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Short Communication

Pleistocene to Holocene continuity and discontinuity in California Northern Channel Island marine invertebrate communities

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ABSTRACT

There is growing interest in analyzing interdisciplinary datasets to better understand the evolution of ecosystems through deep time. One burgeoning area has been the integration of archaeological and fossil data to evaluate the long-term structure and function of habitats, floral and faunal communities, and ecosystems. Here, marine invertebrate data from Holocene archaeological sites and Pleistocene marine terrace deposits on California's Northern Channel Islands are combined to glean insights into the long-term structure of nearshore marine ecosystems, the composition of intertidal marine invertebrate communities, and the formation of archaeological shell middens. While a variety of methodological, analytical, and taphonomic challenges in comparing disparate datasets from fossil and archaeological contexts were identified, we offer perspectives for surmounting these challenges in future research. These findings indicate that the integration of fossil and archaeological data, spanning tens of thousands of years, offers important insights on the evolution of nearshore coastal ecosystems and marine climate change in California and around the world.

1. Introduction

Increasingly, scientists are integrating deep historical data to investigate the long-term evolution of coastal and marine ecosystems around the world (e.g., Crumley, 2021; Rick and Lockwood, 2013). Such perspectives are rapidly becoming important for ecologists, biologists, and resource managers to evaluate the long-term continuity or discontinuity of local flora and fauna. Comparisons of archaeological and modern ecological data have been particularly useful for helping researchers understand long-term ecosystem shifts across centuries to millennia and through natural and anthropogenic change (e.g., Szabó, 2015). Scientists also have used paleontological data, predating the arrival of humans, to provide a context for modern ecological systems and to understand climate change (e.g., Barnosky et al., 2017; Dietl and Flessa, 2011). The integration of archaeological and fossil data is less common, despite being uniquely positioned to document the evolution of environments from the deep geologic past to modern times (see Rick et al., 2016).

Southern California's Channel Islands are an excellent laboratory for exploring the research potential of integrated archaeological and paleontological datasets. These islands are protected by various private and government agencies from modern development and have been a focus of geological and archaeological research for over a century (see Braje et al., 2021). This is the first study from California's Northern Channel Islands that integrates fossil and archaeological marine invertebrate data to investigate the evolution of nearshore island ecosystems (but see Vedder and Norris, 1963). Genus and species-level marine invertebrate identifications from Pleistocene marine terrace deposits are synthesized with Holocene archaeological faunal data from nearby shell midden sites. These data offer important perspectives on the continuity and discontinuity of nearshore ecosystems through deep time and highlight the prospects, potential, and challenges for similar studies in the future.

2. Environmental and cultural setting

California's Northern Channel Islands, consisting of Anacapa, Santa Cruz, Santa Rosa, and San Miguel islands, are in the Santa Barbara Channel region, a unique geographic area of the California Coast that trends east-west for approximately 130 km (Fig. 1). Due to their

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proximity to the mainland (currently ~20–44 km offshore) and productive marine and terrestrial ecosystems, the islands have attracted human settlement for millennia (Erlandson et al., 2011; Johnson et al., 2002). The southern California Coast and Santa Barbara Channel contain one of the most productive fisheries in the world, fueled by upwelling of nutrient-rich marine waters, numerous estuaries along the mainland coast, a complex combination of oceanic currents, and extensive nearshore kelp forests. These variables have resulted in high primary marine productivity that support complex food webs, including a diverse array of marine plants and invertebrates and local and migratory fish, seabirds, and sea mammals (Schoenherr et al., 2003).

The Santa Barbara Channel is a tectonically active region of the eastern Pacific Rim. Along with fluctuating sea levels during the Pleistocene, this helped create uplifted marine terrace landscapes across the islands. Age estimates generated from uranium-series dating of fossil corals and amino acid geochronology of fossil mollusks indicate that San Miguel and Santa Rosa islands were tectonically uplifted at rates of 0.12–0.20 m/ka during the late Quaternary (Muhs et al., 2014), while Anacapa and Santa Cruz islands uplift rates are considerably lower. Santa Cruz Island uplift rates, for example, range from 0.09 m/ka to possibly no uplift at all in the past 120,000 years (Muhs et al., 2021). Along many of these terraces, geologists have identified and dated marine terraces deposits at both the 80,000 and 120,000-year-old high sea stands that contain a geological record of nearshore marine invertebrate communities in the Pleistocene prior to the arrival of humans.

The islands were settled by the ancestors of the Island Chumash at least 13,000 calibrated years ago (Johnson et al., 2002). At the time, the islands were connected as a single landmass, called *Santarosae*, but separated from the mainland by approximately 8 km of open ocean. The Island Chumash had a hunter-gather-fisher economy focused on marine invertebrates, fish, marine mammals, birds, and a wide variety of plant foods (Braje et al., 2021). The Chumash and their ancestors occupied the islands continuously throughout the Holocene and, across millennia, their populations increased and communities became less mobile and more circumscribed. Partly as a response to increasing population densities and resource scarcity, the Chumash developed increasingly sophisticated marine fishing and hunting technologies, long-distance trade networks with mainland communities, and complex socio-political hierarchies (Braje et al., 2021). The region contains one the longest and most well-preserved archaeological records in the Americas, including thousands of shell middens, which contain the remains of past meals, along with a variety of epifauna from coastal foraging (i.e., seaweed harvesting, riders on large marine invertebrates, etc.), marine mammal hunting (i.e., the stomach contents of sea mammals), shell tool and bead production, and other household activities. These archaeological sites are a record of human subsistence and coastal foraging and act as a snapshot of local nearshore ecological communities.

3. Materials and methods

The presence or absence of marine invertebrate species in archaeological midden sites (Fig. 2) and paleontological marine terrace deposits (Fig. 3) from published sources along the Northern Channel Islands were

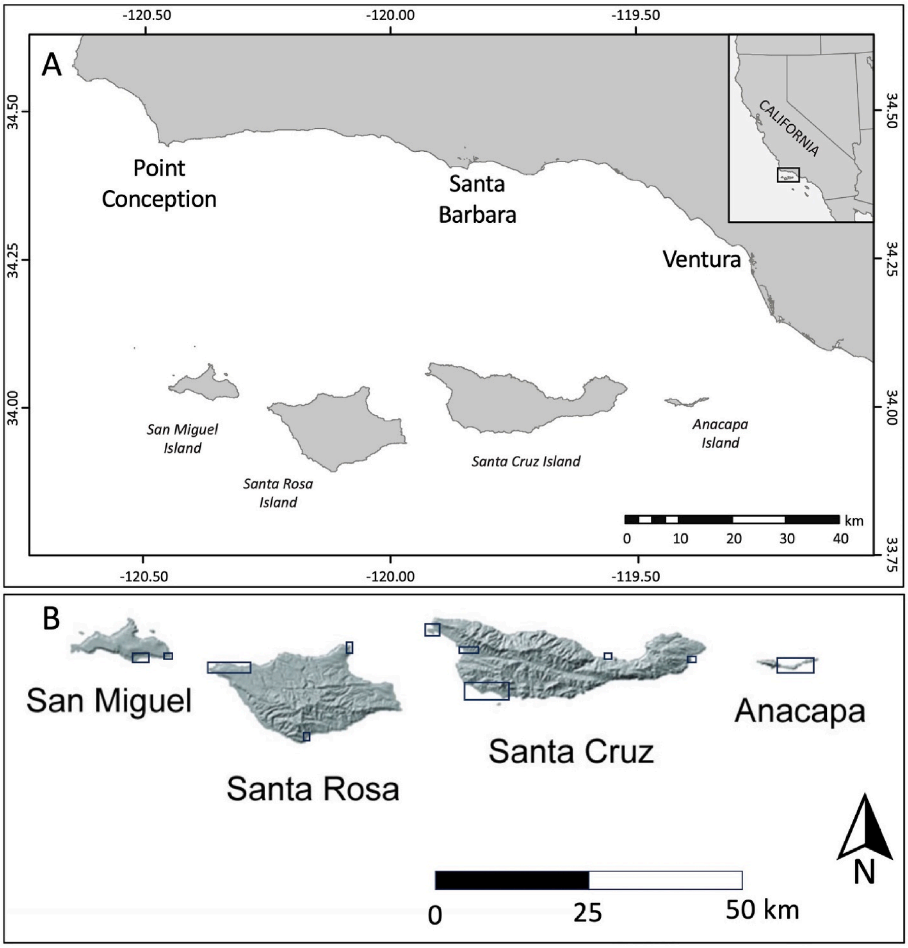

Fig. 1. A) Map of the Santa Barbara Channel region and the Northern Channel Islands, B) Map of the marine terrace/archaeological localities considered in this study. Note: The boxes indicate the general locations of both the marine terrace deposits and archaeological sites used in this study, more precise locations are not provided due to the sensitive nature of these geological and archaeological sites and National Park Service guidelines on disclosing cultural resource localities.

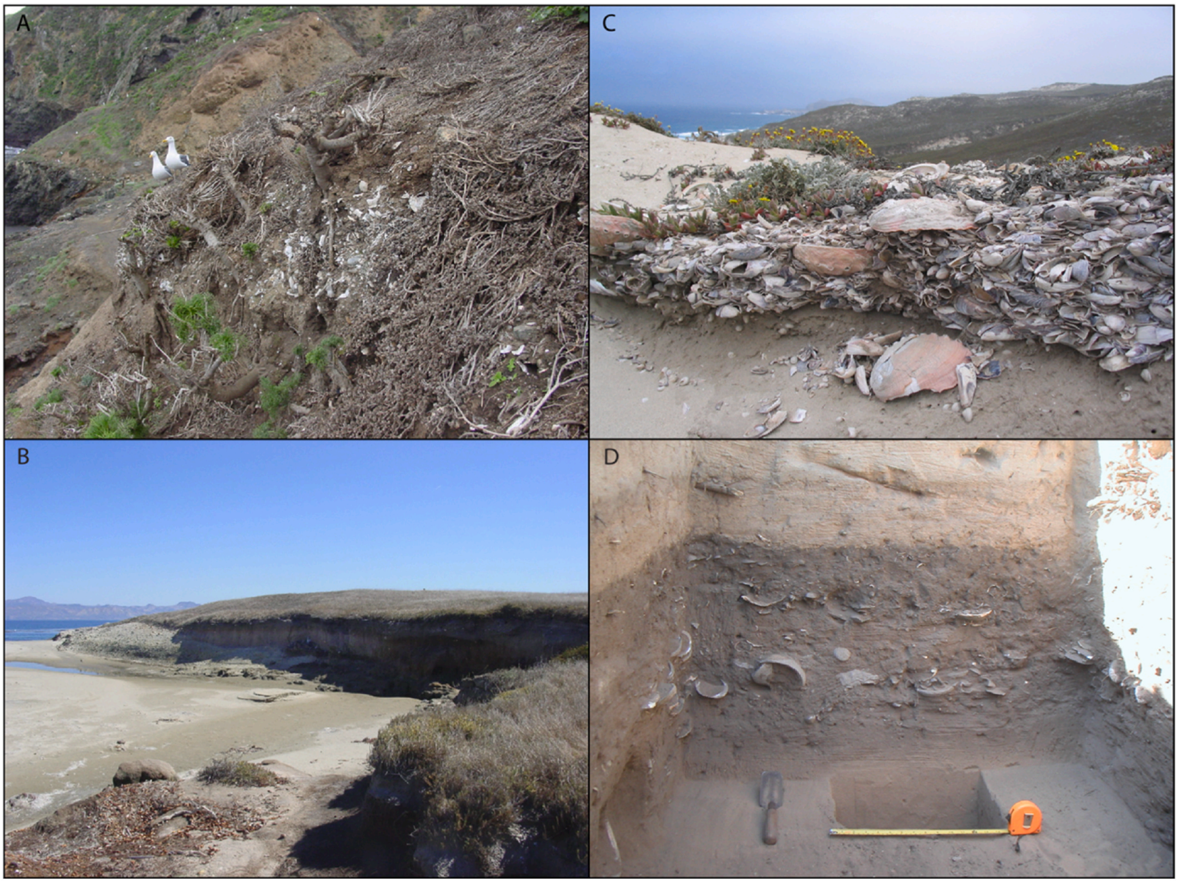

Fig. 2. Images of archaeological sites used in this study from the Northern Channel Islands, California (all photographs by T. Braje and T. Rick): A) A 3000-year-old archaeological deposit eroding from the sea cliff on western Anacapa Island; B) Overview image of a ~1000-year-old archaeological deposit preserved in a coastal terrace from eastern Santa Rosa Island; C) Close up image of a 4500-year-old archaeological site from northern San Miguel Island; and D) Close up image of a 4300-year-old archaeological site from southern San Miguel Island.

compiled (Table 1, Supplemental Table 1). In total, data from 24 archaeological sites (25 site components) were synthesized, with the oldest deposit dated to ca. 9500 cal BP and the youngest dated to the Historic Period (≤1542 AD; Table 2). Six sites come from Anacapa Island, four from Santa Cruz Island, ten from Santa Rosa Island, and four from San Miguel Island. Paleontological data from marine terrace deposits were compiled from 28 localities, all from late Pleistocene, pre-human intervals of either the 80,000 or 120,000 cal BP sea stands. Three localities come from Anacapa Island, ten from Santa Cruz Island, fourteen from Santa Rosa Island, and one from San Miguel Island. Due to the long-time spans represented by the fossil assemblages, archaeological assemblages were grouped into one broad category representing the Holocene. These comparisons allow for a generalized discussion of pre-human Pleistocene fossil assemblages alongside anthropogenic Holocene archaeological assemblages that represent the coarse temporal nature of the datasets.

All fossil assemblages synthesized here are from systematic collections of marine terraces. Archaeological data are all from excavations using standard archaeological procedures, including 1/8-inch screens and recordation of the precise locations and depth of excavation units. For taxonomic identification, many archaeologists focus on major taxa that were key components of human diet, often not identifying small gastropods and other epifauna to genus or species (see Braje et al., 2012). In contrast, marine invertebrates from marine terrace deposits were identified to the most specific taxonomic category possible, resulting in a larger number of species. Due to these differences and to decrease biases between the archaeological and fossil datasets, the focus was on the presence/absence of the 11 most common marine invertebrate food species from Northern Channel Island archaeological sites: California mussel (*Mytilus californianus*), black and red abalone (*Haliotis cracherodii* and *H. rufescens*), black and brown turban snail (*Tegula funebralis* and *T. brunnea*), sea urchin (*Strongylocentrotus* spp.), platform mussel (*Mytilisepta bifurcatus*), chiton, gooseneck barnacle (*Pollicipes polymerus)*, and Venus and pismo clams (*Chione califorrniensis* and *Tivela stultorum*) (Table 1). This analysis also includes purple olive snail shell (*Callianax biplicata*), a critical shell resource for the Chumash in the production of shell beads and, by the late Holocene, standardized currency. All these species are readily identified in both archaeological and paleontological deposits and act as important indicators of local nearshore habitat types in the past (i.e., sandy beaches, rocky shores, estuaries, etc.). While other species such as small gastropods, bivalves, and other epifauna can be excellent indicators of water temperatures, local environmental conditions and habitats, and other natural conditions and human behaviors, they are more difficult to identify and are rarely part of faunal identifications from Holocene deposits on the Northern Channel Islands (for an exception see Ainis et al., 2014).

Marine terrace deposits represent the natural accumulation of marine invertebrates from former beach, shallow embayment, and rocky intertidal habitats, while the archaeological deposits are the result of human selection and deposition in a site. Taphonomic processes from erosion due to wind and rain exposure, livestock trampling, and other activities resulted in fragmentation of both fossil and archaeological assemblages. Despite these processes, both the archaeological and fossil assemblages are relatively well preserved and suitable for reconstructing past environments and human activities.

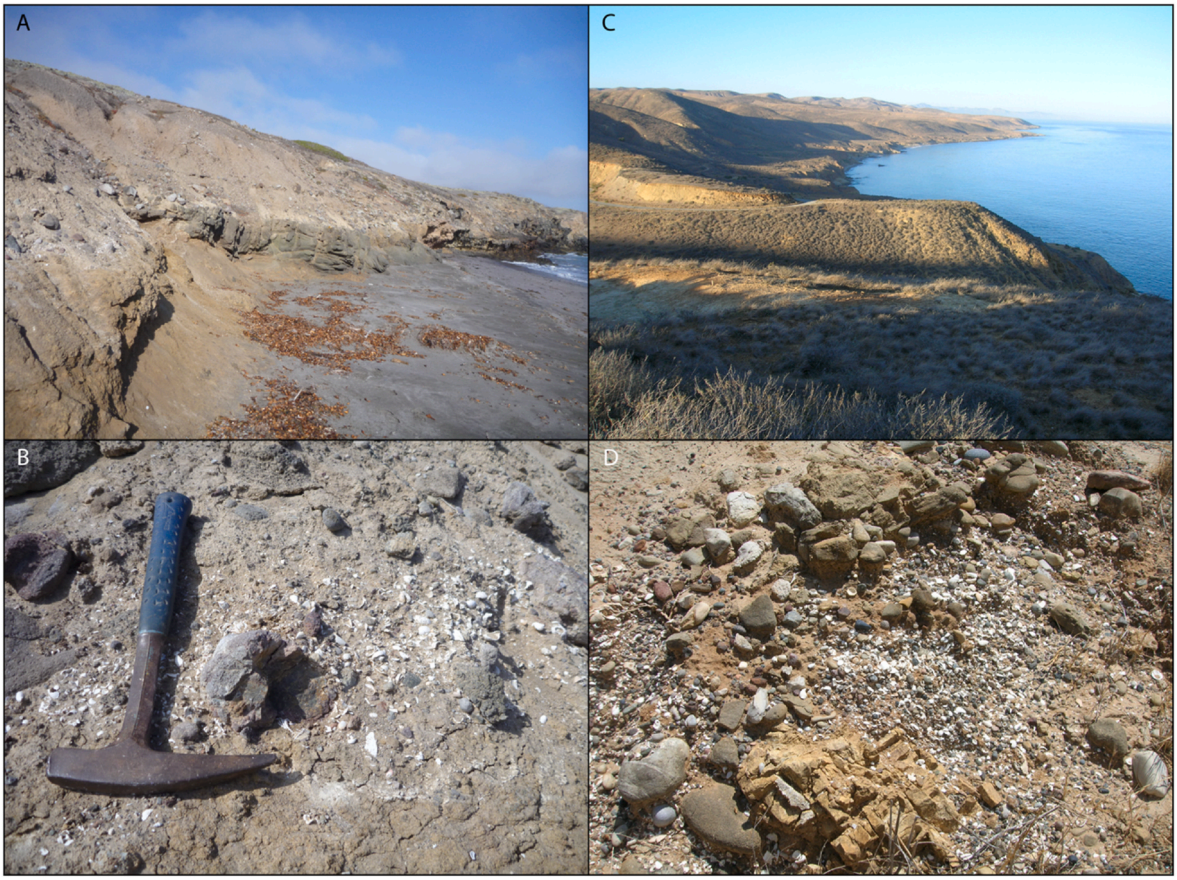

Fig. 3. Images of fossil localities used in this study from the Northern Channel Islands, California (all photographs by D. R. Muhs): A) Overview image of the 120,000-year-old marine terrace at Forney's Cove, northwestern Santa Cruz Island; B) Close up image of the marine terrace deposit from the 120,000-year-old locality at Fraser Point, northwestern Santa Cruz Island; C) Overview image of the 120,000-year-old marine terrace at Johnson's Lee, southern Santa Rosa Island; and D) Close up image of the marine terrace deposit from the 120,000-year-old locality at Johnson's Lee, southern Santa Rosa Island.

Table 1

Summary table of the presence and absence of the most common marine invertebrate food species from the Northern Channel Islands: California mussel (*Mytilus californianus*), black abalone (*Haliotis cracherodii*), red abalone (*H. rufescens*), turban snail (*Tegula* sp.), sea urchin (Echinoidea), platform mussel (*Mytilisepta bifurcata*), chiton (*Cryptochiton stelleri*), gooseneck barnacle (*Pollicipes polymerus*), and Venus and pismo clams (*Chione californiensis*, *Tivela stultorum*) along with purple olive snail shells (*Callianax biplicata*). An "X" indicates presence in fossil or archaeological deposits compiled in this study, a "P" represents presence in other nearby archaeological sites not included in this study, and a "L" represents the likely presence but not represented in our study due, most likely, to sampling error.

Taxa	Anacapa		Santa Cruz		Santa Rosa		San Miguel	
	Fossil	Archaeological	Fossil	Archaeological	Fossil	Archaeological	Fossil	Archaeological
Gastropoda								
Callianax biplicata	X	X	X	P	X	X	X	X
Haliotis cracherodii	X	X	X	X	X	X	X	X
Haliotis rufescens	X		X	X	X	X	X	X
Haliotis sp.	X	X	X	X	X	X		X
Tegula brunnea					X	X	X	X
Tegula funebralis		X	X	X	X	X	X	X
Tegula sp.	X	X	X		X	X		X
Bivalvia								
Chione californiensis	X				L	P		
Chione sp.				X	L	P	X	
Mytilus californianus	X	X	X	X	X	X	X	X
Mytilisepta bifurcata		X	X	X	X	X	X	X
Tivela stultorum				X		X		P
Polyplacophora								
Chiton plates	X	X	X	X	X	X	X	X
Cryptochiton stelleri					X	X	X	X
Arthropoda								
Pollicipes polymerus		X		X		X		X
Echinodermata								
Echinoid spines & plates	X	X	X	X	X	X	X	X

Table 2
Fossil localities, archaeological sites, ages, and citations for marine invertebrates reported in this study.

Fossil Locality	Age (year BP)	Reference	Archaeological Site	Age (cal BP)	Reference
San Miguel Island					
Locality SMI-236	120 ka	Muhs et al. (2014)	CA-SMI-608	9720–8160	Braje (2010)
			CA-SMI-657	7060–6820	Braje (2010)
			CA-SMI-628	1530–1280	Braje (2010)
			CA-SMI-232	1290–1070	Braje (2010)
Santa Rosa Island					
LACMIP-42946	80 ka	Muhs et al. (2023)	CA-SRI-6	9330–9020	Erlandson et al. (1999)
LACMIP-42948	80 ka	Muhs et al. (2023)	CA-SRI-2	1030–150	Rick (2011)
LACMIP-42957	80 ka	Muhs et al. (2023)	CA-SRI-115	4200–1915	Jazwa (2015)
LACMIP-42958	80 ka	Muhs et al. (2023)	CA-SRI-116	6380–4870	Jazwa (2015)
LACMIP-42937	80 ka	Muhs et al. (2023)	CA-SRI-131	3585–2330	Jazwa (2015)
LACMIP-42941	80 ka	Muhs et al. (2023)	CA-SRI-313	1280–565	Jazwa (2015)
LACMIP-42930	120 ka	Muhs et al. (2023)	CA-SRI-333	1325–140	Jazwa (2015)
LACMIP-42935	120 ka	Muhs et al. (2023)	CA-SRI-147	7300–350	Braje et al. (2007)
LACMIP-42936	120 ka	Muhs et al. (2023)	CA-SRI-5	4800–4400	Jazwa (2015)
LACMIP-42947	120 ka	Muhs et al. (2023)	CA-SRI-109	5870–4420	Jazwa (2015)
LACMIP-42940	120 ka	Muhs et al. (2023)			
LACMIP-42938	120 ka	Muhs et al. (2023)			
LACMIP-42939	120 ka	Muhs et al. (2023)			
LACMIP-42942	120 ka	Muhs et al. (2023)			
Santa Cruz Island					
LACMIP-42970	120 ka	Muhs et al. (2021)	CA-SCRI-109	6900–4800	Glassow et al. (2008)
LACMIP-42332	120 ka	Muhs et al. (2021)	CA-SCRI-823	3280–150	Thakar (2014)
LACMIP-42333	120 ka	Muhs et al. (2021)	CA-SCRI-568	3210–840	Thakar (2014)
LACMIP-42334	120 ka	Muhs et al. (2021)	CA-SRI-236	2945–870	Thakar (2014)
LACMIP-42335	120 ka	Muhs et al. (2021)	CA-SCRI-109	2120–1920	Glassow et al. (2008)
LACMIP-42336	120 ka	Muhs et al. (2021)			
LACMIP-42337	120 ka	Muhs et al. (2021)			
LACMIP-42338	120 ka	Muhs et al. (2021)			
LACMIP-42339	120 ka	Muhs et al. (2021)			
LACMIP-42971	120 ka	Muhs et al. (2021)			
Anacapa Island					
LACMIP-42323	120 ka	Muhs and Groves (2018)	CA-ANI-5	5280–5010	Rick and Reeder-Myers (2018)
LACMIP-42322	120 ka	Muhs and Groves (2018)	CA-ANI-8	5030–520	Rick and Reeder-Myers (2018)
LACMIP-42321	120 ka	Muhs and Groves (2018)	CA-ANI-3	3300–3030	Rick and Reeder-Myers (2018)
			CA-ANI-2	3210–2730	Rick and Reeder-Myers (2018)
			CA-ANI-4	3210–2460	Rick and Reeder-Myers (2018)
			CA-ANI-6	630–500	Rick and Reeder-Myers (2018)

4. Results and discussion

In total 220 different marine invertebrate categories (species, genus, and family) were identified in the fossil assemblages and 56 were identified in the archaeological deposits (Table 1; Supplementary Table 1). The higher richness of the fossil assemblages compared to archaeological assemblages are, at least partly, the product of the different identification procedures noted above. In addition, natural fossil accumulations likely contain greater taxonomic richness because they are not influenced by human selectivity as are archaeological middens. However, this pattern will need to be tested in future studies that employ identical analytical procedures.

The most apparent pattern that emerges from these datasets is the long-term stability of rocky intertidal marine invertebrates from the Pleistocene to Holocene. Across all four islands, rocky intertidal marine invertebrate species such as turban snails, black abalone, California mussels, platform mussels, chitons, and sea urchins are present in both marine terrace and archaeological deposits. These species are often the most common ones in modern intertidal marine invertebrate communities today, especially thick beds of California and platform mussels and, although less clustered, turban snails, chitons, and sea urchins (Schoenherr et al., 2003). This indicates considerable stability in the presence, ubiquity, and distribution of rocky intertidal shorelines where these species thrive today, despite massive fluctuations in sea levels and sea surface temperatures through deep time (Kennett and Ingram, 1995; Pak et al., 2012).

Embedded within this general patterning, however, are some deviations. For example, no platform mussels were identified from marine terrace deposits on Anacapa Island, although they occur in similar deposits along the other Northern Channel Islands. Platform mussels are abundant across island rocky intertidal habitats today and in archaeological deposits, and their absence from marine terrace deposits on Anacapa Island may be a sampling issue but requires further investigation. Gooseneck barnacles occur in archaeological deposits across the islands but have yet to be identified in marine terrace deposits. This species is closely associated with California mussels, inhabiting at the same tidal depths and thermal tolerances, and oftentimes found growing on the surfaces of shells (Marchant Rojas, 2014). They were likely collected by Chumash foragers at the same time, along with other intertidal shellfish species as a critical part of their subsistence economies. Gooseneck barnacles have small and delicate shells and their absence in marine terrace deposits may have more to do with preservation issues than their Pleistocene biogeographic distribution.

The presence and absence of certain rocky intertidal marine invertebrate species from marine terrace and archaeological deposits can act as indicator species for past sea surface temperatures across the Santa Barbara Channel through time. For example, in both marine terrace and archaeological deposits on Anacapa and Santa Cruz islands, brown turban snails are absent, while black turban snails occur across all the islands, with the possible exception of marine terraces on Anacapa Island where undifferentiated turban snails have been identified and most likely represent black turban snails. Brown turban snails, a species that lives in the low intertidal or subtidal zones and prefers colder waters, are rare in the warmer intertidal waters along the east end of the Santa Barbara Channel today (Morris et al., 1980). This biogeographic pattern seems to be consistent with the Pleistocene past. Black turban snails, in contrast, prefer warmer waters and live in the high intertidal zone (Cooper, 2010; Morris et al., 1980). They seem to have successfully accessed suitable habitats and temperature regimes more broadly across the Santa Barbara Channel through time, a pattern that remains in place today.

Interesting complications arise, however, when this same logic is applied to the occurrence of abalone species across the Santa Barbara Channel. Red abalone, a cold water-adapted species, occurs across all the islands in both marine terrace and archaeological deposits, apart from archaeological ones on Anacapa Island. On the one hand, warmer water-adapted black turban snails and black abalone show consistency in their widespread distribution in both geological and archaeological deposits across the Northern Channel Islands. On the other hand, the distributions of cold water-adapted brown turban snails and red abalone seem to have undergone some significant changes through time. While red abalone was present across all the islands during the Pleistocene, their range may have contracted during the Holocene with their lack of archaeological identification on Anacapa Island. This was likely related to the presence of cooler sea surface temperatures during the late Pleistocene, which facilitated their range expansion to the east end of the Santa Barbara Channel (for a broader discussion see Braje et al., 2009). During the Holocene, Anacapa Island has been far more protected from cold waters than either San Miguel Island or Santa Rosa Island, which may explain the lack of red abalone in archaeological sites. Surprisingly, cold water adapted brown turban snails have not been similarly identified in Pleistocene deposits on Santa Cruz and Anacapa islands, indicating some interesting biogeographic differences across species through time along the Santa Barbara Channel region. No 80 ka marine terrace deposits have been identified on either Santa Cruz Island or Anacapa Island, likely because of the lower uplift rates on these two islands, which likely explains the lack of cold-water species. However, better understanding these dynamics could be a fruitful avenue of future research. Of particular interest may be species-level identifications of smaller gastropods and other epifaunal marine invertebrates from archaeological shell middens and marine terrace deposits. Many of these species act as reliable indicators of local sea surface temperatures and other environmental conditions, which could help parse out patterning in the Santa Barbara Channel-wide biogeographic distribution of marine invertebrate species (see Ainis et al., 2014).

Species distributions also provide important clues about other nearshore habitats such as sandy beaches and estuaries. Pismo clams, usually found along the intertidal zone of flat beaches along open coasts and the entrances of channels, bays, and estuaries, have yet to be identified in marine terrace deposits but are found in archaeological sites on Santa Cruz and Santa Rosa islands, as well as in surface observations on San Miguel Island (Rick and Eliot, 2013). Pismo clams were an important contributor to Chumash diet when and where available and signal the presence of productive sandy beaches on Santa Cruz, San Miguel, and Santa Rosa islands during portions of the Holocene, similar to their modern distribution (Rick and Eliot, 2013; Thakar, 2011). The absence of pismo clams in marine terrace deposits indicates a markedly constricted biogeographic range during the Pleistocene or their lack of preservation.

California Venus clams and oysters may be an even better harbinger of local ecological systems. These species are commonly found in sandy bays and mudflats and act as an important indicator of an open and productive estuarine habitat. While no estuaries exist today on the Northern Channel Islands, the only known Holocene estuary, the Abalone Rocks Estuary, was located on southeastern Santa Rosa Island at the mouth of Old Ranch Canyon during the early and middle Holocene (Cole and Liu, 1994; Rick et al., 2005), where Venus clams, oysters, and other estuary taxa are commonly found in archaeological deposits dating to ca. 10,000–5000 cal BP (Rick, 2020). Venus clams have also been identified in archaeological deposits on western Santa Cruz Island and may have been transported from the Abalone Rocks Estuary or other now submerged estuary. While Venus clams or oysters were not identified in the marine terrace dataset from Santa Cruz and Santa Rosa islands, there are some interesting indications, including recent sonar mapping and seafloor sampling (Braje et al., 2022), that a large paleoestuary existed during the late Pleistocene in the now submerged paleolandscapes between Santa Rosa and Santa Cruz islands, an area Erlandson (2016) dubbed "Crescent Bay" (see Gusick et al., 2022). It is possible that Chumash foragers gathered estuarine shellfish from this paleoestuary prior to its inundation by raising post glacial seas in the early Holocene. Venus clams and oysters also have been identified in Pleistocene marine terrace deposits on Anacapa and San Miguel islands but are not present in archaeological deposits on these islands. This indicates the presence of Pleistocene estuary habitats on these islands or along nearby now submerged paleolandscapes that closed and infilled prior to the arrival of humans in the late Pleistocene.

A number of challenges exist when attempting to combine archaeological and geological data. For this study of marine invertebrate constituents in marine terrace deposits and archaeological sites, differences in the preservation conditions of archaeological and geological deposits, different practices in marine invertebrate identification across disciplines, and variability in how geological versus archaeological sites are formed are some of the most difficult to resolve. Future research could build upon the work presented here by performing field sampling and analytical procedures using the same methods at marine terrace and archaeological sites, and quantifying marine invertebrate abundance. Such analyses can refine future interpretations and tease apart the differences and similarities between natural marine invertebrate accumulations in marine terraces and the anthropogenic deposits of shell middens. This study does provide, however, broad scale patterning in marine invertebrate communities across time and broad stroke interpretations about environmental change and continuity, oceanographic processes, and ecosystem evolution. There are exciting opportunities in combining these datasets to generate perspectives on the long-term structure and function of habitats, floral and faunal communities, and ecological systems.

CRediT authorship contribution statement

Todd J. Braje: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Natasha Vokhshoori:** Writing – review & editing, Funding acquisition. **Lindsey T. Groves:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Torben C. Rick:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.

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