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Abstract

Archaeologists analyzing shell middens typically focus on larger (>2 cm) mollusks to examine subsistence practices, impacts on littoral habitats, and paleoenvironmental conditions as well as a host of other natural and cultural phenomena. Small (<2 cm), non-dietary gastropods in archaeological shell middens also provide important clues regarding human resource procurement in littoral areas and coastal paleoenvironments. We present data from two sites on the California Channel Islands to demonstrate the range of information that can be gained by analyzing small gastropod shells. Identifications revealed the remains of over 4,500 non-dietary small gastropods from 75 taxa. Human harvesting of marine macrophytes is suggested by the presence of 18 species that are predominantly associated with seaweeds and seagrasses. Quantification measures revealed high diversity and equitability indices, oscillating taxonomic richness, and decreasing densities through time at both sites. Likelihood ratio tests revealed differences in assemblage composition between Early Holocene and later components at one site and demonstrated similarities in the relative composition of non-dietary shell assemblages between both sites during the Middle Holocene. Incorporating detailed studies of less conspicuous "incidental" shellfish remains in archaeological midden studies has the potential to contribute to our understanding of past human land use practices and littoral paleoecology. Our

findings are applicable to archaeologists working in coastal settings around the world, as well as marine ecologists interested in intertidal paleo-habitats and kelp forest ecosystems.

Keywords: coastal archaeology, shell midden analysis, kelp associates, seagrass associates, non-dietary incidental shells, California Channel Islands.

1. Introduction

Small, non-dietary shells are accidentally incorporated in archaeological middens through a variety of mechanisms (see Claassen 1998; Stiner 1999), and can provide significant information through their associations with purposely harvested perishable resources such as marine algae and plants. Marine benthic macrophytes, including seaweeds (multicellular marine macroalgae) and seagrasses (angiosperms, flowering sea plants), provide the foundation for healthy marine ecosystems and vibrant littoral habitats that have attracted human foragers for over 100,000 years (Avery et al. 2008; Erlandson 2001; Klein et al. 2004; Marean et al. 2007; Ramos et al. 2011) and other members of our genus for even longer (Cortéz-Sánchez et al. 2010; Cunane and Stewart 2010; Erlandson 2010; Stiner 1994; Szabó and Amesbury 2011). Roughly 150 species of seaweed are considered edible (Kumar et al. 2008) and used as food worldwide. These species contain various compositions of macro and micro-nutrients (Aaronson 1986; Chapman and Chapman 1980; Dawcyzynski et al. 2006; Druehl 2000; Fleurence 1999; Floreto and Teshima 1998; Guiry and Blunden 1991; Hong et al. 2007; MacArtain et al. 2007; Nisizawa et al. 1987; Turner 2003), with some species boasting mineral contents higher than many land plants (Indegaard and Minsaas 1991; Ito and Hari 1989; Rupérez 2002), making them a valuable food source. Seaweeds and seagrasses are also used for fuel, roofing and matting when dried (McRoy and Helfferich 1980:298-299; Mouritsen 2013:5-21), to underlay and wrap burials for cremation (Photos-Jones et al. 2007), as raw material for the production of cordage, nets, and baskets (Connolly et al. 1995; Scagel 1961; Turner and Bell 1973; Vellanoweth et al. 2003), and to wrap and steam food (Turner and Bell 1973). Unfortunately, Seaweeds and seagrasses rarely survive in the archaeological record and only preserve under the most favorable conditions, for example caves and rockshelters (e.g., Connolly et al. 1996; Vellanoweth et al. 2003) and some

open-air sites such as Monte Verde, Chile, where nine species of marine algae were identified from archaeological features and directly dated to roughly 14,000 years ago (Dillehay et al. 2008). Despite the fact that macrophytes are highly perishable, the small gastropods that live on them have been identified in archaeological contexts dated as far back as the Upper (Colonese and Wilkens 2005) and Lower Paleolithic (Barrière 1969), and hypothesized as indirect evidence that people brought seaweed to cave sites.

In the fossil record, the lack of evidence for kelp (large brown seaweeds in the family Laminariaceae that frequently form large underwater forests) requires researchers to use climatic models and historical distributions of kelp and their associates to infer their evolution and radiation across the world (Estes and Steinberg 1988). As related by Estes and Steinberg (1988:21); seaweed associates include kelp and seagrass limpets that possess unique morphologies and form close associations with particular marine algae and plants. Unlike kelps, seagrasses and associated limpets left evidence of their antiquity in fossil records of Eocene age; however, limpets bearing the unique morphological characteristics of associations with large brown algae only appear in the fossil record about 3 million years ago. The relatively sudden appearance of kelp associated limpets at this time has led researchers to suggest that this was when the widespread proliferation of kelps likely occurred (Estes and Steinberg 1988:21-22). We are proposing to use seaweed associates in a similar fashion, to signal, or infer, the harvesting of seaweeds and seagrasses that have not left direct evidence of their use in the archaeological record.

We present shellfish data from a trans-Holocene multi-component rockshelter on San Miguel Island (ca 8,500 – 1,000 cal BP) and a Middle Holocene open-air dune site on San Nicolas Island (ca 4,800 – 3,600 cal BP), located off the southern California coast (Figure 1). We

4

identify several species of small gastropods that live predominantly (sometimes exclusively) on marine macrophytes (Figures 2 and 3), and we suggest that the presence of these shells in archaeological deposits serve as indirect evidence for human harvesting of these perishable resources. Varieties of other small gastropods are presented here with possible explanations for their presence in archaeological deposits. The aims of this study are to describe small gastropod assemblages from archaeological shell middens by: 1) quantifying non-dietary shells and placing them in habitat based categories; 2) employing heterogeneity measures and cross tabulation frequency distributions to investigate the significance of patterning; 3) examining inferred human harvesting of marine macrophytes through the presence of seaweed and seagrass associates; 4) presenting ethnographic accounts from coastal areas north and south of the Channel Islands as well as on the mainland coast as examples of marine macrophyte use by Native people in the greater region; and 5) exploring possible paleoecological and paleoenvironmental implications signaled by the presence of non-dietary shells, though this discussion remains exploratory.

2. Background

2.1 Ethnohistoric Accounts of Seaweed and Seagrass Use from Western North America

Substantial and varied uses of seaweeds and seagrasses by Native People have been extensively documented for the Pacific Northwest Coast of North American and the Gulf of California. Multiple species of marine macroalgae and angiosperms were harvested, utilized and traded, forming a pivotal role in the lifeways of coastal peoples. Ethnographic accounts have documented a rich linguistic heritage associated with kelps and seagrasses including primary names differentiating stages of growth and aspects of use, suggesting considerable antiquity (Berlin 1973; Felger et al. 1980; Turner 1995, 2003).

5

Several marine macroalgae, including sea wrack (*Fucus gardneri*, *Fucus* sp.), giant kelp (*Macrocystis pyrifera*), bull kelp (*Nereocystis leutkeana*), and red lavers (*Porphyra* spp.) were (and in some cases still are) utilized by Native Peoples of the Pacific Northwest Coast (Ager and Ager 1980; Turner 1995, 2003; Turner and Bell 1973). Several species of brown algal blades (*Egregia menziesii*, *Fucus* sp., *M. pyrifera*, and *N. leutkeana*) were used to catch herring eggs during spawning season. Herring spawn covered blades were dried then bundled and stored for winter use, or traded as a valuable item through extensive coastal and inland networks (Ager and Ager 1980; Turner 1995; Turner and Bell 1973; Turner and Loewen 1998). Kelp blades were also used as heated poultices and the long hollow tubular stipes were used to store oil and grease and to make ropes, fishing nets and lines, and harpoon lines (Turner and Bell 1973).

To a lesser degree, marine seagrasses were also used for food. Surfgrass (*Phyllospadix scouleri* and *P. torreyi*) and eelgrass (*Zostera marina*) plants were dried and formed into cakes for winter consumption, and eelgrass roots and rhizomes were used to flavor meat (Turner 1995:53-54). The *Kwakwaka'wakw* participated in an Eelgrass Feast, in which uncooked rhizomes, stems, and bases were eaten as the food of their mythical ancestors (Turner 1995:54), suggesting antiquity to the practice of consuming eelgrass. In addition, eelgrass and surfgrass were utilized by coastal tribes along western North America, including the Channel Islands, as basket weaving materials (Scagel 1961).

The Seri (*Koŋkáak*) Indians of the Sonoran Desert, Mexico, are the only people known to have extensively harvested the seeds of a submerged marine angiosperm (Felger and Moser 1973, 1976, 1985; Felger et al. 1980). Not only were eelgrass seeds utilized, they were one of the most important traditional foods of the Seri (Sheridan and Felger 1977). Eelgrass flour was of particular importance as a storable food; it was placed in sealed pottery vessels and hidden in

caves with other edible items for times of need (Felger and Moser 1970, 1971, 1976). In addition

to its dietary value, eelgrass was also used to line baskets and sea turtle carapaces for the

placement of meat and other foods, spread over the frame of shelters for shade and roofing, and

in the construction of children's toys (Felger et al. 1980). In addition, eelgrass has been used to

determine seasonality of an archaeological event. In one instance where eelgrass was found

covering a group of burials, the lack of fruit, seeds or flowering structures suggested it was

collected before its reproductive structures emerged, implying the burial event occurred in winter

(Felger et al. 1980:272).

2.2 California Channel Islands: Kelp Forests and Nearshore Environments

The California Channel Islands consist of eight islands located off the coast of southern

California. They are divided into two geographical groupings, the northern Channel Islands,

consisting of Anacapa, Santa Cruz, Santa Rosa, and San Miguel Islands, and the southern

Channel Islands of Santa Catalina, Santa Barbara, San Clemente, and San Nicolas. Although the

Channel Islands are located in relative proximity, a mixture of geographic, oceanographic,

physical, and biological features produce unique nearshore communities on each island, dictating

local marine productivity and contributing to the diversity and abundance of marine resources

along their shores (Engle 1994; Schoenherr et al. 1999). The outer islands, San Miguel and San

Nicolas, reap the benefits of the colder nutrient rich waters of the California Current that extends

down the coast from northern California. Traveling northward and moving up from Baja

California, the California Countercurrent (or Davidson Current) brings warmer waters that bathe

Santa Catalina and San Clemente before moving out to the other islands. Fluctuations in water

temperature associated with these currents produces varying sizes of offshore kelp beds, and

different invertebrate compositions in intertidal environments on a single island, as well as among islands.

Californian kelp forests are composed primarily of large brown algae; the dominant subtidal species include the giant kelp *Macrocystis pyrifera* and the bull kelp *Nereocystis luetkeana* (Abbott and Hollenberg 1976; Mondragon and Mondragon 2003). Based on substantial differences in oceanic conditions among marine habitats along the coast of California, kelp forests surrounding the California Channel Islands have been placed within the "Southern California" biogeographic range extending from Point Conception, California to Punta Banda, Baja California, Mexico (Edwards 2004). These kelp forests are dominated by the canopy-forming giant kelp (*Macrocystis pyrifera*), along with stipitate subcanopy kelps (*Eisenia* and *Pterygophora*) and nonstipitate low-lying kelps (*Dictyoneuropsis* and *Laminaria*), with varying amounts of other kelps such as the surface canopy feather-boa kelp (*Egregia menziesii*) (Dayton 1985; Graham 2004; Graham et al. 2003; Mann 1973; North 1971; Rosenthal et al. 1974). Giant kelp forests sustain extremely varied and dynamic ecological communities, creating an extensive ecological web of interdependent species that benefit from the reduction in current intensity found in their immediate surroundings (Coyer 1986; Dayton 1985; Dayton et al. 1998; Foster and Schiel 1985; Graham 2004; Graham et al. 2003; Jones 1971; North 1971). Coastlines of the Channel Islands also harbor large surfgrass (*Phyllospadix* spp.) and eelgrass (*Zostera* spp.) meadows, anchored in shallow subtidal to sublittoral zones of rocky intertidal areas and exposed during low tides (Mondragon and Mondragon 2003).

Primary intertidal environments on San Miguel and San Nicolas islands include protected outer coast habitats, semi-sheltered coastlines often with offshore kelp beds, and open coast habitats, characterized as unprotected surf pounded shores. Within varying habitat types a range

of physical and biological factors influence the proliferation of associated biota (Brandon and Rokop 1985; Hinton 1987; Lewis 1964; Little et al. 2009; Ricketts et al. 1985; Stephenson and Stephenson 1972). The plethora of shell midden sites on the Channel Islands suggests that rocky intertidal communities were utilized extensively by humans. Rocky shores form relatively stable substrate, promoting high diversity and stable communities of the larger shellfish collected for consumption.

The archaeological sites discussed in this paper are located on the coast, overlooking rocky intertidal habitats with associated kelp beds (Figure 4). Midden constituents consist predominantly of black abalone (*Haliotis cracherodii*), California mussel (*Mytilus californianus*), and black turban snail (*Chlorostoma funebralis*), all of which are found in the upper to middle intertidal zone. Other common shellfish species include red abalone (*H. rufescens*) and wavy top shell (*Megastraea undosa*), found in the lower to subtidal zone, and sea urchin (*Strongylocentrotus* spp.), found in middle intertidal to subtidal zones, demonstrating that people collected from the full range of intertidal zones/habitats. Additional dietary species include brown turban snails (*C. brunnea*), several species of crab and chiton, and numerous limpet species.

2.3 Channel Islands Archaeology

The Channel Islands have a long and continuous record of human occupation, with the northern islands containing archaeological sites dated to almost 13,000 years ago and representing some of the oldest evidence for coastal lifeways on the west coast of North America (Erlandson et al. 2011b; Johnson et al. 2002; Rick and Erlandson 2012). Numerous studies investigating trans-Holocene human-environmental dynamics on the Channel Islands demonstrate that people relied on a relatively consistent suite of key resources through time

(Braje et al. 2012; Erlandson et al. 2005; Rick 2011), showing small-scale variable impacts on intertidal habitats (Braje et al. 2007; Erlandson et al. 2008, 2011a; Rick et al. 2005a, 2008). General subsistence trends for the region suggest that shellfish provided a dietary staple during the Early and Middle Holocene, with the use of near and offshore fisheries increasing through time, replacing shellfish as a dietary staple during the Late Holocene (Braje et al. 2012; Erlandson et al. 2009; Glassow 1993; Kennett 2005; Rick et al. 2005a). The importance of marine mammal and cetacean hunting varied through time depending on location and the productivity of island and offshore rookeries (Braje et al. 2011; Colten and Arnold 1998).

3. Archaeological Sites and Methodology

3.1 Cave of the Chimneys (CA-SMI-603)

Cave of the Chimneys, located on the northeast coast of San Miguel Island, is a multi-component site containing approximately 7,500 years of human occupation. The rockshelter currently sits on a steep cliff face roughly 12 meters above a rocky coastline and is accessible by a narrow ledge on the southeast side of the shelter (Figure 5). The cave consists of andesitic conglomerate in a sandy matrix and appears to have been formed by marine erosion during high interglacial sea levels of the Pleistocene. The rockshelter measures approximately 10 meters deep by 12 meters wide with a skylight measuring roughly 1.5 meters in diameter. The large east facing entrance provides adequate lighting and protection from the strong northwesterly winds that pummel San Miguel Island most of the year (Johnson 1973:63). Sediments fill the site to less than one meter toward the back of the rockshelter and gently slope downward forming an apron at its mouth. Deposits are intact, finely stratified, and extremely well-preserved.

Archaeological excavations revealed seven distinct, chronologically intact stratigraphic layers representing intermittent occupational phases that were radiocarbon dated to between

about 8,600 and 1,000 cal BP (Table 1). A total of 1,588 liters was excavated between 1997 and 1999. The exceptional preservation at this site is evidenced by delicate strands of seagrass cordage found in the basal components and dated to the Early Holocene (Vellanoweth et al. 2003). Faunal constituents, including over 122 kg of shell and over 2 kg of bone (predominantly fish), demonstrate the importance of rocky intertidal and nearshore habitats to site inhabitants (Ainis 2012; Ainis et al. 2011; Ainis and Vellanoweth 2012; Rick et al. 2005b; Vellanoweth et al. 2002).

3.2 CA-SNI-40

Situated on the northwest coast of San Nicolas Island, CA-SNI-40 is a large linear sand dune with paleosols and occupational middens, measuring approximately 1 km long (Figure 6). The surface of the site resembles a red abalone midden, though erosional exposures and controlled excavations revealed several discrete deposits within two main components dated to between 4200 and 3800 cal BP (Table 2). A Middle Holocene cemetery located on the east end of the dune was excavated in the late 1950s and dated to the same time period as the midden (Reinman and Townsend 1960). Many artifacts from the cemetery correspond directly with items uncovered in the midden, suggesting continuity between the cemetery and associated midden at this site. Recent excavations took place between 2010 and 2011. Five loci were sampled and 30 1 x 1 meter units were excavated, removing 8,185 liters of archaeological materials and soil matrix. The samples discussed here are from two 1 x 1 meter units (11 and 12A) in Locus E, located on the top of the dune. The components are primarily comprised of red (*H. rufescens*) and black abalone (*H. cracherodii*), wavy top shells (*Lithopoma undosa*), and other rocky intertidal shellfish and crustacean taxa along with the bones of teleost fishes, elasmobranches, sea mammals and marine birds. A wide variety of artifacts in various stages of production,

11

including several types of Olivella (*Callianax biplicata*)beads, abalone nacre sequins, bone tools, and pendants made from imported soapstone was uncovered during excavations. The relatively large size of the midden deposit at this site and the short temporal chronology of radiocarbon dates suggests CA-SNI-40 was utilized extensively for a brief period of time.

3.3 Analytical Methods

The small gastropods analyzed in this study were excavated from sites CA-SMI-603 and CA-SNI-40 using standard stratigraphic methods of recovery and recordation. The minimum number of individuals (MNI) was calculated for each taxonomic designation using apices (though most shells were whole due to their small size), and all shell remains were weighed using a digital scale to two decimal places. All identifications were made to the lowest taxonomic level possible using comparative collections at the Los Angeles County Natural History Museum, California State University, Los Angeles, and the University of Oregon, as well as multiple reference books (Allen 1969; Brandon and Rokop 1985; Carlton 2007; Hinton 1987; McLean 1978; Morris 1966; Morris et al. 1980; Rehder 1981).

Density measures were calculated by dividing the minimum number of individuals (MNI) for each taxonomic group over the excavated volume (m³) for each stratum and feature. Because identifications of small gastropods were not always possible at the species level, we calculated taxonomic richness of each stratum by counting the total number of taxonomic categories identified therein. An analysis of covariance (ANCOVA) was used to investigate changes in taxonomic richness through time. Along with shifts in foundation species, changes in taxon richness have the potential to illuminate shifts in community composition of intertidal gastropods (e.g., Needles and Wendt 2013). Diversity and equitability measures, utilizing richness and abundance data from each taxonomic category, were used to describe the heterogeneity of

12

analyzed samples. The Shannon-Weaver function (Reitz and Wing 2008) was used to calculate

taxonomic diversity (H') measured as:

$$H' = - \Sigma(p_i) (\text{Log}_e \, p_i)$$

where H' is the heterogeneity measurement of the sample; p_i is the relative abundance of each

species or genus within the sample (calculated using MNI of all identified small gastropods); and

$\text{Log}_e \, p_i$ is the logarithm of p_i. Equitability (V': equivalent to Pielou's evenness index J') was

measured as:

$$V' = H' / \text{Log}_e \, S$$

where H' is the Shannon-Weaver function and S is the total number of taxa (using lowest

possible taxonomic identifications) in each stratum or feature. Analyses of variance (ANOVA)

were computed to determine if significant differences in species density among strata at each site

were present. The use of density values rather than MNI allowed us to factor out sample size as a

contributing variable. Non-parametric contingency tests (G-Test of Independence) were used to

distinguish similarities or differences in community composition of seaweed associates, gravel

dwellers, mollusk associates, and rock and boulder dwellers; and investigate changes in the

relative proportions of shellfish from our four categories (Type 1-4, see Table 3) both within and

between archaeological sites. ANCOVA and ANOVA tests were run in SAS 9.2 and G-Tests

were run in BiomSTAT (Sokal and Rohlf 2012). All G-values are reported with Williams

correction, degrees of freedom (df), and p values expressed as <0.05 with $\alpha = 0.05$ unless

otherwise noted.

4. Results

Excavations of Unit 1 at CA-SMI-603 yielded a total of 122 kg of shell identified to 78

species, 16 genera, and seven higher taxonomic levels (Ainis 2012). A total of 42 kg of shellfish

remains was recovered from Units 11 and 12A at CA-SNI-40 and identified to 42 species, 11 genera, and three higher taxonomic levels. A total of 4,568 individuals belonging to 34 genera and 61 species of small gastropods was identified in this study, excluding larger shellfish taxa known to be of dietary value. We grouped the small, non-dietary gastropod shells into four categories (Type 1-4) based on substrate, habitat, and associations with other shellfish. Our categories are defined in Table 3 and general ecological information for each species is presented in Table 4.

4.1 Application and Interpretation

4.1.1 *Intrasite Analysis: CA-SMI-603*

Analysis of small gastropods from Cave of the Chimneys resulted in the identification of 3,305 individuals belonging to 28 genera and 49 species (Table 5), with seaweed and seagrass associates comprising close to 26% of the MNI of small gastropods. The assemblage is dominated by small limpets and slipper snails (Figure 7). Diversity and equitability indices reveal a high diversity of taxa accompanied by relatively high equitability throughout the deposit (Figure 8), indicating a fairly even distribution of a large variety of taxa. An analysis of covariance demonstrated that there is no linear relationship between taxonomic richness and time (strata) at this site (ANCOVA; $F_{1,4} = 0.13$, $p = 0.7375$). While richness oscillates through time (Table 6), densities follow a downward trend (Figure 9), indicating that although most taxa continue to be present through time their numbers decline. Sample size can be ruled out as a factor affecting the decline in density (from 3,367 MNI/m³ in Stratum VII to 1,285 MNI/m³ in Stratum II), as Strata II and IV contain the largest excavated volumes (see Table 6 and Figure 9 for density values and excavated volumes). Furthermore, we found that differences in species densities among strata are highly significant and not related to sample size (ANOVA; $F_{65,300} =$

6.72, $p < 0.0001$). Overall, we found significant differences between strata and relative

abundances of shells in the four categories were significant (G = 155.868, df = 15, $p = 0$).

However, these data contained non-significant subsets that show similarities among some strata

and the four shell types. These subsets include: Strata VI and VII (G = 23.5391) and Strata II, III,

and VI (G = 22.6048), suggesting that primary differences in frequency patterning occur between

basal deposits and upper components.

Interestingly, these data coincide with reconstructions of post-glacial shifts in giant kelp

forests off the coast of mainland California, which predict increased kelp forest biomass during

the Terminal Pleistocene and Early Holocene before declining rapidly as sea surface

temperatures rose in the Middle Holocene (Graham et al. 2010). Kelp forests surrounding the

Channel Islands were proposed to have reached peak productivity during the Early Holocene

followed by a significant decrease (50-80%) in kelp forest productivity and associated resources

by the later part of the Middle Holocene as climatic conditions warmed (Graham et al.

2010:404). Though tentative, it is possible that data patterning for small gastropod assemblages

at CA-SMI-603 reflect a decline in local kelp biomass between the time when Strata V and IV

were deposited, coinciding with declining kelp productivity as proposed by Graham and

colleagues (2010). On the other hand, changes in human settlement and land use patterns are

equally valid cultural variables that could explain the distribution of small gastropods at this site.

4.1.2 *Intrasite Analysis: CA-SNI-40*

Analysis of small gastropods from two units at CA-SNI-40 revealed 1,263 identifiable

individuals classified to 24 genera and 38 species (Table 7), with seaweed and seagrass

associates making up roughly 22% of small gastropods. This assemblage is dominated by small

limpets (Figure 10). Diversity and equitability measures show relatively high diversity, with

slight drops in transitional strata (Stratum IIB) and discrete features, and consistently high equitability among taxa (Figure 11). We found no linear relationship between taxonomic richness and time (strata) at this site (ANCOVA; $F_{1, 2} = 0.40$, $p = 0.5929$). Although richness is relatively consistent in the two main strata (IIHC and IIHR), it drops in the transitional layer (IIB) and in the distinct component designated as "dark feature" (Table 6). Density measures are highest in the "dark feature" and decrease slightly through time (Figure 12). Percentages of MNI for kelp and seagrass associates confirm density measures, following a similar pattern of lower percentages through time with a spike in the "dark feature" (Table 6). Differences in species densities among strata are significant (ANOVA; $F_{44, 123} = 9.73$, $p = <0.0001$). Overall, differences between strata relative abundances of shells in the four categories are significant (G = 28.3468, df = 9, $p = 0.0008$). However, these data contained non-significant subsets that show similarities among some strata and the four shell types, including Strata IIHR and IIHC (G = 14.6331). This suggests that primary differences occur in the transitional layer and discrete feature.

The small gastropod assemblage from the "dark feature" reveals a drop in taxonomic richness along with an increase in density of seagrass and seaweed associates, which is 239% higher in this feature than in the surrounding midden (IIHC). The seaweed limpet (*Lottia insessa*) reaches its highest density in this component, where it makes up almost 22% of small gastropods, with combined seaweed and seagrass associates composing over 36% of small gastropod MNI, the highest in any deposit discussed here. This high concentration of seaweed associates marks the presence of a distinct activity area where kelp was likely processed in some way and potentially eaten. It is possible that this feature is the partial remains of a "shell bake,"

in which edible shellfish were wrapped in seaweed and steamed, a hypothesis supported by the unusually high density of seaweed associates.

5.1 Intersite Comparison

Data from CA-SMI-603 and CA-SNI-40 are presented and compared to provide examples of inferred seaweed and seagrass harvesting through the identification and analysis of non-dietary shells, and to explore tentative interpretations signaled by the presence of ancillary shells. Our combined analysis of the shells recovered from two distinct site types on the California Channel Islands identified a total of 4,568 small gastropods belonging to 75 taxa. Diversity and equitability measures fall within very similar ranges and persist through time at both sites despite distinct differences in site type, location, and chronology. Consistently high diversity and evenness measures suggest that a wide variety of small gastropods was included in these deposits without dominance of any single taxon. Taxonomic richness fluctuates through time at both sites and is lower at CA-SNI-40 than at CA-SMI-603, possibly reflecting the distance of each site from the coast and/or differential preservation due to the relative protection afforded deposits in rockshelters vs. those left exposed to the elements at open-air dune sites. Alternatively, taxonomic richness could reflect small scale differences in the distribution and abundance of shellfish communities during particular times in the past, configurations controlled by the intensity of shellfish harvesting by humans and other predators, as well as by a variety of environmental factors.

Although richness measures are variable between sites, overall density measures are surprisingly similar (Table 6) as are relative percentages of shells belonging to each of the four categories (Table 3). Although decreasing trends in density are evident at both sites, the trend is more pronounced at CA-SMI-603, which contains a much longer occupational history.

Decreasing trends in density could be reflective of a number of factors pertaining to human decision making and/or the environment, including variables such as changes in human harvesting practices and foraging locations, shifts in site function and settlement, regional or local environmental fluctuations, or decreasing kelp forest biomass as proposed by Graham et al. (2010), which in turn affects species recruitment, settlement, and productivity. Our primary goal for this paper, however, is to highlight the use of marine macrophytes as inferred by epifauna in archaeological contexts and to provide interpretive possibilities for future studies.

Comparing total MNI values for small gastropods at each site reveal differences in community composition (Type 1-4) between sites (G = 20.8549, df = 3, p = .0001). Differences in the composition of small gastropod assemblages for Early (CA-SMI-603, Strata VI and VII), Middle (CA-SMI-603, Strata III-V; CA-SNI-40, all components), and Late (CA-SMI-603, Stratum II) Holocene time periods reveal significant differences among temporal periods (G = 78.6775, df = 9, p < .0), with Middle and Late Holocene components forming a non-significant subset (G = 5.9531). This similarity in relative frequencies between Middle and early Late Holocene components at CA-SMI-603 and CA-SNI-40 indicate that similar proportions of shells from each type were collected during roughly the same time period on two different islands, and that the Early Holocene components vary significantly from later components.

While there are changes in relative percentages and sizes of key shellfish taxa in these deposits, the primary suite of dietary shellfish is fairly consistent, suggesting a slight depression in intertidal productivity due to extensive harvesting during a relatively short time span. If this decrease in density reflects decreasing populations through time, it could be reflective of diminished offshore kelp beds exposing rocky intertidal taxa to increased wave action and disturbance, limiting settlement and survival. The overall trend of consistently high taxonomic

18

diversity at both sites through time testifies to the relative high stability of rocky shore

communities, which rapidly recover from exploitation in most instances (see Dye et al. 1994;

Hockey and Bosman 1986; Moreno et al. 1986), and likely speaks to the knowledge of islanders

who understood how to intensively harvest intertidal shellfish without causing primary species

extinctions or severe ecosystem disruption.

5.2 Behavioral Implications

Although non-dietary shells are likely riders/hitchhikers and thus incidental inclusions to

archaeological middens, the question we wish to explore is, how were they included and what

does their presence in an archaeological shell mound indicate? As some of these small species

live directly on other larger shellfish their presence indicates the harvesting and use of their host

species, while other small gastropods can be used to infer the harvesting of the marine vegetation

they live on and consume.

5.2.1 Shellfish Harvesting Inferences

Small rider species, such as *G. norrisiarum*, can be useful in instances where the host

shell may no longer be present because it was utilized in tool production or for ornamental

purposes. This small slipper shell is known to live predominantly on *Norrisia norrisi*, as implied

by its name. While excavated materials from CA-SMI-603 revealed only one identifiable

fragment of *N. norrisi*, the presence of *G. norrisiarum* in several strata suggests that perhaps *N.*

norrisi was collected and brought to the site but was not incorporated into the midden because

the shell was utilized in the manufacturing of ornaments and fishhooks. Interestingly, these two

species of shellfish appear together in both units sampled from CA-SNI-40; strata containing *N.*

norrisia also contain *G. norrisiarum*, but neither is present in deposits without the other.

5.2.2 Indirect Evidence of Seaweed and Seagrass Harvesting

Preservation biases often exclude perishable materials from being unearthed in archaeological contexts, however, this does not necessarily mean that they were not utilized, but only that their remains did not preserve. Although in most cases direct evidence of seaweed and seagrass harvesting has long disappeared from the archaeological record, either because of human consumption, processing, and/or site-specific taphonomic factors, indirect evidence in the form of seaweed associates is a veritable untapped reservoir of data. We suggest that the presence of Type 1 gastropods in archaeological contexts is the result of kelp and seagrass harvesting by humans in the past. The relative percentages of these shells in sites through time may be able to act as proxies for changes in harvesting intensity and potentially provide information regarding fluctuations in kelp and seagrass patches and regional or local environmental changes.

As described in ethnohistoric accounts from Western North America (see section 2.1), the relative ease of drying and storing seaweeds makes them highly valuable as a storable non-meat food item and potential fuel source. Each family, genus, and species of macroalgae contains variable amounts of humanly digestible nutrients, with relative percentages also varying within species due to oceanographic, climatic, and seasonal differences (Floreto and Teshima, 1998; Kaehler and Kennish, 1996; Mabeau and Fleurence, 1993; Rupérez, 2002). The relatively lower protein content and higher dietary fiber content of brown algae (Laminariales and Fucales) in particular (Khotimchenko et al., 2002; Kumar et al., 2008) allows these "sea vegetables" to fulfill this human dietary requirement lacking in protein-rich marine diets. Marine macroalgae could thus serve as a valuable dietary alternative to terrestrial botanical resources, especially to islanders subsisting predominantly on marine resources. Though no firsthand accounts of Channel Islanders utilizing kelp for food survive, it is imperative to bear in mind that a lack of

direct ethnographic information is anything but definitive. Furthermore, the rich record of coastal people using similar marine resources north and south of the Channel Islands (see section 2.1), where it is similarly plentiful, suggests their possible use by analogy. The bountiful resources provided by lush kelp forests along the Circum-Pacific Coast likely acted as a veritable ocean "highway" (Erlandson et al. 2007), dispensing similar suites of marine resources and coastal habitats as humans ventured further south into the Americas.

5.3 Paleo-environmental Implications

This study highlights the potential utility of identifying and analyzing all shells found in archaeological middens as a suite of species somewhat akin to a fossil assemblage, albeit an archaeologically biased assemblage. While clearly not equivalent to a naturally accumulated death assemblage, the addition of 76 taxa to the frequently analyzed suite of larger dietary mollusks provides the best data set possible for reconstructing the littoral paleo-ecology of coastal areas frequented by humans in the past, especially in the absence of naturally accumulated fossil records. Although we suggest this as a tentative hypothesis, it has been proposed by environmental scientists that the often ignored, small, non-dietary shells in archaeological middens are the most useful for paleoenvironmental reconstructions (Limondin-Lozouet et al. 2013:62).

Type 4 species can contribute to our understanding of intertidal paleoecology and in some cases the health of local kelp patches. Offshore kelp beds, and *Macrocystis* in particular, can be a limiting factor to widespread larval dispersal of intertidal dwelling limpets, as they can decrease currents and wave action in its immediate surroundings (Turner 2003; Shanks et al. i.p.). This links the presence of offshore kelp beds to higher local settlement for limpets living on rocks in the intertidal zone, and suggests that diminishing kelp beds could result in reduced local

populations for these boulder dwelling species and vice versa. Shanks et al. (i.p.) found a significant correlation between local recruitment of *Lottia scabra*, an intertidal rock dwelling limpet, and the presence of *Macrocystis* in the intertidal. In addition, Graham's (2004) study of associated taxa in southern California kelp forests found that several carnivorous mollusks (often found on rocks and boulders) were observed significantly more often in kelp forested habitats over deforested areas. While these species are not direct kelp or seagrass associates in the sense that they do not live directly on marine vegetation, they have a strong association with kelp forest habitats and their presence or absence through time could speak to the relative health of local kelp forest patches. Carnivorous species identified by Graham (2004) and found in the assemblages discussed here include *Fusinus kobelti*, *Homalopoma luridum*, and *Pseudomelatoma torosa*. In addition, the predatory *Conus californicus*, was found by North (1971) to be common in Southern California kelp beds even though it is not a direct kelp associate. Naturally, a wide range of biological, ecological, and environmental factors intersect and must be teased apart to reach a conclusive understanding of what is causing shifts in taxonomic richness and species density. Though this is beyond the scope of this paper, we believe it is an interesting possibility requiring further investigation.

5.4 Methodological and Ecological Implications: Human Impacts

Although temporal scales for archaeological assemblages are often longer than ideal for ecological studies, shell middens around the globe contain substantial evidence that human harvesters impacted the size structure and relative abundances of exploited populations (Jerardino 1997, 2010; Langejans et al. 2012; Mannino and Thomas 2002; Parkington, 2008; Sealy and Galimberti 2011; Tonner 2005; and others). Nevertheless, factors such as species interactions and trophic level dynamics, and changes in oceanographic temperature and sea level

complicate anthropogenic induced effects of predation and its clues in the archaeological record (see Bailey and Milner 2008; Dayton et al. 1998; Mannino and Thomas 2002).

Human harvesters in intertidal shellfish beds exert a disproportionate effect on rocky shore communities, significantly altering community dynamics as they collect much larger quantities with higher efficiency than other predators (Adessi 1994; Castilla and Durán 1985; Hockey 1994; Moreno et al. 1984; Oliva and Castilla 1986; Ortega 1987). Although selective exploitation of shellfish in rocky intertidal areas can disrupt space mosaics causing significant changes in community structure, these disturbances are not permanent due to the dynamic nature of biological systems, and major changes may occur again when exploitation ceases or switches to another species (Durán and Castilla 1989; Dye 1992; Hockey and Bosman 1986; Lasiak 1991; Moreno et al. 1984, 1986; Oliva and Castilla 1986). In addition to impacts on exploited populations, non-targeted species can also experience indirect effects, such as altered size structures and alterations in species abundances (e.g., Roy et al. 2003). Lindberg et al. (1998) found that when the large and dietarily important limpet, *Lottia gigantea*, was removed from intertidal boulders, small limpets, such as *L. scabra,* often increased in density. Suggesting that increases in relative abundances of small, non-dietary limpets may also be indicative of intensive human harvesting of larger dietary species.

We suggest that small, non-dietary shells in coastal middens can contribute to a more complete (though not exhaustive) understanding of nearshore community composition and dynamics in the past. By identifying the full suite of represented species in archaeological assemblages, it is possible to infer the state of littoral ecosystems and how they shifted through time, allowing us to better reconstruct possible consequences of human predation in these heavily utilized primary resource habitats. Relative percentages of small gastropods can be used

in conjunction with reduced abundances and shell size changes of purposefully harvested shellfish to support or negate perceived impacts. The presence of these species as well as their detailed analysis (e.g., stable isotope geochemistry, trace elemental analysis, etc.) can provide the environmental parameters against which anthropogenic impacts of marine resources can be compared. We believe that when all shells, including small, non-dietary mollusks, uncovered in coastal midden deposits are analyzed together as a suite of taxa, a more complete picture of the paleo-community is attainable. Adding ancillary mollusks can increase taxonomic richness counts from 10-20 dietary taxa to close to 100 total taxa as seen at CA-SMI-603 (Ainis 2012), thus greatly increasing the potential for nearshore reconstructions. Reconstructing the most representative population possible can contribute to our understanding of how these ecosystems were affected and potentially managed by humans in the past.

6. Conclusions

This study demonstrates some of the types of data that can be gleaned from non-dietary shells accidentally incorporated in archaeological shell middens and suggests tentative implications for further investigation. The behavioral implications of this study suggest islanders from San Nicolas and San Miguel were utilizing very similar harvesting strategies despite typological, spatial, and temporal differences between sites, conforming to regional patterns and similar nearshore ecology on both islands. The methodological significance of this study lies in the discovery that small, non-dietary shells in coastal middens have stories to tell. Although they may not contain information on direct subsistence strategies, they can be used to infer harvesting of marine resources like kelps and seagrasses and potentially inform us on the community structure and relative health of local kelp forests and intertidal communities in the past. We have demonstrated that small gastropods can be used to infer kelp and seagrass harvesting; the

presence of shellfish species whose shells were utilized and therefore no longer present in an archaeological assemblage; and tentatively support environmental data demonstrating shifts in kelp forest productivity. Furthermore, we suggest the possibility that ancillary shells may be used to signal paleoenvironmental factors such as changes in climate and sea surface temperature and nearshore ecology, though distinguishing between these interrelated factors is beyond the scope of this paper.

Whereas taxonomic identifications presented here are limited to the southern California region, the concept of identifying small shells and investigating the ecological implications they may contain is not limited to any one region or area. The identification of numerous seaweed and seagrass associates is a step towards better understanding the use of these highly perishable but extremely useful resources in the past. The application of these types of data has the potential to reveal new patterns and more in-depth understandings of coastal lifeways around the globe.

Acknowledgments

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Table 1. A Radiocarbon Chronology for Cave of the Chimneys (CA-SMI-603).

Unit 1 Stratum/Level	Lab number	Material dated	Uncorrected ^{14}C age (RYBP)	^{13}C/^{12}C Adjusted	Adjusted age range[2] (cal BP, 1 sigma)
I	OS-85199	Marine Shell	N/A	1700 ± 25	1067 : 956
II / 1	OS-85200	Marine Shell	N/A	2800 ± 25	2311 : 2191
II / 2	OS-85201	Marine Shell	N/A	2930 ± 25	2461 : 2331
II	Beta-115556	Marine Shell	2550 ± 60	2980 ± 60	2575 : 2352
II / 3	OS-85202	Marine Shell	N/A	3560 ± 25	3268 : 3128
II / 4	OS-85203	Marine Shell	N/A	4010 ± 25	3804 : 3672
III	Beta-115557	Marine Shell	3830 ± 70	4270 ± 70	4188 : 3955
Probe B: 15-20 cm	Beta-12454	Marine Shell	N/A	4430 ± 60	4403 : 4207
IV	Beta-115558	Marine Shell	4010 ± 70	4450 ± 70	4426 : 4208
V	Beta-115559	Marine Shell	4030 ± 60	4480 ± 60	4445 : 4245
Probe B: 15-20 cm	Beta-14364A	Charcoal	N/A	3930 ± 60	4497 : 4257
Probe B: 35-40 cm	Beta-14367A	Charcoal	N/A	3940 ± 60	4512 : 4292
Probe B: 35-40 cm	Beta-12455A	Marine Shell	N/A	4560 ± 60	4841 : 4683
VI	Beta-129099	*Olivella bead*	6890 ± 70	7300 ± 70	7623 : 7483
VI	Beta-136695	Marine Shell	7440 ± 60	7300 ± 60	8180 : 8019
VI	Beta-122712	Marine Shell	7690 ± 80	8120 ± 80	8456 : 8268
VII	Beta-122713	Marine Shell	7220 ± 70	7650 ± 70	7963 : 7805
VII	Beta-136696	Marine Shell	7310 ± 80	7740 ± 80	8070 : 7876

Beta dates compiled from Kennett (1998), Vellanoweth et al. (2002), and Vellanoweth et al. (2003). OS dates compiled from Ainis and Vellanoweth (2012). Dates were calibrated via Stuiver and Reimer's (1993, 1999) Calib 6.0.1 using a ΔR of 225 ± 35 years, and adjusted according to Hughen et al. (2004). ^{13}C/^{12}C ratios were determined by the radiocarbon lab.

Table 2. A Radiocarbon Chronology for CA-SNI-40.

Locus	Unit	Stratum/ Level	Lab Number	Material Dated	Un-calibrated ^{14}C Age Range (RYBP)	Calibrated Age Range (BP)	
						One Sigma:	Two Sigma:
Auger	#4	-	OS-105788	*S. bifurcatus*	4720±45	4788-4617	4821-4523
A	1	IA/1	OS-85189	*H. cracherodii*	4360±30	4280-4125	4368-4064
A	2	I/1	OS-85188	*H. rufescens*	4370±20	4282-4141	4357-4082
A	2	IIA/1	OS-85191	*H. cracherodii*	4380±35	4308-4142	4385-4081
B	3	II/1	OS-85195	*H. cracherodii*	4280±30	4147-3995	4232-3935
B	3A	Pit Feature	OS-85192	*H. cracherodii*	4390±30	4318-4157	4389-4099
C	5	I/2	OS-85197	*H. cracherodii*	4340±35	4242-4083	4343-4004
C	6	Ochre Feature	OS-85196	*H. cracherodii*	4130±30	3953-3821	4037-3728
C	6	IIIO/2	OS-96261	*H. cracherodii*	4120±25	3941-3813	3995-3714
C	5/6A	IIHR/1	OS-105787	*H. rufescens*	4440±40	4392-4238	4466-4138
C	5/6A	IIHC/1	OS-105782	*H. cracherodii*	4440±30	4386-4247	4427-4151
C	5/6B	IU/1	OS-96260	*H. cracherodii*	4120±25	3941-3813	3995-3714
D	7	I/4	OS-85190	*H. cracherodii*	4070±25	3861-3726	3931-3671
E	9	IA/1	OS-85194	*H. cracherodii*	4150±30	3969-3836	4064-3774
E	11	IIHC/1 (Dark Feature)	OS-105783	*M. californianus*	4440±30	4341-4182	4401-4118
E	12	IA/1	OS-85193	*H. cracherodii*	4070±35	3867-3719	3951-3661
E	12	II/1	OS-85198	*Diomedeidae*	4480±30	4423-4286	4501-4223
E	12	IIHC/trans	OS-105786	*H. cracherodii*	4370±40	4303-4128	4389-4064
E	12A	IIHC/SU/1	OS-96262	*H. cracherodii*	4170±25	3982-3866	4057-3830
E	12A	IIHR	OS-105789	*H. cracherodii*	4180±25	4011-3871	4078-3826
E	10A/12A	Ash Feature	OS-105784	*Chlorostoma* sp.	4300±30	4206-4050	4264-3961
E	10A/12A	Ash Feature	OS-105785	*M. californianus*	4220±30	4072-3930	4140-3862
E	10A/12A	Ash Feature	OS-96263	*H. cracherodii*	4230±35	4085-3934	4160-3859

Dates were calibrated via Stuiver and Reimer (1993, 1999) Calib 6.0.1 using a ΔR of 225±35 years, and adjusted according to Hughen et al. 2004.

Table 3. Categorical Definitions of Non-Dietary Gastropods in Archaeological Shell Middens.

Category	Characterization	Habitat/ Substrate	Definition and Association	Inference	CA-SMI-603 MNI	CA-SMI-40 MNI
Type 1	Seaweed and Seagrass Associates	Kelpbeds and seagrass meadows	Taxa that live on, or are closely associated with, marine macrophytes; some taxa are species specific to certain kelps and seagrasses.	Can be used to infer harvesting of marine macrophytes and transportation of marine vegetation back to the archaeological site.	852 (27%)	234 (22%)
Type 2	Sand and Gravel Dwellers	Coarse sand and gravely substrate underlying kelpbeds and seagrass meadows	Taxa that live in the coarse sand and gravely substrate often underlying kelpbeds and seagrass meadows; some are also often found on the base and holdfasts of kelps and seagrasses.	Possible use as indicators of marine macrophyte harvesting by pulling up entire stocks including bases and holdfasts.	32 (1%)	23 (<2%)
Type 3	Mollusk Commensals	Live on other larger shellfish in the intertidal zone	Taxa that are known associates of other mollusks in the intertidal zone; some are found on a variety of taxa and others are species specific.	Can be useful in instances where the host shell is no longer present because it was used to manufacture tools or ornaments.	1,392 (44%)	432 (40%)
Type 4	Rock and Boulder Dwellers	Rocks and boulders in upper intertidal to sublittoral zones	Taxa that live on large rocks and boulders at various depths in the intertidal zone; possible associations with all species of shellfish gathered for subsistence purposes.	Possible explanations for the presence of these shells include: scraping of rocks and boulders for mussels, turban snails, etc.; harvesting clusters of shells rather than individuals; accidental dislodging by strands of kelp and seagrasses that were dragged and collected in the intertidal zone.	1,908 (60%)	741 (69%)

Table 4. Ecological Profiles for Mollusk Taxa.

Scientific Name	Common Name	Category/Type (see Table 3)	Habitat Zone	Habitat Notes and Associations	Trophic Type and Food Preference
Acanthinucella (Acanthina) punctulata	Spotted thorn drupe	1, 2	intertidal and sublittoral	clean coarse sand among eelgrass (*Zostera*), coralline algae, and rocks	predators - primarily eats Littorines
Acmaea mitra	Whitecap limpet	3, 4	low intertidal, subtidal	low intertidal/pools	herbivore - eats encrusting algae *Lithothamnion*, *Lithophyllum*
Acteocina culcitella	Pillow barrel-bubble, Western barrel-bubble	2	high intertidal to 46m	bays and lagoons in sand and mud	predator - eats foraminifera
Alia carinata	Carinate dove snail	1	low intertidal to 15m	kelp stipe/holdfast, abundant in surf grass (*Phyllospadix*) and eelgrass (*Zostera*) habitat and in shallow kelp forests	herbivore/detritivore
Alia tuberosa	Variegate dove snail	1	sublittoral zone	Kelp and eelgrass (*Zostera*), drift algae, sand and gravel under kelp	epifaunal predator
Amphissa spp.	Dove shells, Dove snails	4	low intertidal and subtidal	grazer on rocks	herbivore
Amphissa versicolor	Variegate Amphissa,	4	intertidal to 46m	rocky intertidal	carnivore
Callianax biplicata	Purple olive shell	2	low intertidal to 50m	sandy bottoms/beaches	omnivore/detritivore Kelp blades and detritus
Calliostoma canaliculatum	Channeled topsnail	1	low intertidal to 37m	lives on kelp (*Macrocystis* and *Cystoseira*)	herbivore/omnivore - kelp, diatoms, bryozoans, hydroids, detritus
Calliostoma ligatum	Blue topsnail	1	low intertidal to 54m	found in and around kelp beds (on *Macrocystis* and *Cystoseira*) and eelgrass (*Zostera*)	herbivore/omnivore - kelp, diatoms, bryozoans, hydroids, tunicates, detritus
Calliostoma spp.	Top snails	1	low intertidal to sublittoral	species specific to kelps, some species specific to portions of stipe/blades/holdfasts	herbivore/omnivore - kelp, diatoms, bryozoans, hydroids, detritus
Cerithiopsis carpenteri	Carpenter's miniature cerith	4	subtidal to 30m	common under rocks at low tide and in sublittoral	omnivore: primarily sponges
Clathurella canfieldi	-	1, 2	intertidal	in sand among surfgrass/eelgrass roots	predator - polychaete worms
Conus californicus	California cone	2, 4	low intertidal to subtidal	rock crevices, sand pockets	predator - worms, mollusks, crustaceans, buried in sand when not eating
Crepidula aculeata	Spiny slipper snail	4	low intertidal to 60 m	common on rocks and hard debris in shallow subtidal	ciliary feeder on detritus
Crepidula coei	-	3, 4	intertidal	common on gastropods - *Polinices* (moon snails)	ciliary feeder on detritus
Crepidula	Northern white	4	intertidal to	attaches to rocks or dead shells	ciliary feeder on

41

nummaria	slipper snail		subtidal		detritus
Crepidula onyx	Onyx slipper snail	4	intertidal to 90m	smaller males often stack on top of larger females	ciliary feeder on detritus
Crepidula perforans	Western white slipper snail	4	intertidal	under rocks, resides on interiors of dead shells	ciliary feeder on detritus
Crepidula spp.	Slipper snails	4	intertidal to subtidal		ciliary feeder on detritus
Crepipatella lingulata	Wrinkled slipper snails	4	intertidal to 100m	on rocks/snail shells	ciliary feeder on detritus
Diodora arnoldi	Neat-rib keyhole limpet	4	low intertidal to 25m	undersides of rocks	herbivore
Diodora aspera	Rough keyhole limpet	4	low intertidal to subtidal	undersides of rocks	omnivore - prefers encrusting bryozoans but will eat algae
Diodora spp.	Keyhole limpets	4	intertidal to subtidal	undersides of rocks	omnivore
Epitonium tinctum	Tinted wentletrap, White wentletrap	3	low intertidal to subtidal	on sand, at base of sea anemones/feeds on tips of *Anthopleura* tentacles	predator - eats tips of *Anthopleura*
Fissurella volcano	Volcano limpet	4	intertidal, mostly middle intertidal	undersides of rocks	herbivore
Fissurellidae	Keyhole limpets, Slit limpets	4	intertidal to subtidal	on and under rocks and boulders	omnivore - feed on algae and detritus; some are carnivores and feed on sponges
Fusinus kobelti	Kobelt's spindle-shell	2	intertidal	sandy bottoms	carnivorous scavengers
Fusinus luteopictus	Painted spindle-shell	2	low intertidal to 40m	rocks	carnivorous scavengers
Garnotia adunca	Hooked slipper-shell	3	mid to low intertidal	on intertidal snail shells including *Calliostoma*, *Chlorostoma*, *Lirabuccinum*	ciliary feeder on detritus
Garnotia norrisiarum	Norris slipper shell	3	subtidal	commonly and primarily on *Norrisia norrisi* (and sometimes *Promartynia pulligo* shells)	ciliary feeder on detritus
Garnotia spp.	Slipper shells	3		attach to species specific host shells	ciliary feeder on detritus
Hipponix panamensis	Flat hoofsnail	4	intertidal to 46m	clings to rocks, algae	sedentary limpet, obtain food with extensible snout
Hipponix tumens	Ribbed hoofsnail	4	low intertidal	rock crevices	sedentary limpet, obtain food with extensible snout
Homalopoma baculum	Berry dwarf turban	4	mid intertidal	under rocks	epifaunal predator
Homalopoma luridum	Dall's dwarf turban	4	intertidal to sublittoral	rocks (note: shells are often used by hermit crabs)	epifaunal predator
Homalopoma spp.	Dwarf turbans	4	intertidal to sublittoral	rocks	epifaunal predator
Lacuna marmorata	Chink shell	1, 4	mid to high intertidal	rocks, seaweed and seagrasses (*Phyllospadix* and *Zostera*)	herbivore - algae -- is eaten by *Leptasterias*
Lacuna spp.	Chink shell	1	mid to high intertidal	species specific to kelps and sea grasses in moderately shallow water	herbivore

Lirularia spp.	Minute trochids	1, 2	intertidal to sublittoral but mostly sublittoral	on gravel/loose rocks/algae, common at the base of kelp and on eelgrass (*Zostera*)	herbivore
Littorina keenae	Flat periwinkle	4	In the splash zone	rocks in the high tide line	herbivore: diatoms, films
Littorina plena	Black periwinkle	4	high intertidal zone	rocks with algae, mussels and barnacles	herbivore
Littorina scutulata	Checkered periwinkle	4	common in upper intertidal zone, lower than L. planaxis	rocks	herbivore: diatoms, microscopic algae, lichens as well as macroalgae
Littorina spp.	Periwinkles	4	upper and high intertidal	on rocks in shallow water along shoreline	herbivore
Lottia asmi	Black limpet	3	mid to low intertidal	attaches to host shell or rock, can move from one to another, found on *Chlorostoma funebralis* (primarily) or *C. gallina*, but also *Mytilus* and rocks	herbivore: microscopic algae on host shell/rocks
Lottia digitalis	Ribbed limpet, Fingered limpet	4	upper intertidal and splash zone	vertical or overhanging rock faces, exposed rocky coasts, occasionally on gooseneck barnacles (these have lighter morph)	microscopic algae and newly settled barnacles
Lottia fenestrata	Fenestrate limpet, Chocolate limpet	4	mid to low intertidal	reef rocks and boulders adjacent to loose sand	herbivore
Lottia insessa	Seaweed limpet	1	low intertidal	common on stipes and holdfasts of *Egregia* (feather boa kelp)	herbivore: feed directly on the kelp, forming scars and eventually destroying it
Lottia instabilis	Unstable seaweed limpet	1	low intertidal, subtidal	kelp stipes (primarily *Laminaria setchelli* and *Pterygophora californica*)	herbivore: kelp stipes and other algae
Lottia ochracea	Yellow limpet	1, 4	one of few limpet species in sublittoral zone	in sublittoral depths under kelp and surfgrass (*Phyllospadix)* and the undersides of small rocks at low tide	herbivore: kelp stipes and other algae
Lottia palacea	Surfgrass limpet	1	low intertidal	common on blades of surfgrass (*Phyllospadix*) along open coast, occasionally on eelgrass	herbivore: feeds on superficial algae
Lottia paradigitalis	-	3, 4	high and mid intertidal	rocks, shells of turban snails and mussel (*Mytilus*)	herbivore
Lottia pelta (rock morph)	Shield limpet	4	mid to low intertidal	rocky reef, rocks and boulders	herbivore
Lottia pelta (dark seaweed morphology)	Shield limpet	1	mid to low intertidal	stipes and holdfasts of kelps (*Egregia* and others)	herbivore: kelps
Lottia persona	Masked limpet, Speckled limpet	4	high to mid intertidal	rocks	herbivore
Lottia rosacea	Rose limpet	2, 3	common in subtidal	associated with coralline algae	herbivore
Lottia scabra	Rough limpet	4, 3	mid intertidal	rocky reefs and boulders, often found on Owl limpet (*L. gigantea*)	herbivore: algal films

Species	Common name		Zone	Habitat	Feeding
Lottia scutum	Pacific plate limpet	4	mid to low intertidal	rocks	herbivore: algal films, crustose algae
Lottia strigatella	Checkered limpet	1, 4	middle intertidal to sublittoral under kelp	kelp beds, eelgrass (*Zostera*) roots, algae	herbivore: microscopic algae and diatoms
Lucapinella callomarginata	Hard-edged fleshy limpet	4	low intertidal to subtidal	underside of rocks	omnivore: primarily sponges (*Tetilla*), but will consume algal films
Mitromorpha aspera	Rough miter-form	2	intertidal	gravel at low tide and in sublittoral	epifaunal predator
Nucella emarginata	Emarginate dog winkle	3, 4	middle intertidal	rocks, mussel beds, often in association with *O. circumtexta*	predator: prey on *Mytilus*, barnacles (*Balanus*)
Nucella spp.	Dogwinkle	4	shallow intertidal	rocks	predator
Ocinebrina (Ocenebra) circumtexta	Circled rock shell	3, 4	intertidal, common in rocky crevices at midtide	rocks in heavy surf areas, often associated with barnacles (*Balanus*)	predator
Ocinebrina (Ocenebra) interfossa	Sculptured rock shell	4	intertidal to 100m	under rocks	predator, can drill into mollusks and barnacles
Ocinebrina (Ocenebra) lurida	Lurid rock shell	4	intertidal to 200m, common at low tide	on/under rocks, common in low intertidal in northern CA, rare in sublittoral in southern CA	predator, eats *Cryptochiton stelleri* and *Mytilus*
Ocinebrina (Ocenebra) minor	Minor rock shell	1, 2	sublittoral zone	not uncommon in sublittoral zone, particularly under kelp	predator
Ocinebrina (Ocenebra) spp.	Rock shell	4	intertidal to sublittoral	rocks and crevices, rocky bottoms	predator
Odostomia nota	Odostome	1	intertidal, shallow water	common on eelgrass (*Zostera*) roots	may be parasitic on certain molluscs
Pleisiocystiscus jewettii	-	1, 2	low intertidal	gravel of tide pools, with coralline algae, in surfgrass (*Phyllospadix*) holdfasts	predatory snail
Pseudomelatoma torosa	Knobbed tower-shell	4	low intertidal to 30m	rocky areas	predatory snail - polychaete worms
Stylidium (Bittium) eschrichtii	Threaded cerith	1, 2	low intertidal and sublittoral	clean coarse sand among eelgrass (*Zostera*)/rocks/coralline algae	herbivore: algae/detritus
Terebra sp.	Auger shell	2	intertidal to 1000m	offshore sandy bottoms	predator
Trimusculus reticulatus	Reticulate gadinia	4	mid intertidal	rock overhangs	planktivore; primarily pelagic diatoms
Volvarina taeniolata	California marginella	4	intertidal and sublittoral	rocks	predator

Table 5. CA-SMI-603, Unit 1, MNI of Small Gastropods.

Taxa	Stratum II	III	IV	V	VI	VII	Total	%
Acanthinucella punctulata	-	-	-	1	-	-	1	0.0
Acmaea mitra	12	3	20	17	3	1	56	1.7
Alia carinata	10	6	38	12	4	12	82	2.5
Alia tuberosa	1	-	17	8	-	1	27	0.8
Amphissa spp.	-	-	-	-	-	4	4	0.1
Amphissa versicolor	19	2	21	15	-	-	57	1.7
Callianax biplicata	2	-	1	1	1	-	5	0.1
Calliostoma spp.	1	-	-	2	-	-	3	0.1
Clathurella canfieldi	1	1	-	-	-	-	2	0.1
Conus californicus	-	-	2	-	-	1	3	0.1
Crepidula coei	9	1	3	6	12	-	31	0.9
Crepidula nummaria	-	-	-	-	-	2	2	0.1
Crepidula perforans	1	-	-	1	-	-	2	0.1
Crepipatella lingulata	-	1	-	-	-	-	1	0.0
Diodora arnoldi	-	-	1	-	-	-	1	0.0
Diodora aspera	-	-	2	-	-	-	2	0.1
Diodora spp.	-	1	-	-	-	-	1	0.0
Epitonum tinctum	-	-	1	1	-	-	2	0.1
Fissurella volcano	22	3	28	29	6	10	98	3.0
Garnotia adunca	57	5	11	175	166	16	430	13.0
Garnotia norrisiarum	6	-	10	3	12	7	38	1.1
Garnotia spp.	-	-	-	1	6	2	9	0.3
Hipponix panamensis	1	-	3	-	-	2	6	0.2
Hipponix tumens	1	-	2	1	1	-	5	0.2
Homalopoma baculum	-	-	1	10	-	1	12	0.4
Homalopoma luridum	1	6	16	1	-	2	26	0.8
Lacuna marmorata	10	1	-	-	-	1	12	0.4
Lacuna spp.	1	-	1	10	-	1	13	0.4
Lirularia spp.	-	-	8	1	-	-	9	0.3
Littorina keenae	6	2	11	10	1	4	34	1.0
Littorina plena	9	4	14	12	-	-	39	1.2
Littorina scutulata	-	-	-	2	-	-	2	0.1
Littorina spp.	-	-	-	-	1	-	1	0.0
Lottia asmi	4	1	16	72	26	15	134	4.0
Lottia digitalis	48	12	66	48	31	5	210	6.3
Lottia fenestrata	11	6	40	22	17	-	96	2.9
Lottia insessa	8	-	8	6	1	6	29	0.9
Lottia ochracea	1	3	4	9	11	6	34	1.0
Lottia palacea	-	-	2	-	-	-	2	

Lottia paradigitalis	-	6	4	7	38	23	78	2.4
Lottia pelta (rock morph)	21	14	60	69	14	28	206	6.3
Lottia pelta (seaweed morph)	52	10	92	110	111	51	426	12.8
Lottia persona	1	5	7	8	1	-	22	0.7
Lottia rosacea	-	-	-	-	-	2	2	0.1
Lottia scabra	79	28	156	192	88	47	590	17.8
Lottia scutum	7	3	13	44	-	3	70	2.1
Lottia strigatella	10	8	48	44	68	21	199	6.0
Lottia spp.	49	1	19	30	11	19	129	4.0
Nucella emarginata	2	1	3	4	1	2	13	0.4
Nucella spp.	-	1	-	2	-	4	7	0.2
Ocinebrina circumtexta	1	3	-	3	2	-	9	0.3
Ocinebrina interfossa	-	-	1	-	-	-	1	0.0
Ocinebrina lurida	-	-	-	1	-	-	1	0.0
Ocinebrina minor	-	-	-	1	-	-	1	0.0
Ocinebrina spp.	1	-	3	3	-	1	8	0.2
Odostomia nota	1	1	2	3	-	-	7	0.2
Pleisiocystiscus jewettii	-	-	1	-	-	1	2	0.1
Stylidium eschrichtii	-	-	3	-	-	-	3	0.1
Terebra sp.	1	-	-	3	-	-	4	0.1
Trimusculus reticulatus	-	-	-	3	-	2	5	0.2
Volvarina taeniolata	-	-	-	1	-	-	1	0.0
Total	467	139	758	1003	632	303	3305	100

Table 6. Quantitative Measures.

Site (CA-)	Unit(s)	Strata	Excavated Volume (m³)	Taxa Richness	Small Gastropod Density (MNI/m³)	Seaweed and Seagrass Density (MNI/m³)	Seaweed and Seagrass % MNI	Diversity (H')	Equitability (V')
SNI-40	11, 12	IIHR	0.138	30	2021.7	297.1	14.9	2.805	0.825
SNI-40	11, 12	IIB	0.02	16	3000	500	16.7	2.382	0.86
SNI-40	11, 12	Dark Feat.	0.016	14	4312.5	1562.5	36.1	2.343	0.865
SNI-40	11, 12	IIHC	0.2765	35	3045.2	654.6	21.6	2.752	0.773
	Totals:		0.4505	40	2772.5	572.7			
SMI-603	1	II	0.362	34	1284.5	265.2	20.7	2.768	0.778
SMI-603	1	III	0.14	28	992.9	214.3	21.6	2.894	0.869
SMI-603	1	IV	0.461	39	1644.3	485.9	29.5	2.897	0.792
SMI-603	1	V	0.208	44	4822.1	995.2	20.7	2.771	0.733
SMI-603	1	VI	0.127	23	4976.4	1535.4	30.9	2.318	0.738
SMI-603	1	VII	0.09	32	3366.7	1111.1	32.9	2.818	0.812
	Totals:		1.388	59	2377.5	612.4			

Table 7. CA-SNI-40, Units 11 and 12A, MNI of Small Gastropods

Taxa	Stratum IIHR	Stratum IIB	Stratum IIHC	Dark Feature	Total	%
Acanthinucella punctulata	1	-	-	-	1	0.1
Acmaea mitra	13	1	38	-	52	4.1
Acteocina culcitella	-	-	1	-	1	0.1
Alia carinata	10	2	27	4	43	3.4
Amphissa versicolor	9	3	29	2	43	3.4
Callianax biplicata	-	-	14	-	14	1.1
Calliostoma canaliculatum	-	-	2	-	2	0.2
Caliostoma ligatum	-	-	1	-	1	0.1
Cerithiopsis carpenteri	1	-	1	-	2	0.2
Conus californicus	1	-	-	-	1	0.1
Crepidula aculeata	3	2	8	-	13	1.0
Crepidula onyx	-	-	1	-	1	0.1
Crepidula perforans	-	-	3	-	3	0.2
Crepidula spp.	1	-	8	2	11	0.9
Crepipatella lingulata	5	1	10	1	17	1.3
Epitonium tinctum	-	-	1	-	1	0.1
Fissurella volcano	15	4	35	4	58	4.6
Fissurellidae	8	-	5	-	13	1.0
Fusinus kobelti	-	-	1	-	1	0.1
Fusinus luteopictus	-	-	1	-	1	0.1
Garnotia adunca	4	3	13	-	20	1.6
Garnotia norrisiarum	1	-	6	-	7	0.6
Homolopoma baculum	5	-	6	-	11	0.9
Homolopoma luridum	12	3	35	2	52	4.1
Littorina keenae	1	-	8	-	9	0.7
Littorina scutulata	31	4	41	2	78	6.2
Lottia asmi	14	2	55	4	75	5.9
Lottia digitalis	9	3	27	2	41	3.2
Lottia insessa	15	4	93	15	127	10.1
Lottia instabilis	-	-	2	-	2	0.2
Lottia ochracea	3	3	15	3	24	1.9
Lottia pelta (rock morph)	2	-	17	1	20	1.6
Lottia pelta (seaweed morph)	8	1	40	3	52	4.1
Lottia pelta (uncategorized)	1	-	-	-	1	0.1
Lottia scabra	56	20	184	11	271	21.5
Lottia strigatella	1	-	2	-	3	0.2
Lottia spp.	39	4	113	13	169	13.4

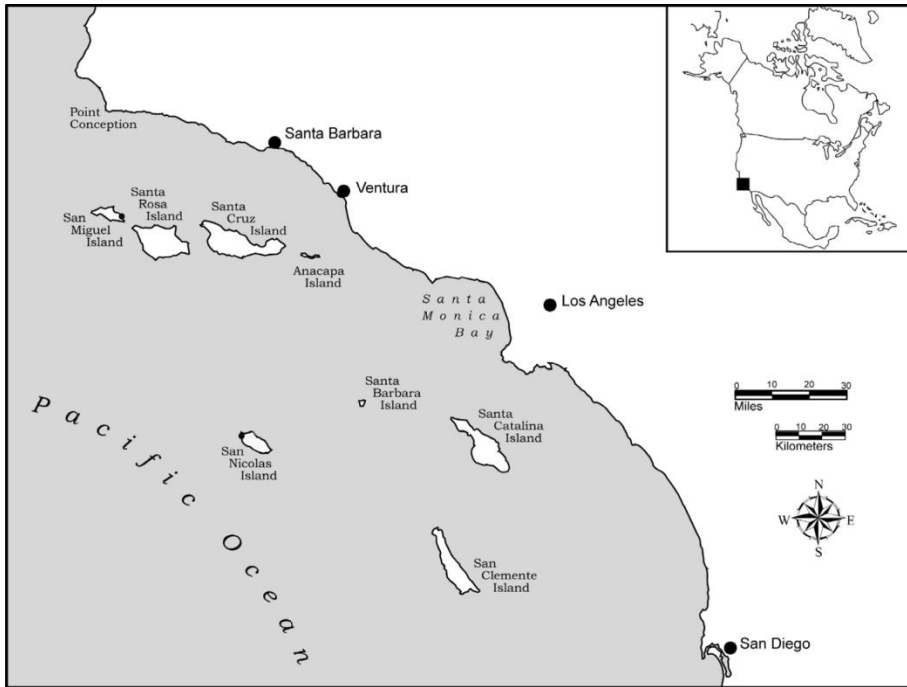|						
Lucapinella callomarginata	1	-	-	-	1	0.1
Mitromorpha aspera	1	-	-	-	1	0.1
Ocinebrina circumtexta	1	-	5	-	6	0.5
Pseudomelatoma torosa	-	-	1	-	1	0.1
Stylidium eschrichtii	3	-	-	-	3	0.2
Trimusculatus reticulatus	4	-	6	-	10	0.8
Total	278	60	855	69	1263	100

Figure 1. Map of the California Channel Islands with CA-SMI-603 demarcated on the northeast coast of San Miguel Island and CA-SNI-40 demarcated on the west end of San Nicolas Island.

Figure 4. View of rocky shore and kelp patches looking out from Cave of the Chimneys (CA-SMI-603, above) and CA-SNI-40 (below).
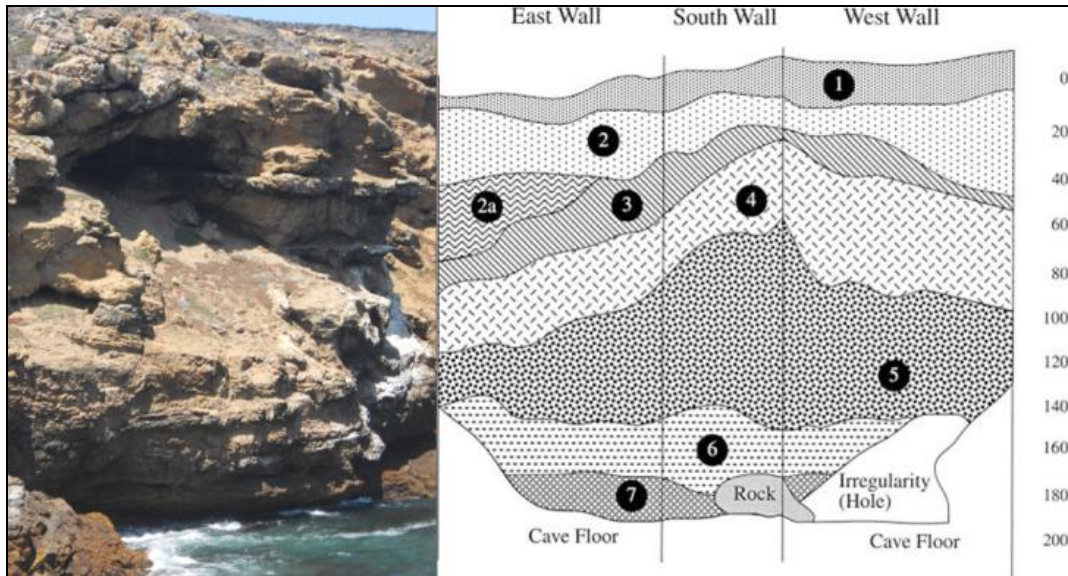
Figure 5. Entrance to Cave of the Chimneys (CA-SMI-603) and stratigraphic profile drawing of Unit 1.
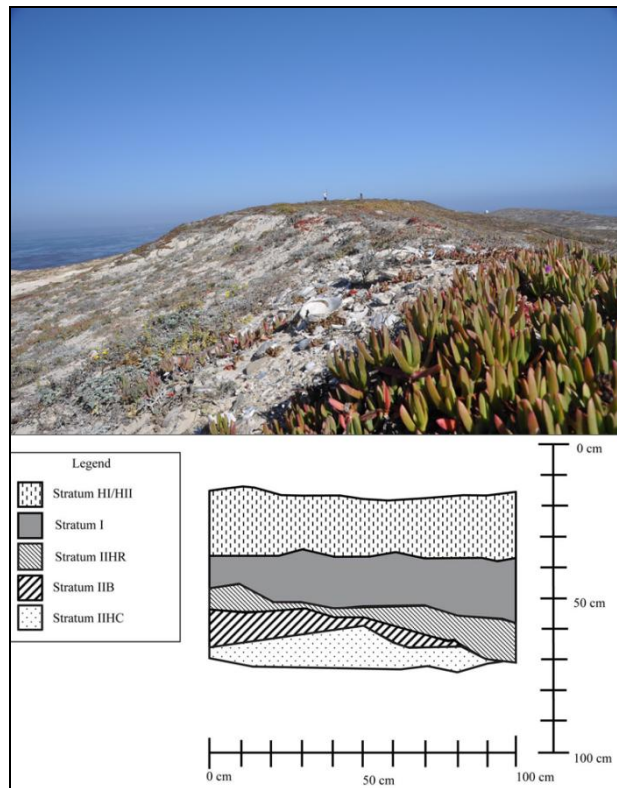
Figure 6. The large dune that comprises CA-SNI-40 (facing west) and stratigraphic profile drawing of Unit 12A.

Figure 2. Archaeological examples of seaweed associates identified in this study (top left to bottom right): *Callisotoma canaliculatum*, *Calliostoma ligatum*, *Acanthinucella punctulata*, *Lacuna marmorata*, *Lacuna unifasciata*, *Lirularia* sp., *Pleisiocystiscus jewettii*, *Alia carinata*, *Alia tuberosa*, *Stylidium eschrichtii*, *Clathurella canfieldi*, and *Odostomia nota*.
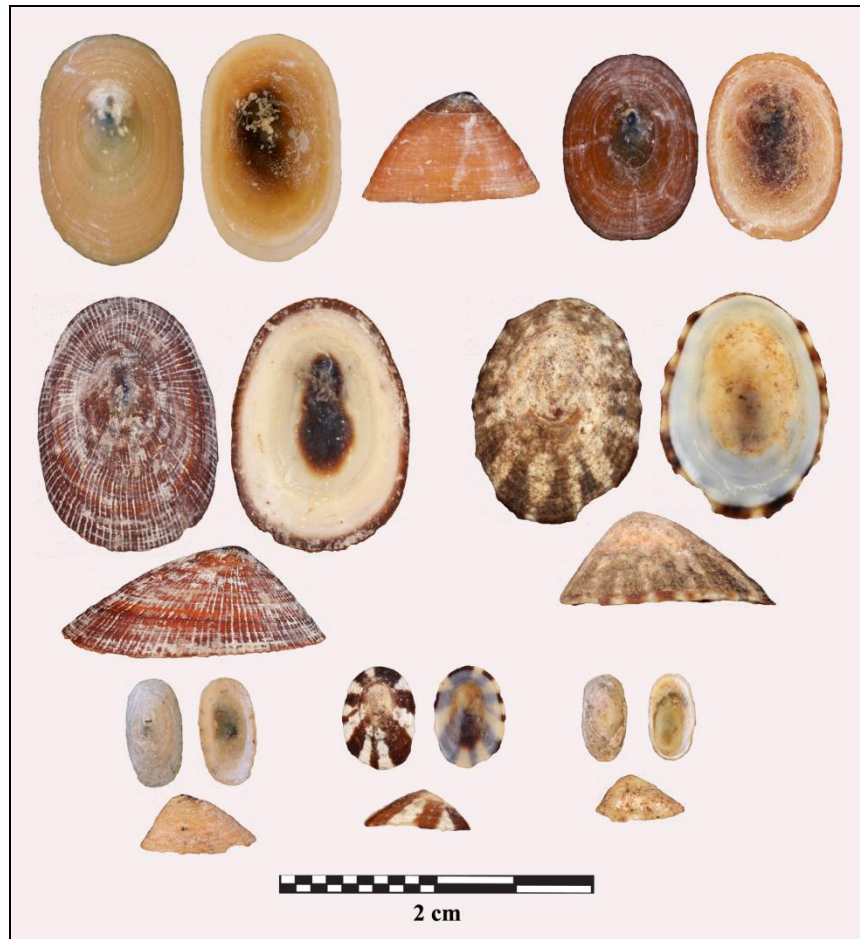
Figure 3. Archaeological examples of seaweed and seagrass limpets identified in this study (top left to bottom right): light and dark morphologies of *Lottia insessa*, *L. pelta* (seaweed morphology), *L. strigatella*. *L. instabilis*, *L. ochracea*, and *L. palacea*.
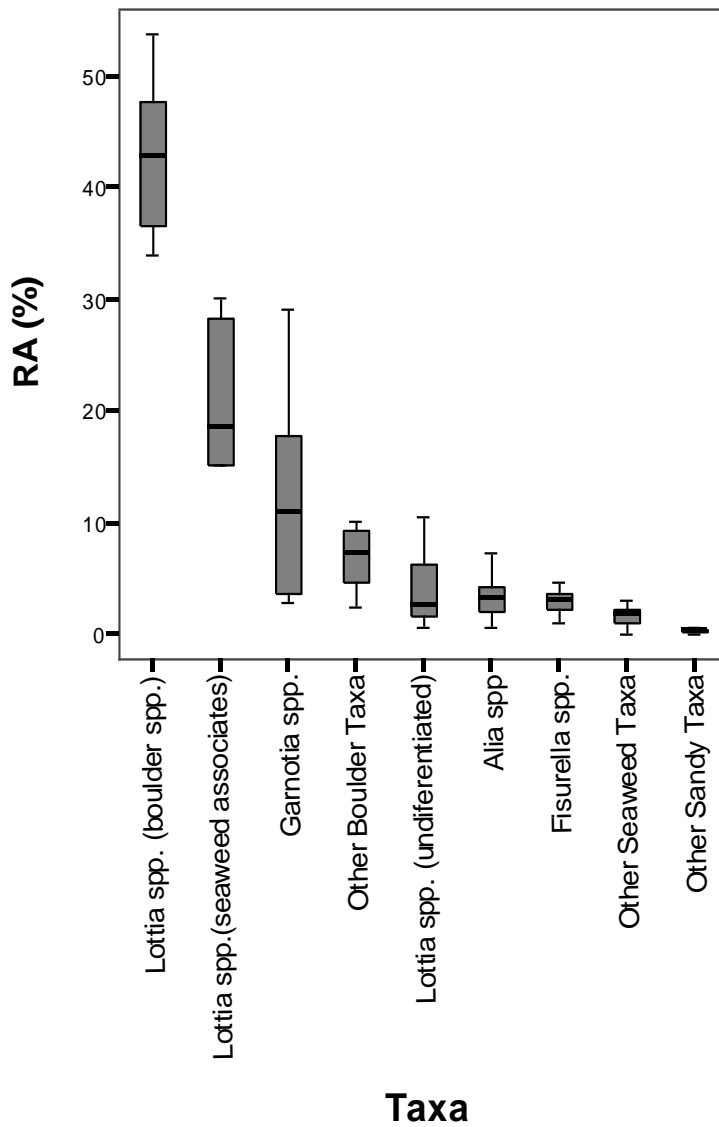
Figure 7. Composition of small gastropod taxa from CA-SMI-603. Boxplots include mean relative abundance and interquartile ranges. Error bars denote full ranges. N = number of analyzed strata (6), RA = relative abundance.
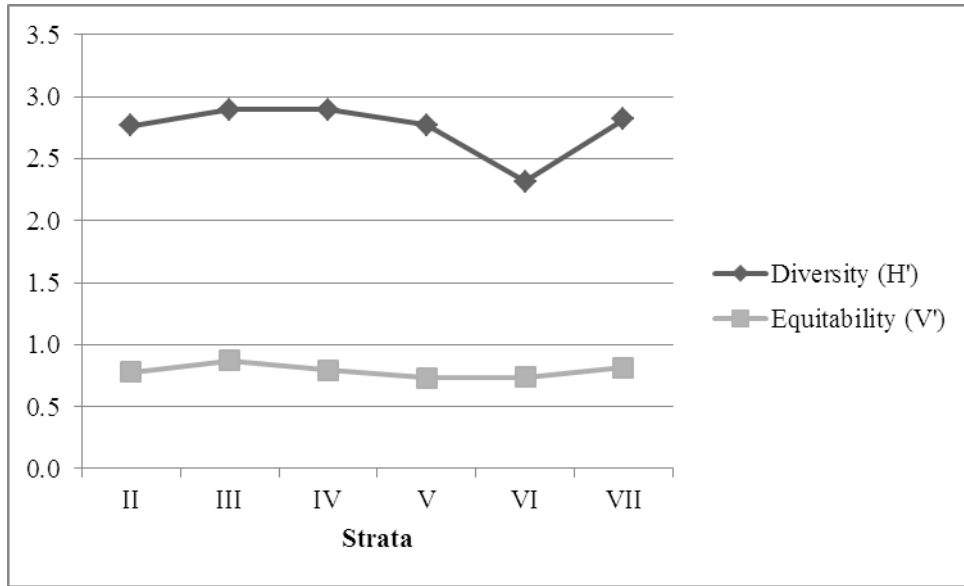
Figure 8. Heterogeneity measures for the small gastropod assemblage from CA-SMI-603. Changes in shellfish diversity and equitability through time are described by the Shannon-Weaver Diversity Function (H') and Equitability Function (V') (Reitz and Wing 2008).
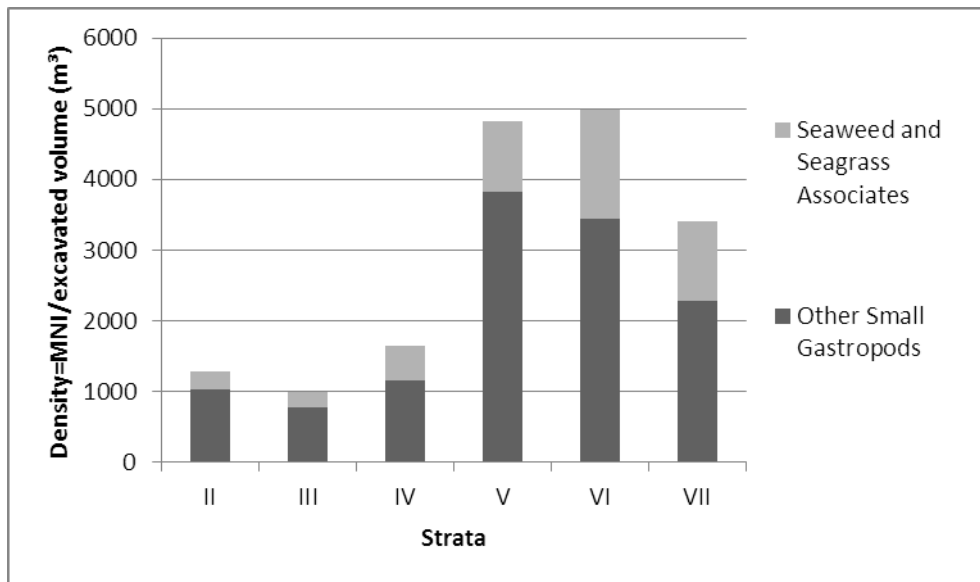

Figure 9. Density measures for small non-dietary gastropods from CA-SMI-603.
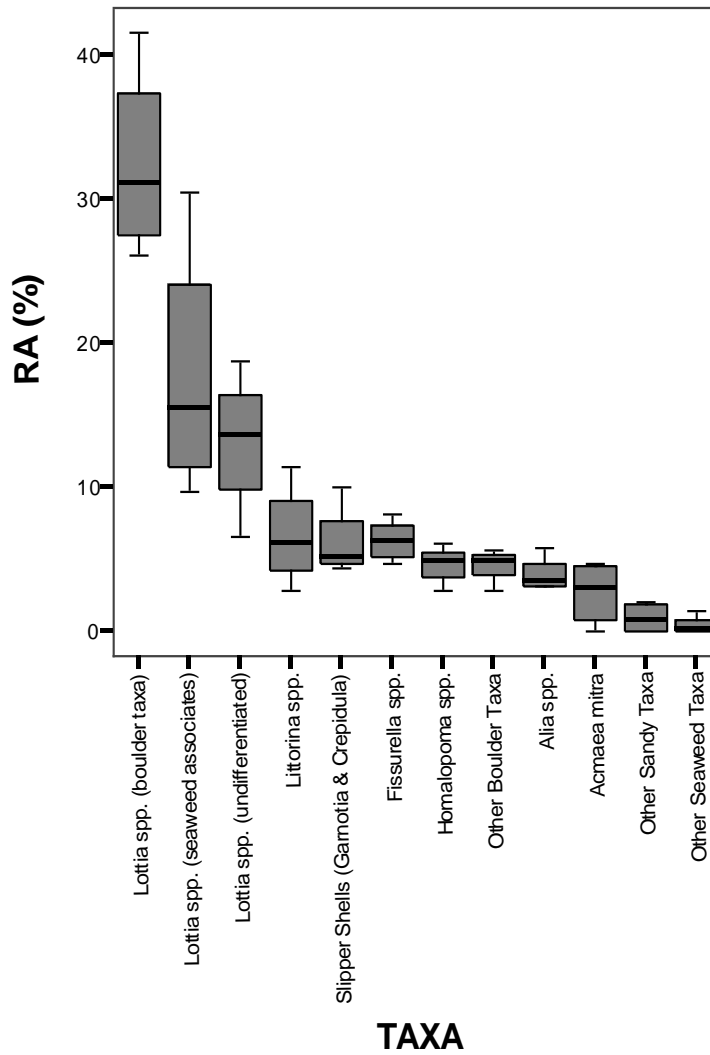
Relative Abundance of CA-SNI-40 Taxa

Figure 10. Composition of small gastropod taxa from CA-SNI-40. Boxplots include mean relative abundance and interquartile ranges. Error bars denote full ranges. N = number of analyzed deposits (4), RA = relative abundance.
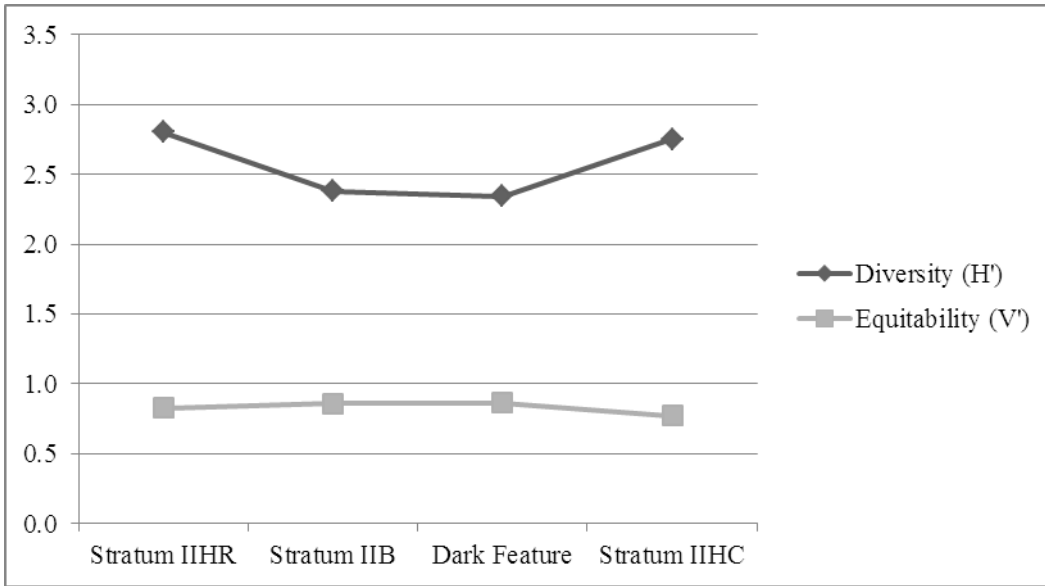
Figure 11. Heterogeneity measures for the small gastropod assemblage from CA-SNI-40. Changes in shellfish diversity and equitability through time are described by the Shannon-Weaver Diversity Function (H') and Equitability Function (V') (Reitz and Wing 2008).
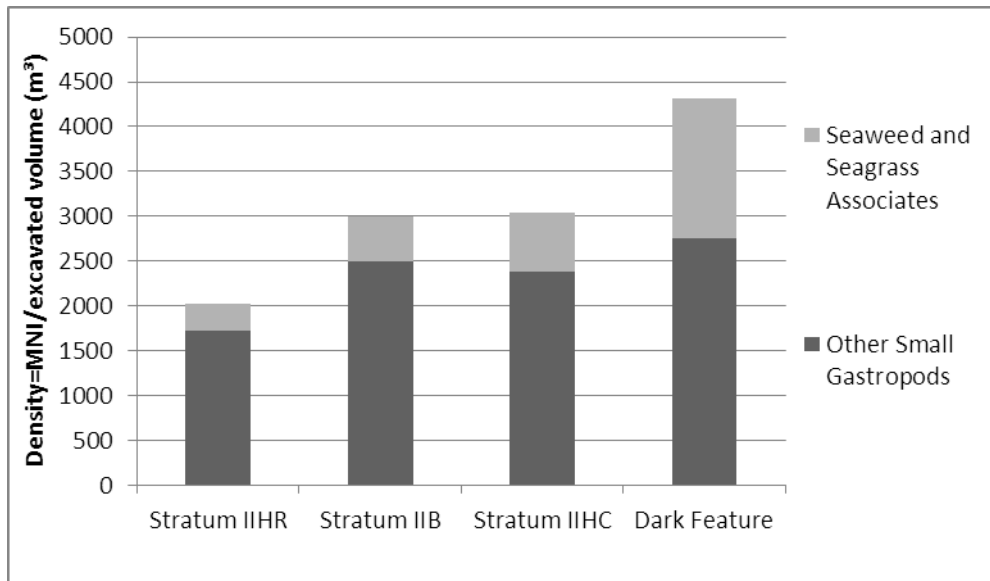

Figure 12. Density measures for small non-dietary gastropods from CA-SNI-40.