands and the main- 458
 459 land. These differences were because of the complex 460
 461 physiography of the region (described above and depicted 462
 463 in figure 2). Island forest area doubled during the first 464
 465 7000 years of marine transgression, peaking *ca* 13 500 466
 467 cal. yr BP owing to flooding of the broad wave-cut ter- 468
 469 races that formerly lined the perimeters of the islands 470
 471 (figure 2). Despite this general increase, however, varia- 472
 473 bility in forest area differed depending on location 474
 475 within the region, even among relatively proximate off- 476
 477 shore islands (figure 2*d*). The principal differences are 478
 479 summarized by comparison of the Santarosae and 480
 481 southern island groups. After reaching a maximum *ca* 482
 483 14 000 cal. yr BP that was 250 per cent above LGM 484
 485 forest area, southern island forest area decreased by 80 486
 487 per cent through the end of the Younger Dryas cool 488
 489 period (*ca* 9000 cal. yr BP), and gradually thereafter, 490
 491 because of a rapid decrease in island perimeter. Santaro- 492
 493 sae island forest area reached a more recent maximum *ca* 494
 495 12 500 cal. yr BP, 190 per cent above LGM forest area, 496
 497 owing to the flooding of an emergent marine terrace. 498
 499 This was followed by a decrease of 60 per cent by *ca* 500
 501 11 000 cal. yr BP, when the sublittoral zone around the 502
 503 large aggregate-island fragmented into the four present- 504
 505 day islands (figure 2*b,c*). The predicted size and 506
 507 distribution of present-day island forests closely matches 508
 509 known giant kelp distributions based on remote sensing 510
 511 surveys (86% concordance at 10 m resolution). 512

482 In contrast to the islands, predicted mainland forest 483
 484 area gradually increased to a mid-Holocene (7500 cal. yr 485
 486 BP) maximum 670 per cent above LGM levels 487
 488 (figure 2*d*). Predicted mainland forest area overestimated 489
 490 known mainland giant kelp distributions (only 22% con- 491
 492 cordance) owing to large sediment deposits offshore of 493
 494 the present-day southern California mainland that origi- 495
 496 nated as sea level stabilized during the late-Holocene 497
 498 *ca* 4000–6000 cal. yr BP (Kinlan *et al.* 2005); similar 499
 500 sediment deposition was much rarer around most of the 501
 502 arid offshore islands. 503

493 The strong response of modern-day kelp forest bio- 494
 495 mass to ocean climate fluctuation suggests that the 496
 497 effects of glacial–interglacial transitions on southern 498
 499 California kelp systems go beyond the simple redistribu- 500
 501 tion of habitat and organisms. Analysis of southern 502
 503 California kelp canopy area and biomass records from 504
 505 1968 to 2002 reveals predictably higher biomass density 506
 507 during periods of high-productivity potential (La Niña) 508
 509 versus low-productivity potential (El Niño; figure 3*a*), 510
 511 presumably owing to nutrient deficiency during El Niño 512
 events (Zimmerman & Robertson 1985; Tegner *et al.* 1997). Furthermore, recently published paleoceanographic records (Hendy *et al.* 2002, 2003, 2004; **Q2** Friddell *et al.* 2003) for the last 20 000 years reveal an abrupt shift in late-Quaternary oceanographic productivity potential, from cold unproductive conditions at the LGM to warmer more productive conditions from 15 600 cal. yr BP to present (figure 3*b*). The low-productivity potential of the LGM may be analogous to long-term El Niño conditions (Ortiz *et al.* 2004).

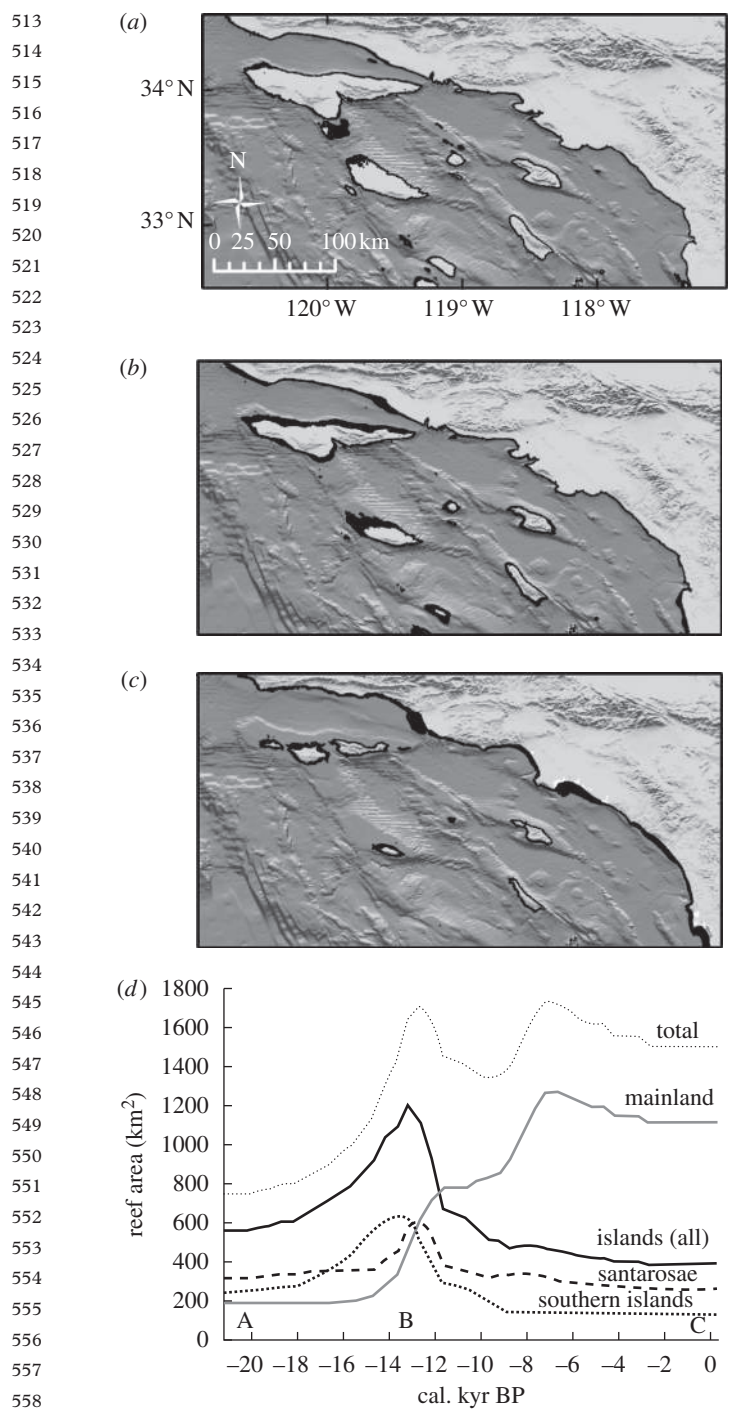


Figure 2. (a–c) Late Quaternary variation in the distribution and area of southern California shallow regions (0–25 m; depicted in black) capable of supporting giant kelp forests (*Macrocystis pyrifera*). (a) Last glacial maximum (21 500 cal. yr BP), (b) peak island reef area (13 500 cal. yr BP) and (c) present (0 cal. yr BP). (d) Time series of 0–25 m inhabitable forest areas for total (islands+mainland), mainland, all southern California islands, and Santarosae and southern island groups. Increments are 500 cal. yr, continuous lines represent linear interpolations between data increments. Letters indicate time periods corresponding to maps (a–c).

The small inhabitable forest areas during the first 5500 years of marine transgression coincided with relatively poor oceanographic productivity, limiting potential increases in kelp biomass relative to LGM levels. Interestingly, the 13 500 cal. yr BP peak in both island and mainland inhabitable forest area occurred after the

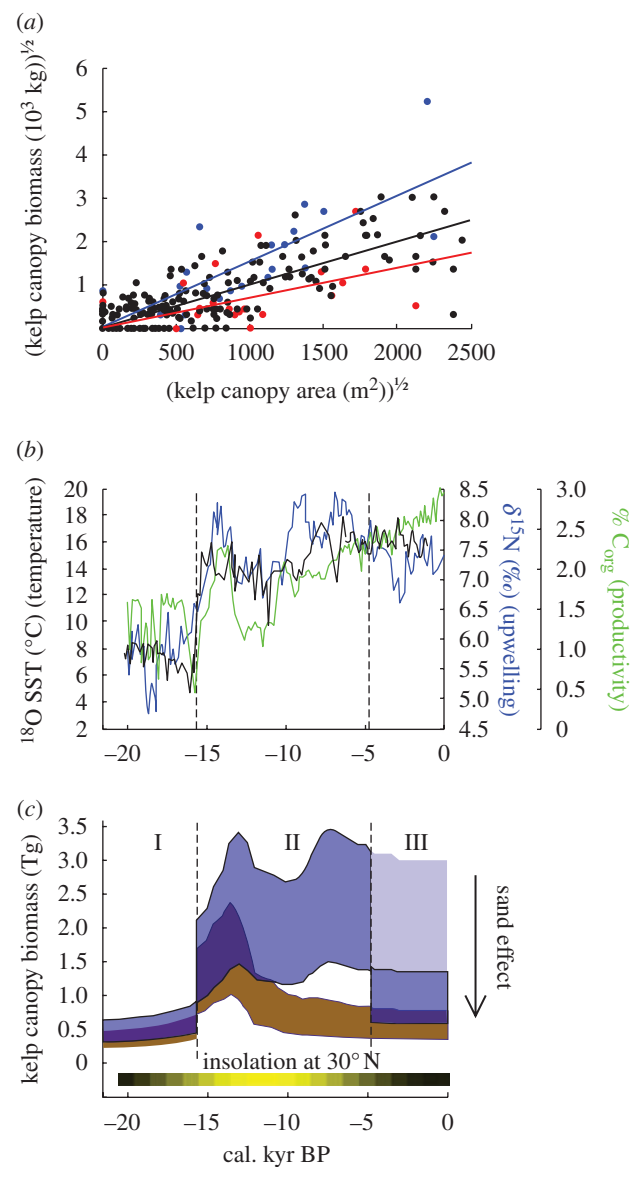


Figure 3. Reconstruction of kelp forest productivity (change in biomass) since the last glacial maximum. (a) Annual maxima in giant kelp canopy biomass (wet weight, kg) versus giant kelp canopy surface area (m^2) in southern California under prevailing El Niño (red), La Niña (blue) and ‘normal’ ocean climates (black). (b) Paleooceanographic conditions in the Southern California Bight: sea surface temperature (SST; black), upwelling ($\delta^{15}N$; blue), and biological productivity (% organic carbon; green; value for most recent 10 000 cal. yr BP is an upper bound). Left vertical reference line at 15 600 cal. yr BP indicates the approximate timing of the Bolling-Allerod warming and marks the beginning of the high productivity period, whereas right vertical reference line at 4750 cal. yr BP marks the approximate onset of mainland sand inundation. (c) Late Quaternary variation in giant kelp canopy biomass (wet weight, teragrams, Tg) for southern California islands (brown) and total (islands+mainland; blue). Period I indicates low-productivity conditions; periods II and III indicate high-productivity conditions, before and after the beginning of mainland sand inundation. The large arrow and shading during period III indicates total giant kelp canopy biomass after removal of the ‘sand effect’ (70% reduction equivalent to modern difference in kelp occupancy between islands and mainland). At the bottom is index of Northern Hemisphere solar insolation (Berger & Loutre 1991), with white as highest ($520 W m^{-2}$) and black as lowest ($460 W m^{-2}$).

oceanographic transition to more productive conditions *ca* 15 600 cal. yr BP, leading to a rapid increase in predicted kelp biomass to 150–325% of LGM levels, dominated by large island-based kelp forests. This enhancement of kelp forest productivity likely lasted through most of the Holocene, although the dominant source of kelp biomass would have shifted from islands to the mainland around 11 000 cal. yr BP. This maximum in kelp forest biomass was interrupted only by the mainland transition to a sand-dominated system *ca* 4000–6000 cal. yr BP (figure 3c; Kinlan *et al.* 2005), whereby mainland forests were likely inundated by sand, restricting the size of the available kelp habitat. We note that, although the direct relationship between solar insolation and kelp productivity is unknown, the pre- to mid-Holocene peak in kelp forest biomass coincides with the peak in late-Quaternary solar insolation at 30° (figure 3c; Berger & Loutre 1991), which would likely have further enhanced kelp productivity during this period.

Finally, it is challenging to synthesize data records that span MULTIPLE temporal and spatial scales and that were collected with different levels of accuracy. Consequently, our results incorporate a degree of inherent error owing to the compounding of data records. Although we could not characterize the extent of such errors, two main sources are likely: (i) spatial errors created during the formation of the bathymetric map that would affect interpretation of distribution and abundance patterns of kelp canopy/forest; and (ii) errors owing to temporal inaccuracies in the oceanographic and sea level records that would primarily affect the timing of changes in reef area and kelp canopy biomass. The high spatial resolution of the bathymetric map and temporal resolution of the oceanographic and sea level records, however, suggest that subsequent errors would be small relative to the conspicuous predicted shifts in kelp forest reef area (hundreds of square kilometres) and the timing of such shifts (thousands of years). The generality of our conclusions does not hinge on finer-scale patterns. Instead, our aim is to represent broad-scale (>1 km) changes in the long-term (more than centennial) average distribution of kelp forest biomass.

4. DISCUSSION

The overall pattern emerging from these reconstructions is one of climate-driven redistribution of coastal kelp forest resources since the LGM. Near the LGM, most inhabitable kelp forest areas existed around large offshore islands, due primarily to the steepness of the mainland coast during the low sea level stand. As such, the islands likely represented focal points for the aggregation of kelp forest organisms, similar to the glacial refugia of terrestrial systems (Hewitt 2000). With the transition to interglacial conditions, the productivity of these kelp systems likely increased owing to changes in oceanography, again similar to that of temperate forests (Davis & Shaw 2001); this pattern was because of an increase in upwelling despite increased warming of surface waters, evidenced by independent paleo-oceanographic proxies of temperature and productivity. However, after the first 7500 years, the size of the island forests decreased rapidly, and they fragmented and increased in isolation distance, opposite

to the commonly observed pattern of expansion and coalescence of terrestrial glacial refugia (Hewitt 2000).

Our reconstructions predict high fragmentation and recent isolation of Santarosae island giant kelp forests relative to their southern counterparts as a result of marine transgression. In contrast, coalescence of Santarosae island components would occur during regressive seas. Repetition of this pattern with each glacial–interglacial cycle (approx. 100 000 yr frequency) could result in greater genetic homogeneity among Santarosae island group populations of kelp forest organisms in comparison with southern ones. Southern Californian black surfperch (*Embiotoca jacksoni*) a near shore reef fish that lacks a pelagic larval stage and thus has limited ability to disperse among islands, exhibit a phylogeographic pattern consistent with this expectation (Bernardi 2000). Mitochondrial control-region sequences from populations in the southern California mainland and each of the eight present-day islands showed low average pairwise divergence (0.3%), and haplotype diversity (0.58) among the Santarosae island group relative to the southern islands (0.97 and 0.86%, respectively). Thus, similar to many terrestrial systems (Hewitt 2000), climate-forced habitat fragmentation/coalescence cycles may provide a useful framework for interpreting genetic signals in the structure of temperate marine species.

The predicted response of marine foundation species to glacial–interglacial fluctuations has important implications not only for predicting the long-term effect of past and future climate change on global distribution of biodiversity and productivity, but also the flux of resources across the land–sea interface to human and other communities. For instance, the redistribution of kelp forest resources implies that early human populations on the northern and southern islands (colonized by approx. 12 000 and 9000 cal. yr BP, respectively; Erlandson 1994) experienced a 50–80% decrease in the availability of kelp forest-based resources by the end of the mid-Holocene. Erlandson *et al.* (2005) showed a decline in the remains of sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus*) and red and black abalone (*Haliotis cracherodii*, *H. rufescens*) in island middens over the last 800 years, suggesting decreased availability of these species owing to either decreasing kelp productivity (Graham 2004), fishing or both. Such changes could have contributed to an intensification and diversification of Native American fisheries evident on the California islands during the late Holocene (Kennett 2005).

Recent work in terrestrial paleoecology has highlighted the strong regional variation of ecosystem responses to climate change. Our reconstructions of late Quaternary southern California kelp forest distribution reveal how different habitats within a region may exhibit distinct responses to climate-forcing. Ecosystems at the interface between habitats, such as coastal areas, may therefore exhibit particularly complex responses to millennial-scale climate change. These responses can be traced to interactions and feedbacks among forcing processes in the atmosphere (precipitation, alongshore winds), ocean (sea level rise, nutrient flux) and lithosphere (uplift, subsidence, physiography, sediment deposition).

We have focused on the southern California Bight because it supports the most productive, extensive and well-studied modern kelp forests in the world

769 (Foster & Schiel 1985; Dayton *et al.* 1999; Graham *et al.*
 770 2007), and because of the availability of detailed bathy-
 771 metric and oceanographic data, an excellent paleo-
 772 oceanographic record (Kennett & Ingram 1995), and a
 773 wealth of archeological data documenting human use of
 774 kelp forest resources throughout the Holocene (Erlandson
 775 2002; Erlandson *et al.* 2005; Kennett 2005). At present
 776 this combination of data does not exist for any of the
 777 other major kelp forest systems of the world. However,
 778 because the processes leading to kelp forest redistribution
 779 are general, glacial–interglacial cycles may have driven
 780 similar major fluctuations in kelp forest distribution and
 781 productivity in coastal upwelling systems worldwide.
 782 Moreover, the response of global kelp forest ecosystems
 783 to sea level change is likely characterized by strong
 784 regional signatures owing to differences in the physiogra-
 785 phy of coastal margins, geological processes that
 786 determine relative sea level and sediment deposition,
 787 and oceanographic processes that influence productivity.
 788 This point is supported by the extreme variability of
 789 present-day near-shore physiography among major
 790 coastal upwelling regions inhabited by canopy-forming
 791 kelps, with bathymetric profiles that contain unique fea-
 792 tures likely to influence paleo-forest areas, including
 793 high or low relief, shoals and offshore islands. The depen-
 794 dence of kelp forest responses to post-glacial change on
 795 nonlinear bathymetries implies that near-shore benthic
 796 marine ecosystems will not generally follow the same
 797 post-glacial trajectories of abundance, productivity, diver-
 798 sity and connectivity as adjacent terrestrial or pelagic
 799 marine habitats. Although the impact of a predicted 1 m
 800 rise in future sea levels rise will likely be minimal on rela-
 801 tively linear temperate coastlines, the nonlinear
 802 bathymetries of coastal islands may result in more con-
 803 spicuous impacts to insular kelp forests; using our
 804 bathymetric map, predicted losses of kelp forest habitat
 805 in the northern Channel Islands are approximately 6
 806 per cent for a 1 m sea level rise.

807 The decoupling of marine and terrestrial responses to
 808 sea level rise implies large changes in the relative impor-
 809 tance of marine versus terrestrial production in coastal
 810 ecosystems over glacial–interglacial cycles. Flux of
 811 marine productivity across the coastal interface during
 812 periods of low terrestrial resource availability could alter
 813 patterns of coastal diversity and community structure as
 814 it does in arid coastal regions today (Polis & Hurd
 815 1996), and may have also facilitated expansion of human
 816 settlements into otherwise unfavourable regions, including
 817 such fundamental events in human cultural evolution as
 818 the crossing from Asia to North America (Erlandson
 819 2002; Erlandson *et al.* 2007). Given their continuing
 820 importance as centres of human economies, populations
 821 and impacts, the complexity of coastal ecosystem responses
 822 to global climate change, past and present, represents an
 823 important avenue of emerging research.

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