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INTERPRETING THE PALEOZOOGEOGRAPHY AND SEA LEVEL HISTORY OF THERMALLY ANOMALOUS MARINE TERRACE FAUNAS: A CASE STUDY FROM THE LAST INTERGLACIAL COMPLEX OF SAN CLEMENTE ISLAND, CALIFORNIA

Daniel R. Muhs^{1,3}, Lindsey T. Groves², and R. Randall Schumann¹

ABSTRACT.—Marine invertebrate faunas with mixtures of extralimital southern and extralimital northern faunal elements, called thermally anomalous faunas, have been recognized for more than a century in the Quaternary marine terrace record of the Pacific Coast of North America. Although many mechanisms have been proposed to explain this phenomenon, no single explanation seems to be applicable to all localities where thermally anomalous faunas have been observed. Here, we describe one such thermally anomalous fossil fauna that was studied on the second emergent marine terrace at Eel Point on San Clemente Island. The Eel Point terrace complex is a composite feature, consisting of a narrow upper bench (terrace 2a) and a broader lower bench (terrace 2b). Terrace 2b, previously dated from ~128 ka to ~114 ka, was thought to date solely to marine isotope stage (MIS) 5.5, representing the peak of the last interglacial period. Nevertheless, the fauna contains an extralimital northern species and several northward-ranging species, as well as an extralimital southern species and several southward-ranging species. Similar faunas with thermally anomalous elements have also been reported from San Nicolas Island, Point Loma (San Diego County), and Cayucos (San Luis Obispo County), California. U-series dating of corals at those localities shows that the thermally anomalous faunas may be the result of mixing of fossils from both the ~100-ka (cool-water) and the ~120-ka (warm-water) sea level high stands. Submergence, erosion, and fossil mixing of the ~120-ka terraces by the ~100-ka high-sea stand may have been possible due to glacial isostatic adjustment (GIA) effects on North America, which could have resulted in a higher-than-present local sea level stand at ~100 ka. The terrace elevation spacing on San Clemente Island is very similar to that on San Nicolas Island, and we hypothesize that a similar mixing took place on San Clemente Island. Existing fossil records from older terraces elsewhere in California also show thermally anomalous elements, indicating that the scenario presented here for the last interglacial complex may have applicability to much of the marine Quaternary record for the Pacific Coast.

RESUMEN.—Durante más de un siglo, se reconocieron faunas marinas de invertebrados con combinaciones de fauna extralimital del norte y extralimital del sur, denominadas faunas de anomalía térmica, en el registro de terrazas marinas cuaternarias de la Costa Pacífica de Norteamérica. Se propusieron muchos mecanismos para explicar este fenómeno, sin embargo no se puede utilizar la misma explicación en todas las localidades en las cuales se observó. En este estudio describimos fósiles de una fauna de anomalía térmica que se estudió en la segunda terraza marina emergente en Eel Point (Punta Anguila), en la Isla San Clemente. El complejo de la terraza de Eel Point es un compuesto, que consiste en una elevación superior angosta (“terrace 2a”) y una elevación inferior más ancha (“terrace 2b”). Se consideró que la terraza 2b, de aproximadamente 128 mil años a 114 mil años, databa únicamente de la época de los estadios isotópicos marinos (MIS, por sus siglas en inglés) 5.5, que representan el punto máximo del último período interglaciar. Sin embargo, la fauna contiene una especie extralimital del norte y especies que tienden a ubicarse en el norte y una especie extralimital del sur y especies que tienden a ubicarse en el sur. También se registraron faunas de características similares con elementos de anomalía térmica en la Isla de San Nicolás, Point Loma (condado de San Diego) y Cayucos (condado de San Luis Obispo), California. La datación con el método de Series de Uranio de corales en esos lugares muestra que las faunas de anomalía térmica pueden ser el resultado de la mezcla de fósiles de hace aproximadamente 100 mil años (aguas frescas) y 120 mil años (aguas tibias). La mezcla de fósiles, el sumergimiento y la erosión de las terrazas de hace aproximadamente 120 mil años por el nivel del mar alto de hace aproximadamente 100 mil años han sido posibles debido a los efectos de ajuste isostático glacial (GIA, por sus siglas en inglés) en Norteamérica, que podría haber dado como resultado un nivel del mar local más elevado que el actual. El espaciado de la elevación de la terraza en la Isla San Clemente es similar al de la Isla de San Nicolás, y suponemos que en la Isla San Clemente se produjo una mezcla similar. Los registros de fósiles existentes de terrazas más antiguas en otros lugares de California también muestran la existencia de elementos con anomalía térmica, lo cual indica que es posible que la hipótesis que presentamos en el este trabajo de investigación sobre el último complejo interglaciar se pueda aplicar a una parte considerable del registro cuaternario marino de la Costa del Pacífico.

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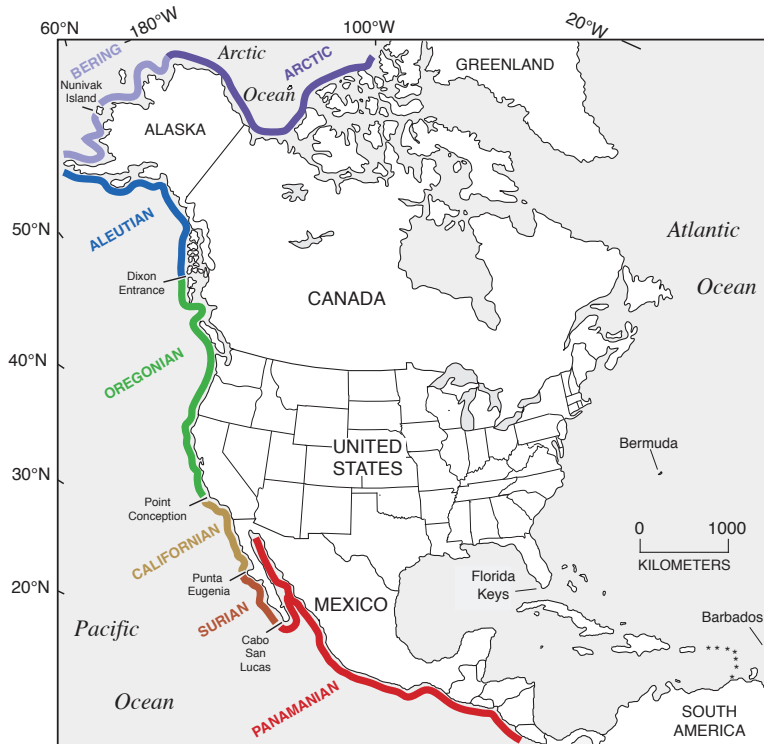


Fig. 1. Faunal provinces, or “biogeographic units” (cf. Belanger et al. 2012), of the Pacific and Arctic coasts of North America, as defined by Valentine (1973).

With the prospect of a warmer future earth, there is considerable interest in studying past warm periods in the geologic record. One such period that has received attention is the last interglacial period (LIG), when global ice volume was significantly lower than today, based on sea level studies (Kopp et al. 2009, Muhs et al. 2011, Dutton and Lambeck 2012). Reconstructions of sea surface temperatures (SSTs) from deep-sea core data (foraminifera, radiolarians, diatoms, coccoliths, and alkenones) show that while globally the LIG was only slightly warmer than present, there were significant regional differences from the global average (Turney and Jones 2010, McKay et al. 2011). These latter studies show that in middle to high latitudes (30°N to 70°N) of both the Atlantic Ocean and Pacific Ocean, LIG SSTs may have been significantly warmer than present, by up to ~4 °C. In order to assess the possible implications of such regional warming in the future, it is important to confirm that the deep-sea core record of past warming is reliable.

In addition to marine cores, estimates of LIG paleotemperatures in middle- to high-latitude regions can be generated from fossils of shallow-water marine invertebrates, particularly mollusks. Faunal provinces for marine invertebrates, also referred to as global biogeographic units, have been developed by a number of investigators over many decades. Two of the best-known attempts are those of Valentine (1973) and Spalding et al. (2007). The Valentine (1973) scheme (Fig. 1) is based largely on shared species and species diversity, whereas the Spalding et al. (2007) scheme is based mostly on patterns of endemism. Belanger et al. (2012) showed that biogeographic units for both schemes can be predicted with 89%–100% accuracy by a very limited number of variables—principally temperature, salinity, and productivity. In fact, temperature alone correctly predicts 53%–99% of the biogeographic structure along coastlines globally. Thus, fossil marine invertebrate records from emergent marine terraces provide a powerful means of estimating marine paleotemperature ranges.

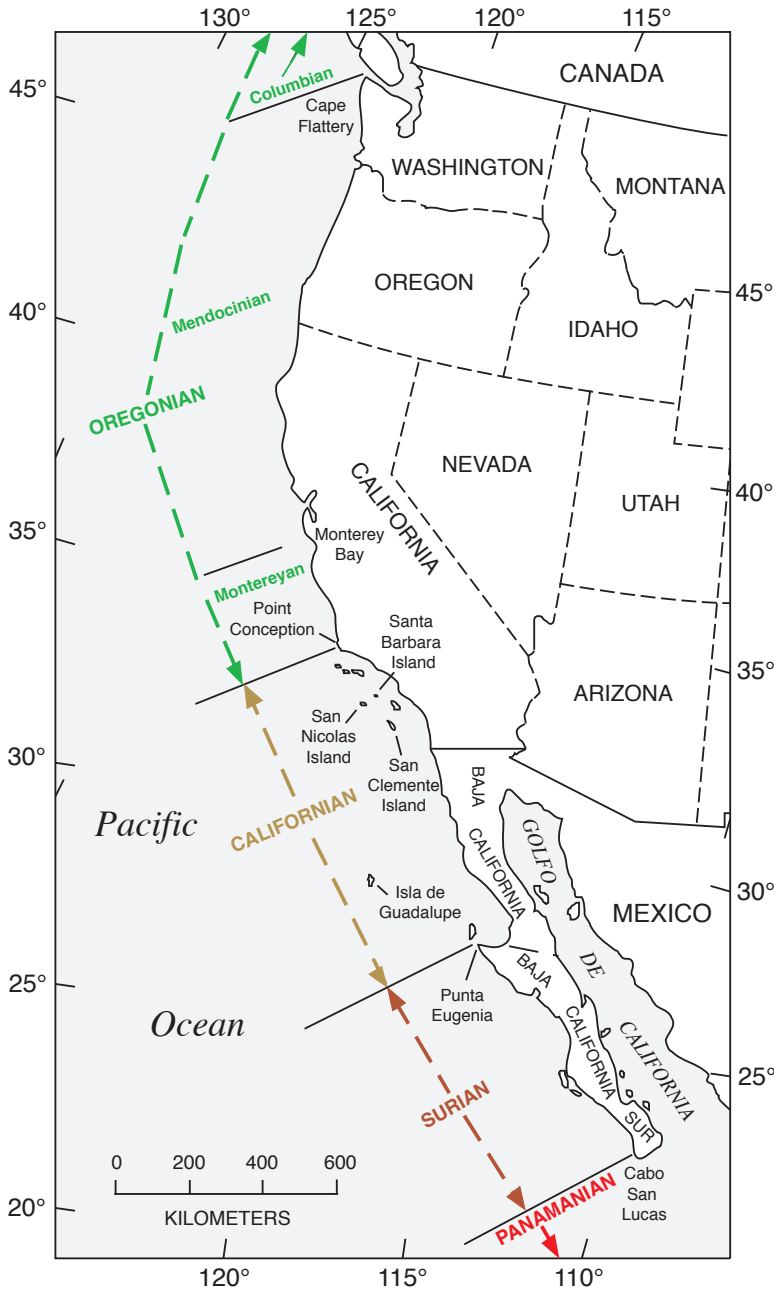


Fig. 2. Detailed depiction of faunal provinces and subprovinces of the Pacific Coast of North America, as defined by Valentine (1966, 1973). Also shown is the location of San Clemente Island and other localities referred to in the text.

On the Pacific Coast of North America, faunal province boundaries correspond, at least in part, to major changes in the physical geography of the continental margin, such as shifts in the orientation of the coastline that modify ocean currents (Fig. 2). Comparisons of fossil

mollusks in marine terrace deposits to modern faunal provinces along the Pacific Coast has allowed inferences about changes in marine paleoclimate. For example, fossil localities within what is now the Californian province might contain species that today are found

only within the Surian or Panamic (or Panamanian) province, thus implying warmer waters in the past. Similarly, fossil localities in what is now the Californian province that contain species now found only in the Oregonian province would imply cooler-than-present waters in the past.

For more than a hundred years, the Quaternary fossil record of Pacific Coast marine terraces has generated a rich literature on past marine climates (Arnold 1903, Grant and Gale 1931, Woodring et al. 1946, Woodring 1957, Valentine 1958, 1961, 1962, 1980, Kanakoff and Emerson 1959, Valentine and Meade 1961, Vedder and Norris 1963, Addicott 1966, Lipps et al. 1968, Kern 1977, Kennedy 1978, 2000, Susuki and Stadum 1978, Emerson 1980, Lindberg et al. 1980, Emerson et al. 1981, Kennedy et al. 1982, 1992, Muhs et al. 2002a, 2006, 2012a). One problem that has long been recognized in marine terrace fossil studies on the Pacific Coast is the existence of fossil assemblages with elements that imply contradictory paleoclimatic interpretations when set in the context of their modern zoogeography. For example, a given fossil fauna might contain some species that presently live only to the south of that locality (extralimital southern species), as well as some species that currently live only to the north of it (extralimital northern species). Such faunas with mixed fossils have been referred to as “thermally anomalous” assemblages.

The cause of these anomalies has been debated for the better part of a century, with various mechanisms proposed. These include (1) northward and southward shifts in marine isotherms over the course of the Pleistocene (Smith 1919); (2) reworking of fossils from older units (Crickmay 1929, Woodring et al. 1946, Woodring 1957, Vedder and Norris 1963); (3) non-temperature-related factors that govern the composition of a marine community, such as species competition (Grant and Gale 1931); (4) presence of a cold-water upwelling cell adjacent to a protected, warm embayment or at least near a zone where upwelling is less intense (Valentine 1955, 1980, Vedder and Norris 1963); (5) storm-wave and longshore-current transportation (Woodring et al. 1946); (6) changes in coastal geography (Woodring et al. 1946, Vedder and Norris 1963); (7) changes in physiology that would alter tolerances of species to different temperature ranges (Wood-

ring et al. 1946, Woodring 1957, Vedder and Norris 1963, Kern et al. 1971); (8) local and temporary current changes bringing extralimital taxa into regions where they do not usually live (Zinsmeister 1974); (9) response of individualistic species to climate change (Roy et al. 1995); and (10) greater seasonality due to orbital forcing in some interglacial periods compared to the present (Kennedy 2000).

No one mechanism has proved to be completely satisfactory in explaining the thermally anomalous aspects of some of the Pacific Coast fossil faunas. Valentine (1955) pointed out that Smith's (1919) mechanism of northward and southward shifts in marine isotherms does not explain how cool-water and warm-water fossils can be found at a single locality. Changes in physiology and species competition mechanisms, as proposed by several investigators, are almost impossible to test given present techniques. Modifications in coastal geography, proposed by Woodring et al. (1946) and Vedder and Norris (1963), do not explain thermally anomalous faunas when there is no geologic evidence that such changes occurred over the time period of interest. An upwelling cell adjacent to a warm embayment, proposed by Valentine (1955, 1980) and Vedder and Norris (1963), fails to explain fossil mixtures that are found on outer/exposed and particularly insular coastlines where such thermal contrasts do not exist. Reworking of fossils from older units, also proposed by several investigators cited above, cannot be invoked in those areas where older, fossil-bearing units are lacking. Although Coan et al. (2000) report that there have been migrations of southern bivalves beyond their historic northern range endpoints during warm El Niño years (supporting the Zinsmeister [1974] model, at least in part), Roy et al. (1995) point out that such a mechanism is not likely to explain extralimital southern forms that are abundant at a given fossil locality. Emerson (1980) also noted that this explanation is not consistent with the diversity of extralimital forms.

Development of amino acid geochronology explains some of the problems of thermally anomalous faunas. Aminostratigraphic studies with good paleontological characterization show that the assumption of an identical age for the lowest marine terrace along the Pacific Coast is incorrect (Wehmiller et al. 1977, Kennedy 1978, Kennedy et al. 1982). Using the marine

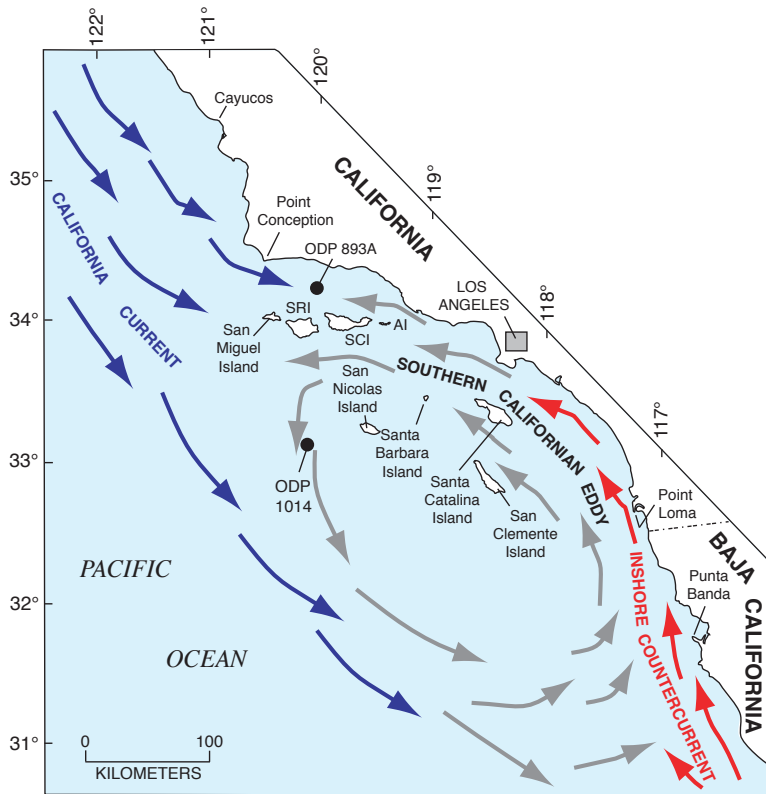


Fig. 3. Map of southern California showing ocean currents (modified from Hendy 2010), location of San Clemente Island, ODP hole 893A and 1014, and other localities referred to in the text. SRI, Santa Rosa Island; SCI, Santa Cruz Island; AI, Anacapa Island.

oxygen isotope stage (MIS) terminology of Martinson et al. (1987), these studies show that marine terrace deposits with cool-water faunas correlate to MIS 5.1 (~80 ka) or possibly MIS 5.3 (~100 ka) and those with neutral (exposed coasts) or warm-water (protected coasts) faunas are probably correlative with MIS 5.5 (~120 ka). Subsequent U-series dating of corals from many of these terraces confirms the aminostratigraphic interpretations (Muhs et al. 2002a, 2006, 2012a).

Here, the LIG fossil record from the second, Eel Point terrace (terrace 2b) on San Clemente Island, California, is examined. San Clemente Island is ~230 km southeast of Point Conception and is situated well within the Californian faunal province (Fig. 2). The California Channel Islands have an unusual diversity in modern marine invertebrate faunas. San Nicolas Island, for example, is situated far enough southwest of mainland California that it is bathed by the innermost part of the cold,

southward-moving California Current but is west of the warm, northward-flowing Inshore (Davidson) Countercurrent (Fig. 3). Thus, marine invertebrates off San Nicolas Island and San Miguel Island have closer zoogeographic affinities with Cayucos, California (~120 km northwest of Point Conception; see Fig. 3), than they do with the other Channel Islands or mainland southern California to the south and east of Point Conception (Little 1980, Seapy and Little 1980, 1993, Eernisse et al. 2007). In contrast, Santa Catalina Island and San Clemente Island, farther south, are closer to the California mainland and are influenced more by the warm Inshore Countercurrent (Fig. 3). Despite the proximity of some islands to each other and their position within the Californian faunal province, cluster analyses of modern marine invertebrate populations clearly distinguish the northern and outer islands, such as San Miguel and San Nicolas Islands, from the southern and inner islands,



Fig. 4. Map showing Quaternary deposits and inferred inner edges of marine terraces on northern San Clemente Island (from Muhs 1983, as modified by Muhs et al. 2002a) and fossil localities at Eel Point.

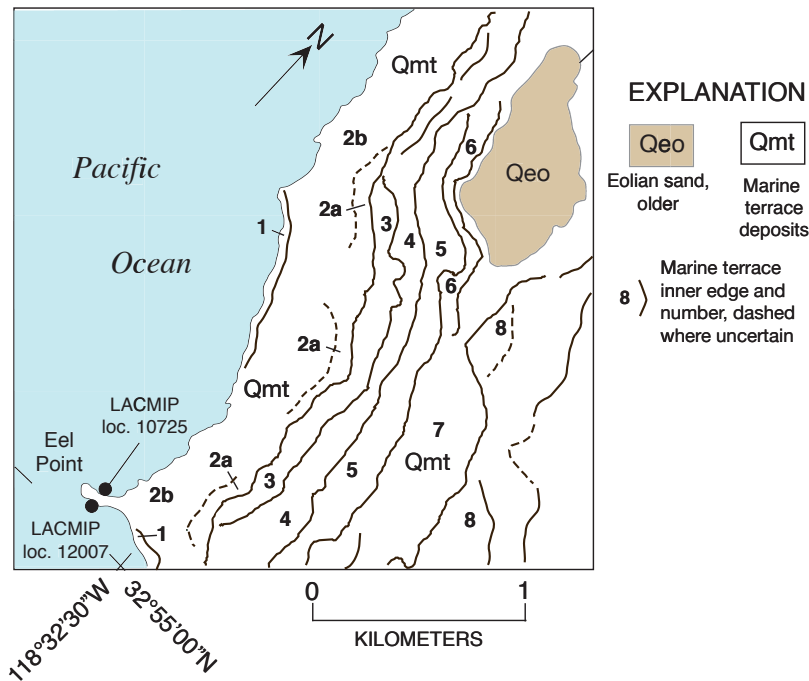
such as Santa Catalina and San Clemente Islands (Seapy and Littler 1980).

GEOMORPHOLOGY OF SAN CLEMENTE ISLAND

Marine terraces are well expressed geomorphologically on San Clemente Island (Figs. 4, 5), and terraces on the northern part of the island were mapped by Muhs (1983). In the Eel Point area (Fig. 5), at least 9 terraces have been mapped. The second marine terrace was informally named “the Eel Point terrace” by

Muhs and Szabo (1982). Muhs et al. (2002a) proposed an important modification to the earlier mapping of Muhs (1983) with the recognition that what was mapped originally as the Eel Point terrace contains 2 distinct terrace platforms (Kennedy et al. 1995, Adler 2003). A narrow, discontinuous inner terrace found at a slightly higher elevation was designated “terrace 2a” by Muhs et al. (2002a); and a broader, continuous outer terrace at a lower elevation was designated “terrace 2b” (Figs. 4, 5). At places, there is a still-lower terrace, mostly

(a) Eel Point study area and fossil localities



(b) view of marine terraces near Eel Point, looking south

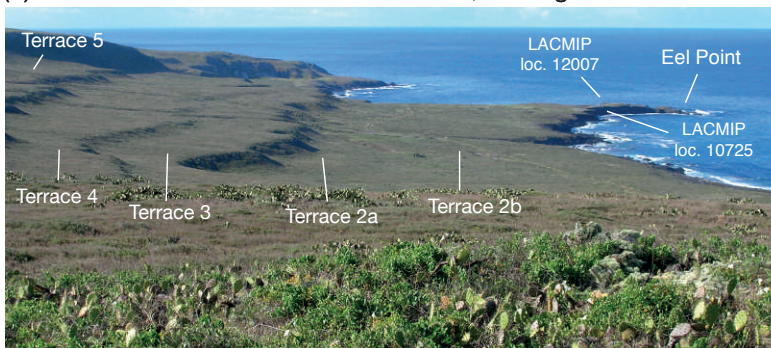


Fig. 5. (a) Detailed map of Quaternary deposits and marine terrace inner edges in the Eel Point area of San Clemente Island (from Muhs 1983, as modified by Muhs et al. 2002a). (b) View to the south of the Eel Point area, showing the lowest marine terraces and fossil localities shown in (a).

discontinuous, inset against terrace 2b and designated "terrace 1."

In the present work, elevations of the Eel Point terrace complex were determined using differential global positioning system (GPS) measurements. Differentially correcting the GPS elevations usually results in horizontal and vertical uncertainties of 30 cm or less. Comparison of GPS-derived elevations with benchmarks and taped elevations elsewhere on the Channel Islands shows good agreement within

the limits of instrumental uncertainty. Two elevation transects show the geomorphic relationships of the Eel Point terrace complex and adjacent terraces (Fig. 6). Near West Cove, on the northern part of the island (Fig. 4), only low terraces 1, 2b, and 3 are present. Terrace 1 is a narrow feature above the modern bench and has a shoreline angle (a junction of the wave-cut bench with the former sea cliff) elevation of 7.8 m. Terrace 2b is a much broader landform, and thin, nonfossiliferous marine

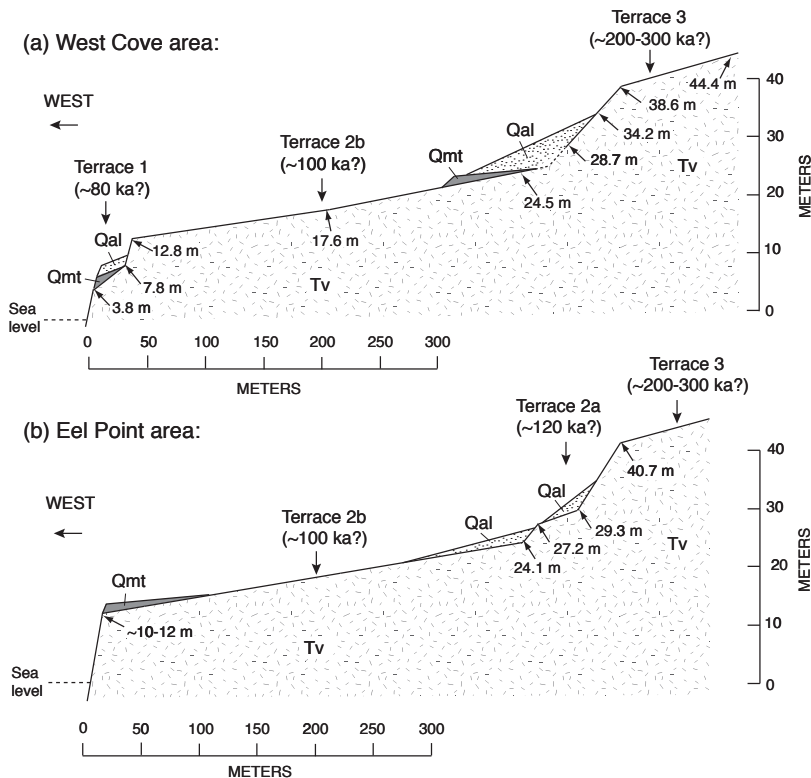


Fig. 6. Marine terrace cross sections from 2 shore-normal transects across terraces 3, 2a, 2b, and 1. All elevations are from differential GPS measurements. Qal, Quaternary alluvium and/or colluvium; Qmt, Quaternary marine terrace deposits; Tv, Tertiary volcanic rocks.

gravels overlie the wave-cut bench near the inner edge, at an elevation of 24.5 m. This elevation is slightly below that of the shoreline angle, which is not exposed. The lowest exposed sea cliff elevation above the shoreline angle is 28.7 m. Extrapolating the bench elevations landward and the cliff elevations downward, we infer the shoreline angle to be at an elevation of ~ 25 m. Near Eel Point itself, terrace 1 is found both to the south and over a distance of ~ 1 km to the north (Fig. 4). Unlike the West Cove area, however, both terraces 2b and 2a are present, with shoreline angle elevations of 24.1 m and 29.3 m, respectively. Whereas terrace 2b is a broad (~ 370 m), well-expressed landform (Fig. 5), terrace 2a is barely 40 m wide where it occurs inland of Eel Point (Fig. 6). This geomorphology is very similar to what Muhs et al. (2012a) also called terraces 2b and 2a on San Nicolas Island. Marine terrace deposits on San Clemente Island are largely absent from both terraces in this area, except

at Eel Point itself. Here, 2 localities were once present (Los Angeles County Museum Invertebrate Paleontology [LACMIP] locs. 10725 and 12007); but as of 2006, only the latter remains, as sea cliff retreat on the north side of Eel Point removed what was once LACMIP loc. 10725. The present bench elevation near where LACMIP loc. 10725 was situated is ~ 12.4 m above sea level. LACMIP loc. 12007 is ~ 10.3 m above sea level and is between 2 stacks: one at ~ 16.3 m on the west side and one at ~ 14.3 m on the east side. Fossils at both localities are (or were) hosted by ~ 0.5 m of calcareous sand and gravel. Eolian sand overlies the marine terrace deposits in places at Eel Point.

AGE OF THE EEL POINT TERRACE ON SAN CLEMENTE ISLAND

Corals (*Balanophyllia elegans*) from both fossil localities on the Eel Point terrace (terrace 2b) date to the peak of the last interglacial

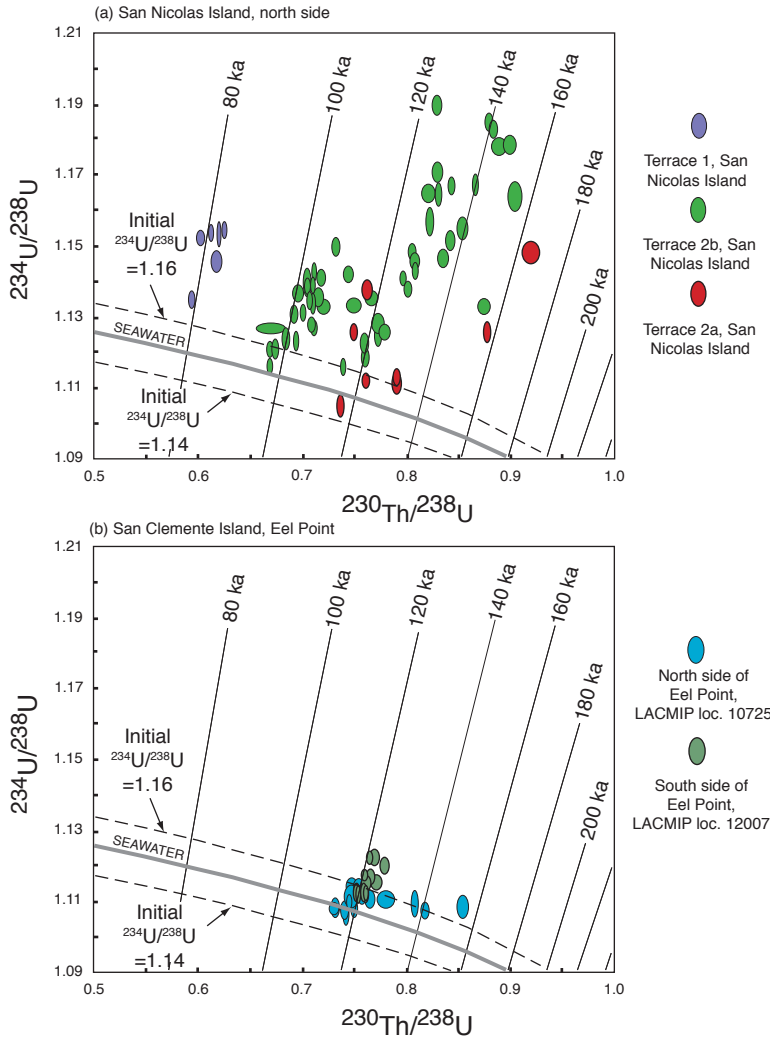


Fig. 7. Isotopic evolution curves (dashed lines) showing sympathetic variation in $^{230}\text{Th}/^{238}\text{U}$ and $^{234}\text{U}/^{238}\text{U}$ activity ratios over time in materials with no initial ^{230}Th and with 3 different initial $^{234}\text{U}/^{238}\text{U}$ activity ratios that define the bounds of modern seawater (from Chen et al. 1986). Age in thousands of years (ka) is shown by isochrons (thin solid lines): (a) Measured values of the solitary coral *Balanophyllia elegans* from the 3 lowest terraces on San Nicolas Island. Solid-colored ellipses define the measured values and 2-sigma uncertainties (data from Muhs et al. 2012a); (b) Similar data for the 2 fossil localities at Eel Point on San Clemente Island (data from Muhs et al. 2002a).

period, ~ 128 ka to ~ 114 ka (Muhs et al. 2002a). All corals from Eel Point have U contents of 3.4–4.6 ppm, similar to the range for modern dead-collected specimens of *B. elegans*. With 2 exceptions, corals from Eel Point show very high $^{230}\text{Th}/^{232}\text{Th}$ activity values, indicating little or no inherited ^{230}Th . For San Nicolas Island, many corals analyzed by Muhs et al. (2012a) plot well above a theoretical isotopic evolution pathway that is expected if these fossils had behaved as ideal closed systems with

respect to initial ^{238}U , ^{234}U , and ^{230}Th (Fig. 7a). Corals from San Clemente Island, in contrast, generally plot much closer to the ideal closed-system isotopic evolution pathway, although a number of corals still show evidence of at least some open-system behavior (Fig. 7b). In all, 19 of 29 corals analyzed by Muhs et al. (2002a) have initial $^{234}\text{U}/^{238}\text{U}$ values that range from 1.149 to 1.159, which are indicative of mostly closed-system ages. At worst, according to the model of Gallup et al. (1994),

samples with the highest initial $^{234}\text{U}/^{238}\text{U}$ values are biased old by only ~ 2500 years. Overall, apparent ages of the 19 best-behaved corals from San Clemente Island range from ~ 128 ka to ~ 114 ka. This age range is in good agreement with the ages of LIG corals dated elsewhere in California (Muhs et al. 2002a, 2006, 2012a), as well as on Hawaii, the Florida Keys, and Curaçao (Muhs et al. 2002b, 2011, 2012b).

The age range of corals from terrace 2b on San Clemente Island, ~ 128 ka to ~ 114 ka, is similar to that from terrace 2a on San Nicolas Island (Fig. 7a). Muhs et al. (2012a) analyzed corals from 4 localities on terrace 2b of San Nicolas Island. Of these 4 localities, 2 gave mixed ages of corals (~ 120 ka and ~ 100 ka), one gave only ~ 100 ka ages, and one gave only ~ 120 ka ages. In contrast, at Eel Point, the coral population of terrace 2b is represented only by fossils of the ~ 120 ka sea stand. Repeated searches on San Clemente Island for corals from terrace 2a and other localities on terrace 2b were unsuccessful.

PALEONTOLOGY AND PALEOZOOGEOGRAPHY

There have been few Quaternary fossil studies on San Clemente Island. Cockerell (1939) reported a fauna with 33 species of mollusks from a high (~ 245 – 260 m) terrace ~ 3 km northeast of Eel Point. Susuki and Stadum (1978) studied Quaternary marine terrace fossils from several localities on the northern part of the island, some of which are at higher elevations than the Eel Point terrace. One of their localities (UCLA loc. 6325 = LACMIP loc. 26325), however, is on the east side of San Clemente Island and is considered to be about the same age as the Eel Point localities of Muhs (1983), based on amino acid ratios in *Epilucina californica*. At this locality, Susuki and Stadum (1978) report 18 species of mollusks, 2 of which (*Norrisia norrisii* and *Volvarina taeniolata*) are mostly southern forms that do not range north of Point Conception. These investigators also report a gastropod, *Lottia scutum*, which lives mostly north of San Clemente Island today, based on records from the Natural History Museum of Los Angeles County. Other localities of Susuki and Stadum (1978) cannot be placed confidently in the framework of terrace mapping shown in Fig. 4. Lipps (1966) reported a fossil fauna from a low marine terrace near Horse Cove on the south end of San Clemente

Island. This terrace has a shoreline angle elevation of ~ 30 m and probably correlates with some part of the Eel Point terrace complex. The fauna from Horse Cove is discussed in more detail below.

Only the most abundant elements in the terrace fauna from the Eel Point localities on San Clemente Island have been reported previously. Muhs et al. (2002a) noted the presence of the bivalves *Crassadoma gigantea*, *Cumingia californica*, *Epilucina californica*, *Glans subquadrata* (= *Glans carpenteri*), and *Mytilus californianus*. Gastropods reported by these workers include *Acmaea mitra*, *Crepidatella lingulata* (incorrectly reported as *C. dorsata*), *Diodora arnoldi*, *Fissurella volcano*, *Haliotis cracherodii*, *Megathura crenulata*, *Norrisia norrisii*, *Chlorostoma funebris*, *Zonaria spadicea*, and several species of *Lottia*. In addition, 2 extralimital southern gastropods, *Mexacanthina lugubris* and *Stramonita biserialis* (the latter reported by Kennedy et al. 1995), were noted. The presence of all these taxa is confirmed here, with the exception of *Stramonita biserialis*, which was not found in any of the Eel Point collections.

In the present study, collections made in 1989 and 1999 (reported in Muhs et al. 2002a) and later collections made in 2006, 2007, and 2012 (reported here) were examined. A much more diverse fauna is evident in these later collections (Table 1). The paleozoogeographic significance of the fauna was assessed by ascertaining the modern ranges of the species using the latest available sources, including Keen (1971), Abbott (1974), McLean (1978, 2007), Abbott and Haderlie (1980), Haderlie and Abbott (1980), Coan et al. (2000), Coan and Valentich-Scott (2012), and collections of the Natural History Museum of Los Angeles County, Malacology Section (LACM; see <http://ip.nhm.org/nhmsearch/findlots.php>).

At the Eel Point fossil localities on San Clemente Island, 73 gastropods that could be identified to species were found, with another 5 that could be identified only to genus. Of the bivalves, 20 could be identified to species, with another 2 only to genus. Of the chitons, 3 species could be identified to species and one only to genus. Overall, the assemblage of more than 100 taxa represents one of the largest from open-coast localities in the California Channel Islands reported thus far. The collection is comparable to the assemblage from a low terrace

TABLE I. Marine fossils from Eel Point terrace, San Clemente Island, California.

Taxon/species	LACMIP 10725	LACMIP 12007
MOLLUSCA: Gastropoda		
<i>Acanthinucella punctulata</i> (Sowerby, 1835)	x	
<i>Acmaea funiculata</i> Carpenter, 1864	x	
<i>Acmaea mitra</i> Rathke, 1833	x	x
<i>Agathistoma eiseni</i> (Jordan, 1936)		x
<i>Alia tuberosa</i> (Carpenter, 1864)	x	x
<i>Alvinia purpurea</i> (Dall, 1871)		x
<i>Amphissa versicolor</i> Dall, 1871	x	x
<i>Antisabia panamensis</i> (C.B. Adams, 1862)	x	x
<i>Barleeia</i> sp.	x	
<i>Bellaspira grippi</i> (Dall, 1908)		x
<i>Bittium</i> sp.		x
<i>Caecum californicum</i> Dall, 1885		x
<i>Calliostoma supragranosum</i> Carpenter, 1864	x	x
<i>Calliostoma</i> sp., indet.	x	
<i>Ceratostoma nuttalli</i> (Conrad, 1837)		x
<i>Cerithiopsis</i> sp., indet.	x	
<i>Chlorostoma funebris</i> (A. Adams, 1855)	x	
<i>Chlorostoma gallina</i> (Forbes, 1852)	x	
<i>Chlorostoma gallina</i> var. <i>multifilosa</i> (Stearns, 1893)	x	
<i>Conus californicus</i> Reeve, 1844		x
<i>Coronadora simonsae</i> Bartsch, 1946		x
<i>Crepidula perforans</i> Valenciennes, 1846		x
<i>Crepidula</i> spp., indet.	x	x
<i>Crepidatella lingulata</i> (Gould, 1846)	x	x
<i>Cymakra aspersa</i> (Carpenter, 1864)	x	
<i>Dentiscalia funiculata</i> (Carpenter, 1857)		x
<i>Diodora arnoldi</i> McLean, 1966		x
<i>Diodora aspera</i> (Rathke, 1833)	x	
<i>Epitonium tinctum</i> (Carpenter, 1864)		x
<i>Fissurella volcano</i> Reeve, 1849	x	x
<i>Fissurellidea bimaculata</i> Dall, 1871		x
<i>Haliotis cracherodii</i> Leach, 1814	x	
<i>Haliotis fulgens</i> Philippi, 1845	x	
<i>Haliotis rufescens</i> Swainson, 1822	x	
<i>Haliotis</i> sp., indet.	x	x
<i>Harfordia</i> sp.	x	x
<i>Hesperato columbella</i> (Menke, 1847)		x
<i>Hesperato vitellina</i> (Hinds, 1844)		x
<i>Hipponix tumens</i> Carpenter, 1864	x	x
<i>Homalopoma luridum</i> (Dall, 1885)		x
<i>Homalopoma radiatum</i> (Dall, 1918)		x
<i>Homalopoma</i> sp., indet.		x
<i>Lacuna unifasciata</i> Carpenter, 1857		x
<i>Liotia fenestrata</i> Carpenter, 1864	x	x
<i>Lirobittium purpureum</i> (Carpenter, 1864)	x	
<i>Lirobittium</i> sp., cf. <i>L. quadrifilatum</i> (Carpenter, 1864)		x
<i>Lirobittium</i> sp.		x
<i>Lirularia succincta</i> (Carpenter, 1864)	x	
<i>Littorina keenae</i> Rosewater, 1978	x	x
<i>Littorina scutulata</i> Gould, 1849	x	x
<i>Lottia asmi</i> (Middendorff, 1847)		x
<i>Lottia digitalis</i> (Rathke, 1833)	x	
<i>Lottia gigantea</i> Sowerby, 1834 [midden?]		x
<i>Lottia scabra</i> (Gould, 1846)		x
<i>Lottia</i> sp., indet.	x	x
<i>Lucapina constantinae</i> (Kanakoff, 1953)		x
<i>Lucapinella callomarginata</i> (Dall, 1871)	x	
<i>Maxwellia gemma</i> (Sowerby, 1879)		x
<i>Megastrea undosa</i> (Wood, 1828)		x
<i>Megathura crenulata</i> (Sowerby, 1825)	x	x
<i>Megasurcula carpenteriana</i> (Gabb, 1865)		x

TABLE I. Continued.

Taxon/species	LACMIP 10725	LACMIP 12007
<i>Mexacanthina lugubris</i> (Sowerby, 1822)	x	
<i>Mitra idae</i> Melvill, 1893		x
Muricidae, indet. [fragments]		x
<i>Norrisia norrisii</i> (Sowerby, 1838)	x	x
<i>Petalocochnus montereyensis</i> Dall, 1919	x	x
<i>Ocenebrina atropurpura</i> (Carpenter, 1865)		x
<i>Ocenebrina gracillima</i> (Stearns, 1871)	x	
<i>Ocenebrina lurida</i> (Middendorff, 1848)		x
<i>Ocenebrina minor</i> (Dall, 1919)		x
<i>Ocenebrina</i> sp., indet.		x
<i>Pomaulax gibberosa</i> (Dillwyn, 1817)	x	x
<i>Promartynia pulligo</i> (Gmelin, 1791)	x	x
<i>Pusula californiana</i> (Gray, 1827)		x
<i>Pusula solandri</i> (Sowerby, 1832)		x
<i>Seila montereyensis</i> Bartsch, 1907	x	x
<i>Serpulorbis squamigerus</i> (Carpenter, 1857)	x	x
<i>Stearnsium reginum</i> (Stearns, 1892)		x
<i>Stylidium eschrichtii</i> (Middendorff, 1849)	x	
<i>Triphora pedroana</i> Bartsch, 1907	x	
<i>Turbonilla</i> (s.l.) sp./spp.		x
Turridae, indet.		x
<i>Vermicularia fewkesi</i> (Yates, 1890)	x	x
<i>Volvarina taeniolata</i> Mörch, 1860		x
<i>Williamia peltoides</i> (Carpenter, 1864)	x	x
<i>Zonaria spadicea</i> (Swainson, 1823)		x
MOLLUSCA: Bivalvia		
<i>Acar bailyi</i> Bartsch, 1931		x
<i>Chama arcana</i> Bernard, 1976		x
<i>Chlamys hastata</i> (Sowerby, 1842)	x	
<i>Chlamys</i> sp., indet.	x	x
<i>Crassadoma gigantea</i> (Gray, 1825)	x	x
<i>Cumingia californica</i> Conrad, 1837	x	x
<i>Epilucina californica</i> (Conrad, 1837)	x	x
<i>Gari fucata</i> (Hinds, 1845)		x
<i>Glans carpenteri</i> (Lamy, 1922)	x	x
<i>Hiatella arctica</i> (Linnaeus, 1767)	x	x
<i>Kellia suborbicularis</i> (Montagu, 1803)		x
<i>Kurtiella pedroana</i> (Dall, 1899)	x	
<i>Kurtiella</i> sp., indet.	x	
<i>Modiolus carpenteri</i> Soot-Ryen, 1963	x	x
<i>Mytilus californianus</i> Conrad, 1837	x	x
<i>Neaeromya californica</i> (Dall, 1899)		x
<i>Ostrea lurida</i> Carpenter, 1864		x
Pectinidae, indet.		x
<i>Philobrya setosa</i> (Carpenter, 1864)	x	
<i>Pododesmus macroschisma</i> (Deshayes, 1839)	x	
<i>Pseudochama exogyra</i> (Conrad, 1837)		x
<i>Semele rupicola</i> Dall, 1915		x
<i>Septifer bifurcatus</i> (Conrad, 1837)	x	x
Tellinidae sp., indet.	x	
MOLLUSCA: Polyplacophora		
<i>Callistochiton crassicostratus</i> Pilsbry, 1893	x	x
<i>Callistochiton palmulatus</i> Pilsbry, 1893		x
<i>Callistochiton</i> sp., indet.	x	x
<i>Placiphorella</i> sp., indet.	x	
? <i>Stenoplax conspicua</i> (Pilsbry, 1892)		x
Polyplacophora, unidentified (multiple species)	x	x
PORIFERA: Demospongiae		
Clionidae, indet. (borings in shells)	x	x
CNIDARIA: Anthozoa		
<i>Astrangia</i> sp.		x
<i>Balanophyllia elegans</i> (Verrill, 1864)	x	x

TABLE I. Continued.

Taxon/species	LACMIP 10725	LACMIP 12007
CNIDARIA: Hydrozoa		
<i>Stylaster californicus</i> (Verrill, 1866)	x	x
ECTOPROCTA: Gymnolaemata		
<i>Phidolopora pacifica</i> (Robertson, 1908)	x	x
Cheilostomata, erect branching forms, unidentified	x	x
Cheilostomata, encrusting forms, unidentified	x	x
Cheilostomata, encrusting species on <i>Crepidatella</i>	x	x
ANNELIDA: Polychaeta		
Serpulidae, indet. (sp. A)		x
Serpulidae, indet. (sp. B)	x	x
Spionidae, indet. (borings)		x
Spirorbidae, indet.		x
ARTHROPODA: Crustacea (Cirripedia)		
<i>Megabalanus californicus</i> (Pilsbry, 1916)	x	x
<i>Pollicipes polymerus</i> Sowerby, 1833		x
<i>Tetraclita rubescens</i> Darwin, 1854	x	x
" <i>Balanus</i> " (s.l.) spp.		x
ARTHROPODA: Crustacea (Malacostraca)		
Canceridae, indet. appendages	x	x
<i>Paraxanthias taylori</i> (Stimpson, 1860)		x
Hermit crab appendages, indet.		x
ECHINODERMATA: Echinoidea		
<i>Dendraster</i> sp., ? <i>D. excentricus</i> (Eschscholtz, 1831)		x
<i>Strongylocentrotus franciscanus</i> (Agassiz, 1863)	x	x
<i>Strongylocentrotus purpuratus</i> (Stimpson, 1857)	x	x
CHORDATA: Osteichthyes		
<i>Lutjanus</i> sp., indet.		x
<i>Semicossyphus</i> sp., cf. <i>S. pulcher</i> (Ayres, 1854)		x
PROTOCTISTA: Rhodophyta		
Rhodophyceae, indet.	x	x

on Santa Barbara Island (Lipps et al. 1968), although not as rich as the low-terrace assemblage on San Nicolas Island (Vedder and Norris 1963, Muhs et al. 2012a). The abundance of the bivalves *Cumingia californica*, *Epilucina californica*, *Glans carpenteri*, and *Mytilus californianus* and the gastropods *Acmaea mitra*, *Diodora arnoldi*, *Fissurella volcano*, and *Haliotis cracherodii* show that this is a typical littoral to adlittoral, open-coast, rocky-shore assemblage, similar to those found at many localities on the California Channel Islands. In addition to mollusks, the invertebrate fauna contains corals, hydrocorals, bryozoans, polychaete worms, decapod crustaceans, barnacles, and sea urchin remains (Table 1). Also found were 2 species of bony fish, determined on the basis of teeth, and a calcareous red alga.

Most of the mollusks identified at Eel Point have modern geographic ranges that extend well to the north and south of San Clemente Island and thus are not very useful in paleozoogeographic reconstruction. Indeed, a number of species (Table 1) have modern geographic

ranges that span the Oregonian, Californian, Surian, and Panamanian provinces, with at least 20 species having modern ranges extending into the Aleutian province (Fig. 1). Two bivalves (*Hiatella arctica* and *Pododesmus macroschisma*) have modern ranges from the Arctic province to the Panamanian province. Kennedy (2000) noted that it is common for outer, open-coast fossil localities, such as the west side of San Clemente Island, to be dominated by zoogeographically "neutral" species (i.e., taxa that today range well to the north and south of a given locality).

Warm-Water Indicators

The fauna at Eel Point contains a number of warm-water indicators, including one likely extralimital southern species (Figs. 8, 9). The gastropod *Mexacanthina lugubris*, found at LACMIP loc. 10725, is commonly cited as an extralimital southern species elsewhere in other southern California fossil studies (Valentine 1962, Lipps et al. 1968, Kennedy et al. 1992, Muhs et al. 2002a). The modern range of this

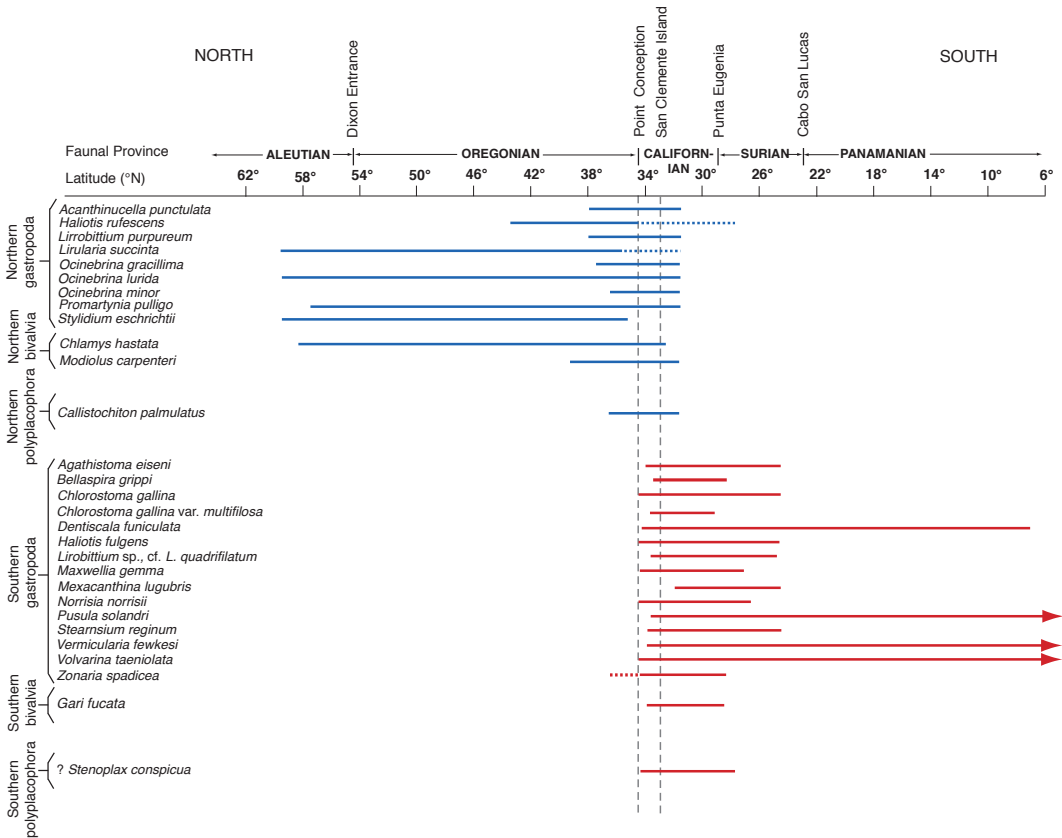


Fig. 8. Graph showing the modern distribution, by latitude, of extralimital northern and southern and northward- and southward-ranging taxa found on terrace 2b on San Clemente Island. All paleontological data are from this study. Geographic distributions are taken from Keen (1971), Abbott (1974), McLean (1978, 2007), Abbott and Haderlie (1980), Coan et al. (2000), Coan and Scott (2012), and records from the Natural History Museum of Los Angeles County (LACM).

species is unclear. Keen (1971) states that it ranges from “southern California” (without specific locations) to Bahía Magdalena, Baja California; whereas Abbott (1974) reports that the species lives in Baja California and ranges no farther north than San Diego. Radwin (1974) and Hertz (1995) reported finding *M. lugubris* in the San Diego area, but both pointed out that sightings of the species there are rare. McLean (1978) does not list it among gastropods living in southern California waters today. Modern specimens of *M. lugubris* at the Natural History Museum of Los Angeles County (examined in the present study) are all from Baja California on both the Pacific and Gulf of California coasts and islands in the Gulf of California. Specimens recorded at the Museum of Comparative Zoology at Harvard

University (not examined personally in this study) were collected only from Ensenada to Bahía Magdalena, Baja California Sur, and in the Gulf of California (as far north as Cholla Bay, in the uppermost part) in the Surian and Panamanian provinces (Fig. 9). Apart from one unverified specimen reported to have been collected near Ventura, California, other modern North American specimens of *M. lugubris* in collections at the California Academy of Sciences are either from the Pacific Coast of Baja California (as far north as Ensenada) or the Gulf of California. Based on the above data, *M. lugubris* may not range much north of the San Diego, California–Ensenada, Baja California area, and is therefore interpreted as an extralimital southern species with regard to its occurrence on San Clemente Island.

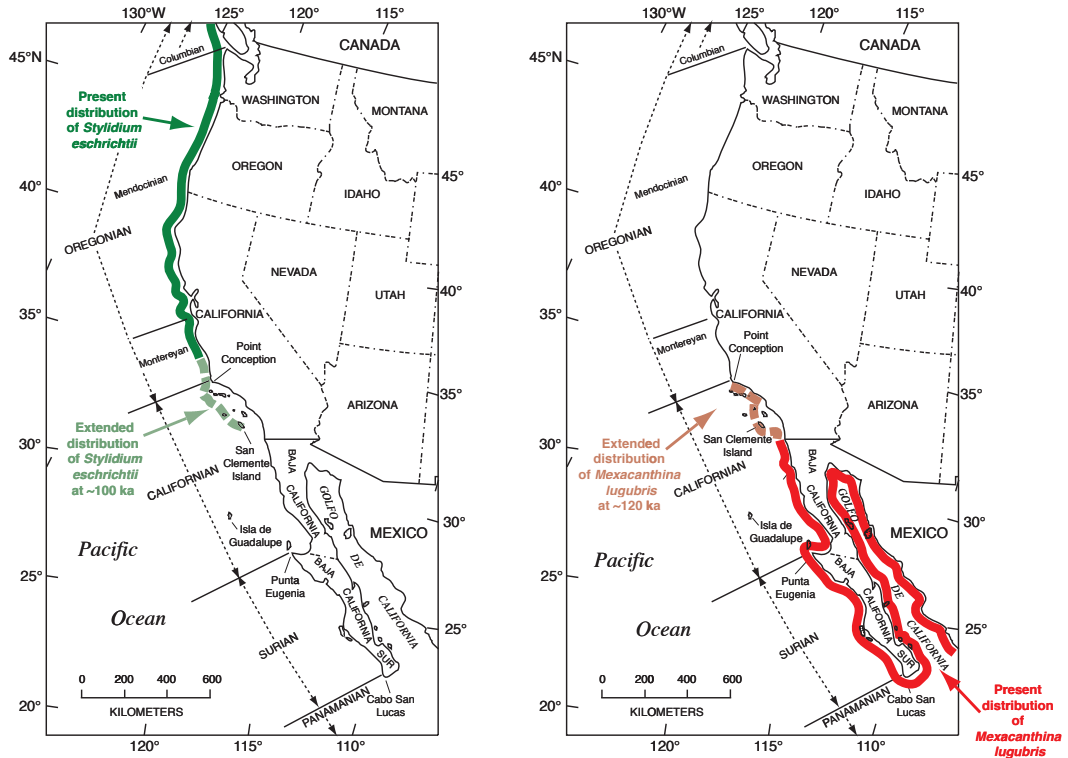


Fig. 9. Maps of a portion of the Pacific Coast of North America, showing location of San Clemente Island; provinces and subprovinces of marine invertebrate faunas (Valentine 1966); modern (dark green) and extended (light green, ~100 ka [?]), distributions of *Styliidium eschrichtii*; modern (red) and extended (orange, ~120 ka), distributions of *Mexacanthina lugubris*. Modern distribution data for *S. eschrichtii* are taken from Abbott (1974), Harbo (1997), and collections at the Natural History Museum of Los Angeles County (LACM). Modern distribution data for *M. lugubris* are taken from collections at the Natural History Museum of Los Angeles County (LACM); the California Academy of Sciences (CAS); the Museum of Comparative Zoology, Harvard University; Abbott (1974); Radwin (1974); and Hertz (1995). Extended last interglacial distribution data for *S. eschrichtii* are compiled from Valentine (1958), Vedder and Norris (1963), and Lipps (1966), with chronology from Muhs et al. (2002a, 2012a). Extended last interglacial distribution data for *M. lugubris* are compiled from Valentine (1962), Lipps et al. (1968), Kern (1977), Kennedy et al. (1992), and this study, with chronology from Kennedy et al. (1992) and Muhs et al. (1992, 2002a, 2010, 2012a).

The deposits at Eel Point contain other warm-water indicators in addition to *M. lugubris*. Three other species of gastropods (*Chlorostoma gallina* var. *multifilosa*, *Lirobittium* sp. cf. *L. quadrifilatum*, and *Pusula solandri*) have northern range endpoints in the Santa Monica–Palos Verdes Hills–San Pedro area; and a fourth, *Bellaspira grippi*, has its northern range endpoint at Santa Barbara Island. All these northern range endpoints are very close to San Clemente Island. Thus, these 4 species constitute an assemblage of southward-ranging taxa. An additional 12 species of mollusks currently live no farther north than Point Conception or Santa Barbara, and thus range mostly to the south of San Clemente Island (Fig. 8). Four

gastropods (*Dentiscala fuciculata*, *Pusula solandri*, *Vermicularia fewkesi*, and *Volvarina tae-niolata*), in addition to being southward-ranging species, are found well into tropical latitudes at present (Keen 1971). These taxa are interesting to consider in light of the “out of the tropics” and “bridge species” model of Jablonski et al. (2013).

Cool-Water Indicators

The Eel Point localities also yielded mollusks that range predominantly to the north of Point Conception and are treated herein as cool-water forms. The only strictly extralimital northern species identified, *Styliidium eschrichtii*, ranges from the Kenai Peninsula of

Alaska only as far south as Shell Beach, San Luis Obispo County, California (LACM records). Thus, its presence on San Clemente Island places it ~300 km south of its present southernmost range endpoint (Fig. 9). *Stylidium eschrichtii* was also reported by Lipps (1966) from the fossil locality at Horse Cove, southern San Clemente Island, described above. This species is not common in the southern California fossil record, but it has also been reported from 2 other localities where there is a mix of corals dated by U-series to ~100 ka and ~120 ka: Cayucos, California (Valentine 1958, Muhs et al. 2002a), where it is just slightly north of its southern range endpoint; and San Nicolas Island, California (Vedder and Norris 1963, Muhs et al. 2012a), where it is ~230 km south of its nearest modern occurrence.

Two other gastropods, rarely found south of Point Conception, are also present. *Haliotis rufescens* ranges from Sunset Beach, Coos County, Oregon, to as far south as Bahía San Bartolome, Baja California, but McLean (1978) points out that the species is most common in northern California. Lipps (1966) also reports this species in the marine terrace deposits at Horse Cove on San Clemente Island. *Lirularia succincta* is an interesting species in that it seems to have a disjunct distribution at present. Based on LACM collections, it has been reported at Punta Santo Tomás, in northern Baja California, but its continuous distribution is apparently from Cook Inlet, Alaska, to Point Piedras Blancas, in San Luis Obispo County, California. One bivalve, *Chlamys hastata*, presently lives from Afognak Island and the Kenai Peninsula of Alaska only to San Diego (Coan et al. 2000). Eight other species of mollusks have southern range endpoints in the Santo Tomás–Punta Banda area of northern Baja California (~31°45′) and thus range mostly to the north of San Clemente Island (Fig. 8).

DISCUSSION

Paleontology, Age, and Sea Level History

Given that San Clemente Island is situated well within the Californian faunal province (Fig. 2), is ~100-km offshore (Fig. 3), and has a western coast that is well exposed to the open ocean, a zoogeographically neutral fossil fauna at Eel Point might be expected. The Eel Point terrace deposits on San Clemente Island contain both an extralimital southern species

(*Mexacanthina lugubris*) and an extralimital northern species (*Stylidium eschrichtii*). The modern southern range endpoint of *S. eschrichtii* and the modern northern range endpoint of *M. lugubris* are nearly 600 km apart (Fig. 9). The fauna also has a significant number of both southward-ranging species and northward-ranging species of mollusks. The U-series ages on coral from this locality all clearly place the age of the deposit within one high-sea stand, MIS 5.5 at ~120 ka (Fig. 7b). As is the case with a number of other fossil localities on the Pacific Coast, the Eel Point terrace fauna on San Clemente Island can be considered thermally anomalous.

Three other localities in Southern California with terraces long thought to date solely to the peak of the last interglacial period (~120 ka) are now known to contain corals of more than one age. Muhs et al. (2012a) reported that the broad, geomorphically well-expressed terrace 2b on San Nicolas Island, alluded to earlier, contains corals that date to both ~120 ka and ~100 ka. Similar mixes of ~120-ka and ~100-ka corals have been reported from the low terrace at Cayucos, California (Stein et al. 1991, Muhs et al. 2002a), and the Nestor terrace at Point Loma, near San Diego (Ku and Kern 1974, Muhs et al. 2002a). At all 3 localities (San Nicolas Island, Cayucos, and Point Loma), there is a mix of extralimital southern, southward-ranging, extralimital northern, and northward-ranging species within the faunal assemblages (Valentine, 1958, Valentine and Meade 1961, Vedder and Norris 1963, Kern 1977, Muhs et al. 2002a, 2012a).

New marine terrace mapping on San Nicolas Island shows the complex and often subtle nature of the last interglacial marine terrace record in Southern California and helps explain some of these seemingly contradictory records. Although San Nicolas Island has a low, broad 2nd terrace that rims most of the island (Vedder and Norris 1963), Muhs et al. (2012a) found fragments of a narrow terrace (terrace 2b) a few meters above the second terrace (terrace 2a). Corals from terrace 2a date only to the ~120-ka sea stand, and the fossil assemblage contains several southward-ranging species but no northward-ranging or northern extralimital species. The broader terrace 2b on San Nicolas Island, a few meters below terrace 2a, has a mix of ~100-ka and ~120-ka corals and warm-water and cool-water mollusks. Muhs et

al. (2012a) interpreted these data to mean that terrace 2a formed during the ~120-ka high-sea stand but was then eroded and many of its fossils reworked during the ~100-ka high-sea stand, which formed terrace 2b. Assuming that the ~120-ka sea stand was ~6–8 m above present (Kopp et al. 2009, Muhs et al. 2011, Dutton and Lambeck 2012) and assuming a constant uplift rate, the paleo-sea level at ~100 ka that formed terrace 2b on San Nicolas Island can be calculated from its elevation and age. The ~100-ka high-sea stand is estimated to have been +2 to +6 m above present on San Nicolas Island, which would explain how the ~120-ka terrace was eroded and its fossils reworked, even on an uplifting coast. Muhs et al. (2012a) proposed that a similar sequence of events could have taken place at Cayucos and Point Loma, although only one terrace representing the 2 high-sea stands (~100 ka and ~120 ka) is present at those localities. With a lower uplift rate at both Cayucos and Point Loma, the original ~120-ka terrace was probably completely overtaken and eroded away by the ~100-ka high-sea stand.

Although this scenario seems to provide an explanation for the thermally anomalous faunal elements and mixes of coral ages at Cayucos, San Nicolas Island, Point Loma, and possibly San Clemente Island, it is contradicted by paleo-sea level evidence from other parts of the world. Studies on Barbados (Cutler et al. 2003, Potter et al. 2004, Speed and Cheng 2004) and New Guinea (Chappell et al. 1996) show that constructional coral reef terraces are well expressed geomorphically and date to the ~80-ka, ~100-ka, and ~120-ka high-sea stands. Using the same method of calculating paleo-sea level via uplift rates based on the age, elevation, and paleo-sea level of the ~120-ka high-sea stand, the ~100-ka sea stand is estimated to have been ~15–20 m below present at these tropical localities. If sea level during the ~100-ka high-sea stand was this low on the California coast, it is not possible for the ~100-ka high stand to have completely submerged and eroded the ~120-ka terrace, even in areas of low uplift rate, such as at Cayucos.

Glacial Isostatic Adjustment (GIA) Effects

Reconciliation of the vastly different estimates of paleo-sea level on San Nicolas Island from those on Barbados and New Guinea is

possible by considering glacial isostatic adjustment (GIA) processes. During a glacial and subsequent interglacial phase of a climate cycle, GIA-induced effects on sea level lead to departures from eustasy that have a complex geometry and history (Mitrovica and Peltier 1991, Mitrovica and Milne 2002, Potter and Lambeck 2003, Milne and Mitrovica 2008, Tamisiea and Mitrovica 2011). The GIA signal includes changes in the direct gravitational attraction of the time-varying ice-plus-ocean load and perturbations in both crustal and sea-surface heights in response to load-induced deformation. Thus, apparent sea level records will differ from coast to coast depending on proximity to large ice sheets, such as the Laurentide ice sheet that covered much of North America. GIA effects on apparent sea level will generate a geologic record that departs from a purely eustatic one most dramatically on coastlines near large ice sheets (“near-field” localities), whereas coastlines distant from ice sheets (“far-field” localities) will record a more purely eustatic sea level history.

Barbados and New Guinea are both in far-field regions where the eustatic signal dominates. The Atlantic Coastal Plain of the United States and the island of Bermuda, in contrast, are situated closer to where the former Laurentide ice sheet of North America advanced during the past 2 glacial periods (MIS 2 and 6). Thus, even though Bermuda is tectonically stable, ~80-ka (MIS 5.1) marine deposits are well dated and are found 1–2 m above present sea level (Muhs et al. 2002b). Wehmiller et al. (2004) also reported that ~80-ka marine deposits are found a few meters above modern sea level on the tectonically stable Atlantic Coastal Plain of the United States. Potter and Lambeck (2003) explain these higher-than-expected elevations at northern localities to be the result of GIA effects, which are minimal on Barbados, increase slightly moving northward to the Florida Keys, and increase dramatically at the Atlantic Coast of the United States and Bermuda (Fig. 1). San Nicolas Island, also close to North America, is situated within an “intermediate field” region where GIA effects are still expected to be significant. Modeling of GIA effects for San Nicolas Island (and applicable elsewhere on the California coast) by J.X. Mitrovica (*in* Muhs et al. 2012a) shows that both the ~80-ka (MIS 5.1) and ~100-ka (MIS 5.3) sea stands are predicted to

record higher relative paleo-sea levels on the California coast than on Barbados and New Guinea. The geologic record of terraces 1, 2b, and 2a (~80, ~100 [+120 ka, reworked], and 120 ka, respectively) on San Nicolas Island agree with the GIA model results.

For San Clemente Island, we hypothesize that terrace 2a represents the ~120-ka high-sea stand and terrace 2b represents the ~100-ka high-sea stand. This hypothesis requires that the ~120-ka corals on terrace 2b of San Clemente Island were all reworked from terrace 2a during the ~100-ka high-sea stand, similar to what is documented on San Nicolas Island. Rigorous testing of this hypothesis requires identification of coral-bearing fossil localities on terrace 2a on San Clemente Island (which should contain only ~120-ka fossils), as well as other coral-bearing fossil localities on terrace 2b (which should contain both ~100-ka and ~120-ka fossils). Because other fossil localities have yet to be located, only geomorphic tests of this hypothesis are possible. Assuming terrace 2a on San Clemente Island formed during the ~120-ka high-sea stand, one can calculate an uplift rate assuming that sea level was +6 m relative to present at that time (Kopp et al. 2009, Muhs et al. 2011, Dutton and Lambeck 2012). Near Eel Point, terrace 2a has a shoreline angle elevation of 29.3 m, indicating 23.3 m of uplift in 120 ka, or an uplift rate of $0.194 \text{ m} \cdot \text{ka}^{-1}$. Assuming that terrace 2b, with a shoreline angle of 24.1 m, is ~100 ka and was uplifted at the same rate, one can back out the paleo-sea level and compare it to what Muhs et al. (2012a) reported for this high-sea stand on San Nicolas Island. At an uplift rate of $0.194 \text{ m} \cdot \text{ka}^{-1}$, terrace 2b on San Clemente Island would have experienced 19.4 m of uplift in ~100 ka, implying a paleo-sea level of +4.7 m relative to present. Muhs et al. (2012a) estimated paleo-sea level elevations for the ~100-ka high-sea stand on San Nicolas Island to be +2 to +6 m relative to present, which brackets the +4.7 m paleo-sea level estimate for San Clemente Island. Thus, we conclude that terrace 2b on San Clemente Island *could* have formed during the ~100-ka high-sea stand. During the time of formation of terrace 2b, the ~100-ka high stand could have eroded terrace 2a shoreward until just a small fragment of it remained (Fig. 10). In so doing, the ~100-ka high-sea stand could have reworked

most of the fossils on terrace 2a into the assemblage on terrace 2b.

Comparison of Paleotemperature Interpretations with Deep-Sea Core Data

The sequence of events just described assumes that warmer-than-present waters prevailed along San Clemente Island during the ~120-ka high-sea stand and cooler-than-present waters bathed the island during the ~100-ka high-sea stand. It is difficult to obtain independent evidence of these conditions from the marine terrace record, however, since GIA effects and fossil mixing could also have occurred on coastlines with similar or lower uplift rates to San Nicolas Island and San Clemente Island. An independent estimate of the relative difference in marine paleotemperatures off southern California during the ~100-ka and ~120-ka high-sea stands can be made from planktonic foraminiferal records in deep-sea cores. Like marine mollusks, planktonic foraminiferal assemblages provide a proxy for marine paleotemperatures. As with mollusks, planktonic foraminiferal assemblages can be identified by distinct, temperature-controlled biogeographic zones (Bé 1977). Unlike terrace mollusks, however, foraminiferal records in deep-sea cores are not subject to fossil mixing by repeated high sea levels. One of the most complete planktonic foraminiferal records of paleoclimate off southern California, back to ~160 ka, is from ODP Site 893A (Fig. 3) in the Santa Barbara Basin, studied by Kennett (1995), Kennett and Venz (1995), and Hendy (2010). Planktonic foraminifera from this core show that conditions as warm or warmer than present can be identified by the abundance of dextral-coiled *Neogloboquadrina pachyderma* (now referred to as *N. incompta*; see Darling et al. 2006), one of the dominant species today in the Santa Barbara Basin area. This species prefers water temperatures warmer than ~10 °C (Kennett and Venz 1995). In waters cooler than ~10 °C, sinistral-coiled *N. pachyderma* increases in abundance, and this species is dominant in water temperatures cooler than ~6 °C. In addition to *N. incompta*, there are 4 other warm-water species that are useful for paleoclimatic interpretations in the eastern Pacific Ocean: *Globigerinoides ruber*, *Neogloboquadrina dutertrei*, *Globorotalia inflata*, and *Orbulina universa* (Kennett and Venz 1995).

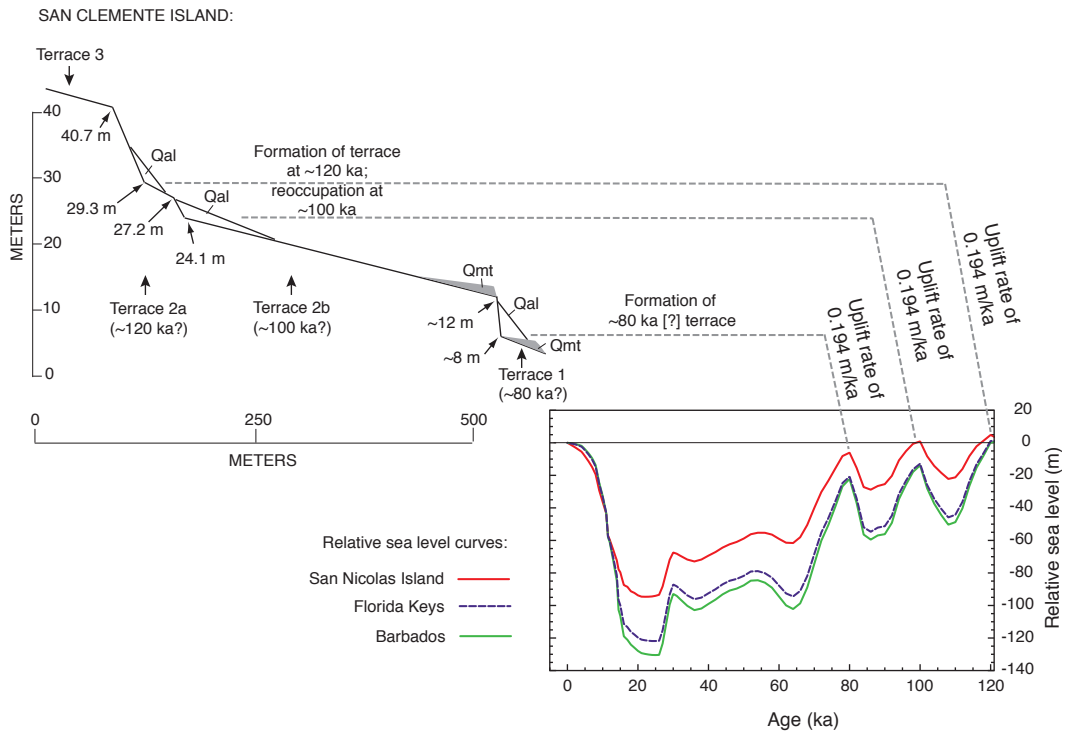


Fig. 10. Composite cross section of the lowest marine terraces on San Clemente Island (taken from Fig. 6); modeled sea level curve for San Nicolas Island, the Florida Keys, and Barbados (from J.X. Mitrovica in Muhs et al. 2012a); and link between sea level history and uplift rate and terrace geomorphology. Qal, Quaternary alluvium and/or colluvium; Qmt, Quaternary marine terrace deposits.

Using these warm-water indicators, the Santa Barbara Basin record shows that MIS 1 (the Holocene) and MIS 5.5 (~120 ka) are by far the warmest 2 periods of the past ~160 ka. Abundances of *N. incompta* reach maximum values during MIS 5.5 and the early Holocene (MIS 1). Glacial periods—represented by MIS 6, 4, and 2—generally show low abundances of *N. incompta*. In addition, MIS 5.3 (~100 ka) and MIS 5.1 (~80 ka) show very low abundances of *N. incompta*. Overall, the planktonic foraminiferal record indicates conditions as warm as or warmer than present in some parts of the Holocene (early MIS 1) and the peak of the last interglacial period (MIS 5.5). In contrast, the records for MIS 5.3 and 5.1 indicate much cooler water temperatures off Santa Barbara than present. Although zoogeographic data are not available, oxygen isotope measurements in planktonic foraminifera (considered to be primarily a temperature indicator) from ODP core 1014 in Tanner Basin near San Nicolas Island (Fig. 3) also show the same

paleotemperatures as in ODP 893A, with MIS 5.1 and 5.3 considerably cooler than MIS 5.5 (Hendy and Kennett 2000).

Using the Santa Barbara Basin and Tanner Basin planktonic foraminiferal records as guides, we interpret the extralimital southern and southward-ranging forms in the Eel Point terrace deposits to represent MIS 5.5 (~120 ka) and the extralimital northern and northward-ranging forms to represent MIS 5.3 (~100 ka). Geomorphic considerations of marine terrace elevations and estimates of paleo-sea level permit the interpretation that this fossil mixing took place during the ~100-ka high-sea stand, when GIA-influenced sea level could have stood +2 m to +6 m higher than present. At this time, terrace 2a—hypothesized to have formed during the ~120-ka high-sea stand—would have been uplifted only a few meters. Thus, the seaward portions of terrace 2a would have been “captured” or overtaken by the higher-than-present ~100-ka sea stand. Formation of terrace 2b could have

taken place at this time, and the process of its formation eroded much of terrace 2a, other than its higher, inland parts.

Implications for the Last Interglacial Fossil Record Elsewhere on the Pacific Coast

If the scenario presented here for San Clemente Island is correct, then there should be other evidence of thermally anomalous faunas in dated, last-interglacial deposits elsewhere on the Pacific Coast. Sea level history and GIA processes should have had similar effects within the same intermediate-field region of California and adjacent Baja California. Earlier, we discussed the evidence for San Nicolas Island, Cayucos, and Point Loma. We can identify 4 other localities (Bahia Tortugas, Punta Camalú, Santa Barbara Island, and Newport Bay) where terrace deposits of probable LIG age have thermally anomalous faunas (Fig. 11).

In Baja California, amino acid data from both Bahía de Tortugas (Emerson et al. 1981) and Punta Camalú (Valentine 1980) indicate that low-elevation terraces at these localities correlate broadly to the LIG. Faunas from both localities contain mixes of southern and northern species of mollusks (Emerson 1980, Valentine 1980). On Santa Barbara Island, aminostratigraphic data using fossil *Tegula* (= *Chlorostoma*) indicate that the lowest terrace there (~7–10 m above sea level) correlates with other southern California terraces that have U-series ages of ~120 ka or have a mix of ~100-ka and ~120-ka ages (Muhs et al. 2010). Lipps et al. (1968) reported an extensive fauna from this terrace. Examination of their data indicates that there are at least 20 extralimital southern or southward-ranging species and 3 extralimital northern species (*Lottia scutum*, *Crepidula nummaria*, *Lacuna carinata*) as well as a northward-ranging species (*Chlorostoma montereyi*).

Perhaps one of the most dramatic examples of thermally anomalous faunas, however, is from Newport Bay, California. U-series ages on coral from a terrace at ~33–34 m are ~120 ka (Grant et al. 1999). Kanakoff and Emerson (1959) report a fauna from this terrace that must contain one of the greatest numbers of taxa in California, with at least 436 species of mollusks. The fauna contains abundant warm-water species, with at least 13 extralimital southern species of bivalves alone (based on updated zoogeography in Coan et al. 2000),

plus many species of southward-ranging gastropods. The fauna also contains 3 extralimital northern bivalves (*Macoma inquinata*, *Patinopecten caurinus*, and *Modiolus modiolus*) as well as *Chlamys rubida*, which ranges south of Newport Bay but is normally rare south of Puget Sound, Washington (Coan et al. 2000). There were also at least 5 extralimital northern or northward-ranging species of gastropods in the Newport Bay fauna (*Acmaea persona*, *Crepidula nummaria*, *Ocenebra barbarensis*, *Ocenebrina lurida*, and *Chlorostoma montereyi*). Because 4 species of corals have been reported from this deposit (Kanakoff and Emerson 1959), it would be worthwhile to do additional U-series analyses to determine if a mix of ~100-ka and ~120-ka corals is present.

Reconciliation of the Oxygen Isotope Record with the Paleontological Record

In some early experiments estimating SSTs from the oxygen isotope compositions of fossil bivalves in marine terraces, Muhs and Kyser (1987) found evidence for what appeared to be cooler conditions during the ~120-ka high-sea stand. These inferences were based on oxygen isotope compositions in fossil *Epilucina californica* from the Nestor terrace in San Diego, as well as from what are now referred to as terrace 2b on San Clemente Island and terrace 2b on San Nicolas Island. Data were also obtained from fossil *E. californica* from the first terrace on San Nicolas Island and from the lowest terrace at various localities in the Palos Verdes Hills; these terraces are now known to date to the ~80-ka high-sea stand (Muhs et al. 2006). Fossil *E. californica*, from what were then thought to be strictly ~120-ka terrace fossils (Nestor, San Clemente Island terrace 2b, San Nicolas Island terrace 2b), have significantly heavier oxygen isotope compositions compared to modern specimens of this species, indicating cooler waters in the past. Still heavier oxygen isotope compositions were found in fossil *E. californica* from the ~80-ka terraces on San Nicolas Island and the Palos Verdes Hills (even after accounting for ice volume effects), also indicating much cooler-than-present SSTs off the California coast (Fig. 12). The oxygen isotope values for the ~80-ka fossils indicating cooler SSTs are consistent with the ~80-ka marine terrace paleontological record, which consistently shows the presence of extralimital northern

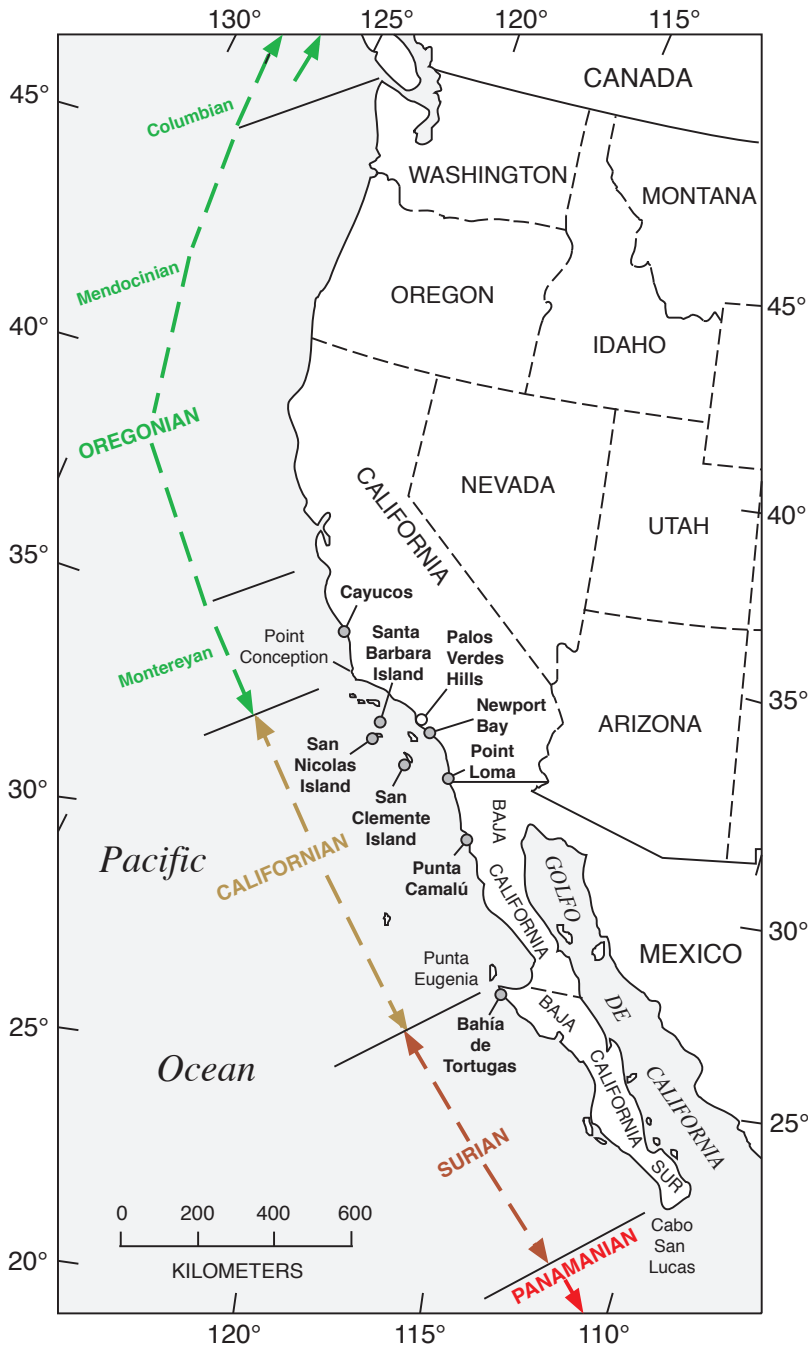


Fig. 11. Faunal provinces and subprovinces on the Pacific Coast of North America, showing marine terrace localities dated or correlated to the last interglacial period where thermally anomalous faunas have been recorded (gray circles). Data sources are as follows: Cayucos—Valentine 1958, Muhs et al. 2002a; Santa Barbara Island—Lipps et al. 1968, Muhs et al. 2010; San Nicolas Island—Vedder and Norris 1963, Muhs et al. 2012a; Newport Bay—Kanakoff and Emerson 1959, Grant et al. 1999; San Clemente Island—Muhs et al. 2002a, this study; Point Loma—Valentine and Meade 1961, Kern 1977, Muhs et al. 2002a; Punta Camalú—Valentine 1980; and Bahía de Tortugas—Emerson 1980, Emerson et al. 1981. Also shown is the location of the Palos Verdes Hills (white circle) referred to in Fig. 12.

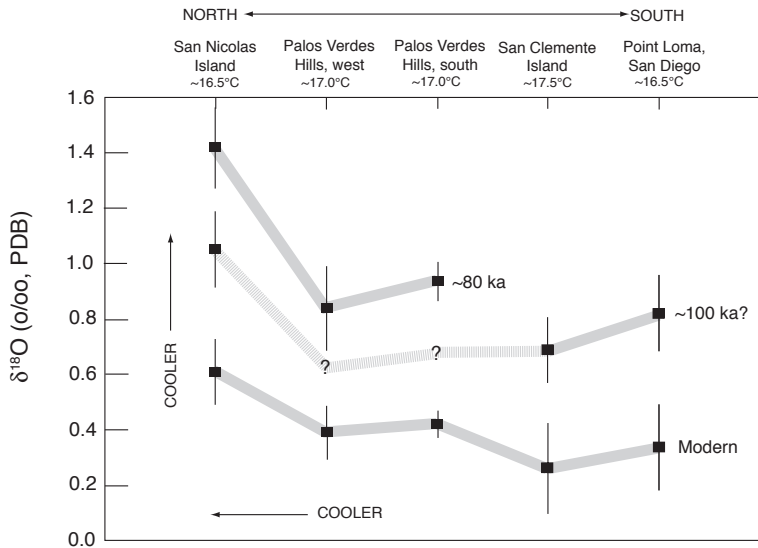


Fig. 12. Oxygen isotope compositions of *Epilucina californica* taken from modern beaches (San Nicolas Island, Palos Verdes Hills, Point Loma, and San Clemente Island; see Fig. 11) and ~80-ka marine terrace deposits (San Nicolas Island and the Palos Verdes Hills). Also shown are similar values for fossil *Epilucina californica* from marine terraces where ages of coexisting corals have been dated to ~100 ka and ~120 ka (San Nicolas Island and Point Loma) and ~120 ka (San Clemente Island). Solid squares are mean values of several valves; vertical lines represent one standard deviation around the mean. Temperatures given below each locality name are approximate average sea surface temperatures estimated from National Oceanic and Atmospheric Administration, Office of Satellite and Product Operations map data, <http://www.ospo.noaa.gov/data/sst/contour/californ.fc.gif>. Oxygen isotope data are from Muhs and Kyser (1987) and Muhs et al (1992).

species and no extralimital southern species or southward-ranging species at many localities from southern Oregon to northern Baja California (Muhs et al. 2002a, 2006). However, the cooler-than-modern SSTs from what were thought to be ~120-ka terraces were not consistent with the paleontological records from these terraces that had warm-water forms. Given the results presented here, as well as those in Muhs et al. (2002a, 2012a), an explanation for this pattern might be that the *E. californica* populations from the Nestor terrace and terraces 2b on San Nicolas and San Clemente Islands date not to the ~120-ka high-sea stand but to the ~100-ka high-sea stand. A worthwhile future effort to test this hypothesis would be to do oxygen isotope analyses of a larger number of taxa from these terraces. If fossil mixing has occurred, some should indicate cooler-than-modern SSTs and others should indicate warmer-than-modern SSTs.

Implications for Older Marine Terraces on the Pacific Coast of North America

Based on the evidence presented and reviewed here, fossils of 2 ages but from the

same interglacial complex (MIS 5) are found on a single terrace at a minimum of 3 localities and possibly 5 or more other localities. Whenever uplift rates have been low enough that the ~120-ka terrace was not raised sufficiently to avoid subsequent erosion by the ~100-ka high-sea stand, mixing of fossils is likely and should be expected. Thus, older interglacial complexes could also show evidence of fossil mixing in marine terraces on low-uplift-rate coasts. The SPECMAP oxygen isotope record of Imbrie et al. (1984) shows that there are substages within the interglacial complexes represented by MIS 7, 9, 11, 13, and 15, as well as MIS 5. Since ~600 ka, glacial-interglacial cycles seem to have followed a 100,000-year cycle linked to the eccentricity of the earth's orbit (Bassiot, 2007). Prior to ~600 ka, however, glacial-interglacial cycles, at least as manifested in the oxygen isotope record, show a closer link to the 41,000-year cycle of obliquity of the Earth's axis. Thus in the marine terrace record, one should expect to see fossil mixing *within* interglacial complexes of the past ~600 ka, at least on low-uplift-rate coasts. Prior to ~600 ka, one might expect to see fossil mixing

both within and *between* interglacial periods on low-uplift-rate coasts. Fossil records from high-elevation marine terraces on the Palos Verdes Hills (Woodring et al. 1946, Valentine 1962, Marincovich 1976) and San Nicolas Island (Vedder and Norris 1963) do in fact show that northward-ranging and southward-ranging forms exist together and have been noted as thermally anomalous by those workers who reported them.

CONCLUSIONS

Based on studies of the fossil record from the Eel Point terrace on San Clemente Island, the following conclusions have been reached:

(1) The Eel Point terrace is a composite feature consisting of a narrow upper bench (terrace 2a) with a shoreline angle elevation of ~29 m and a broader lower bench (terrace 2b) with a shoreline angle elevation of ~24–25 m. In some places, formation of terrace 2b has eroded most or all evidence of terrace 2a.

(2) Terrace 2b—previously dated from ~128 ka to ~114 ka and thought to date to MIS 5.5, the peak of the last interglacial period—has a rich fauna, with more than 100 species of fossil mollusks, as well as a variety of other marine invertebrates. This constitutes one of the richer fossil faunas on the California Channel Islands.

(3) The fauna from terrace 2b at Eel Point contains both an extralimital southward-ranging species, an extralimital northward-ranging species, and quite a number of northward- and southward-ranging species. Coexistence of these warm-water and cool-water forms constitutes an example of what paleontologists have termed “thermally anomalous” faunas.

(4) The origin of thermally anomalous faunas in Pacific Coast marine terrace deposits has been debated for more than a century, but no one mechanism explains most of the observed faunas satisfactorily. U-series dating of corals on San Nicolas Island, Point Loma, and Cayucos, however, shows that the thermally anomalous faunas at those localities could be the result of mixing of fossils from both the ~100-ka (cool-water) and ~120-ka (warm-water) high-sea stands. Submergence, erosion, and fossil mixing of the ~120-ka terraces by the ~100-ka high-sea stand was possible because glacial isostatic adjustment (GIA) effects on North America could have resulted in a

higher-than-present local sea level stand at ~100 ka. Terrace geomorphology on San Clemente Island is very similar to that on San Nicolas Island, with 2 closely spaced terraces present at low elevations. The higher terrace (terrace 2a) may be the remains of the terrace that formed during the ~120-ka high-sea stand, with the broader, lower terrace 2b having formed during the ~100-ka high-sea stand but including fossils eroded from terrace 2a.

(5) Examination of the fossil records from other localities on the Pacific Coast of North America, all dated at least broadly to the last interglacial complex of MIS 5, shows that similar fossil mixing may have occurred from central Baja California to central California.

(6) Recognition of a cool-water fossil population in several California marine terrace deposits of last interglacial age may explain oxygen isotope compositions of fossil bivalves that have previously not been understood. The oxygen isotope compositions indicate apparent cool-water conditions at a time when SSTs were considered to have been warmer, based on the paleontological record.

(7) Consideration of older glacial-interglacial cycles of the Quaternary, based on the oxygen isotope record, indicates that fossil mixing during older interglacial complexes should be expected in the older marine terrace record as well. Existing fossil records from some of these older terraces in California do show thermally anomalous faunas, indicating that the scenario presented here for the last interglacial complex may have applicability to much of the Pacific Coast marine Quaternary record.

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Leslie H. Harris (Collection Manager of Polychaetes) identified the polychaete tubes; Richard F. Feeney (Collection Manager of Ichthyology) identified the fish teeth; James H. McLean (Malacology Emeritus Curator) confirmed several gastropod identifications; and Janice Lipeles (Malacology volunteer) picked the sediment samples for microspecimens. George Kennedy also assisted in the fossil identification and reviewed a draft of the manuscript. Jeff Pigati, Diane Stephens, Tom Judkins (all U.S. Geological Survey), Torben Rick (Smithsonian Institution), and 2 anonymous reviewers made helpful comments on an earlier draft of the manuscript.

LITERATURE CITED

- ABBOTT, D.F., AND E.C. HADERLIE. 1980. Prosobranchia: marine snails. Pages 230–307 in R.H. Morris, D.P. Abbott, and E.C. Haderlie, editors, *Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
- ABBOTT, R.T. 1974. *American seashells: the marine mollusca of the Atlantic and Pacific coasts of North America*. 2nd edition. Van Nostrand Reinhold Company, New York, NY.
- ADDICOTT, W.O. 1966. Late Pleistocene marine paleoecology and zoogeography in central California. U.S. Geological Survey Professional Paper 523-C.
- ADLER, J.A. 2003. Chronology, morphology, and deformation of the marine terraces on San Clemente Island, California. Master's thesis, San Diego State University, San Diego, CA. 153 pp.
- ARNOLD, R. 1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. *Memoirs of the California Academy of Sciences* 3:1–420.
- BASSINOT, F.C. 2007. Oxygen isotope stratigraphy of the oceans. Pages 1740–1748 in S. Elias, editor, *Encyclopedia of Quaternary Sciences*. Elsevier, Amsterdam.
- BÉ, A.W.H. 1977. An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera. Pages 1–100 in A.T.S. Ramsay, editor, *Oceanic micropalaeontology*. Academic Press, London, U.K.
- BELANGER, C.L., D. JABLONSKI, K. ROY, S.K. BERKE, A.Z. KRUG, AND J.W. VALENTINE. 2012. Global environmental predictors of benthic marine biogeographic structure. *Proceedings of the National Academy of Sciences* 109:14046–14051.
- CHAPPELL, J., A. OMURA, T. ESAT, M. MCCULLOCH, J. PANDOLFI, Y. OTA, AND B. PILLANS. 1996. Reconciliation of late Quaternary sea levels derived from coral terraces at Huon Peninsula with deep sea oxygen isotope records. *Earth and Planetary Science Letters* 141:227–236.
- CHEN, J.H., R.L. EDWARDS, AND G.J. WASSERBURG. 1986. ^{238}U , ^{234}U , and ^{232}Th in seawater. *Earth and Planetary Science Letters* 80:241–251.
- COAN, E.V., AND P. VALENTICH-SCOTT. 2012. *Bivalve seashells of tropical west America*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- COAN, E.V., P. VALENTICH-SCOTT, AND F.R. BERNARD. 2000. *Bivalve seashells of western North America: marine bivalve mollusks from Arctic Alaska to Baja California*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- COCKERELL, T.D.A. 1939. Pleistocene shells from San Clemente Island, California. *Nautilus* 53:22–23.
- CRICKMAY, C.H. 1929. The anomalous stratigraphy of Deadman's Island, California. *Journal of Geology* 37:617–638.
- CUTLER, K.B., R.L. EDWARDS, F.W. TAYLOR, H. CHENG, A. ADKINS, C.D. GALLUP, P.M. CUTLER, G.S. BURR, AND A.L. BLOOM. 2003. Rapid sea-level fall and deep-ocean temperature change since the last interglacial period. *Earth and Planetary Science Letters* 206:253–271.
- DARLING, K.F., M. KUCERA, D. KROON, AND C.M. WADE. 2006. A resolution for the coiling direction paradox in *Neogloboquadrina pachyderma*. *Paleoceanography* 21:PA2011, <http://dx.doi.org/10.1029/2005PA001189>.
- DUTTON, A., AND K. LAMBECK. 2012. Ice volume and sea level during the last interglacial. *Science* 227:216–219.
- EERNISSE, D.J., R.N. CLARK, AND A. DRAEGER. 2007. Polyplacophora. Pages 701–713 in J.T. Carlton, editor, *The Light and Smith manual: intertidal invertebrates from central California to Oregon*. 4th edition. University of California Press, Berkeley, CA.
- EMERSON, W.K. 1980. Invertebrate faunules of late Pleistocene age, with zoogeographic implications, from Turtle Bay, Baja California Sur, Mexico. *Nautilus* 94:67–89.
- EMERSON, W.K., G.L. KENNEDY, J.F. WEHMILLER, AND E. KEENAN. 1981. Age relations and zoogeographic implications of late Pleistocene marine invertebrate faunas from Turtle Bay, Baja California Sur, Mexico. *Nautilus* 95:105–116.
- GALLUP, C.D., R.L. EDWARDS, AND R.G. JOHNSON. 1994. The timing of high sea levels over the past 200,000 years. *Science* 263:796–800.
- GRANT, U.S., IV, AND H.R. GALE. 1931. *Catalogue of the marine Pliocene and Pleistocene mollusca of California and adjacent regions*. San Diego Society of Natural History Memoir 1 [reprinted 1958]:1–1036.
- GRANT, L.B., K.J. MUELLER, E.M. GATH, H. CHENG, R.L. EDWARDS, R. MUNRO, AND G.L. KENNEDY. 1999. Late Quaternary uplift and earthquake potential of the San Joaquin Hills, southern Los Angeles Basin, California. *Geology* 27:1031–1034.
- HADERLIE, E.C., AND D.P. ABBOTT. 1980. Polyplacophora: the chitons. Pages 412–428 in R.H. Morris, D.P. Abbott, and E.C. Haderlie, editors, *Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
- HARBO, R.M. 1997. *Shells and shellfish of the Pacific Northwest: a field guide*. Prolong Press Limited, Hong Kong.
- HENDY, I.L. 2010. The paleoclimatic response of the southern Californian margin to the rapid climate change of the last 60 ka: a regional overview. *Quaternary International* 215:62–73.
- HENDY, I.L., AND J.P. KENNETT. 2000. Stable isotope stratigraphy and paleoceanography of the last 170 K.Y.: Site 1014, Tanner Basin, California. *Proceedings of the Ocean Drilling Program, Scientific Results* 167:129–140.
- HERTZ, J. 1995. *Acanthina lugubris* found again in San Diego. *The Festivus* 27:110.
- IMBRIE, J., J.D. HAYS, D.G. MARTINSON, A. MCINTYRE, A.C. MIX, J.J. MORLEY, N.G. PISIAS, W.L. PRELL, AND

- N.J. SHACKLETON. 1984. The orbital theory of Pleistocene climate: support from a revised chronology of the marine delta ^{18}O record. Pages 269–305 in A. Berger, J. Imbrie, H. Hays, G. Kukla, and B. Saltzman, editors, *Milankovitch and climate: understanding the response to astronomical forcing*. D. Reidel Publishing, Dordrecht, The Netherlands.
- JABLONSKI, D., C.L. BELANGER, S.K. BERKE, S. HUANG, A.Z. KRUG, K. ROY, A. TOMASOVYCH, AND J.W. VALENTINE. 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences* 110:10487–10494.
- KANAKOFF, G.P., AND W.K. EMERSON. 1959. Late Pleistocene invertebrates of the Newport Bay area, California. *Natural History Museum of Los Angeles County Contributions in Science* 31:1–47.
- KEEN, A.M. 1971. Sea shells of tropical west America. Marine mollusks from Baja California to Peru. 2nd edition. Stanford University Press, Stanford, CA.
- KENNEDY, G.L. 1978. Pleistocene paleoecology, zoogeography and geochronology of marine invertebrate faunas of the Pacific Northwest Coast (San Francisco Bay to Puget Sound). Doctoral dissertation, University of California–Davis, CA. 824 pp.
- _____. 2000. Zoogeographic correlation of marine invertebrate faunas. Pages 413–424 in J.S. Noller, J.M. Sowers, and W.R. Lettis, editors, *Quaternary geochronology*. American Geophysical Union Reference Shelf 4, Washington, DC.
- KENNEDY, G.L., J.A. ADLER, AND T.K. ROCKWELL. 1995. Middle and late Pleistocene neotectonic activity and sea level history: the marine terrace record on San Clemente Island, southern California. *Geological Society of America Abstracts with Programs* 27(6):A-375.
- KENNEDY, G.L., K.R. LAJOIE, AND J.F. WEHMILLER. 1982. Aminostratigraphy and faunal correlations of late Quaternary marine terraces, Pacific Coast, USA. *Nature* 299:545–547.
- KENNEDY, G.L., J.F. WEHMILLER, AND T.K. ROCKWELL. 1992. Paleoecology and paleozoogeography of late Pleistocene marine-terrace faunas of southwestern Santa Barbara County, California. Pages 343–361 in C.H. Fletcher III and J.F. Wehmiller, editors, *Quaternary coasts of the United States: marine and lacustrine systems*. SEPM [Society for Sedimentary Geology] Special Publication No. 48.
- KENNETT, J.P. 1995. Latest Quaternary benthic oxygen and carbon isotope stratigraphy: hole 893A, Santa Barbara Basin, California. Pages 3–18 in J.P. Kennett, J.G. Baldauf, and M. Lyles, editors, *Proceedings of the Ocean Drilling Program, Scientific Results, Volume 146 (Part 2)*.
- KENNETT, J.P., AND K. VENZ. 1995. Late Quaternary climatically related planktonic foraminiferal assemblage changes: Hole 893A, Santa Barbara Basin, California. Pages 281–293 in J.P. Kennett, J.G. Baldauf, and M. Lyles, editors, *Proceedings of the Ocean Drilling Program, Scientific Results, Volume 146 (Part 2)*.
- KERN, J.P. 1977. Origin and history of upper Pleistocene marine terraces, San Diego, California. *Geological Society of America Bulletin* 88:1553–1566.
- KERN, J.P., T.E. STUMP, AND R.J. DOWLEN. 1971. An upper Pleistocene marine fauna from Mission Bay, California. *San Diego Society of Natural History Transactions* 16:329–338.
- KOPP, R.E., F.J. SIMONS, J.X. MITROVICA, A.C. MALOOF, AND M. OPPENHEIMER. 2009. Probabilistic assessment of sea level during the last interglacial stage. *Nature* 462:863–868.
- KU, T.-L., AND J.P. KERN. 1974. Uranium-series age of the upper Pleistocene Nestor Terrace, San Diego, California. *Geological Society of America Bulletin* 85:1713–1716.
- LINDBERG, D.R., B. ROTH, M.G. KELLOGG, AND C.L. HUBBS. 1980. Invertebrate megafossils of Pleistocene (Sangamon interglacial) age from Isla de Guadalupe, Baja California, Mexico. Pages 41–62 in D.M. Power, editor, *The California Islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- LIPPS, J.H. 1966. Age and environment of a marine terrace fauna, San Clemente Island, California. *Veliger* 9:388–398.
- LIPPS, J.H., J.W. VALENTINE, AND E. MITCHELL. 1968. Pleistocene paleoecology and biostratigraphy, Santa Barbara Island, California. *Journal of Paleontology* 42:291–307.
- LITTLER, M.M. 1980. Overview of the rocky intertidal systems of southern California. Pages 265–306 in D.M. Power, editor, *The California Islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- MARINCOVICH, L. 1976. Late Pleistocene molluscan faunas from upper terraces of the Palos Verdes Hills, California. *Natural History Museum of Los Angeles County Contributions in Science* 281:1–28.
- MARTINSON, D.G., N.G. PISIAS, J.D. HAYS, J. IMBRIE, T.C. MOORE JR., AND N.J. SHACKLETON. 1987. Age dating and the orbital theory of the ice ages: development of a high-resolution 0 to 300,000-year chronostratigraphy. *Quaternary Research* 27:1–29.
- MCKAY, N.P., J.T. OVERPECK, AND B.L. OTTO-BLIESNER. 2011. The role of ocean thermal expansion in Last Interglacial sea level rise. *Geophysical Research Letters* 38: L14605, <http://dx.doi.org/10.1029/2011GL048280>
- MCLEAN, J.H. 1978. Marine shells of southern California. *Natural History Museum of Los Angeles County Science Series*, 24.
- _____. 2007. Gastropoda. Shelled gastropoda. Pages 713–753 in J.T. Carlton, editor, *The Light and Smith manual: intertidal invertebrates from central California to Oregon*. 4th edition. University of California Press, Berkeley, CA.
- MILNE, G.A., AND J.X. MITROVICA. 2008. Searching for eustasy in deglacial sea-level histories. *Quaternary Science Reviews* 27:2292–2302.
- MITROVICA, J.X., AND G.A. MILNE. 2002. On the origin of late Holocene sea-level highstands within equatorial ocean basins. *Quaternary Science Reviews* 21:2179–2190.
- MITROVICA, J.X., AND W.R. PELTIER. 1991. On postglacial geoid subsidence over the equatorial oceans. *Journal of Geophysical Research* 96:20053–20071.
- MUHS, D.R. 1983. Quaternary sea-level events on northern San Clemente Island, California. *Quaternary Research* 20:322–341.
- MUHS, D.R., AND T.K. KYSER. 1987. Stable isotope compositions of fossil mollusks from southern California: evidence for a cool last interglacial ocean. *Geology* 15:119–122.
- MUHS, D.R., G.H. MILLER, J.F. WHELAN, AND G.L. KENNEDY. 1992. Aminostratigraphy and oxygen isotope

- stratigraphy of marine terrace deposits, Palos Verdes Hills and San Pedro areas, Los Angeles County, California. Pages 363–376 in C.H. Fletcher III and J.F. Wehmiller, editors, Quaternary coasts of the United States: marine and lacustrine systems. SEPM [Society for Sedimentary Geology] Special Publication No. 48.
- MUHS, D.R., J.M. PANDOLFI, K.R. SIMMONS, AND R.R. SCHUMANN. 2012b. Sea-level history of past interglacial periods from uranium-series dating of corals, Curaçao, Leeward Antilles islands. *Quaternary Research* 78:157–169.
- MUHS, D.R., K.R. SIMMONS, G.L. KENNEDY, K.R. LUDWIG, AND L.T. GROVES. 2006. A cool eastern Pacific Ocean at the close of the last interglacial complex. *Quaternary Science Reviews* 25:235–262.
- MUHS, D.R., K.R. SIMMONS, G.L. KENNEDY, AND T.K. ROCKWELL. 2002a. The last interglacial period on the Pacific Coast of North America: timing and paleoclimate. *Geological Society of America Bulletin* 114:569–592.
- MUHS, D.R., K.R. SIMMONS, R.R. SCHUMANN, L.T. GROVES, S. DEVOGEL, D. PATTERSON, AND D.V. RICHARDS. 2010. Last interglacial sea-level history on Santa Barbara and Anacapa islands, Channel Islands National Park, California. *Geological Society of America Abstracts with Programs* 42(5):563.
- MUHS, D.R., K.R. SIMMONS, R.R. SCHUMANN, L.T. GROVES, J.X. MITROVICA, AND D. LAUREL. 2012a. Sea-level history during the last interglacial complex on San Nicolas Island, California: implications for glacial isostatic adjustment processes, paleozoogeography and tectonics. *Quaternary Science Reviews* 37:1–25.
- MUHS, D.R., K.R. SIMMONS, R.R. SCHUMANN, AND R.B. HALLEY. 2011. Sea-level history of the past two interglacial periods: new evidence from U-series dating of reef corals from south Florida. *Quaternary Science Reviews* 30:570–590.
- MUHS, D.R., K.R. SIMMONS, AND B. STEINKE. 2002b. Timing and warmth of the last interglacial period: new U-series evidence from Hawaii and Bermuda and a new fossil compilation for North America. *Quaternary Science Reviews* 21:1355–1383.
- MUHS, D.R., AND B.J. SZABO. 1982. Uranium-series age of the Eel Point terrace, San Clemente Island, California. *Geology* 10:23–26.
- POTTER, E.-K., T.M. ESAT, G. SCHELLMANN, U. RADTKE, K. LAMBECK, AND M.T. MCCULLOCH. 2004. Suborbital-period sea-level oscillations during marine isotope substages 5a and 5c. *Earth and Planetary Science Letters* 225:191–204.
- POTTER, E.-K., AND K. LAMBECK. 2003. Reconciliation of sea-level observations in the western North Atlantic during the last glacial cycle. *Earth and Planetary Science Letters* 217:171–181.
- RADWIN, G.E. 1974. *Acanthina lugubris* reappears in San Diego. *The Festivus* 5:114.
- ROY, K., D. JABLONSKI, AND J.W. VALENTINE. 1995. Thermally anomalous assemblages revisited: patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks. *Geology* 23:1071–1074.
- SEAPY, R.R., AND M.M. LITTLER. 1980. Biogeography of rocky intertidal macroinvertebrates of the southern California Islands. Pages 307–323 in D.M. Power, editor, *The California Islands: proceedings of a multidisciplinary symposium*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- _____. 1993. Rocky intertidal macroinvertebrates of the Southern California Bight: an overview and checklist. Pages 293–322 in F.G. Hochberg, editor, *Third California Islands Symposium: recent advances in research on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- SMITH, J.P. 1919. Climatic relations of the Tertiary and Quaternary faunas of the California region. *Proceedings of the California Academy of Sciences* 9: 123–173.
- SPALDING, M.D., H.E. FOX, G.R. ALLEN, N. DAVIDSON, Z.A. FERDAÑA, M. FINLAYSON, B.S. HALPERN, M.A. JORGE, A. LOMBANA, S.A. LOURIE, ET AL. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Science* 57:573–583.
- SPEED, R.C., AND H. CHENG. 2004. Evolution of marine terraces and sea level in the last interglacial, Cave Hill, Barbados. *Geological Society of America Bulletin* 116:219–232.
- STEIN, M., G.J. WASSERBURG, K.R. LAJOIE, AND J.H. CHEN. 1991. U-series ages of solitary corals from the California coast by mass spectrometry. *Geochimica et Cosmochimica Acta* 55:3709–3722.
- SUSUKI, T., AND C.J. STADUM. 1978. A Neogene section, northeastern San Clemente Island, California. *Natural History Museum of Los Angeles County Contributions in Science* 299:1–24.
- TAMISIEA, M.E., AND J.X. MITROVICA. 2011. The moving boundaries of sea level change: understanding the origins of geographic variability. *Oceanography* 24: 24–39.
- TURNER, C.S.M., AND R.T. JONES. 2010. Does the Agulhas Current amplify global temperatures during super-interglacials? *Journal of Quaternary Science* 25: 839–843.
- VALENTINE, J.W. 1955. Upwelling and thermally anomalous Pacific Coast Pleistocene molluscan faunas. *American Journal of Science* 253:452–474.
- _____. 1958. Late Pleistocene megafauna of Cayucos, California, and its zoogeographic significance. *Journal of Paleontology* 32:687–696.
- _____. 1961. Paleoeccological molluscan geography of the Californian Pleistocene. *University of California Publications in Geological Sciences* 34:309–442.
- _____. 1962. Pleistocene molluscan notes. 4. Older terrace faunas from Palos Verdes Hills, California. *Journal of Geology* 70:92–101.
- _____. 1966. Numerical analysis of marine molluscan ranges on the extra-tropical northeastern Pacific shelf. *Limnology and Oceanography* 11:198–211.
- _____. 1973. Evolutionary palaeoecology of the marine biosphere. Prentice-Hall, Englewood Cliffs, NJ.
- _____. 1980. Camali: a Pleistocene terrace fauna from Baja California. *Journal of Paleontology* 54:1310–1318.
- VALENTINE, J.W., AND R.F. MEADE. 1961. Californian Pleistocene paleotemperatures. *University of California Publications in Geological Sciences* 40:1–45.
- VEDDER, J.G., AND R.M. NORRIS. 1963. *Geology of San Nicolas Island California*. U.S. Geological Survey Professional Paper 369.
- WEHMILLER, J.F., K.R. LAJOIE, K.A. KVENVOLDEN, E. PETERSON, D.F. BELKNAP, G.L. KENNEDY, W.O. ADDICOTT, J.G. VEDDER, AND R.W. WRIGHT. 1977. Correlation and chronology of Pacific coast marine terrace deposits of continental United States by fossil amino acid stereochemistry—technique evaluation, relative ages, kinetic model ages, and geologic

- implications. U.S. Geological Survey Open-File Report 77-680. 196 pp.
- WEHMILLER, J.F., K.R. SIMMONS, H. CHENG, R.L. EDWARDS, J. MARTIN-MCNAUGHTON, L.L. YORK, D.E. KRANTZ, AND C.-C. SHEN. 2004. Uranium-series coral ages from the U.S. Atlantic Coastal Plain—the “80 ka problem” revisited. *Quaternary International* 120:3–14.
- WOODRING, W.P. 1957. Marine Pleistocene of California. Pages 589–597 in H.S. Ladd, editor, *Treatise on marine ecology and paleoecology*. Geological Society of America Memoir 67.
- WOODRING, W.P., M.N. BRAMLETTE, AND W.S.W. KEW. 1946. Geology and paleontology of Palos Verdes Hills, California. U.S. Geological Survey Professional Paper 207.
- ZINSMEISTER, W.J. 1974. A new interpretation of thermally anomalous molluscan assemblages of the California Pleistocene. *Journal of Paleontology* 48:84–94.

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