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Living on the edge - interdisciplinary perspectives on coastal and marine ecosystems in human prehistory

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Published in
Frontiers in Earth Science

ISSN 1664-8714
ISBN 978-2-8325-2546-3
DOI 10.3389/978-2-8325-2546-3

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May 2023

Living on the edge - interdisciplinary perspectives on coastal and marine ecosystems in human prehistory

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Citation
Will, M., Green, A., Erlandson, J. M., Villagran, X. S., Jerardino, A., eds. (2023). *Living on the edge - interdisciplinary perspectives on coastal and marine ecosystems in human prehistory*. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-8325-2546-3

Table of contents

frontiers | Frontiers in Earth Science

TYPE Editorial
PUBLISHED 11 May 2023
DOI 10.3389/feart.2023.1209842

OPEN ACCESS

EDITED AND REVIEWED BY
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RECEIVED 21 April 2023
ACCEPTED 02 May 2023
PUBLISHED 11 May 2023

CITATION
Will M, Jerardino A, Villagran X, Green A and Erlandson JM (2023), Editorial: Living on the edge—interdisciplinary perspectives on coastal and marine ecosystems in human prehistory. *Front. Earth Sci.* 11:1209842. doi: 10.3389/feart.2023.1209842

Editorial: Living on the edge—interdisciplinary perspectives on coastal and marine ecosystems in human prehistory

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KEYWORDS

archaeology, marine ecosystem, coast, interdisciplinary, ocean

Editorial on the Research Topic
Living on the edge—interdisciplinary perspectives on coastal and marine ecosystems in human prehistory

Introduction

Coastal and marine ecosystems dominate the world's surface area. Since the beginnings of the discipline, prehistoric archaeology has had an interest in the human use and habitation of these environments, may it be in the form of seafaring or impressive shell middens (e.g., Forchhammer et al., 1852). In 1968, however, the influential archaeologist Lewis Binford relegated intensive human use of aquatic resources to a set of "post-Pleistocene adaptations" that included the development of agriculture. For most of the 20th century, interest in coastal and maritime cultures focused on the Holocene period that shows much evidence for hunter-fisher-gatherer, farming, and early state communities around the globe having diverse ties to shores and oceans. Deeper time perspectives on the role of these ecosystems in human evolution have received attention only recently, with empirical data still limited, due largely to the effects of post-glacial sea level rise.

Since the beginning of the new millennium, ongoing work on the relationship between humans, coasts and oceans worldwide has become decidedly interdisciplinary, with research expanding further back in time to include the whole timespan of human existence, and potentially even before then (e.g., Zilhão et al., 2020). Inspired by the seminal work of Erlandson (2001) and others, the archaeology of aquatic adaptations saw an increase in scholarly publication based on quantitative and scientific approaches—including zooarchaeology, geoarchaeology and marine geology, genomics, isotopic biochemistry, sclerochronology, and modelling studies—and intensified work on the Pleistocene (e.g., Marean, 2014; Villagran, 2014; Jerardino, 2016; Klein and Bird, 2016; Will et al., 2019). This Research Topic brings together articles interested in deep-time, diachronic, and multidisciplinary perspectives on the varying role of coastlines, oceans and marine resources for past societies and human evolution, including ecological, geographical and geological aspects.

Interdisciplinary perspectives on coastal and marine ecosystems in human prehistory

The articles in this Research Topic synthesise interdisciplinary data ranging from the late Middle Pleistocene to the recent past, covering archaeological sequences from South America, North America, Europe and Africa.

Bicho and Esteves review evidence for coastal adaptations of Pleistocene hunter-gatherers during the Middle and Upper Paleolithic in Atlantic Iberia including behavioral, geographic and geological aspects. They find that Neanderthals and modern humans inhabited coastal ecosystems and consumed diverse marine foods in a similar way, with most differences between sites likely stemming from variable distances to the ocean.

Wurz et al. report new results of U-Th dating, taxonomy and taphonomy of the shell midden deposits from the Middle Stone Age (MSA) site of Klasies River, South Africa. The interdisciplinary approach demonstrates that groups of early modern humans exploited coastal ecosystems in a stable and systematic manner by at least 110,000 years ago. Working at the same site, Reynard performed the first taphonomic analysis of its faunal remains. Combined with existing taxonomic and contextual data, his results provide a diachronic overview from MIS 5-3 on the relationship between human behavior and paleoenvironments by reconstructing occupation intensity in the local paleoecological context.

Will et al. combine archaeological findings with coastal geomorphology, GIS modelling and offshore marine geophysical investigation to assess the extent of potential Pleistocene coastal adaptations in eastern South Africa. The review concludes that while sites are still scarce, people settled coastal landscapes and consumed marine resources during both the MSA and LSA, with most past evidence likely being submerged.

The Zanzibar Archipelago during the last 20,000 years and the relation between humans and the intertidal zone constitute the focus of Faulkner et al. Reviewed environmental, archaeological, and modern socio-ecological evidence shows the long-term but complex and changing connections of societies with different socio-economic structures and these coastal ecosystems and potential drivers behind these patterns are discussed.

In a methodology-focused article, Simões and Aldeias employ micromorphological analyses with microscopic FTIR of shells to demonstrate macroscopically invisible fire use in midden deposits. Combined with experimental work, these methodological insights are applied to two Mesolithic shell midden contexts from Portugal, yielding novel evidence for the cooking of shellfish.

Gusick et al. report on the exploration of an extensive submerged landscape located around California's Northern Channel Islands, which have lost ~75% in area to rising seas since the last glacial maximum. They use remote sensing and coring to reconstruct this drowned landscape and document the presence of intact soils beneath the seafloor, suggesting that Late Pleistocene sites may be found with additional research.

Dillehay et al. examine the development of mixed maritime and terrestrial economies along the arid coast of Peru between 14,500–3,800 years ago. Between ~7,500–5,000 years ago, adding agricultural production to rich local fisheries led to the rise of complex civilization marked by social differentiation, proto-urban populations, monumental public architecture, elaborate ritual iconography, and intensive landscape modification.

Reyes et al. focus on the influence that permeable geographical barriers in western Patagonia's archipelago could have had on the circulation and contact among canoe populations. Most interesting are emerging geographical patterns indicating differences in cultural trajectories among the canoe groups that inhabited this fragmented part of the southern Pacific coastal region.

Sanchez et al. study the indigenous engagement with coastal resources for over ~7,000 years on the central California coast. Using a historical ecological framework, the authors identify the use of diverse marine and terrestrial resources by mobile groups who intensified their economies by the Late Holocene, and created habitat mosaics by fire management that are still visible today.

The British Columbia (Canada) clam gardens are studied by Holmes et al. using an integrated approach combining GIS, drone imagery, and radiocarbon dates. The study reveals a close, temporal relationship between the clam gardens and increased human settlements in Kanish and Waiatt Bays, indicating the need for sustainable food production to support larger populations.

Summary and outlook

A golden thread throughout the Research Topic concerns the feedback between changing landscapes, climate, ecology and human behavior. The articles illuminate the deep-seated and complex connections of humans with coastlines, oceans, and the organisms living there, while also highlighting the long-term influences our species had on them. Considering current global climate change and the biodiversity crisis that affects some ecosystems more strongly than others, the UN declared 2021-30 the "Decade of Ocean Science for Sustainable Development." Archaeological research demonstrates the deep history of humanity's role as active agents of ecosystem changes with implications for modern ecological, socio-cultural, and economic systems (Boivin et al., 2016; Stephens et al., 2019). Archaeology can provide unique windows into the positive and negative ways in which humans have lived in and engaged with shores and oceans. Future research in island and coastal archaeology—examining the timing, duration, impact, magnitude, and possible reversibility of anthropogenic change in the past—may also provide important knowledge and baselines for more effective restoration of beleaguered coastal and other aquatic ecosystems and fisheries in the future.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 15 August 2022
DOI 10.3389/feart.2022.964423

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 08 June 2022
ACCEPTED 13 July 2022
PUBLISHED 15 August 2022

CITATION
Will M, Bader GD, Sommer C, Cooper A and Green A (2022), Coastal adaptations on the eastern seaboard of South Africa during the Pleistocene and Holocene? Current evidence and future perspectives from archaeology and marine geology.
Front. Earth Sci. 10:964423.
doi: 10.3389/feart.2022.964423

Coastal adaptations on the eastern seaboard of South Africa during the Pleistocene and Holocene? Current evidence and future perspectives from archaeology and marine geology

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The use of marine resources and the settlement of coastal settlements may have influenced the bio-cultural evolution and dispersal of Pleistocene *Homo sapiens* in Africa. In order to test such scenarios, however, we require evidence for these behaviours deriving from an expanded spatio-temporal archaeological record. The Stone Age of South Africa documents the richest and longest record of coastal adaptations. In contrast to abundant evidence of coastal sites on the western and southern seaboard, the eastern Indian Ocean coast has not played a role in recent discussions. Considering the important and well-known Middle and Later Stone Age (MSA/LSA) record from inland sites of KwaZulu-Natal (KZN), this region may be an underappreciated area for further study. Here we provide a systematic overview of marine resource use and the settlement of coastal landscapes during the Late Pleistocene and Holocene in KZN. For the first time, we contextualize these archaeological findings with a review and new data on the changing marine and coastal geomorphology in the context of GIS modelling and offshore marine geophysical investigations. Our review finds evidence for long-term dietary and non-dietary use of marine resources during the MSA and LSA from a few stratified sites, with many more surface occurrences particularly for the MSA along the modern KZN coastline indicating human habitation. Comparisons to other areas of South Africa, GIS modelling and geological considerations suggest that current data on the eastern seaboard are not reflective of the original extent and nature of the consumption of marine foods and settlement of coastal landscapes. By contextualizing the biased and patchy MSA and LSA record with results on the dynamic marine and coastal geomorphology of KZN, we develop productive lines of future studies to assess open questions on potential coastal adaptations in this region. These research strategies include the identification of areas with high potential for finding new sites within a

10 km transect along the current coastline as well as dedicated off-shore projects including underwater archaeology aided by new marine geological work in the southwest Indian Ocean.

KEYWORDS

middle stone age, later stone age, marine geomorphology, GIS model, offshore & marine, paleolithic archaeology, palaeolithic

1 Introduction

Humans have a deep-seated connection with oceans, coasts and the organisms inhabiting these ecosystems: today, more than 600 million people live in coastal communities, beaches are highly popular natural attractions to tourists and seafood is a major source of diet found around the globe. Archaeologists and paleoanthropologists have long been interested in the evolutionary roots of this relationship. Coastal foraging by hunter-fisher-gatherers during the Holocene and in recent times has been among the main research topics of archaeology since its inception (Forchhammer et al., 1852; Morse, 1877; Uhle, 1907). In contrast, the prevailing view on the Pleistocene use of beaches and oceans during most of the 20th century has been rather negative. With a few notable exceptions (e.g. Sauer 1962), the majority opinion has been that shorelines were marginal, dangerous and unattractive ecosystems, with many coastlines being uninhabitable and barriers to expansion due to a lack of potable water, resulting in a lack of evidence for a deep-time engagement of people with oceans such as manifested in the form of shell middens (e.g. Binford, 1968; Washburn and Lancaster, 1968; Meighan, 1969; Osborn, 1977; Waselkov, 1987; Yesner, 1987; for discussion see Erlandson, 2001).

A renewed interest in the topic coupled with novel archaeological data has challenged this picture. Over the past 20 years, the earliest habitations of coastal landscapes and the exploitation of seafood have become important topics for understanding the bio-cultural evolution of *Homo sapiens* during the Pleistocene (Erlandson, 2001; Parkington, 2003; Jerardino and Marean 2010; Marean, 2014; Jerardino 2016; Will et al., 2019). The potential of coastal landscapes to facilitate dispersals of early modern humans from Africa has likewise been a major theme of recent research (e.g., Field and Lahr, 2006; Mellars et al., 2013). While there is still ongoing debate and the actual relevance of these behaviors for human evolution and dispersal have been criticised (see Bailey, 2009; Boivin et al., 2013; Groucutt et al., 2015; Blinkhorn et al., 2017; Rabett, 2018), there is now good evidence for some populations of both Neanderthals and modern humans having adapted to coastal ecosystems and marine food resources in a systematic way over a period of many tens of thousands of years stretching back to the late Middle Pleistocene (e.g. Will et al., 2019; Zilhão et al., 2020).

Throughout the article we follow our recent definition of the term ‘coastal adaptations’ as a multifaceted array of behavioral traits in a population beneficial to their fitness, consisting of the regular and systematic acquisition, consumption and use of marine resources as well as an expansion of settlement systems that included repeated and planned occupation of coastal landscapes (for a more detailed discussion of the concept see Will et al., 2016: 70; Will et al., 2019: 36; for an even broader approach of ‘coastal engagement’ see Faulkner et al., 2021). The majority of evidence on such Pleistocene use of coasts by *Homo sapiens* has come from the African Middle Stone Age (MSA), with the longest record for the consumption of marine resources deriving from sites in northern and particularly southern Africa (for northern Africa see Steele and Alvarez-Fernández, 2011; Campmas et al., 2016). In South Africa, the oldest known collection of edible shellfish derives from Pinnacle Point Cave 13B at ~164 ka (Jerardino and Marean, 2010), one of the very few localities in Africa with evidence predating the Eemian interglacial. During Marine Isotope Stage (MIS) 5e, systematic shellfish gathering has been documented at Ysterfontein 1 (120–113 ka; Niespolo et al., 2021) and Hoedjiespunt 1 (130–100 ka; Will et al., 2013; Kyriacou et al., 2014; Tribolo et al., 2022). Multiple localities with ample evidence for coastal adaptations as defined above date to between ~110 ka and 50 ka, including Klasies River (Thackeray, 1988), Blombos Cave (Langejans et al., 2012), Die Kelders Cave 1 (Grine et al., 1991), Klipdrift Shelter (Henshilwood et al., 2014) and Herolds Bay Cave (Brink and Deacon, 1982) on the southern Indian Ocean coast, an Diepkloof (Klein and Steele, 2013), Varsche Rivier 003 (Steele et al., 2016) and Sea Harvest (Volman, 1978) on the western Atlantic coast. In sum, ample archaeological data exists for coastal adaptations during the Late Pleistocene in sites which escaped high sea level of the Holocene and Eemian interglacials.

Yet, the archaeological record of coastal occupation and resource use is not equally distributed along African shorelines. Vast gaps in knowledge plague the African record, such as in western or eastern Africa (see e.g. Niang et al., 2020; Faulkner et al., 2021), and even in regions that are comparatively well-studied such as South Africa. In contrast to abundant evidence of Pleistocene coastal sites on the western and southern seaboard, the eastern Indian Ocean coastline and the province of KwaZulu-Natal (KZN; Figure 1) in particular have not played any role in recent discussions due to the perceived scarcity of relevant data, and those often deriving from old publications. The recently excavated coastal site of Waterfall Bluff dated to ~38–10 ka, located in Eastern Pondoland ca. 50 km

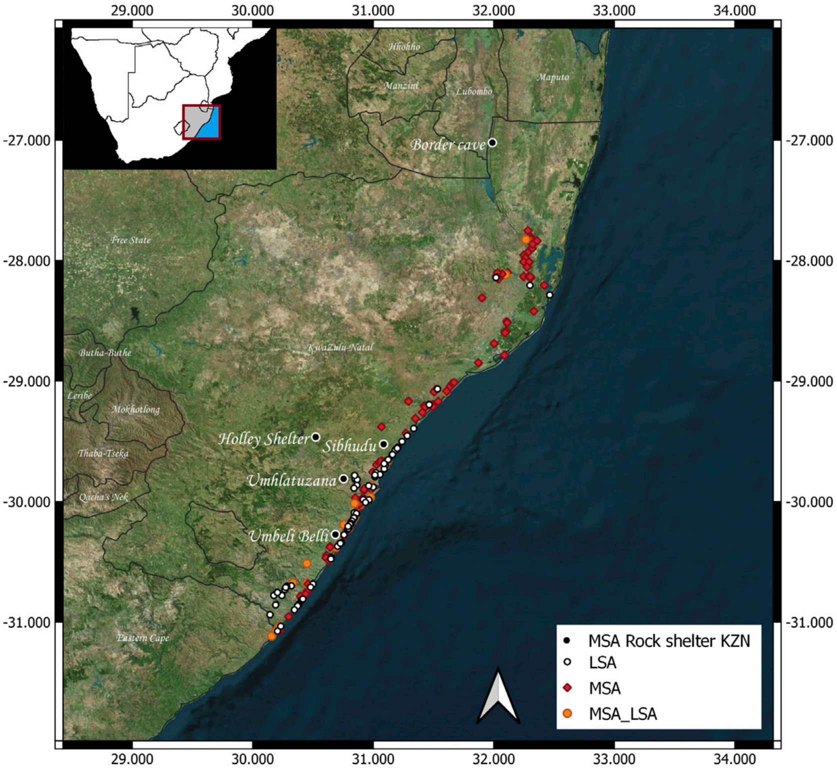

FIGURE 1
Overview map of the province of KwaZulu-Natal in southern Africa (see inset top left) with named key MSA rockshelter sites as well as MSA, LSA and mixed MSA/LSA sites from an exhaustive database of sites within a transect of 20 km from the modern shoreline.

southwest of KZN, is a notable exception (Esteban et al., 2020; Fisher et al., 2020). Considering this recent evidence and the important MSA and LSA archaeological record from inland sites of this region, the seaward sectors of KZN may be an underappreciated area for further study (Bader and Will, 2017). The specific coastal and marine ecology of KZN likely impacted the currently known archaeological record of this region. Most importantly, the Indian Ocean coast features a different terrestrial biome and lower marine productivity compared to the Fynbos and nutrient-rich waters of the Atlantic ocean coast (e.g. Kyriacou, 2017).

Connected to this research gap are the more general issues of the relevance and spread of coastal adaptations in early humans. Some scholars see the current evidence as geographically isolated behaviors, derived primarily from the highly productive marine ecosystems such as the Atlancic ocean coast in southwestern South Africa (Bailey 2009; Boivin et al., 2013; Blinkhorn et al., 2017). Such a pattern could imply that Pleistocene people were limited in their capability to adapt to variable coastal ecosystems and only able to exploit the most prolific shorelines in an efficient manner. The record is further biased towards specific areas by climate and geology, particularly Pleistocene changes in sea-levels with only few sites close to the ocean having escaped erosion during sea-level highstands (Bailey and Flemming, 2008; Bailey, 2009; Bailey et al., 2015). In order to test scenarios for the spatial bias, selective advantages and dispersal capabilities of coastal adaptations, we require more evidence for these behaviours deriving from an expanded spatio-temporal archaeological record from diverse ecological, geographical and geological settings.

Here we examine the understudied region of KZN which differs in its marine ecology and offshore geology from the well-known record of western and southern South Africa. We are interested in how such areas can contribute to a better understanding and evaluation of the evolutionary relevance of coastal adaptations. This goal requires a joint approach of archaeology, marine geology and geography. The KZN shoreline is an ideal test case. For one, the region possesses a mostly steep offshore bathymetric profile with a mix of narrow and broader continental shelves. As a result, coastal sites in some regions had a chance of escaping erosion by post-glacial sea-level rise due to limited coastline movements across glacial/interglacial cycles. At the same time, the marine ecosystem of this region is less productive compared to the western Atlantic coast. Here we provide a systematic overview of marine resource use and the settlement of coastal landscapes during the Late Pleistocene, considering localities within 20 km of the current coastline of KZN. We contextualise these archaeological findings with a review and both new and existing data on the changing marine and coastal geomorphology in this area in the context of GIS modelling and offshore marine geophysical investigations. We start by introducing the general geological and physiographic setting of the region.

2 Geological and physiographic setting

The KZN continental margin comprises a sheared passive margin that formed during the breakup of Gondwana (Martin and Flemming, 1988). The margin is currently tectonically stable, and has been so since the late Pliocene, following several pulses of hinterland uplift that deposited most of the KZN shelf edge sequences (Green, 2011; Green and Garlick, 2011). The KZN shelf can be divided into three main zones. The southern KZN shelf, from the Mzimkulu River to Durban, is narrow with an average width of 8 km (Bosman, 2012; Green et al., 2018; Pretorius et al., 2019). In some places, this is decreased where submarine canyons intersect the shelf break (Flemming, 1981). From Durban to Port Durnford, the shelf widens to a maximum of ~40 km offshore the Thukela River (Martin and Flemming, 1988; Engelbrecht et al., 2020), before narrowing to a minimum of 4 km from Richards Bay to the Mozambique border (Green et al., 2022a). The area between Durban and Port Durnford is known as the Natal Bight, and is underlain by a Kimmeridgian to Cenozoic-aged submerged fan delta complex formed by the Thukela River, termed the Thukela Cone (Hicks and Green, 2016). The shelf break throughout KZN occurs at a uniform depth of 100 m, though its expression varies from distinct in the south and north, to relatively gradual in the central areas offshore the Thukela River.

To the south and north of Durban, the acoustic basement comprises Cretaceous-aged siltstones into which several fluvial valleys associated with the Pleistocene lowstands are incised (Green, 2009a; Green, 2011; Pretorius et al., 2019). The acoustic basement of the Natal Bight comprises Pliocene-age siltstones of the Thukela Cone (Hicks and Green, 2016). Throughout KZN, the acoustic basement forms a shallow feature covered by only a thin veneer of Holocene sediment (Flemming, 1978; Flemming, 1981). Unconsolidated sediment cover, up to 30-m-thick, may be found on the inner shelf, decreasing to no more than a few meters at the ~50 m isobath (Flemming, 1981; Green and Garlick, 2011; Green et al., 2022a). Seaward of the 50 m isobath, the shelf is increasingly sediment starved with mostly exposed bedrock mantled by patches of palimpsest bioclastic gravels (Green, 2009b; Green and Garlick, 2011; Pretorius et al., 2019; Green et al., 2022a).

Of special importance to this paper are several aeolianite and beachrock features that are commonplace along the mid to outer shelf of KZN (Cawthra et al., 2012; Green et al., 2018; Pretorius et al., 2018). Beachrocks are lithified beach sediments cemented by high-Mg calcite precipitated in the mixing zone of seawater and meteoric waters (Mauz et al., 2015). They are known to form particularly rapidly along the KZN coastline, often within a span of 80 years or less (Wiles et al., 2018; Falkenroth et al., 2022). The coastal aeolianites of KZN formed through the precipitation of low-Mg calcite from CO_2-saturated meteoric waters in coastal dunes (Cooper and Green, 2016). The narrow, steep and bedrock-framed coastline of KZN means that beachrock and aeolianite often occur in tandem with each other due to the limited accommodation space that arises from such coastal topography (Cooper and Flores, 1991; Kelly et al., 2014). Their presence on the shelf reflects *inter alia* multiple cycles of shoreline inheritance and occupation throughout the mid Pleistocene to Holocene (Bosman, 2012; Pretorius et al., 2016).

Much of the shelf is exposed and presents a relict topography due, in part, to the strong sweeping effects of the Agulhas Current, a fast, poleward-flowing western boundary current (Lutjeharms, 2006). This current hugs the shelf break and periodically impinges into the mid-shelf areas (Flemming, 1978). In tandem with the vigorous wave regime (Smith et al., 2010) that forms a particularly strong wave ravinement (Pretorius et al., 2018), and when coupled to the narrow shelf widths of the area, the current results in the expression of well-exposed hardgrounds and paleo-landsurfaces from the mid shelf to seaward.

3 Materials and methods

3.1 Archaeological database

The review of archaeological data focusses on MSA and LSA sites in KZN with potential evidence of coastal adaptations, including traces of various behaviors such as the regular consumption and systematic acquisition of marine food resources and the expansion of settlement systems to include coastal and near-coastal zones as occupation spots on a regular and planned basis (Will et al., 2016; Will et al., 2019). The presentation of new and published data consists of two parts: 1) Key MSA and LSA sites of KZN with relevant data on coastal resource use deriving from the published literature and our own recent work. 2) An overview of excavated and known Stone Age sites in KZN in a strip of 20 km along the modern coastline from a large database. The latter is a modified version of the KZN Museum database in Pietermaritzburg which was kindly provided by G. Whitelaw. It contains a systematic collection of archaeological sites and surface collections conducted by researchers since the early 20th century. Much of this data comes from early systematic and extensive surveys of the KZN coast by Oliver Davies (1952, Davies (1970) and members of the KZN Museum reporting on ESA, MSA and LSA stone tools among various beach deposits within a strip of ~10 km along the coastline. Davies had a profound knowledge of southern African archaeology and he dedicated most of his later years towards a comprehensive investigation of KZN, with a focus on coastal areas. More detailed information on the sites and the sources of their data can be found in SOM Supplementary Table S1. We treated Lake St. Lucia (Isimangaliso Wetland Park) like a coastal area as there is clear evidence for the lake being fully marine at certain points within the time frame of this study, indicated by corals growing on the landward shorelines at Listers Point, False Bay (Cooper et al., 2013; Benallack et al., 2016).

3.2 Material and methods of GIS modelling

We investigated the spatiotemporal variations of the continental shelf during the Late Pleistocene and Holocene with a dynamic GIS model. Our approach is based on bathymetry and paleo sea-level reconstructions and thus aims to 1) simulate displacements of the shoreline, 2) estimate the exposed shelf area, and 3) measure the shore-distances of selected coastal sites at sea level lowstands. The modelled area spans the South African East Coast from 28.1 to 31.2°S covering parts of the KZN South Coast, the Durban Basin and the Zululand Basin (Figure 1). The bathymetric model was extracted from a regional dataset produced by de Wet and Compton (2021) from single-beam echo-sounding, which features a high spatial resolution of ~290 m and has proven suitable for the study of sea level fluctuations on the continental margin. The temporal extent of the model covers the last 119,000 years and is informed by a global sea level reconstruction by Waelbroeck et al. (2002). The dataset provides a total of 81 timesteps for every 1,500 years in our timeframe with information on relative mean sea level as well as upper and lower margins.

Our model is similar to the approaches presented in Fisher et al. (2010) and Bader et al. (2022) relying on the vectorization of isobaths for relevant time steps and their respective relative sea levels. Due to the high tectonic stability (Erlanger et al., 2012) and negligible effects of glacial isostatic adjustment in the region, we consider the passive flood or "bathtub" approach (Anderson et al., 2018) to be a suitable basis for our calculations. Further, the very limited sediment cover seaward of the 50 m isobath provides a reliable paleo-bathymetric surface on which our model is contextualised. The model was realised in the statistical software "R" v. 4.1.2 (R Core Team 2022) using the geospatial libraries "stars" v.0.5–5 (Pebesma 2021) for raster data (bathymetry) and "sf" v.1.0–7 (Pebesma 2018) for vector data handling. In the first step, we generated paleo-shorelines by deriving isobaths from the bathymetric data, which relate to the relative sea levels in the past, and measured their length. Short isobaths, representing either smaller inland depressions or small islands off the coast, were excluded with a threshold. In a second step, we estimated the Euclidean distances between coastal archaeological sites and the closest segment of the modelled paleo-shorelines with the 'geosphere' library v.1.5–14 (Hijmans 2021). Due to the properties of the bathymetric model, relative sea levels higher than 1 m were excluded from this study. As a result, the model computes shoreline distance measurements for each site and each paleo sea level lowstand in the time range between 0 and 119,000 years ago. Since the sea level reconstruction by Waelbroeck et al. (2002) reports uncertainty estimates, these were used to calculate shore distance uncertainty. Figure 2 shows the input sea level reconstruction (A) and the resulting shoreline distances (B) for two example sites, Sibhudu and Umbeli Belli.

3.3 Materials and methods of coastal and offshore geomorphology

The offshore geological and geomorphological data base used in this study stems from data collected using a series of geophysical techniques. Bathymetric data were collected using a WASSP WMB 3250 multibeam sonar system (Green et al., 2018; Pretorius et al., 2019). The positioning was achieved using a Hemisphere VS.330 Real Time Kinematic (RTK) and heading system, with the RTK base correction. Motion correction was applied by a xSens MTi-G motion reference unit mounted at the WMB 3250 transducer. Sound velocity profiles were collected with a Valeport MiniSVP, and the data were tidally corrected using the RTK input. The data were then exported as a 2 × 2 m grid.

Two different types of seismic reflection data are employed in this paper. High-resolution seismic profiles were collected using a 200 J Applied Acoustics boomer, coupled to an 18-element hydrophone array, the data acquisition and processing parameters of which are outlined in Green et al. (2013a). Ultra-high resolution seismic reflection data were collected using a Kongsberg Topas PS18 parametric sub-bottom profiler. Data were collected using a Chirp pulse and match filtered with the Kongsberg SBP utility where transducer motion was also modelled using the inputs from a Kongsberg Seapath 200 Inertial Motion Unit. The final segy data were exported using the secondary low frequency data between 0.5 and 6 kHz, with a resolution of <10 cm. All data were converted from two way travel time to depth using a standard sound velocity of 1500 m/s and 1,600 m/s for water and sediment respectively. Several vibracores were collected to examine the subsurface lithology, the collection and handling of which is outlined in Pretorius et al. (2016). AMS 14C dating on selected deposits representative of palace-land surfaces or processes were carried out, the intricacies of which are further documented in Pretorius et al. (2016; Pretorius et al. (2019).

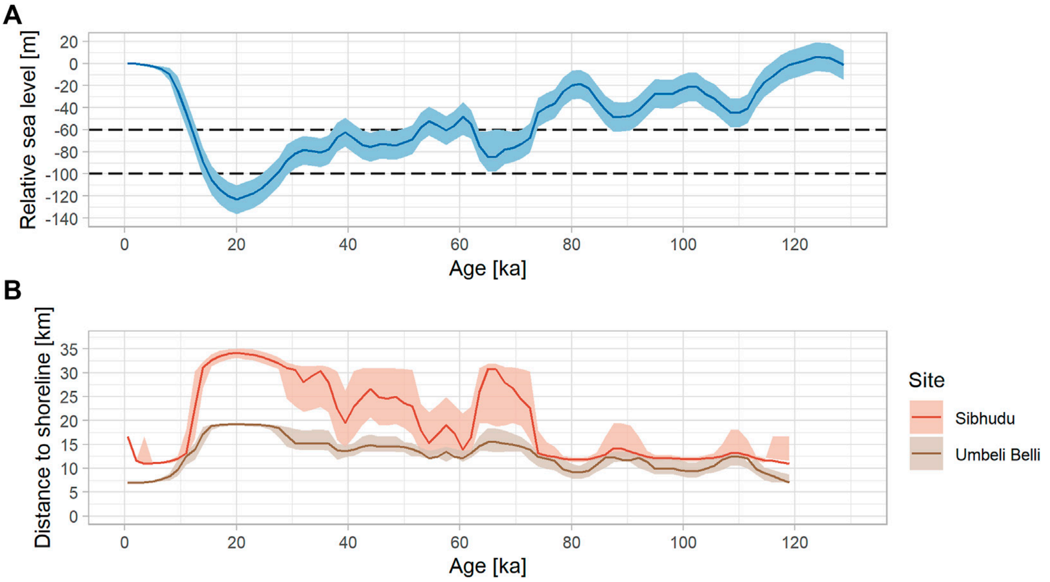

FIGURE 2
Input and output of the GIS model. **(A)** Sea level curve by Waelbroeck et al. (2002) with error margins. The dashed lines indicate the depths of aeolianite shoreline positions at −60 and −100 m. **(B)** Shoreline distance variation of two exemplary sites, Sibhudu and Umbeli Belli, in response to sea level lowering. The error margins are derived from the uncertainties of the sea level reconstruction.

4 Results

4.1 MSA and LSA archaeology

The few key stratified MSA sites in KZN all derive from rock shelters and encompass Border Cave, Holley Shelter, Sibhudu, Umbeli Belli and Umhlatuzana (Figure 1). None of these sites is closer than 7 km to the current coastline, showing a remarkable absence of excavated localities on the modern Indian Ocean coast. No MSA engagement with marine resources is recorded from Umhlatuzana and Holley Shelter, which are >30 km distant from the modern shoreline. Unfortunately, Umbeli Belli features no organic preservation in the MSA (Bader et al., 2016) potentially erasing any relevant traces, considering that the LSA layers with more favourable taphonomic conditions have yielded shellfish remains (see below). In the following, we first summarise the published work on key MSA and LSA sites on the known evidence, followed by our new data from an exhaustive archaeological database.

The site of Sibhudu (Figure 1) has provided evidence of a low number of edible marine shellfish from a maximum of 8 different species - with the most frequent being *Perna perna* (MNI=36) coming from its late MSA until pre-Still Bay layers (~77–48 ka) but also some rare marine animals, fish, crustaceans and turtle (Plug, 2006). In addition, the Still Bay occupations feature a total of eight potential ornamental shell beads with anthropogenic perforation from the marine gastropod *Afrolittorina africana* and one humanly-modified bead from *Nassarius kraussianus* deriving from the Late MSA layers, with further marine shells with natural perforations occuring in the Howiesons Poort and pre-Still Bay strata (d’Errico et al., 2008; Vanhaeren et al., 2019). New excavations directed by N. Conard since 2011 have added a small number (NISP=26 specimens >2 cm; plus hundreds of smaller fragments) of unpublished mollusks - both edible and non-edible—from layers spanning the Howiesons Poort until pre-Still Bay occupations (>80–60 ka) that require further zooarchaeological analysis. Combined, the data from Sibhudu indicate long-term engagement with the coasts both for dietary but also non-dietary reasons over the entire MSA occupations and at least during >80–38 ka, even though the distance to the coast during these occupations has fluctuated between 12–38 km to the shoreline. The low quantity of evidence in particular for the consumption of marine foods is likely a function of site-distance to the coast which exceeds the daily foraging radius. At Border Cave (Figure 1), the association of two beads of marine *Conus ebraeus* shell with the potential burial of a child at ~74 ka (d’Errico and Backwell, 2016) and the presence of two perforated specimens of *Nassarius kraussianus* in layers dated to ~44–42 ka (d’Errico et al., 2012) also indicate the special and planned use of marine resources as ornaments from sites far inland at the time (>50 km). Unfortunately, data on potential marine faunal remains are currently unpublished, precluding further assessment of their dietary use.

Regarding LSA localities, the most prevalent feature is the presence of marine shell ornaments - most often beads - at several inland sites in KZN. These beads (n=78) occur in variable frequency at a minimum of 11 LSA sites that span the time period ~13.000–300 uncal. BP (Mitchell, 1996). All of these sites are >20 km away from the present coastline, some up to 180 km. While a variety of marine gastropod species were used for ornamental purposes, *Nassarius kraussianus* accounts for >90% of all specimens (Mitchell, 1996). In general, there are few excavated stratified shell middens or localities of associated shellfish and LSA stone tools. Among the rare published stratified LSA sites along the modern coastline, Davies and MacDonald (1978) report on a shell midden with frequent mussels but also oysters found together with "Smithfield" stone tools dated to ~500 uncal. BP at Umhlanga Rocks on the modern coastline. About 7 km away from the Indian Ocean, shellfish exploitation for consumption is also evidenced in the LSA layers at Umbeli Belli (1,140±50 and 200±50 uncal. BP; Figure 1) dominated by *Perna perna* with >95% (Cable, 1984). Most interestingly, Shongweni (Davies, 1975), currently 30 km away from the coast, features shells of *Perna Perna* in LSA occupations between 4,000–1,000 uncal. BP which are most likely associated with dietary use.

Instead of relying on a biased picture from rock shelters alone, human presence during the Stone Age can be traced on a much broader scale by including open air sites and surface scatters. Our review of archaeological sites from an exhaustive database led to the identification of 228 coastal localities providing evidence for human activities during the MSA and LSA (see SOM Supplementary Table S1). Figure 1 shows the distribution of these sites. In contradiction to our expectations, MSA sites are more common than LSA sites (114 pure MSA sites and 29 MSA/LSA sites vs. 85 pure LSA sites). This seems counterintuitive, considering the large shell middens typically associated with late LSA occupants elsewhere in southern Africa. Furthermore, MSA sites also appear to be more widely distributed along most of the KZN coast, whereas LSA sites are more restricted to the southern part of the province. Since the overall majority of the data from our database derives from Oliver Davies' work it is hard to imagine that the LSA was simply 'overlooked' in the northern areas. In a recent study, Bader et al. (2022) also found comparatively little evidence for late Pleistocene/early Holocene LSA sites in this area, where substantial gaps in occupation after the end of the MSA (~28.000 cal BP) before the LSA occur, sometimes lasting more than 20.000 years. In sum, the database (SOM Supplementary Table S1) and Figure 1 provide clear evidence that the (modern) coastal area of KZN was frequently visited during both the MSA and the LSA. The data suggest that the majority of the original coastal occupations during the Stone Age may lie beyond this modern border but are currently submerged offshore.

4.2 Coastal distance modelling

4.2.1 Shelf exposure

We used the GIS model informed with sea level fluctuations to translate the bathymetric data into a map showing the temporal extent of the shelf exposure during sea level lowstands during the last 119,000 years (see Figure 3). According to the sea level curve, the maximum sea level lowstand at 123 m r.m.s.l was reached around 20,000 years ago, which corresponds to the greatest exposed area confined by the steep shelf edge (0 ka isochrone). The geography of the uncovered shelf is dictated by its geological setting. The shelf south of Durban and north of Richards Bay is steep and narrow, so that isochrones trend in narrow and coast-parallel fashion, indicating minor coastline displacements by time increments. The situation is more complex in the Natal Bight between Durban and Richards Bay, with a shallow northern and a deeper southern shelf. The 60 ka isochrones serve as a good indicator, showing that substantial areas of the northern shelf sector, with a shoreline partly (>30 km) displaced from the modern one, were subaerially exposed during 50% of the timeframe investigated. In the southern part of the Natal Bight, larger areas were only uncovered during deeper relative sea levels, but still account for one third of the studied timeframe (40 ka isochrone). Areas with long exposure times (80–100 ka isochrones) are the Aliwal Shoal north of Scottburgh, the Durban Bay and especially the northern Natal Bight in the area offshore the uMlalazi River/Port Durnford.

4.2.2 Shoreline distance of MSA and LSA coastal sites

The sea level fluctuations since the Eemian (MIS 5e) have caused considerable displacements of the shoreline. Here we present results of our GIS simulation, showing how these variations have affected the shoreline distance of MSA/LSA coastal sites from our database and thus, the potential access to marine resources during these times. Since many of the sites are surface finds that lack radiometric dates, we could not reconstruct the situation at the time of deposition. However, we were able to define broad geographic regions along the KZN coast based on the variability and timing of their response to sea level fluctuations. We analysed 172 archaeological sites situated within 15 km from the modern shoreline and subdivided these into four regions following our results of the shelf exposure model (see above). These regions include the 'North Coast' north of 28.8°S (n=5 sites), the 'Northern Natal Bight' between 28.8°–29.3°S (n=19 sites), the 'Southern Natal Bight' between 29.3°–29.8°S (n=45 sites) and the 'South Coast' south of 29.8°S (n=103 sites). Our results are presented in Figure 4 and show that sites on the North and South Coast lay predominantly within the typical maximum foraging distance

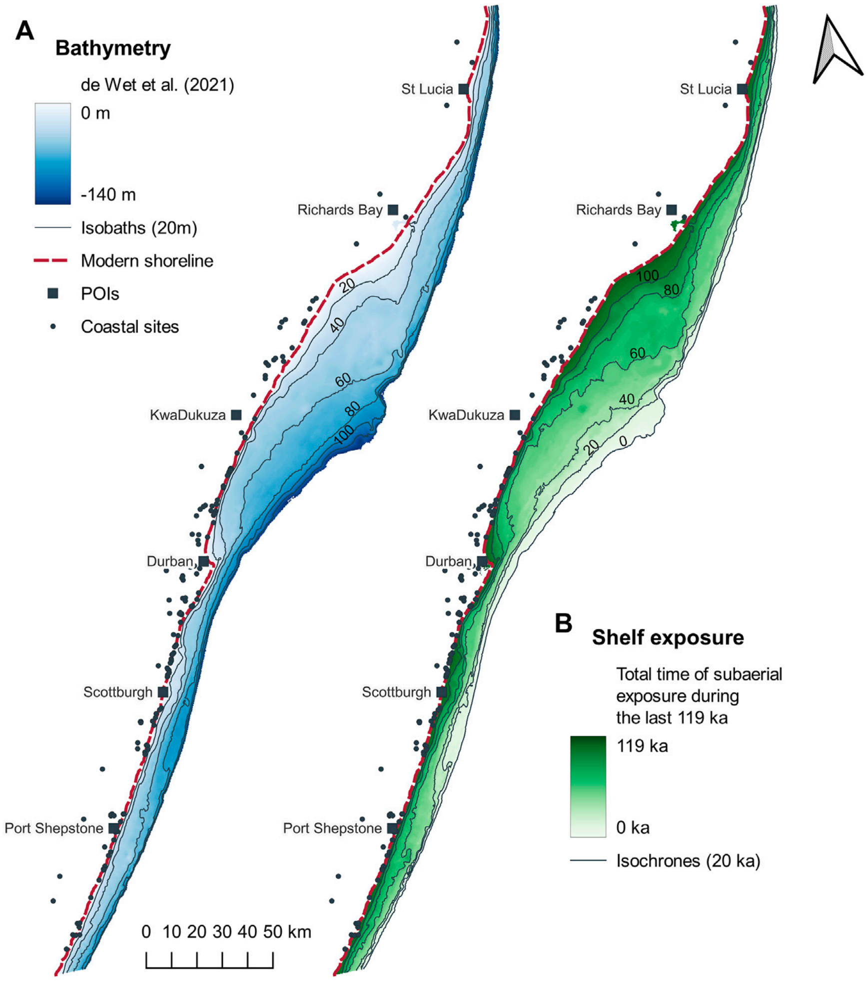

FIGURE 3
How long has the shelf been exposed during the last 119,000? **(A)** Bathymetric model by de Wet and Compton (2021) shows the modern-day water depths in the study area between 28.1–31.2° S in the sea level affected zone between 0 and 140 m. The result of the GIS model **(B)** shows the cumulative exposure time of the affected areas. The colours and isochrones indicate how long an area has been uncovered *in total* during the timeframe between 0–119,000 years ago. Note that the exposure time can be contiguous or the sum of multiple exposures, due to sea level fluctuations derived from the mean sea level curve by Waelbroeck et al. (2002). The isochrones do not indicate absolute dates of paleo-shorelines.

of 10 km to the shoreline over the last 119 ka. Even during the LGM (123 m, 20 ka) the average coastal distance of these sites was only ~14 km (South Coast) to ~18 km (North Coast) from potential marine resources. Much higher variability is found on the coast of the Natal Bight. In the southern part the average shoreline is only within daily foraging range prior to 72 ka, during a short window around 60 ka, and then again after 12.5 ka. During the LGM, the average site is 24 km from the coast with a maximum of 38 km. In the Northern Natal Bight, the sites are only occasionally situated within foraging distance in the timespan before 77 ka and after 11 ka. During the period between, no known site is in foraging distance and the average distance during the LGM reaches >40 km.

4.3 Offshore geology and geomorphology of the KZN shelf: a review and new interpretations

Using a broad array of geophysical data, we examine the morphology and stratigraphy of the shelf offshore the KwaZulu-Natal coast (Figure 5). We focus here on sites that occur adjacent to the MSA occupations of the coast and hinterland, from the Mzimkulu River in the south to KwaDukuza in the north (Figure 5). Between these locations, the shelf widens from 12 km to nearly 30 km offshore the important MSA site of Sibhudu, and houses a variety of submerged landscapes that formed when sea levels were lower than present.

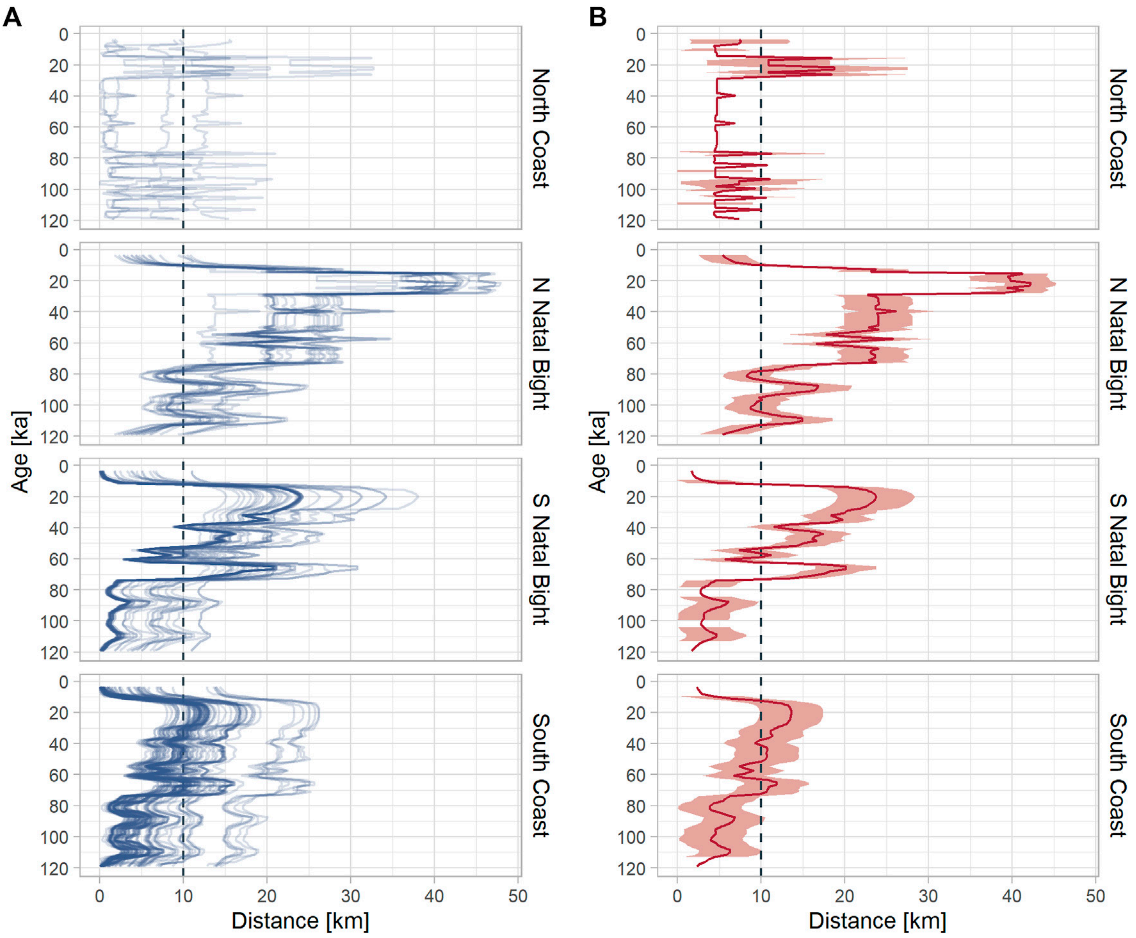

FIGURE 4
Variation of the distance of archaeological sites to the coast over time. **(A)** Coastal distances for 172 archaeological sites from the North Coast (n=5), Northern Natal Bight (n=19), Southern Natal Bight (n=45), and South Coast (n=103). Light blue lines show the time series of single sites and dark blue lines indicate overlapping of multiple time series. **(B)** Temporal aggregates of the time series show the mean (dark red line) and one standard deviation (bright red ribbon) coastal distances. The dashed lines at 10 km in **(A)** and **(B)** mark the upper boundary of daily foraging range of modern Hunter-Gatherer groups.

4.3.1 Paleo-fluvial courses

Many of the rivers observed on the modern coast can be traced seaward of their current mouths where they were incised during the penultimate glacial maximum (MIS6), and the last glacial maximum (LGM) lowstands. During these periods, much of the shelf was exposed to subaerial processes producing a flat coastal plain interspersed with multiple river valleys that terminated at the shelf break where sea level resided (Figures 6, 7). The intervening periods, notably from MIS4 to MIS2 saw the shoreline placed at a minimum of >60 m lower than present, with these rivers forming a series of estuaries and lagoons along the coast in response to higher sea levels drowning the seaward edges of the river valleys. Pretorius et al. (2019) reveal a series of river courses of the Mzimkulu River, some of which are still exposed on the shelf, that were generated during MIS6 and the LGM which have been infilled by estuarine materials (Figure 7). Several key seabed features are: 1) a paleo-lagoon located at a depth of ~85 m and 2) rivers draining into the head of a submarine canyon to form a coastline analogous to the modern one at Waterfall Bluff, ~ 95 km to the southwest.

To the south of Durban and offshore the Isipingo and paleo-Umlasi River mouths, a well-developed meandering river system is evident from seismic reflection data (Figure 6). These river valleys occur two valleys to the south of the Umhlatuzana Rock shelter. The paleo-Umhlatuzana River itself has formed a prominent incised valley in the Durban Bay, where several other smaller rivers merged and exited out to the shelf to combine with a series of incised valleys related to the Mgeni River (Figure 6). These

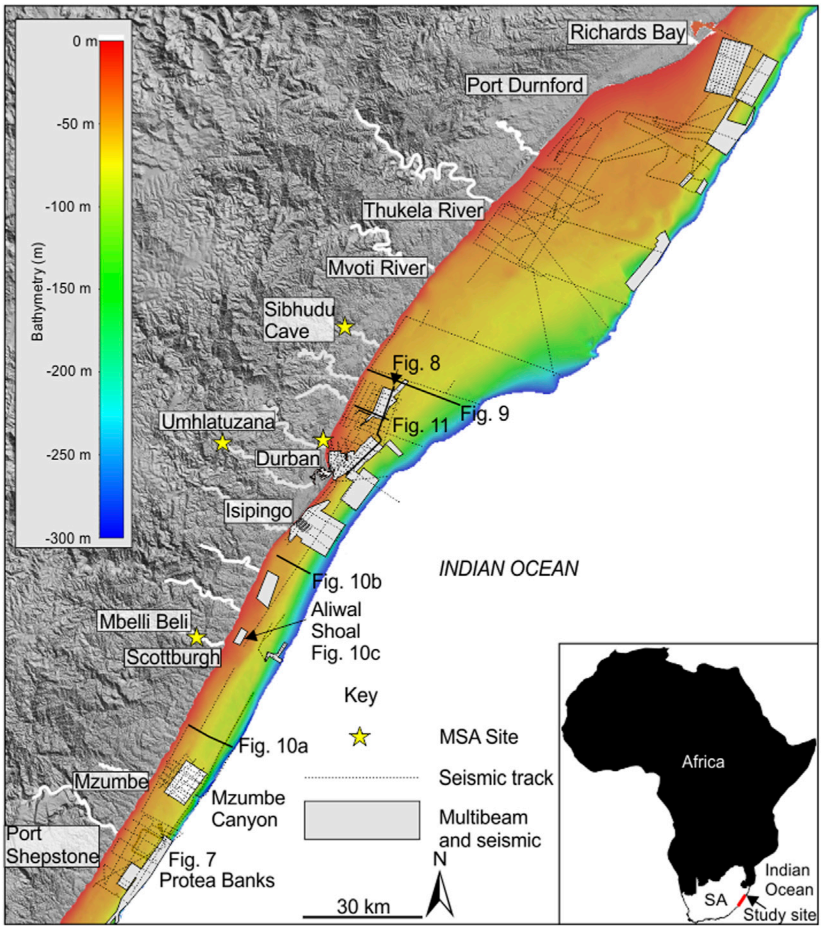

FIGURE 5
Geophysical data coverage of the KwaZulu-Natal shelf, superimposed on the general shelf bathymetry (after de Wet and Compton, 2021). Key data localities discussed in the paper are highlighted in bold.

incised valleys and adjoining subaerial paleo-landscape are marked by circular depressions that occur in the subsurface at elevations of between −60 and −70 m (Figure 6). When viewed in profile, these depressions reflect broad topographic lows associated with an older generation of incised valleys, and now filled by a set of reflections that prograde in from the depression margins (Figure 8). Cores reveal this infilling material to comprise a stiff lagoonal clay dated to 39,636 ± 592 cal. BP. This lagoonal sequence is in turn truncated in various parts by LGM-age incised valleys (Pretorius et al., 2016) and overlain by Holocene age aeolianite and beachrock, the surface outcrop of which marks a second lagoon now preserved on the shelf over the MIS 3 example (Green et al., 2013b) (Figure 8).

Across KZN, a similar pattern emerges. In Richards Bay, radiocarbon dates of 39,100 and 45,200 14C yr B.P. (Pta-4142; Pta-4140) from wetland peats (at depths of 46 and 52 m) within a back-barrier sequence provide a maximum indication of lower than present sea levels at that time (R.R. Maud, personal communication, 2000). In the Umlaas canal in Durban, a date of >48,000 14C yr B.P.was obtained from peats and diatomites from -35 m amsl (R.R. Maud, personal communication, 2000) and in Durban Bay, King (1972) reported an age of 24,950 14C yr B.P. (GaK-1390) for a peat at -22 m amsl.

Directly offshore of Sibhudu, seismic profiles reveal a series of compound incised valleys occurring to landward of a subcropping submerged shoreline at between depths of 60 and 70 m (Figure 9). The truncations of each paleo-subaerial surface reveal up to four generations of incision, with subsidiary smaller channels stacked within the associated fills. These smaller channels resemble the tidal channels found in back-barrier estuarine systems of the modern large lagoons of SE Africa (Benallack et al., 2016; Dladla et al., 2019). We view these as a series of incised valleys associated with a back-barrier/estuary/lagoon environment, fronted by a submerged barrier shoreline.

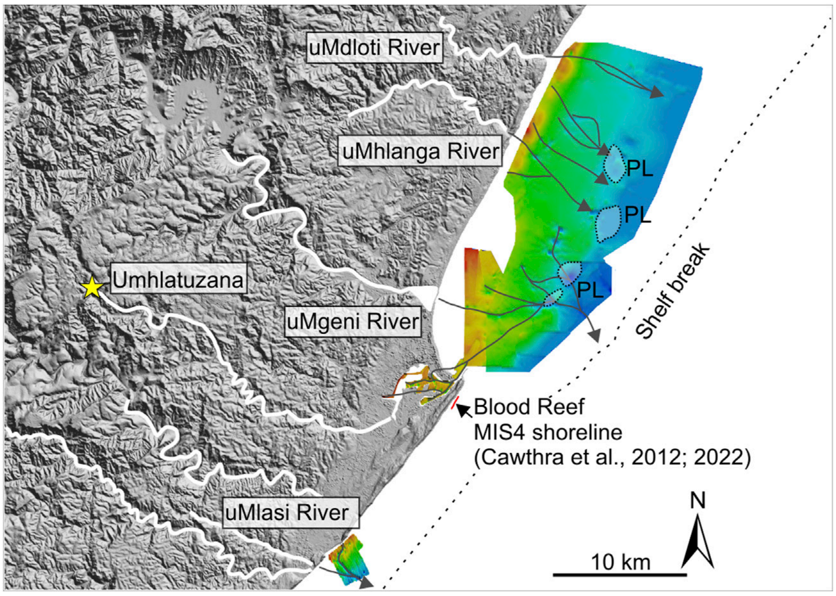

FIGURE 6
Bedrock surface offshore the greater Durban area based on available seismic data. The surface represents several periods of amalgamated subaerial exposure, reflected in the drainage patterns. PL = paleo-lagoon. The MIS 4 shoreline of Cawthra et al. (2012, 2022) is highlighted. Suspected drainage.

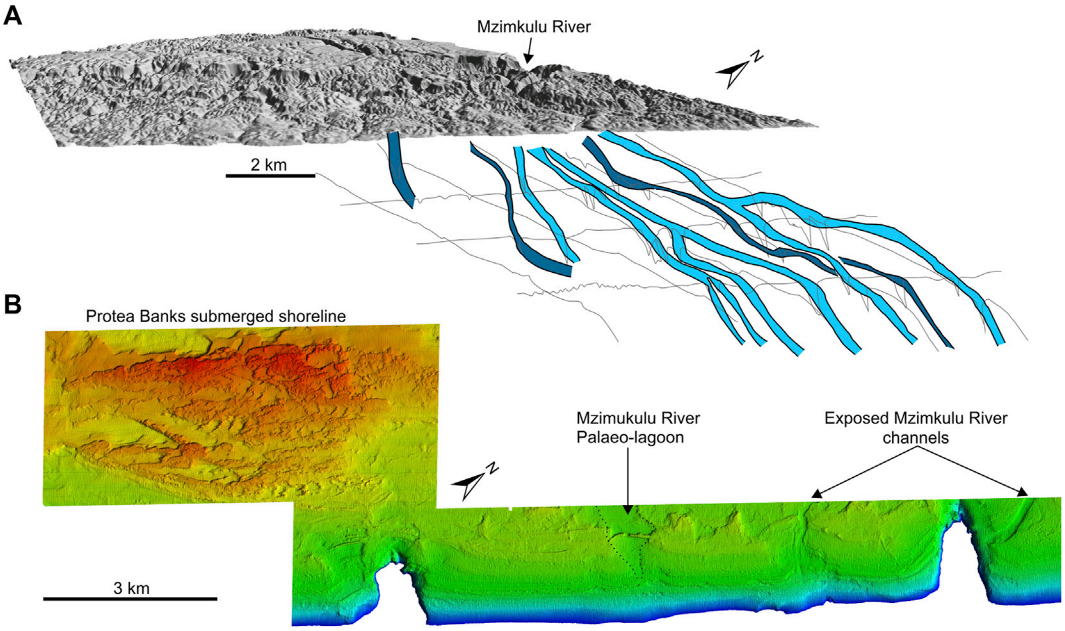

FIGURE 7
(A) 3D representation of the drainage pattern offshore the Mzimkulu River, just to the north of Mpondoland. Dark blue represents an older subaerial channel network, likely MIS 6, the lighter blue represents the LGM drainage system (after Pretorius et al., 2019). **(B)** Multibeam bathymetry of the Protea Banks shelf immediately offshore the Mzimkulu River. Note the development of a lagoon, with several LGM channels still exposed at the seabed, one of which entering a submarine canyon and likely forming a waterfall akin to the Waterfall Bluff site of Mpondoland.

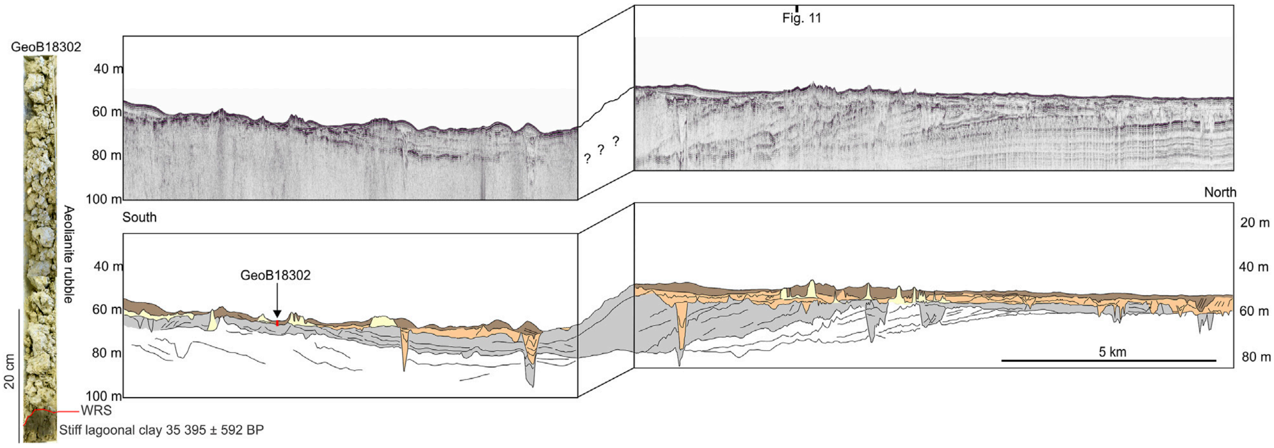

FIGURE 8
Interpreted (top) and raw (bottom) seismic reflection data offshore Durban. The data highlight a series of incisions into paleo-land surfaces. The base of the grey represents an older MIS 3 lagoonal depression (penetrated by GeoB18302-left), which was re-incised by younger LGM channels that later formed younger, Holocene-age lagoons above the older MIS 3 materials.

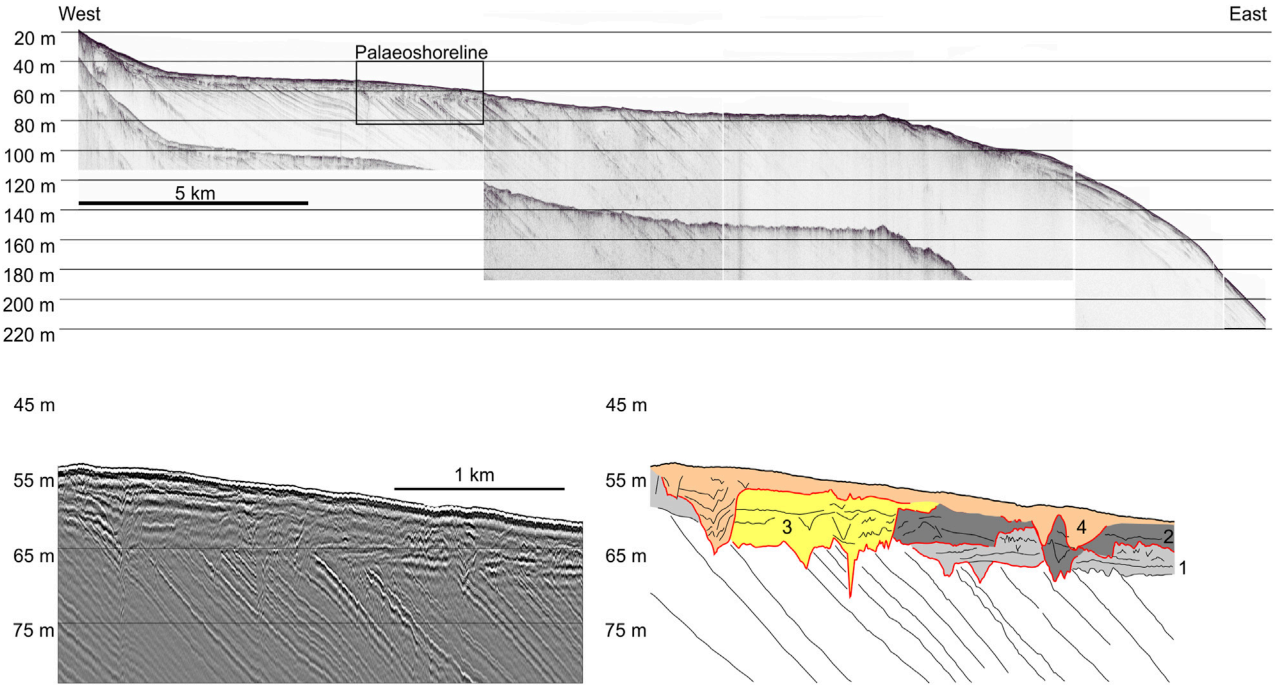

FIGURE 9
Seismic reflection profile offshore Sibhudu Cave. The below interpretation highlights at least four phases of channel incision and lagoon development behind an aeolianite to seaward, spanning a possible MIS 12 to MIS 2 age range.

Their compound nature implies multiple shoreline occupation at that depth over successive sea level cycles, including the most recent lowstand of the LGM and the lowstands of MIS 12 and 6 too.

4.3.2 Coastal aeolianite and beachrock shorelines

Both regional and focused bathymetric and seismic reflection surveys reveal a nearly continuous set of submerged shorelines at

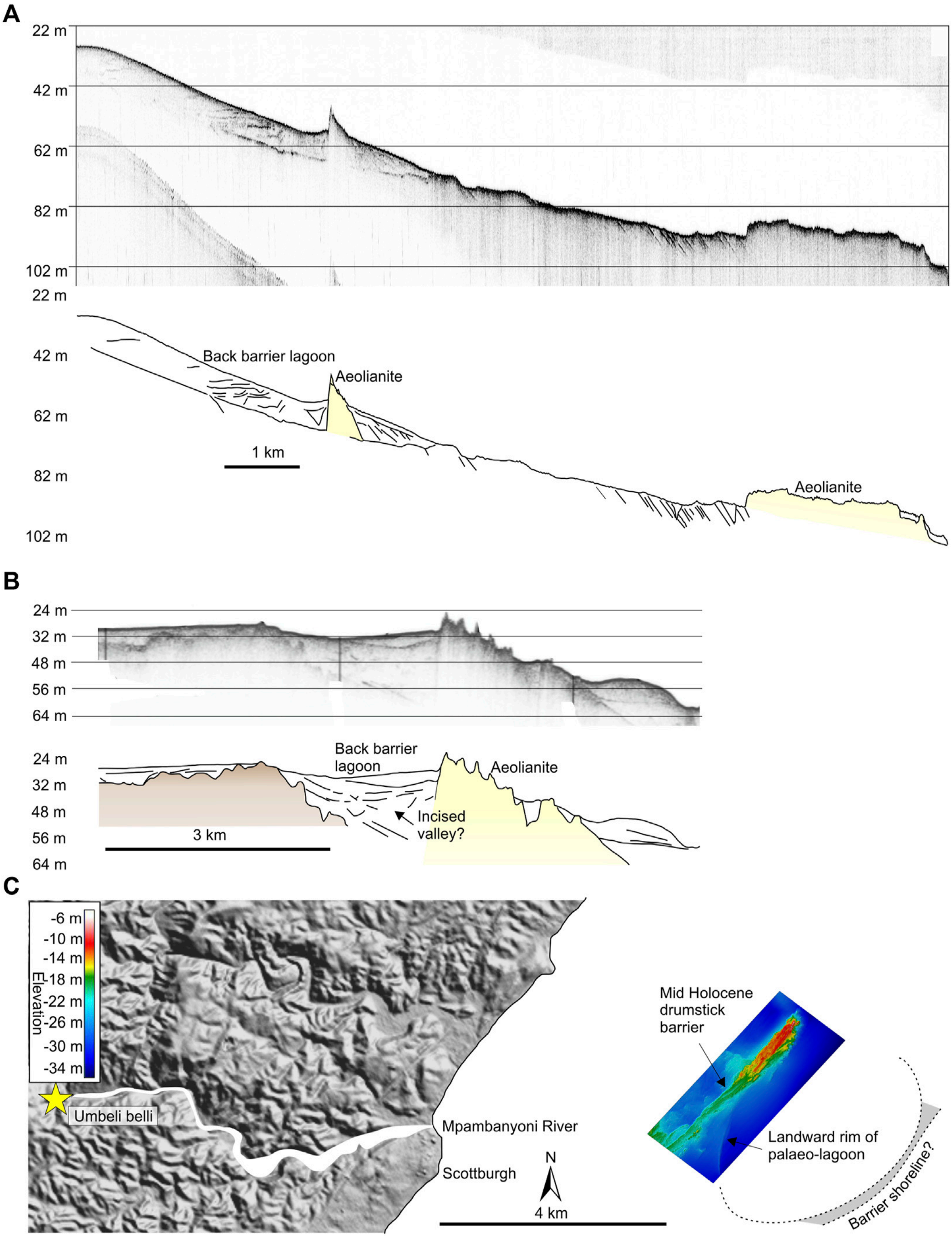

FIGURE 10
(A) Seismic reflection profile from the KZN south coast offshore Mtwalume. Note the two clear phases of aeolianite development at -100 m and 60 m. There is a prominent back barrier lagoon complex housed behind the 60 m shoreline. **(B)** Seismic reflection profile offshore the Amanzimtoti area. Note the similar seismic architecture to **(A)** Data adapted from Gribble (2021). **(C)** Multibeam bathymetry of the Aliwal Shoal, juxtaposed with the location of Umbeli Belli. The shoal forms a drumstick barrier, fringed to seaward by an arcuate ridge that we interpret as the landward rim of a paleo-lagoon.

depths of 20–30, 60–70 and 90–100 m on the shelf. Offshore the Mzimkulu River, the Protea Banks comprises a large upstanding block of aeolianite, with several small coastal spits and barriers found to seaward of the feature at a depth of 100 m (Pretorius et al., 2019) (Figure 8). Offshore the Mtwalume River, seismic profiles show a prominent aeolianite pinnacle with a basal depth

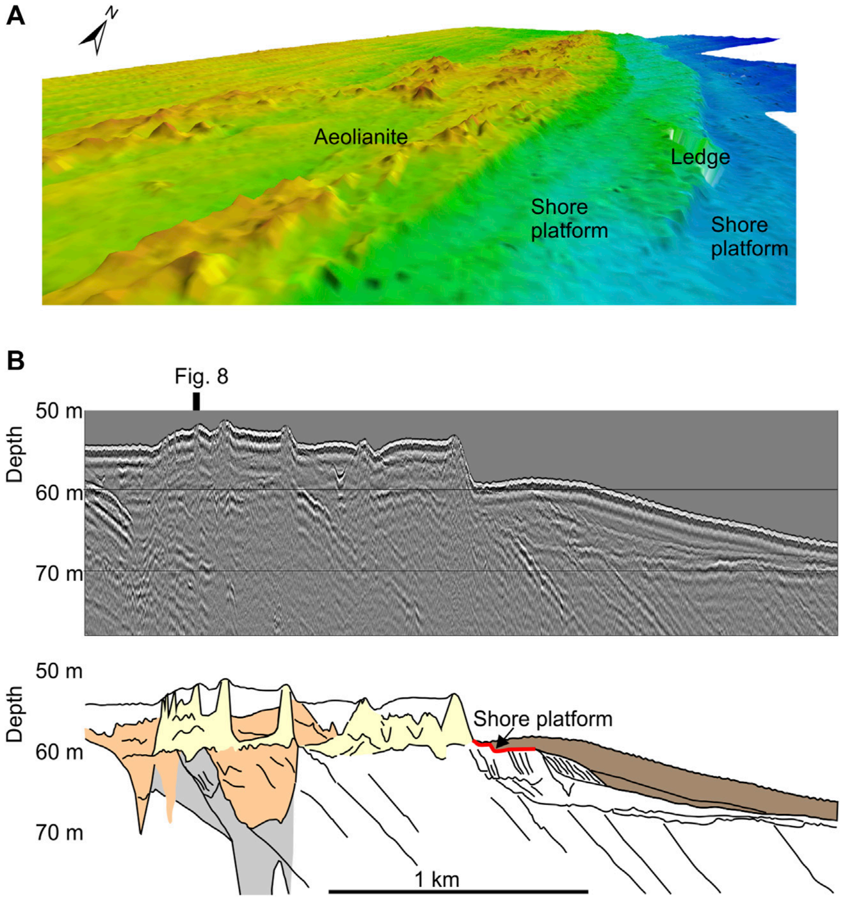

FIGURE 11
(A) 3D multibeam representation of the seabed offshore uMhlanga/uMdloti. Note the landward aeolianite with two shore platforms benched into the rock surface, denoting a rocky shoreline occupation at 60 m **(B)**. Interpreted (top) and uninterpreted (bottom) seismic reflection profiles through the above aeolianite. Note the underlying incised valley, the back barrier system to landward of the aeolianite, and the bench to seaward of the aeolianite, into the fringing material at 60 m.

of ~65 m, fronted to seaward by a flat erosional platform (Figure 10). To landward of the pinnacle, a series of low amplitude, draped reflections onlap the pinnacle and are truncated by a series of small (3 m-deep and 20 m-wide) channels marked by higher acoustic reflection. Likewise, off Amanzimtoti, a similar arrangement is observed, with a well-developed aeolianite onlapped to landward by a prominent incised valley fill.

Bosman (2012) examined a well-developed aeolianite offshore Scottburgh, the Aliwal Shoal, and using OSL dating, placed an early to mid-Holocene age on its development. However, more detailed multibeam mapping shows that the Shoal forms a drumstick barrier that overlies an older arcuate ridge of aeolianite to seaward that is formed at a depth of 30–34 m (Figure 10). These arcuate ridges are commonly associated with paleo-lagoons, forming semi-circular depressions on the seabed bounded by aeolianite and beachrock spits (Green et al., 2013b). This suspected paleo-lagoon occurs 5 km seaward of the Mpambanyoni River, on which the Umbeli Belli site is located, ~ 12 km directly landward of the Aliwal Shoal.

Offshore Durban, between Umhlanga and Umdloti, 19 km southeast of Sibhudu, a well-developed rocky shore platform has been mapped for almost 9 km along coastal strike at a depth of 60 m (Figure 11). Seismic reflection profiles reveal this to be the surface expression of an eroded set of prograding moderate amplitude reflections that are distinct from, and located adjacent to, a prominent aeolianite with a basal depth of 60 m. These are likely remnants of an old rocky platform related to debris collapse of a fringing aeolianite (Green et al., 2018). The upstanding aeolianite block overlies the older MIS 3 and Late Pleistocene incised valleys that comprise the same paleo-lagoon complex shown in Figure 7.

For almost the entire 160 km length of this study, the same trend emerges where shorelines at ~60–70 m water depth comprise upstanding blocks of aeolianite fronting an onlapping sequence of lower amplitude reflections that fill an incised valley. We consider these sequences to represent back-barrier lagoonal environments, with small tidal channels that formed behind a substantial coastal dune cordon that had developed on the shelf (cf. Benallack et al., 2016; Dladla et al., 2019; Green et al., 2022b). The shoreline ages are less-well constrained outside of Durban, though it is clear that the shorelines represent multiple phases of shoreline occupation. The majority of work has placed these as Holocene in age, though undoubtedly, the previous phases of shoreline occupation, especially the paleo-lagoons, appear to relate to MIS 3. The barriers may correspond with a stilstand at -60 m at ~55 ka. According to the core and age data of the submerged lagoons, their presence implies a prolonged period of sea-level stability up to ~39 ka (Pretorius et al., 2016). In addition, lagoonal remnants crop out as far north as the Thukela River shelf (Green and MacKay, 2016), where they were dated at 40,650 uncal. BP (Flemming, 1978), to which we correlate these deposits.

5 Discussion

5.1 Coastal adaptations in KZN during the Pleistocene and Holocene?

In contrast to the Western and Eastern Cape, little is known about the habitation and use of coastal ecosystems in KZN by modern humans during the Late Pleistocene and Holocene. Here we provide the first systematic review of potential coastal adaptations during the MSA and LSA of the eastern Indian Ocean coast. A review of published sites shows important but rare and mostly low-density evidence through the MSA. Key data regarding dietary use comes from Sibhudu where transport and consumption of marine shell (particularly *Perna Perna*) but also low numbers of mammals, fish and crustaceans, is apparent. Both Sibhudu and Border Cave feature shell beads, showing that MSA people procured shells from the beaches, wore them as ornaments and left them at the site, sometimes even as potential grave goods. This evidence spans roughly >80–40 ka, suggesting a long-term engagement with coastal and marine ecosystems. Importantly, both sites were up to 30 km (Sibhudu) or >60 km distant during the relevant times as shown in this study. Based on a large database of Stone Age sites in KZN, our study demonstrates that many open-air scatters of MSA stone tools occur along most of the modern coastline, hinting at a much longer and more intense settlement along the shores as currently known from stratified inland Pleistocene sites.

During the LSA, there are few to no shell middens properly excavated and published from KZN, and the ones that do exist all date to the Holocene. This being said, consumption of marine resources - mostly *Perna perna* - is well-evidenced from sites such as Umbeli Belli and Shongweni within the last 4,000 years. The archaeological database of the region provides evidence for more LSA occupations on the modern shore clustered around the southern part of the province, though interestingly less compared to the MSA. Our shoreline reconstruction over the past 119.000 years has shown that the coast in southern KZN has not dramatically changed during the late Pleistocene and Holocene providing a possible explanation for a multitude of both MSA and LSA occupations along the modern day shoreline. In the northern part of KZN though, shoreline extension was more variable, especially during LSA times (<28.000 cal. BP) during which the coast would have mostly been more than 10 km away from the modern one and thus outside the typical daily foraging radius. The most recurrent pattern of LSA people engaging with coastal resources comes from nearly a dozen inland sites, up to 180 km from the modern shoreline, with evidence for marine shell beads spanning ~13.000–300 uncal. BP. The consistent and predominant use of *Perna perna* for food and *Nassarius krassanius* for beads during both the MSA and LSA shows remarkable consistency in dietary and non-dietary choices across the last ~80.000 years in the region.

Summing up these observations, KZN has a deep-time record of the use of marine resources and the occupation of coastal landscapes in the Late Pleistocene and Holocene, but one which currently differs in the quantity, quality and diversity from the southern Indian Ocean and Atlantic Ocean coast. In the latter regions, over 10 MSA and dozens of LSA sites indicative of systematic coastal adaptations are known starting already at ~120 ka, shell middens occur both in the MSA and frequently in the LSA (also as so-called "megamiddens") and sites are often associated with a wide array of consumed marine mammals, birds and fish from intense occupations directly on the coasts (e.g., Jerardino, 2010; Will et al., 2016). How can we explain these different patterns in the archaeological record? We briefly discuss two potential explanations, though others are conceivable: 1) Behavioral differences based on differences in marine ecology; 2) Research bias due to issues of site preservation, intensity of research and differences in (marine) geology.

Regarding the first hypothesis, the Western Cape and KZN differ strongly in their coastal and marine ecology. Along the Atlantic coast, the Benguela Upwelling system creates highly nutrient-rich waters that sustain a productive marine ecosystem. In contrast, the Indian Ocean coast in KZN is mesotrophic with lower productivity but higher species diversity, driven in part by upwelling along the shelf edge associated with the oligotrophic western boundary of the warmer waters transported by Agulhas Current (De Lecea et al., 2013; Kyriacou et al., 2021). Variable shelf widths and the flow of the Agulhas Current may have changed the nutrient status of the KZN marine ecosystem, though it seems that during lowstands, the Agulhas Current would have been situated close inshore to the shelf edge or paleo-coastline (e.g. Green et al., 2022a) and oligotrophic conditions may have been dominant. The Indian Ocean coast of KZN with its lower marine biomass and different variety of marine food resources might have thus been either unsustainable for intense coastal exploitation, or people in the MSA were not able to efficiently extract resources from such an environment. Modern ethnographic data on coastal foraging in KZN by local subsistence shellfish gatherers show, however, that collecting large amounts of diverse shellfish and crab species is possible (Kyle et al., 1997a; Kyle et al., 1997b). Interestingly, well-defined, stratified Iron Age middens with large amounts of shell (particularly *Perna Perna*) such as Mpambanyoni (Robey, 1980), Emberton Way (Horwitz et al., 1991), Umhlanga Rocks (Beater and Maud, 1963) or several midden sites around Durban Bluff (Schoute-Vanneck, 1958) also demonstrate the viability of extensive coastal adaptations and extracting large amounts of edible seafood from the Indian Ocean, at least in more recent times by more sedentary societies. Whether MSA and LSA people used it in a comparable manner thus becomes a question requiring further research instead of excluding the option *a priori*.

Modern ethnographic studies of shellfish exploitation in the nearby Transkei and other regions (Bigalke, 1973; Siegfried et al., 1985; Hockey et al., 1988), have generally found that people living up to 5 km from the sea regularly exploited shellfish while those living 10 km away visit the coast less frequently, possibly on a monthly basis. These visits often coincided with favorable tides, and required transport when available. No sheltered MSA and LSA sites—generally being good sediment traps allowing the accumulation of a longer record and with faunal remains—occurs closer than 7 km to the current shoreline. From ethnographic observations we would expect few marine remains to be transported to these sites, and this matches the archaeological record. On the shore itself there are few to no sheltered localities, with open-air deposits rarely allowing *in situ* archaeological remains to accumulate and persist. In the Western Cape, almost all sites with good evidence for MSA coastal adaptations come from caves or rock shelters within 10 km from the modern shoreline—such as Klasies River, Blombos or Pinnacle Point - though rare open-air sites exist as well (e.g. Will et al., 2013). Many of the differences between the western and eastern seaboard might be attributable to these differences in relevant sediment traps. Even worse, changes in Pleistocene and Holocene sea-levels along the KZN coastline as modelled here, pushing the shore often 10–40 km from its current location, might have erased or inundated the evidence of open-air deposits on past shorelines. In sum, our key MSA and LSA sites are too far away to record the regular use of marine resources (see also Kyriacou, 2017). More archaeological exploration within a 10 km radius from the shore is needed, especially where the offshore record has identified possible paleo-landscapes that may have provided suitable shelter and/or resources. The lack of caves, rock shelters or sheltered areas on or close to the shoreline and the erosion or flooding of open-air deposits, however, might even require completely new research strategies that we discuss in the next section.

The points made above can be further supported by the example of a recently successful research project on coastal adaptations at the site of Waterfall Bluff along the Indian Ocean coast in Pondoland and only ~50 km south-west from the KZN border (Esteban et al., 2020; Fisher et al., 2020). Here, excavations at a rockshelter site directly on the modern shoreline below a waterfall created by the run-off of the Mlamobomkulu River into the Indian Ocean has provided ample evidence for coastal adaptations between 36–10 ka. The evidence encompasses not only the systematic collection of marine shellfish and fish but also marine shell beads. The authors ascribe the presence of these archaeological remains, usually scarce in the region, to the narrow continental shelf, with the site thus being close to the ocean during the Late Pleistocene and early Holocene even when sea levels changed. This is likely an important determinant, and given the narrow shelf widths in KZN, such as south of Durban or north of Richards Bay, these too would have been within the ca. 10 km daily foraging radius. The submerged landscapes we discuss below, especially offshore these locations, are thus an especially important future exploration target.

In conclusion, archaeological data and contextual observations suggest that the current evidence on the use of marine resources and coastal landscapes during the MSA and LSA in KZN is more likely the result of a complex research and geological bias instead of an inability of Stone Age hunter-gatherers to exploit these resources efficiently in this specific environment: Sheltered sites with well-known records occur mostly >10 km from the modern coasts where sparse transport of dietary marine resources can be expected, little archaeological fieldwork has been carried out directly on the coasts and much of the evidence that might have once been present would have been erased by changes in sea-level. However, since our archaeological review showed that there is a large untapped potential, the next section aims to highlight how best to exploit this by combining archaeological knowledge with our results on the changing coastline's position and nature over various sea level cycles.

5.2 Combining archaeology and coastal geomorphology: Pathways to future research

The most fruitful way to further the exploration of potential coastal adaptations during the Stone Age in KZN consists of combining existing archaeological data with results on the GIS modelling of paleo-shorelines and offshore marine geology and geomorphology. Based on the results of the GIS model, the most interesting areas for finding MSA/LSA archaeology on land should be south of Durban and north of Richard's Bay, both areas of which feature little displacement of the shorelines during the last 120 ka and mostly within <10 km. We especially highlight the Aliwal Shoal region offshore Umbeli Belli, where a proposed lagoon has been identified ~12 km from the site. Interestingly, this area matches with some of the (scant) excavated, and much of the surface, MSA and LSA archaeological evidence available on land. This is always frequent in the southern part of KZN. Likewise, the series of lagoons and estuaries evident from the seismic record offshore Sibhudu (Figure 9) point to a potential submerged resource in existence since at least MIS 12. Cawthra et al. (2022) recently highlighted an MIS 4 shoreline offshore the Durban coast in shallow waters, and link this to the Sibhudu, providing an interesting comparison of wind conditions and climate for the MSA settlement period that can be done for almost all the sites mentioned here.

Conversely, offshore exploration would be particularly interesting in the wider shelf of the Natal Bight, with large exposures of land now submerged up to 60 km from the modern shoreline. Here, observations on offshore marine geology and geomorphology are a key guide for future research. In many of the submerged shorelines, there is strong potential for cave and rockshelter features to form: Overhangs, notches and caves are common in the submerged beachrocks and aeolianiates of the SE African margin (Green and Uken, 2005; Bosman, 2012), and may have provided similar environments as the Pinnacle Point caves of the southern Cape coast and offshore (Cawthra et al., 2018; 2020). Notable examples include offshore the Thukela River and throughout the Aliwal Shoal, where the foresets of aeolianites weather to form overhangs up to 2 m high and several meters wide (Bosman, 2012; Engelbrecht et al., 2020). Based on their relative stability and ages (from the Holocene to at least MIS 3), the now submerged paleo-shorelines and lagoons around modern-day Durban appear to be further attractive possibilities for uncovering submerged MSA and LSA occupations. Coastal lagoons are productive and biodiversity-rich marine ecosystems, featuring diverse and rich communities of marine fauna, and they provide easy access in their generally shallow (<2 m) water depths (Alvarez-Borrego, 1994; Kjerfve, 1994). Present-day Lake St. Lucia may be seen as a close analogue to these submerged ecosystems in the Late Pleistocene. Our modelling shows the once open marine shorelines of the False Bay region were within 10 km of the closest MSA site, a situation we consider analogous to the submerged environments offshore Durban.

The submerged coastal lagoons along the KZN coast are also relatively close to important MSA and LSA sites on the coast of Durban, such as Sibhudu, Umbeli Belli and Umhlanga Rocks, each of which have good evidence for longer-term occupation and the active use of shellfish and other marine resources. The along-coast shoreline variability of these submerged lagoons should be noted. Offshore Umhlanga Rocks, these transform into paleo-rocky shore coastlines with cliffs and wave-cut platforms, the modern equivalents of which are host to abundant marine shellfish such as the oyster *Crassostrea* sp, barnacles such as *Belanus* sp., and the bivalve *Perna perna* (Cooper and Green, 2016). In addition, fluvial systems were an important attractor for human settlements during the Pleistocene, providing drinking water and access to other animal resources. Many rivers on the modern coast, such as the Isipingo, Mgeni, Mzimkulu and Umlasi Rivers, can be traced offshore via seismic reflection data. These are well-incised due to the overall narrow shelf and shallow shelf break, which was exposed repeatedly during the lowstands of the Pleistocene (Green et al., 2013a). Their paleo-courses, in addition to the other major seaward expressions of KZN's paleo-drainage, present another attractive target for submerged archeological exploration.

Based on these observations and the foregoing discussion we propose several pathways for further research. In terms of archaeological exploration, the different geomorphic landforms show different likelihood for past settlements, suitability as sediment traps and are associated with certain preservation conditions. The latter relate to lagoon and coastal dune features that represent sediment-abundant conditions, though the two vary in their respective energy regimes. The tranquil back barrier shorelines of the submerged lagoons would seemingly be an attractive area to explore, given the high degree of possible preservation potential of sediment and archaeological archives. Relict rocky coast paleo-shorelines may provide good shelter and foraging potential, however these need to form and then be stranded by falling sea levels so that the shelter potential is not quickly submerged, and the ensuing occupation record remains preserved from marine erosion. Some of the aeolanites offshore the Sibhudu area are important in this regard (Engelbrecht et al., 2020). Other landforms such as present and paleo-river valleys and mouths constitute another primary target for identifying potential Stone Age settlements along the coasts.

Increasingly detailed and high resolution geomorphological mapping, on- and off-shore, may help to identify new sites or prevent surveying archaeological badlands. We in particular identify two regions such as the South Coast and the southern Natal Bight as relevant on-shore and the submerged lagoons, offshore the Protea Banks, Aliwal Shoal and Durban shelf, as relevant off-shore areas for new and better informed explorations. On-shore explorations will be comparatively easy to carry out via foot surveys, informed by local geomorphology and assisted by drones followed by dedicated excavation of documented *in situ* archaeology or other human traces such as footprints. Similar approaches have shown to be feasible in other coastal areas of South Africa (e.g. Parkington et al., 1988; Morrissey et al., 2020) and recently implemented by us in other areas of KZN. In contrast, off-shore work will be much more demanding in terms of logistics and costs. As a first step, we suggest the initial survey of the identified high-potential areas, using a combined multibeam and side scan sonar approach for underwater detection of lithics wherever possible (see Grøn et al., 2021; Morris et al., 2022). Side scan sonar, with its superior resolution, is especially important to detect lithic artefacts if exposed on seafloors. Given the sediment-denuded character of much of the mid to outer shelf of KZN, this is an especially attractive option. Additional high resolution to ultra-high resolution Chirp seismic reflection data should also be collected to provide stratigraphic context to the ensuing sampling campaign. Small-scale suction dredging for potential stone tools from recovered sediments and localised small core-drillings to identify archaeological traces should follow in this regard. More systematic core drilling over larger areas via research vessels and dedicated underwater archaeology by scuba diver survey and excavation (e.g. Bailey et al., 2015; Bailey et al., 2017; Flemming, 2017; Bailey et al., 2020) on identified Stone Age habitation areas would be a final, much more elaborate step in this exploration. The great potential of KZN offshore areas to yield evidence for Stone Age archaeology associated with early coastal adaptations justifies such an approach in the future.

Other ways to further our current knowledge lie in the interpretation of geomorphological maps as ‘resource maps’, showing past resource spaces with a focus on relevant ecological attributes (e.g. rocky vs. sandy shores; molluscs and sea turtles from marine vs. hippos from estuarine environments), informed by archaeological data. Concerning basic archaeological studies, more detailed analyses are required of both old and new faunal collections from MSA and LSA sites in KZN with a focus on the marine components to assess how far the harvesting of these resources was systematic and optimised (see e.g. Langejans et al., 2012). Re-analysing these assemblages might also uncover more evidence for non-dietary use of shells, with many of the MSA shell beads at Sibhudu only found by in-depth analysis of original material. Outstanding zooarchaeological studies of the large faunal collections from the Conard excavations at Sibhudu since 2011 from the large and small-fraction have great promise to shed further light on the connections of MSA humans to coasts. Likewise, excavated faunal samples from the MSA of Border Cave or the LSA of Shongweni should be studied with a focus on the potential of recovering mollusks derived from dietary use.

6 Conclusion

Present archaeological data indicates that early modern humans during the MSA and LSA were capable of inhabiting the eastern Indian Ocean coast and using its variable resources for dietary and non-dietary purposes, even though marine productivity is comparatively low in this area. The inhabitants engaged with coastal and marine ecosystems in various forms over many thousands of years. The relatively small number of sites and reduced density of shellfish remains could in part be a result of the less productive of the coastal and marine ecosystems in KZN. This being said, current evidence for potential coastal adaptations in KZN appears to be heavily biased in comparison to other regions of South Africa. Chances are therefore high that the current record of the region constitutes only the tip of the iceberg of what was once present. The exact nature and extent of coastal resource use and the settlement of coastal landscapes over the Late Pleistocene by early modern humans thus remains a target for future research. Independent data from archaeology, GIS modelling and offshore geomorphology demonstrate that the shorelines of KZN - both present and past - constitute promising areas for recovering further traces for coastal adaptations in the MSA and LSA. This work can provide key insights from different ecological and geological contexts, and following from the application of novel research strategies. We will only be able to evaluate the full extent and broader relevance of the use of marine resources and the occupation of coastal ecosystems for human evolution in KZN, southern Africa and beyond once new interdisciplinary research on both onshore and offshore areas along the avenues outlined here has been performed.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

MW designed the study; MW; GB performed the archaeological analyses; CS performed the GIS modelling; AG; AC performed the marine geology and geomorphology; MW, GB, and CS; AG wrote the manuscript; all authors commented and proofread the final text version.

Funding

The Funding for the data presented in this paper comes from the Deutsche Forschungsgemeinschaft (grant WI 4978/3-1) and the ROCEEH project (The Role of Culture in Early Expansions of Humans) of the Heidelberg Academy of Sciences. We further acknowledge funds from the BMBF (project MA-RAIN; Grant No. 03F0731A).

Acknowledgments

We acknowledge support by the Open Access Publishing Fund of University of Tübingen. The authors thank Gavin Whitelaw for kindly sharing the KwaZulu-Natal Museum archaeological database on Stone Age sites with us. his paper uses data collected through the scientific surveys with the research vessel Dr Fridtjof Nansen as part of the collaboration between the Food and Agriculture Organization of the United Nations (FAO) on behalf of the EAF-Nansen Programme and South Africa. The EAF-Nansen Programme is a partnership between the FAO, the Norwegian Agency for Development Cooperation (Norad), and the Institute of Marine Research (IMR) in Norway for sustainable management of the fisheries in partner countries and regions. Figure 5 is based on an original draft by Lauren Pretorius, whom we acknowledge accordingly. We further acknowledge Obscape Pty Ltd. for the provision of the multibeam image of the Aliwal Shoal in Figure 8.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.964423/full#supplementary-material

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frontiers | Frontiers in Earth Science

TYPE Review
PUBLISHED 16 August 2022
DOI 10.3389/feart.2022.946732

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment, a section of the journal Frontiers in Earth Science

RECEIVED 17 May 2022
ACCEPTED 14 July 2022
PUBLISHED 16 August 2022

CITATION
Reyes O, Méndez C, San Román M, Belmar C and Nuevo-Delaunay A (2022), Biogeographic barriers in the circulation and interaction of hunter-gatherer marine fishers: The role of the Taitao Peninsula and the Gulf of Penas (~ 47°S) in the differentiation of the cultural trajectories of West Patagonia. *Front. Earth Sci.* 10:946732. doi: 10.3389/feart.2022.946732

Biogeographic barriers in the circulation and interaction of hunter-gatherer marine fishers: The role of the Taitao Peninsula and the Gulf of Penas (~ 47°S) in the differentiation of the cultural trajectories of West Patagonia

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Archaeological research on the settlement of the Patagonian archipelago in the extreme South of South America by groups of hunter-gatherers, fishers or canoeists involves both an understanding of the various modes of subsistence and the possible flows of goods and human interactions that could have occurred from the middle Holocene in this extensive territory. Therefore, the study of how the geographical barriers occurring in Western Patagonia operated is fundamental because it allows to evaluate and discuss not only the characteristics and particularities of the occupation of the archipelagic territory but also its role in the circulation and contact of canoe populations, their relevance in the settlement and occupation of the Patagonian archipelago and their possible impact on the differentiation of the cultural trajectories of the canoe groups that inhabited it. We review and discuss the archaeological record of the areas adjacent to the geographical barrier formed by the Taitao Peninsula and the Northeastern and Southern coast of the Gulf of Penas (47°S) in West Patagonia. This extensive geographical area acted as a permeable barrier, conditioning, over time, maritime mobility and circulation routes, channeling or limiting the access and contact between the canoe groups on both sides.

KEYWORDS

West Patagonian channels, Holocene, biogeographic barriers, marine hunter-gatherer-fishers, cultural trajectories

1 Introduction

In this Review, we discuss the archaeological evidence surveyed in the areas adjacent to the Taitao Peninsula/Gulf of Penas (47°S), both in the Chonos archipelago to the North (Porter, 1993; Stern and Curry, 1995; Reyes et al., 2007; Reyes et al., 2015; Reyes et al., 2019a; Reyes et al., 2019b; Reyes, 2020) and in the central archipelagos that extend toward the Southern portion of the Patagonian archipelago (Laming-Emperaire, 1972; Curry, 1991; Legoupil and Sellier, 2004; Legoupil et al., 2007; San Román and Morello, 2007) (Figure 1). We evaluate the differences of the archaeological record that indicate the continuities and divergences observed in the cultural trajectories of these Patagonian canoe groups (*sensu* Fitzhugh, 1997) and the particular conditions for human circulation. For this reason, and to circumscribe the discussion, we tangentially approach part of the archaeological discussion of the dynamics of human occupation in the geographical extremes of the Patagonian archipelago. A future stage of research includes the archaeological characterization of this extensive continental and insular territory through surveys and archaeological excavations, testing the concepts and discussions of this Review.

When considering the concept of geographic barriers with regard to hunter-gatherers (e.g., Veth, 1989; Rockman and Steele, 2003; Borrero, 2004; Borrero, 2018; Barberena, 2008; Friesen and O'Rourke, 2019) and their influence on archaeological characteristics and on the geographic distribution of human occupations, we do not assume that this barrier is insurmountable nor that the mere presence *defines* the occupation of a territory and its cultural trajectories (David and Thomas, 2016). Rather, we consider that such barriers correspond to interpretations of distributional limits of specific processes (Rosen, 1988). The used spaces are defined qualitatively and quantitatively according to the presence of these barriers and the temporal context in which they could or could not be overcome (e.g., Neme and Gil, 2008; Borrero and Borrazzo, 2011; McNiven, 2015; Lovis and Whallon, 2016; Barberena et al., 2017; Franco et al., 2018) in interactions with the environment and with regard to the structure of available resources (Kelly, 1983; Kelly, 1995; Binford, 1990, Binford, 2001; Bailey, 2004). In this case, the study of these barriers lies in understanding how marine fisher hunter-gatherers innovate to overcome such barriers and what subsistence and technological strategies were used and since when (e.g., Llagostera, 1982; Mandryk, 1993; Erlandson, 2001; Legoupil et al., 2011; Orquera et al., 2011; San Román, 2016; Zangrando et al., 2016) and how they define limits or not in the distribution of the archaeological record on multiple temporal and spatial scales (*sensu* Foley, 1981; Dincauze, 2000). In addition, such studies allow identifying particularities with respect to adjacent areas that are equally occupied, in what is understood as a hierarchy in the human use of various occupied spaces (Borrero, 1989; Borrero, 1994; Belardi, 2003; Borrero, 2004; Keegan et al., 2008), understanding archaeological sites as "distributed long-term observation networks of the past", making it possible to record the conditions of ecosystems and their period of time during human interactions (Sandweiss et al., 2020: 8276).

The movement of human groups can be understood through the flow of materials and resources (Gamble, 1999). Stable isotopes analysis inform on the dietary composition of individuals (e.g., Zangrando et al., 2004; Borrero and Barberena, 2006; Barberena, 2008). These movements consider routes built under social and technological variables (Gamble, 1996; Gamble, 1999; Pallo, 2011; Pallo and Borrero, 2015) in addition to biogeographic variables that allow or limit access to other regions (Borrero and Borrazzo, 2011; Borrero, 2018) or discourage access (Cameron and Tomka, 1993; Mandryk, 1993). However, we understand the settlement of a region as a concept that integrates different moments, including the initial occupation of an unpopulated area by human groups (Borrero, 2004). These moments can be understood as phases that are characterized by different articulations between settlement systems and types of sites, mobility, subsistence, and technology, among other operational parameters, which allow us to discern a human process of occupation of a given space. This model is also based on the logic of maintaining active social networks (Whallon, 2006) and a hierarchy of spaces within a landscape (*sensu* Belardi, 2003) related to the concrete distribution of usable resources within the habitat of a human group (e.g., Binford, 1980; Binford, 1982; Kelly, 1983; Kelly, 1995; Erlandson, 2001; Fitzpatrick et al., 2016). In this way, the spaces used depend on this pattern of distribution, on the mobility of resources, and the biogeographic characteristics of an area (Butzer, 1971; McNiven, 2015; Borrero, 2018), in a process of continuous settlement (Borrero, 1989-90; Borrero, 1999; Borrero, 2004; Borrero and Franco, 1997) and where groups that occupy the same region may show a greater probability of sharing similar cultural traits with each other than with groups that live more distant (Miller-Atkins and Premo, 2018).

This extensive biogeographic barrier formed by the Taitao Peninsula and the Gulf of Penas also defines the coastal maritime circulation of human groups. This would be from and to the North and South of the Patagonian channels, in complex navigation crossings influenced by cold fronts associated with the Southern Westerlies system that bring precipitation to Southernmost western part of South America (Garreaud et al., 2013) and the low bathymetries that cause intense and permanent waves with Pacific groundswells. Navigation with canoes and portages or "Indian steps", that reduce distances and risks between extensive marine areas (Borrero, 1997; Prieto et al., 2000; Coppinger, 2007; Legoupil et al., 2011; Pallo, 2011; Reyes, 2020), undoubtedly constitute subsistence strategies that address geographical barriers (e.g., García, 1889; Byron, 1901). These technological solutions and logistical displacements enabled the transfer and contact of groups while maintaining active social

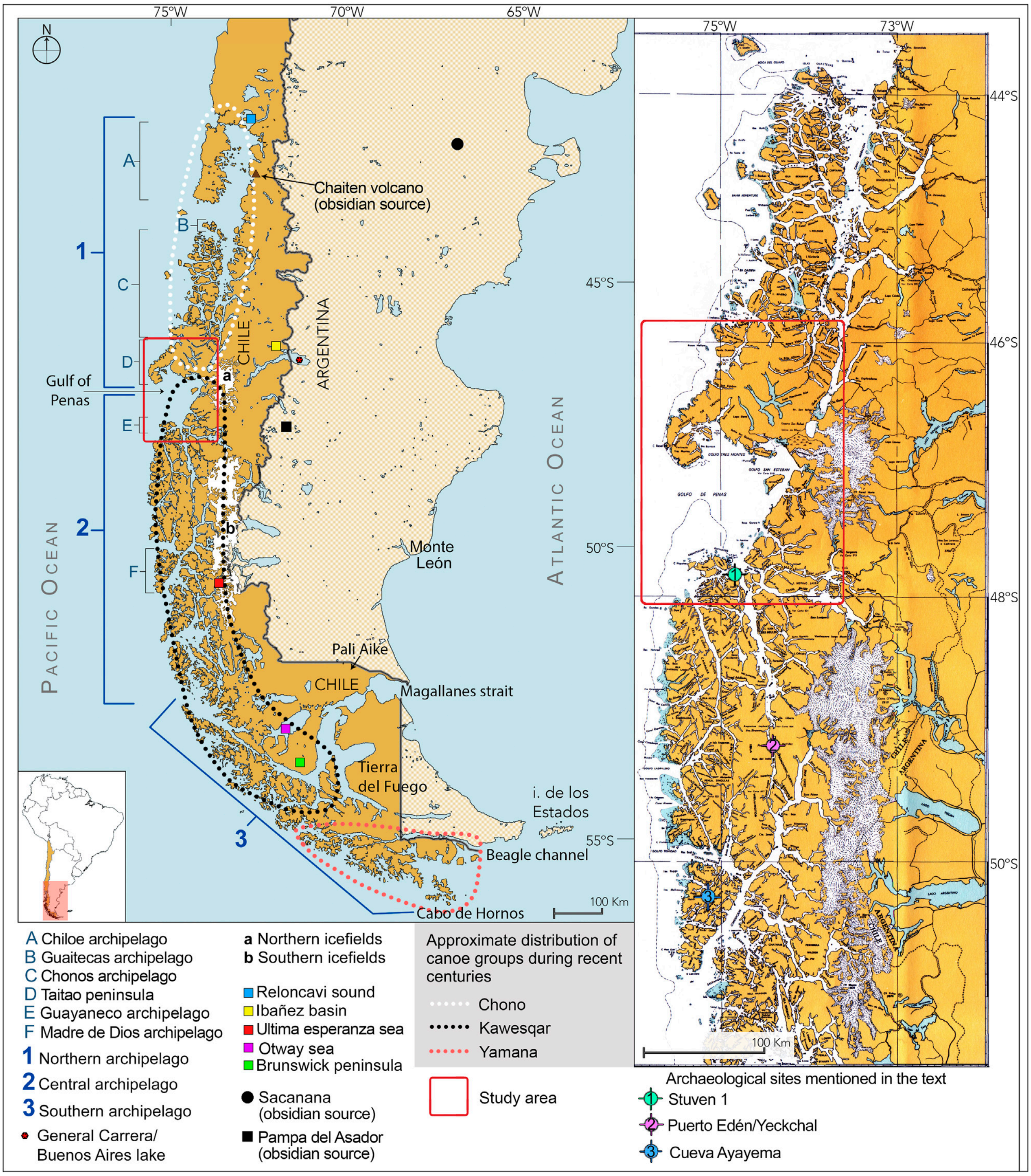

FIGURE 1
West Patagonia. Principal geographical features and archaeological sites mentioned in the text.

networks (*sensu* Whallon, 2006) as well as the flow of goods and information (e.g., Gamble, 1996; Borrero and Barberena, 2006; Pallo and Borrero, 2015). However, in this barrier, the use and articulation of its space has not yet been investigated. Different themes can be addressed, such as the functionality of the types of archaeological sites and their geographic distribution, the material records, differences in settlement patterns, the presence of indicators of extended family units (i.e., distribution of the bioanthropological record, such as the ossuaries, Reyes, 2020), and evidence for the selective transfer of raw materials, techno-typological and subsistence changes and continuities (distinctions in the artifactual and archaeofaunal records and those in fauna and human isotope values, among others), along with an essential set of dates that define the intensity of human occupation (Erlandson and Moss, 1999; Steele, 2010; Williams, 2012) and the evaluation of the preservation of the material record in areas with active coastal edges (Waters and Kuehn, 1996; Bailey and Flemming, 2008; Reyes et al., 2016; Reyes et al., 2018). Consequently, we understand that cultural transmission depends on the degree of connection between different groups and is affected both by the degree, strength and directionality of those interactions as well as by their spatial distribution (Whallon, 2006; Miller-Atkins and Premo, 2018).

FIGURE 2
Coastal modelling by the ice sheet of the Last Glacial Maximum. Steep coasts and fjords can be observed throughout the West Patagonia. The ground rises hundreds of meters and the sea bed descends to similar depths. View mainland coast area to the South of the Gulf of Penas.

2 Regional overview

2.1 Geography

A complex network of channels, fjords and hundreds of islands called West Patagonia extends along the Pacific coast of the South American region (e.g., Steffen, 1944; Bird, 1946; Bird, 1988; Emperaire, 1963). This area, extending ~1,600 km in North–South longitude (~41°–56°S), includes ~50,000 km of coastline in an approximate area of 240,000 km^2 (cf. Bird, 1988; Camus, 2001). Traditionally, it is subdivided into three large macroregions (*sensu* Dincauze, 2000) corresponding to marine and coastal biogeographic districts, limited by biogeographic and ecological barriers that prevent, restrict and/or filter the passage, development and/or access of various species (Viviani, 1979; Camus, 2001; Sievers and Silva, 2006; Velásquez et al., 2016). These limits are not absolute, producing areas of biota transitions and overlaps, conferring characteristics of a biogeographic barrier (Ferro and Morrone, 2014). Thus, the Northern archipelago extends from the Reloncaví basin to the Taitao Peninsula (41°30′–46°50′S), the central portion of the Patagonian channels extends from the Taitao Peninsula/Gulf of Penas to the western entrance of the Strait of Magellan (46°50′–52°30′S), and the southern end (52°30′–55°30′S) of this extensive archipelagic system projects to Cape Horn (Figure 1).

The Northern and central archipelagos are separated by the extensive geographical barrier of the Taitao Peninsula and the Gulf of Penas, covering an area of ~15,000 km^2 and more than ~1,200 km of Pacific coastline, channels and inland estuaries, which delimit the periglacial marine environment closest to the equatorial line of the planet (Stuardo and Valdovinos, 1992). This territory is located to the West of the Andes Mountains and was intensely shaped by Quaternary glacier action with the consequent formation of a series of islands, channels and fjords. The abrupt topography includes slopes of hundreds of meters, in the fjords and channels (Figure 2). During the Last Glacial Maximum, the advances and retreats of large glaciers shaped the landscapes (Aniya, 1999; Heusser, 2002; Glasser and Ghiglione, 2009; Davies et al., 2020). The coastline shifts are associated with changes in global sea level, and with the vertical deformation caused by isostatic glacial rebound and the subduction of the South American plate (Milne et al., 2005; Lange et al., 2008; Dietrich et al., 2010). This region also has an active subduction zone dominated by tectonic plates known as the *Chilean Triple Junction* (the Nazca, South American and Antarctic plates) and large tectonic faults that converge in the Taitao Peninsula (46°–47° S; Lange et al., 2008; Ramos, 2005). These are responsible for major earthquakes and tsunamis, which continually modify the coast (Plafker and Savage, 1970; Vargas et al., 2013). Finally, natural phenomena, such big storms, also modify the coastlines through erosion or by incorporating new sedimentary material (Morton et al., 2007).

The paleoenvironmental information obtained from the record on the Taitao Peninsula (Lumley and Switsur, 1993; Mássaferro and Brooks, 2002), shows warm, dry conditions between 11,000 and 8000 years cal. BP, and wet conditions between 8000 and 4,000 years cal. BP. The most remarkable change is the decline of *Pilgerodendron uviferum* (Ciprés de las Guaitecas) and *Weinmannia trichosperma* (Tenío) and the expansion of the Podocarpaceae and *Nothofagus* spp. Around 2,700 years cal. BP. This shift indicates an increase in precipitations and/or a fall in temperatures in the area and may be linked to the neoglacial activity (Davies et al., 2020).

Other pollen records from the same archipelago (Haberle et al., 2000; Haberle and Bennett, 2004), show the expansion of *Tepualia stipularis* (Tepú) and *Weinmannia trichosperma* between approximately 12,000 and 7,000 years cal. BP, which has been interpreted as a warm, dry episode. The present floral assembly of *Nothofagus*, *Pilgerodendron* and *Tepualia* is thought to have formed around 7,000 years cal. BP, suggesting an increase in precipitation in the area. There are also brief expansions of thermophilous taxa during the Mid and Late Holocene, suggesting warmer, drier moments in this basically colder, wetter period.

The region's climate is typically oceanic with a strong influence of the westerly winds, which cause significant precipitation (>4,000 mm per year) to the West of the Andes. Temperatures are strongly influenced by the sea. The annual average temperatures are approximately ~10°C. This climate is classified as temperate with oceanic influence (Luebert and Pliscoff, 2006; Garreaud et al., 2013). In the Andean range, where the highest elevations in the region are found (>1,000 masl), there is a reduction in mean annual temperatures, resulting in the persistence of large expanses of ice, remnants of the last glacial period. The largest of these are the Northern (4,200 km^2) and Southern (13,000 km^2) Ice Fields (Aniya, 1999; Heusser, 2002; Davies et al., 2020).

The regional vegetation is controlled by precipitation and temperature gradients that change with latitude and altitude. It is dominated by *Nothofagus*, *Weinmannia*, and conifers forming the temperate rainforest of the interior area of the fjords, which is typical of cold and humid regimes. Coastal areas between 45° and 51° S, are characterized by temperate *Donatia* and *Oreobolus* coastal peatland (Luebert and Pliscoff, 2006).

The rich fauna in the study area is represented by a diversity of sea mammals: 18 species of cetaceans, two pinnipeds, two seals, and two mustelids (Aguayo et al., 2006; Zamorano et al., 2010), in addition to 22 species of mollusks (bivalves and gastropods), crustaceans and echinoderms (Osorio and Reid, 2004), 29 species of fish (Navarro and Pequeño, 1979), and 46 species of birds (Vuilleumier, 1985). In contrast, the terrestrial fauna on the islands is scarce (small rodents). On the continental coastline there are two species of deer, the *pudu* (*Pudu pudu*) and the *huemul* (*Hippocamelus bisulcus*) (González et al., 2009).

2.2 Ethnohistory and ethnography

These biogeographic areas also coincide with cultural differences within indigenous groups separated by this barrier (Figure 1), especially linguistic and technological distinctions (e.g., use of different boats) observed by 16th and 18th century chroniclers and expeditions (Goicueta, 1879; García, 1889; Byron, 1901; Bibar, 1966) and by 19th-20th century ethnographic studies about the distribution of the canoe groups known ethnohistorically as *Chono* (Northern archipelago) and *Kawésqar* (central archipelago) (e.g., Skottsberg, 1913; Cooper, 1917; Cooper, 1946; Hammerly, 1952; Emperaire, 1963). The *Chono* were the first of the indigenous groups, generically identified as canoeists, to disappear as a culture toward the 18th century. There are very few written and material records (García, 1889; Cooper, 1917; Emperaire, 1963). The *Kawésqar*, on the other hand, although suffering cultural transformations, still remain as a community in different parts of the Patagonian archipelago (Skottsberg, 1913; Cooper, 1917; Cooper, 1946; Latcham, 1930; Bird, 1946; Hammerly, 1952; Emperaire, 1963; Laming-Emperaire, 1972; Casamiquela, 1973; Gusinde, 1982; Medina, 1984; Quiroz and Olivares, 1988; Aguilera, 2008; Aguilera, 2011). For sea travel, the *Chono* used a canoe made of three boards sown together called a *Dalca*, very different from the vessels used by the *Kawésqar,* i.e., tree bark canoes (Cooper, 1917; Latcham, 1930; Medina, 1984). Later studies propose that the canoe was probably a technology derived from Huilliche territory, from further North, since these forest-dwelling groups were specialists in the use of wood; and that later spread to the Chonos Archipelago (Medina, 1984). After European contact and the forced migrations of many Chono (Urbina, 2016; Urbina et al., 2020), or their flee to safer areas south of the Taitao Peninsula (47°S), the *dalca* would have gradually replaced the bark canoe used by Kawésqar groups (Cooper, 1917; Latcham, 1930; Lothrop, 1932; Finterbusch, 1934; Medina, 1984). For both groups, linguistic and subsistence differences led historians and ethnographers to classify them as different canoe groups of the extreme South of South America (Goicueta, 1879; García, 1889; Byron, 1901; Skottsberg, 1913; Cooper, 1917; Cooper, 1946; Hammerly, 1952; Emperaire, 1963; Casamiquela, 1973; Gusinde, 1982). From the first chroniclers, the idea was installed that the Taitao Peninsula and its Southern area, the dreaded Gulf of Penas (~46°50′S), constituted a geographical barrier in which indigenous canoe groups entered, mainly when serving as guides and navigators or when fleeing European dominance (García, 1889; Byron, 1901; Emperaire, 1963; Urbina, 2010; Urbina, 2016; Martinic, 2013; Álvarez et al., 2015). Undoubtedly, this traditional ethnographic division is not a monolithic classification; in its construction underlies biases in the accounts and observations in a dynamic post-European contact border (Orquera and Piano, 1995; Álvarez, 2002; Urbina et al., 2020).

2.3 Archaeological framework

The Northern Patagonian archipelago (~41°30′-46°50′S) includes the Reloncaví basin, the Chiloé archipelago and its adjacent continental edge, and the Guaitecas and Chonos archipelagos. Although there is evidence from the Late Pleistocene that indicates the use of coastal resources by hunter-gatherer groups (Dillehay et al., 2008), the first indications of human occupations by canoe hunter-gatherer groups in the Reloncaví area to the North and in Chiloé are ~6,400 cal years BP (Gaete et al., 2004; Gaete and Navarro, 2004; Ocampo and Rivas, 2004; Quiroz and Sánchez, 2004; Legoupil, 2005; Rivas and Ocampo, 2010; Campbell and Quiroz, 2015; Massone et al., 2016; Sierralta et al., 2019; Sierralta et al., 2021; Reyes et al., 2020; Munita et al., 2021; Rebolledo et al., 2021). The archaeological record of the transition to the late Holocene and even historical times is characterized by an increase in the number of archaeological sites and the diversity of deposits and site types, such as large multicomponent monticular shell middens, deposits with ceramic materials, fishing corrals, funerary sites and sites with paintings and rock carvings (Bird, 1988; Ladrón de Guevara et al., 2003; Munita, 2007; Sáez, 2008; Álvarez et al., 2008; Flores et al., 2010; Rodríguez et al., 2010; Flores and Correa, 2011; Mena et al., 2011; Munita et al., 2011; Labarca et al., 2016; Labarca et al., 2021; Reyes et al., 2020).

Archaeological investigations carried out on the Chonos archipelago (~43°50′-46°50′S), immediately North of the Taitao Peninsula/Gulf of Penas, revealed initial occupations at ~ 6,200 cal years BP (Porter, 1993; Reyes et al., 2016; Reyes et al., 2019a). These contexts formed by marine hunter-gatherers, recorded until ~4,200 cal years BP, are of an exploratory and specialized nature. They are mediated by deep occupational hiatuses associated with important coastal remodeling processes (Reyes et al., 2018). Entering the third millennium, there was a relative increase in the intensity of occupation by these canoe groups (such as the records of the first shell midden sites) and in their distribution throughout the archipelago. Later, we observed a *peak* of occupation around ~1,300 cal years BP, with a greater number and variety of archaeological sites [e.g., shell midden camps, ossuaries (formed by the funeral arrangement of bodies on the surface and inside of rocky shelters, deposited synchronously or at different temporal moments, Reyes et al., 2015), and sighting points]. In a regional context of marginal occupation in terms of the frequency/density of the archaeological record (Borrero, 2004), it represents a discontinuous occupation over time (Reyes et al., 2019a; Reyes, 2020).

In the Chonos archipelago, we evaluated the influence of the multiple geographical barriers that appear toward the east as *a continuous barrier* and that would have influenced the hierarchy in the human use of occupied spaces (Borrero and Franco, 1997; Borrero, 1999; Borrero, 2004; Belardi, 2003). The marine distances that separate this archipelago from the continental edge and the Andean massif and the dense montane forests, volcanoes and ice fields that flank it from the rest of the continent led us to implement theoretical and methodological designs that allowed us to postulate that these are poorly permeable barriers with regard to the possibility of contact by land with extra-Andean or steppe terrestrial hunter-gatherer groups (Méndez and Reyes, 2008; Reyes et al., 2009). This situation does occurs in the North geographical extremes (Reloncaví basin area) and South (Strait of Magellan and Tierra del Fuego) of the extensive Patagonian archipelago (e.g., Borrero, 1997; Gaete et al., 2004; Zangrando et al., 2009; Morello et al., 2012; Morello et al., 2015). In fact, the lack of evidence of contact between marine and terrestrial hunter-gatherer groups, both in the Andean forests and in the steppe and archipelago, can be interpreted as a product of the effective action of the various geographical barriers. This is confirmed through the distribution and differentiation of technotypological criteria and artifactual assemblages, circulation of lithic raw materials (e.g., grey porphyritic obsidian source from the Chaitén volcano, Pampa del Asador, and Sacanana) and the archaeofaunal record recovered from excavated contexts. These barriers hindered contact and human circulation in an East–West direction in this region throughout the Holocene, with two cultural spheres that until now are configured as completely separate, with circuits of mobility and contact in a general North–South direction (Reyes et al., 2007; Reyes et al., 2009; Reyes et al., 2015; Reyes et al., 2019a; Méndez and Reyes, 2008; Méndez et al., 2018; Reyes, 2020).

Another line of evidence corresponds to the bioanthropological information of human remains from the steppe and the archipelago. DNA analyses suggest that population flow independently with respect to the Pacific fringe and the extra-Andean steppe (Moraga et al., 2009; De la Fuente et al., 2018; Nakatsuka et al., 2020). Furthermore, the information from the craniometric analyses on human remains recovered from the Chonos archipelago shows very little affinity with the groups East of the Andes, less than 140 km East–West, and a greater biological affinity with various groups along the Pacific coast (Kuzminsky et al., 2018). Finally, the human diet patterns inferred from the comparisons of δ^{15}N and δ^{13}Ccol values indicate subsistence modes with high specificity, coastal occupations with marine diets and inland groups with terrestrial diets (Méndez et al., 2014; Reyes et al., 2019b). This supports other lines of evidence regarding the influence of biogeographic barriers in the marked segregation of two cultural traditions of marine and terrestrial hunter-gatherers. In the middle course of the Ibáñez River valley in Aisén (General Carrera Lake area/Buenos Aires), the occupations of terrestrial hunter-gatherers detected in the montane deciduous forest are noticeably reduced toward the west, with no deep material record in the forest and in the mountain foothills (García and Mena, 2016). Nuevo-Delaunay et al. (2022) argue that the presence of a Western limit of occupations of terrestrial hunters, toward the foothills of the Northern Ice Field, practically creating a dead end to the West.

To the South of the Taitao Peninsula and the Gulf of Penas (~47°S), the central portion of the extensive Patagonian archipelago extends for more than 600 km and is largely isolated from the continental territory by the presence of

TABLE 1 Descriptive statistics of the δ15N and δ13Ccol values of the canoe groups that inhabited the Patagonian archipelago. References used: Alfonso-Durrruty et al., 2015; Barberena 2002; Borrero et al., 2001; Kochi 2017; Panarello et al., 2006; Reyes et al., 2019b, 2022; Tafuri et al., 2017; Tessone et al., 2003; Yesner et al., 2003.

Region	Southern archipelago		Central archipelago		Northern archipelago (de los chonos)		Northern archipelago (de chiloé)	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
N	14	14	5	5	36	36	17	17
Media	−12,9	17,2	−12,8	17,6	−11,4	17,2	−11,4	18,7
Standard deviation	2,2	2,5	1,4	1,6	0,9	0,9	1,4	1,7
Minimum	−18,5	10,6	−14,1	15,8	−13,9	15,3	−16,0	13
Maximum	−11,1	19,2	−10,6	20,0	−9,3	18,8	−9,2	20,3

another extensive barrier, the Southern Ice Field. In this area, archaeological studies are even scarcer and more dispersed than elsewhere. There are records of the 1741 shipwreck of the frigate *Wager* in the Guayaneco archipelago (Byron, 1901; Carabias, 2009) and the excavation of a shell midden at the Northern entrance of the Messier channel at the Stuven one site on the homonymous island, ~2,200 years BP, with an important artifactual and archaeofaunal record (Legoupil et al., 2007). Then, 150 km farther South, a series of sites, mainly shell middens, were identified near Puerto Edén (Emperaire, 1963; Bird, 1988), dated post 1,800 years BP. These sites have been discussed in the framework of the evaluation of ethnographic observations on the mobility and settlement patterns of canoe groups in this area (Curry, 1991). Adjacent to Puerto Edén is the Yekchal site, a shell midden that accounts for an important archaeofaunal complex and a burial that dates to ~1,000 cal years BP (San Román and Morello, 2007; De la Fuente et al., 2018). Finally, 150 km South of Puerto Edén, funerary caves and rock art are recorded on the Madre de Dios archipelago (Jaillet et al., 2009; Sepúlveda, 2011). Among these sites, the Ayayema Cave burial stands out, with human skeletons dating to ~4,500 years BP (Legoupil and Sellier, 2004), corresponding to the oldest records of an indigenous presence in the central portion of the Patagonian channels and whose evidence of ancient DNA would indicate different population flow (Nakatsuka et al., 2020).

The area of the central archipelago has been the subject of regional analyses of the presence, distribution and density of the archaeological record. It has been characterized as "taphonomically active" (Borrero, 2014), requiring the necessary integration of environmental dynamics with the presence and interpretation of the material record. It is "marginal", in terms of the evaluation of the frequency and density of the archaeological record in a territory occupied/exploited discontinuously (Borrero, 2004). It is also defined as an "empty zone" (Laming-Emperaire, 1972), in terms of the spatial distribution with respect to the intensity of occupations in the Southern archipelagos, and as a "circulation route" (Borrero, 1982; Pallo, 2011), in terms of the availability of resources and/or the technological feasibility of access to certain locations permanently or seasonally (e.g., Bailey and Parkington, 1988; Ames, 2002).

3 Discussion

3.1 Variations in the canoe subsistence patterns on either side of the Taitao Peninsula and the Gulf of Penas

The archaeological investigations carried out North and South of the Taitao Peninsula/Gulf of Penas record unravel the subsistence patterns of these canoe groups, specifically with respect to the technological, archaeofaunal and bioanthropological assemblages recovered (Curry, 1991; Legoupil and Sellier, 2004; Legoupil et al., 2007; Reyes et al., 2007; Reyes et al., 2015; Reyes et al., 2016; San Román and Morello, 2007; Christensen, 2016; Reyes, 2020).

δ^{15} N and δ^{13} Ccol analyses of human remains from the Patagonian archipelago (Borrero et al., 2001; Barberena, 2002; Tessone et al., 2003; Yesner et al., 2003; Zangrando et al., 2004; Panarello et al., 2006; Alfonso-Durrruty et al., 2015; Kochi, 2017; Tafuri et al., 2017; Reyes et al., 2019b) revealed statistically significant differences (Mann–Whitney *p*=0,000,008) in the spectrum of marine diets between canoe groups to the North and South of the Taitao Peninsula/Gulf of Penas (Table 1) that, beyond the ecological diversity and local availability of resources, obey diverse cultural trajectories with respect to the subsistence patterns defined in the late Holocene for these canoe groups (Reyes et al., 2019b; Reyes et al., 2022). Thus, in the Chonos archipelago, terrestrial fauna did not provide a relevant contribution to the diet; in contrast, the isotopic values for human osteological assemblages south of Taitao indicate a relevant role of huemul (*Hippocamelus bisulcus*) in the diet.

The recovered archaeofaunal assemblages also indicate an important difference with respect to the consumption of this terrestrial mammal, very present in contexts South of the Taitao Peninsula/Gulf of Penas (e.g., Emperaire, 1963; Curry, 1991; Legoupil et al., 2007; San Román and Morello, 2007; Fernández et al., 2016) and poorly represented to the North, in the Chonos archipelago, even though they are biogeographically available (Reyes et al., 2019a; Reyes, 2020). Similarly, greater consumption of marine mammals (Otariidae) has been documented in archaeological sites in Southern Taitao Peninsula/Gulf of Penas (Curry, 1991; Orquera and Piana, 1999; Legoupil et al., 2007; San Román and Morello, 2007; San Román, 2010; Tivoli and Zangrando, 2011) compared to the archaeofaunal assemblages excavated to the North of this barrier, where this resource is not common (Reyes et al., 2019b). At the macroregional scale, bioindicators of subsistence (human isotope values and archaeofaunal assemblages) have revealed evident differences for both areas on either side of the barrier. These data indicate differences in the spectrum of marine diets among the different groups of hunter-gatherer fishers throughout the Patagonian archipelago, probably obeying both the ecological diversity present in this extensive territory and diverse cultural trajectories in relation to patterns of subsistence and the consumption of wildlife resources.

These differences are also evident when comparing the technological assemblages recorded on both sides of the Taitao Peninsula/Gulf of Penas. The bone industry in the Chonos archipelago, after excavating/probing 16 archaeological sites (14.18 m^2 total), is practically nil, with only a pair of bone awl have been found (Reyes et al., 2007; Reyes, 2020). In contrast, in the south of the Taitao Peninsula/Gulf of Penas, the archaeological record indicates great technofunctional diversity that includes awls, wedges and harpoons, among other artifacts (Legoupil et al., 2007; San Román and Morello, 2007; Christensen, 2016; San Román, 2018) that indicate various domestic and hunting activities. At the Stuven one site, instruments made from cetaceans and huemuls are recorded (Legoupil et al., 2007). Bone harpoons, are not found in the Chonos archipelago, except for a vague mention in Guaitecas (Barros, 1931), being documented thus far at a very low frequency ($N = 5$) in only some contexts of Reloncaví in the Northern archipelago (Gaete et al., 2004; Munita et al., 2021). These few harpoons differ greatly from those recorded in practically all the sites South of the Taitao Peninsula/Gulf of Penas (Christensen, 2016).

Regarding the lithic assemblages, we also observed differences. The material culture of the hunter-gatherer fishers of the Chonos archipelago did not exhibit major variations throughout its temporal sequence (~6,200–300 cal years BP, Reyes et al., 2019a). It was characterized by the use of bifacial tools, stone axes and net weights (Porter, 1993; Reyes et al., 2007; Reyes et al., 2015; Reyes et al., 2016). The raw materials used show extensive ranges of mobility/exchange along 600 km of the northern archipelago and part of the southern coast of Chile. This is evidenced from the distribution of grey porphyritic obsidian from the Chaitén volcano throughout the Chono sites. None of these knapped artifacts (lanceolate lithic heads and lithic axes) nor the grey porphyritic obsidian are reported in the excavated contexts of the central archipelagos, from the South of the Taitao Peninsula/Gulf of Penas to Ultima Esperanza, in Magallanes (Morello et al., 2002; Legoupil et al., 2007; San Román et al., 2016). The Chaitén obsidian, however, has an extensive geographic "jump," being very scarcely identified at some sites in Monte León, on the Atlantic coast, and in the border volcanic zone of Pali Aike, both in Argentina. Its dispersion covers over 1,400 km (Stern et al., 2012; Stern, 2018). Regarding the lithic points, a similar geographical "jump" also occurs; beyond the Chonos archipelago, they are found in the Strait of Magellan/Otway Sea (Morello et al., 2002; Legoupil, 2003; San Román, 2005) and the Beagle Channel (Orquera et al., 1977) mostly associated with dates close to ~5,000–4000 BP. Some researchers propose that these are technological and subsistence elements used as defense against a second cultural group ("Ponsonby tradition" Legoupil and Pigeot, 2009) that would occupy the inland seas at least between 5,000–4,000 years BP and possibly into the next millennium (Morello et al., 2002; Morello et al., 2004). Technological and temporal similarities with the northern Chiloé/Reloncaví Basin (Díaz and Garreton, 1972; Gaete et al., 2004; Gaete and Navarro, 2004; Ocampo and Rivas, 2004; Munita, 2007; Reyes et al., 2020; Munita et al., 2021; Rebolledo et al., 2021; Sierralta et al., 2021) presumed a northern influence that would differ from the earliest contexts of maritime adaptation recorded in the middle Holocene in Fuego-Patagonia (Morello et al., 2015; San Román et al., 2016), defined as the Englefield Culture (between ~6,500 and 5,000 years BP; Emperaire et al., 1961; Ortiz Troncoso, 1975; Legoupil, 1997; San Román, 2005, San Roman, 2010). In contrast, from the north coast of the Beagle Channel, the presence of such elements is explained as the diffusion of technological innovation, without population replacement or migration (Piana and Orquera, 2007; Orquera et al., 2011). Both positions, however, suggest technological projection from the northern archipelago to the south during the middle Holocene. In this discussion, recent ancient DNA analysis in human remains from Fuego-Patagonia propose the arrival of new groups that carry a different stone tool assemblage in the Western Archipelago and Beagle Channel regions that between ~5,500 and 3,100 bp. There would be an, interruption of the use of green obsidian and the presence of large biface projectile points (Nakatsuka et al., 2020).

We observe differences at the macroscale level. Since the late Holocene, hunting activities, diet and subsistence patterns indicate particularities in the strategies for the supply and utilization of faunistic resources on both sides of the Taitao Peninsula/Gulf of Penas. It could be argued that taphonomic factors and dissimilar archaeological records produce bias; however, these are taken into account and discussed in the investigations carried out on both sides. Another plausible explanation, according to the known archaeological record and the close relationship of hunter-gatherers with their environment (e.g., Kelly, 1995; Binford, 2001), is that faunal variability can originate from the same canoe groups and that the material record responds rather to the biogeographic distribution and local availability of resources and raw materials. Such an explanation, however, does not fully justify the differences in the presence and/or absence of lithic and bone technological components, beyond their frequency, and the differentiated marine diets (isotope values) among the human groups sampled on both sides of this barrier.

The archaeological documentation evaluated indicates that the Taitao Peninsula/Gulf of Penas is a geographical barrier that, although permeable, effectively influenced the differentiation of cultural trajectories of hunter-gatherer fishers who inhabited either side of this barrier. Therefore, subsequent ethnographic distinctions (especially linguistic and technological) referred to a process of differentiation that had undoubtedly began centuries before. It is hoped that with this evaluation at hand, the further archaeological studies to be carried out in the area will be able to characterize the various material assemblages. Obviously, this effort will need to take into account the diversity and intensity of canoe people occupations that could have formed these contexts over time and also be able to understand at what point in time of the chronological sequence archaeological contexts began to differentiate the cultural trajectories of either side of the Taitao Peninsula and the Gulf of Penas.

Author contributions

OR designed the research; OR, CM, MS, CB, and AN-D. wrote the paper.

Funding

This research was funded by ANID-FONDECYT 1210045; ANID-Regional R20F0002.

Acknowledgments

We acknowledge to Corporación Nacional Forestal (CONAF XI Región).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 25 August 2022
DOI 10.3389/feart.2022.957214

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted
to Quaternary Science,
Geomorphology and
Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 30 May 2022
ACCEPTED 11 July 2022
PUBLISHED 25 August 2022

CITATION
Bicho N and Esteves E (2022),
Pleistocene hunter-gatherer coastal
adaptations in Atlantic Iberia.
Front. Earth Sci. 10:957214.
doi: 10.3389/feart.2022.957214

Pleistocene hunter-gatherer coastal adaptations in Atlantic Iberia

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Coastal prehistoric hunter-gatherers in Atlantic Iberia were particularly important to understanding Paleolithic human innovation and resilience. This study will focus on Middle and Upper Paleolithic adaptations to the Iberian Atlantic border. Elements such as intensity and diversity of marine foods, site location, distance to shore, submerged platform, and bathymetry are discussed for the region between Gibraltar and the Gulf of Biscay.

KEYWORDS

middle paleolithic, upper paleolithic, hunter-gatherers, coastal adaptations, Iberia

Introduction

Charles Darwin, some 170 years ago, wrote in his *Journal and Remarks*, describing the Tierra del Fuego coastal hunter-gatherers, “To knock a limpet from the rocks does not require even cunning, that lowest power of mind. Their skill in some respects may be compared to the instinct of animals. . .” (Darwin 1839:296–297). This plainly negative and biased perspective of coastal adapted human societies set the pace for the scientific notion of the importance of coastal landscapes and resources for human evolution for most of the 19th and 20th centuries. This same view was still deeply rooted in *Man the Hunter*, edited in 1968 by Lee and DeVore: hunter-gatherers hunt, gatherer, live in small groups, and move around a lot (Lee and De Vore 1968).

Only in the last 2 decades, authors such as Bailey (e.g., Bailey and Milner 2002; Bailey 2004; Bailey and Flemming 2008) or Erlandson (Erlandson 2001; Erlandson and Scott 2006; Erlandson 2008), among others, have published a great deal trying to reverse the generalized misconception of archaeologists towards marine and aquatic environments in early Prehistory. Marine foods are not perceived anymore as fallback resources in a time of demographic pressure and low resource availability (Bailey and Milner 2002; Bailey 2004; Erlandson and Scott 2006; Bicho and Haws 2008; Erlandson 2008; Bicho, Haws, and Davis 2011; Marean 2011; Marean 2014). On the contrary, they likely stimulated reduced mobility, increased human demographics and population packing (Fitzhugh 1972; Yesner et al., 1980; Keeley 1988; Renouf 1988; Ames and Maschener 1999; Bailey and Milner 2002; Marean 2014), increased complex technology, and economic and social inequality, as seen in the archaeological and ethnographic record (e.g. and examples within Marean 2014; Price 1985; Price and Feinman 2010, 1995). According to Binford (2001:216), the ethnological data show that c. 40% of the mobile human groups in the equatorial and tropical regions use aquatic resources. In the boreal zone, however, 97% of the sedentary hunter-gatherers base their economy and diet on coastal resources.

The time and spatially predictable, and in many cases, easily accessible and in great quantities, coastal resources have provided in the long timeline of the human career the prolonged use of specific areas. These were a perfect set up for the development of human societies that based their social system on social inequality, group identity, territoriality, and respective territorial land markers. All these are characteristics of complex hunter-gatherer groups (Ames 1994; Arnold 1996; Prentiss and Kuijt 2004) also named affluent when applied to coastal hunter-gatherers (e.g., Price, 1985; Koyama and Uchiyama, 2006; Ames, 2007). These aspects are now well accepted by the archaeological community that deals with late Pleistocene and early Holocene human populations in many areas of the world. It was only, however, in the last 15 years that coastal resources become important in the discussion of the emergence of human modernity (e.g., McBrearty and Brooks 2000; Erlandson 2001; Parkington 2001; Bailey and Milner 2002; Bailey et al., 2008; Bicho and Haws 2008; Fa 2008; Finlayson 2008; Marean 2010, 2014; Cortes-Sanchez et al., 2011; Marean 2011; Jerardino 2016; Will, Kandel, and Conard 2019) in both Africa and Europe. Perhaps the first and main reason for the acknowledgment of the importance of marine resources in the diet of early modern humans is that there are nutritional elements fundamental to human health, including the development of the nervous system as well as the pregnancy and early childhood, and that are not produced in the human body (Broadhurst et al., 2002; Jensen 2006; Milligan and Bazinet 2008). The argument has been, thus, within the evolutionary context of early human adaptation, that marine resources may have played a very important role in the adaptation of archaic modern humans due to the changes in the brain and general nervous system (Henshilwood and Marean 2003; Hockett and Haws 2005; Bicho, Haws, and Davis 2011; Marean 2011; Hockett 2012; Marean 2014). In fact, according to Marean (2011), the use of marine resources in South Africa implies a necessary complex cognitive jump shown by the relation between the availability and accessibility of resources and the astronomical calendar through the lunar and tidal cycles.

Marean (2014) has also offered another very interesting hypothesis stemmed on the idea of systematic use of marine resources with direct and important implications for human origins: the use of marine resources, specifically shellfish, provided a perfect context with predictable, both in time and space, coastal resources that allowed reduced mobility, increase human packing due to higher numbers of people. In turn, the sense of territoriality increased as did inter-group conflict, resulting in developed pro-social behavior, based on the presence of predictable high rank dietary resources and social boundary defenses.

In the two perspectives regarding the importance of marine resources for the emergence of human modernity (i.e., human health and brain development and prosocial behavior), the basis is the recognition in the archaeological record of the prolonged use of marine resources also known as coastal adaptations (Erlandson and Scott 2006; Marean 2014). Two problems stem from these concepts. In the archaeological literature, not all authors have used the same definitions or even the same scale for sporadic and systematic use of coastal resources and for coastal adaptations. Naturally, the differences in scale in the use of marine resources likely had different repercussions in human evolution. To solve that problem, Marean (2014), proposed that the only unequivocal proxy was the presence of a shellmidden context. Shellmiddens are contexts where the sediment is shell supported, shells are inter-fingered, and the fine sedimentary matrix fills in the spaces among the shells. The second issue is that a coastal adaptation can be more than just the use of shellfish for dietary reasons seen in a shellmidden context.

In this paper, we will present a survey of coastal or near-coastal Middle and Upper Paleolithic sites in the 2000 km-long coastal region of the Iberian Atlantic coastal margin, from the Gulf of Biscay, in the north, to the Strait of Gibraltar, in the south. In addition, we will also discuss aspects of Paleolithic coastal adaptations in Iberia based on a statistical model, and the importance in the general context of human evolution and the consolidation of our species in the region.

Coastal settings and resources in human evolution

Human evolution is closely linked with the occasional dispersal and migration of various hominin species across time. Many, if not all, major migration episodes in our past are the result of sea and coastal settings. This is the case of *Homo erectus* in Indonesia at ~800 ka (Morwood et al., 1998) as well *H. floresiensis* on the island of Flores (Brown et al., 2004). They offer tantalizing evidence for very early sea crossing capability in East Asia. Petraglia and Rose have also argued for a Red Sea crossing from Eastern Africa (Kenya, Somalia, Djibouti, and Eritrea) to the Arabian Peninsula (Oman and Yemen), for the dispersion of modern humans out of Africa and into Asia (Petraglia and Rose 2009; Rose et al., 2011; Rose and Marks 2014) (Petraglia and Rose 2009; Rose et al., 2011). Findings in the United Arab Emirates seem to confirm this perspective (Armitage et al., 2011). More recently, the sea was a fundamental factor on the dispersal of modern humans to many archipelagos in the Indian and the Pacific oceans, including Sri Lanka (>45 ka), New Guinea/Papua (>35 ka), Australia (>40 ka), New Ireland (30 ka) and the Japanese islands (26 ka) (Allen, Gosden, and White 1989; Gillespie 2002; O'Connell and Allen 2004; Roberts, Jones, and Smith 1990; Storm et al., 2013; Thorne et al., 1999; Wedage et al., 2019; Wedage et al., 2020). The peopling of the New World seems to be pretty much accepted as a coastal migration out of Asia (e.g., Erlandson et al., 2007; Erlandson, Braje, and Graham 2008;

Davis 2011) probably sometime during the Last Glacial Maximum (Bennett et al., 2021).

Coastal settings are highly rich in biomass and offered, both in the past and in the present, numerous easily accessible and predictable dietary resources for hunter-gatherers on the move. Not surprisingly, the earliest evidence for human settlement at each continent and region frequently included the use of coastal resources.

In 1979, Thomas and Koyama (1979), applied the term *Affluent Foragers* to complex coastal temperate forager societies. This term was used in a conflicting perspective to that of Sahlins' 1968 argument of simple, small-scale highly mobile hunter-gatherers with an egalitarian socioeconomic structure, minimal food storage technology and no sense of territoriality. Although the discussion on the meaning of hunter-gathering complexity is very important, it is not the focus of this article. It is, however, rather fundamental the notion that Affluent societies were (commonly?) characterized by the presence of large group sizes and sedentary lifestyles. Binford (1978, 1982) pointed out that high levels of demographic packing are conditioned by local and temporal carrying capacity and only achieved if resources are available in more productive ecosystems. The technological and economic systems are then marked by the presence of both resource intensification procurement and increasing storage capacity and technology. In his seminal work, *Constructing Frames of Reference*, Binford (2001) argued based on a huge ethnographical data set that when a landscape is highly packed with hunter-gatherers, these become less mobile. The result is that resource intensification pressure tends to occur, frequently based on territorial marking and defense, favoring the development of exchange of food and non-food items, both locally and regionally. The likely consequence is the transformation of social and territorial boundary arrangements, as well as their economic and technological structure with the presence of storage equipment and, ultimately, with production of food surplus. Testart (1982), for instance, believed that social stratification and inequality may be a consequence of intensification and diversification of resource acquisition, storage and sedentism. In many coastal hunter-gatherer cases there seems to be an association between abundance of marine resources and reduced mobility in highly packed populations with storage facilities (e.g., Ames and Maschener 1999; Bailey and Milner 2002; Prentiss and Kuijt 2004).

Many seafoods are potentially storable (e.g., Yesner 1987, 1998), and seasonal species (such as salmon) and various mollusks can be easily salted, smoked and dried for later consumption. Though in same cases there must be an important investment in storing, these have very little processing costs, in contrast to meat from large mammal prey species that have high to very high processing costs, more so in temperate and low latitudes. Still, in many cases, it seems that highly productive marine environments, more so in continental shelf ecosystems (Erlandson and Scott 2006), are associated to more limited terrestrial resources (Bailey and Milner 2002).

In areas where upwelling systems are present, such as Southern Africa and Southwestern Iberia, the biomass greatly increases seasonally during the windy months. This is the case in the summertime in coastal Portugal, producing today great amounts of fish and shellfish near the shore. At least in southern Iberia, it is clear that during the Late Pleistocene the biomass was many times higher than today (Abrantes 1991, 2000), creating an extremely rich coastal environment for human exploitation. These areas, thus, would be potentially good systems for increasing human population packing and decrease in mobility, but certainly for the exploitation of marine resources and coastal lifeways.

Coastal populations are frequently characterized by high population packing (Binford 2001; Yesner et al., 1980; Kelly 1995; Pálsson 1991, 1988) and reduced residential mobility (Binford 1980; Kelly 1995) due to the high biomass productivity and availability. They also tend to present the highest levels of social complexity (Pálsson 1991; Binford 2001; Prentiss and Kuijt 2004; Koyama and Uchiyama 2006), likely resulting in high levels of social conflict, both at the intra- and inter-group level (Lambert and Walker 1991; Moss, 1993; Lambert 1997; Marean 2014), as predicted by Dyson-Hudson and Smith (1978), probably based on passive territorial boundaries (Peterson 1975).

According to Marean, (2014), coastal hunter-gatherers have the highest levels of territoriality and inter-group conflict recorded among hunter-gathering societies. Marean has recently argued for the origin of prosocial behavior in early human societies in Southern Africa. The argument is based on a logical consideration, based on the facts stated above: when humans included in their diet marine resources, these provided a highly stable, very predictable, and dense high ranked staple food—mobility decreased and population packing increased with an improvement in complex technologies, resulting in economic and social differentiation and a more intensive and extensive gifting and exchange. The consequence was that the use of coastal ecosystems triggered the sense and need for territoriality and in a second phase the development of inter-group conflict. Mechanisms of adaptation and selection provided the appearance of prosocial behavior, a late addition to the modern human cognitive package.

As stated above, it is now believed by some that the importance of marine resources for early modern humans reside at least on the fact there are crucial nutritional elements for human health, specifically for the development of the brain and the retinal organs. These elements are omega 3 and omega 6, long-chain polyunsaturated fatty acids, such as the Docosahexaenoic acid (DHA) and Arachidonic acid (AA) (Crawford et al., 1999; Parkington 2001; Broadhurst et al., 2002; Langdon 2006; Uauy and Dangour 2006; Carlson and Kingston 2007; Cunnane et al., 2007). These fatty acids, also invaluable during pregnancy and early childhood, are not produced in the human body (Broadhurst et al., 2002; Jensen 2006; Milligan and Bazinet 2008) but occur naturally in aquatic plants and animals, if not exclusively, at least frequently in higher concentrations than in terrestrial food elements. The natural outcome, thus, is that marine resources most likely played a fundamental role in the development of the human brain during the evolutionary process of early human adaptation (McBrearty and Brooks 2000; Henshilwood and Marean 2003; Hockett and Haws 2005; Bicho, Haws, and Davis 2011; Marean 2011; Hockett 2012; Marean 2014).

Existing data suggest the use of coastal settings and even resources back to the Middle Pleistocene in the European continent. This was a time when a significant leap in the encephalization quotient occurred with the appearance in Europe of *H. heidelbergensis* (Ruff, Trinkaus, and Holliday 1997). There might be an important cause-effect connection between the two, so far, unrelated facts since no data are available to even suggest the possibility. If in fact, marine resources were a positive factor in human brain development and expansion related to the emergence of anatomical modern humans or even prior human species, then determining the antiquity of coastal adaptations and their scale is a critical research question.

Following Darwin's perspective, most researchers up to the end of the millennium, saw coastal resources as low-ranking dietary elements, second quality food assets. They were perceived as limited and unreliable, costly to process or to harvest and, in general, as poor sources of nutrition (Osborn 1977), basically, as starvation foods or fallback resources that people used only in moments of terrestrial scarcity or land resource pressure (for a general discussion on the topic, see Bailey and Milner 2002; Erlandson 2001; Erlandson and Scott 2006). In addition to this view, or perhaps because of it, water and coastal settings were also perceived as a major barrier for human development. In the words of Washburn and Lancaster (1968:294), "During most of human history, water must have been a major physical and psychological barrier and the inability to cope with water is shown in the archaeological record by the absence of remains of fish, shellfish, or any other object going deeply into water or using boats. There is no evidence that resources of river and sea were utilized until late pre-agricultural period. (. . .) For early man, water was a barrier and a danger, not a resource." Binford in his 2001 seminal work, *Constructing frames of references*, shows to a certain degree the type of bias: "So far my discussion of habitats has focused on the properties of terrestrial biotypes because human beings are terrestrial animals who are biologically incapable of living in aquatic environments without technological help. (. . .) Although human actors are capable of direct participation, ecologically speaking, in a terrestrial setting, they may be thought of as outsiders in aquatic biomes; they intrude at times, but always at very restricted locations and under rather specific conditions. To exploit aquatic resources, humans must be positioned on aquatic-terrestrial ecotones. This positioning, together with the fact that successful human exploitation of an aquatic biome is severely limited (. . .)." (Binford 2001:166–167). In fact, many of the propositions and generalizations related to the "aquatic biome" offered by Binford (2001) are based more on riverine and lacustrine environments than on coastal settings. Still, and unlike what was argued by Washburn and Lancaster in the 1968 *Man the Hunter* volume, there is a fairly wide range of early sites with marine and other aquatic elements (e.g., Erlandson 2001; Bailey and Milner 2002; Erlandson and Scott 2006; Bicho and Haws 2008; Finlayson 2008; Bicho, Haws, and Davis 2011; Villa et al., 2020). In the last 3 decades of literature focusing on the Paleolithic times, it is possible to find multiple references to the use of marine resources covering the time span from c. 400,000 years ago to the end of the Paleolithic and from the North Atlantic, in England, to South Africa, from the Mediterranean, the Atlantic and the Indian coasts of Africa. The countries with Mediterranean coast are also represented in this early evidence for the use of marine resources (fish, mollusks, and mammals). Many of these references (more so in the case of the earlier cases) are simple lists of species without any critical review of either how they got there or their importance in terms of hunter-gatherer adaptation. It is important, however, to note that coastal resources are not limited to mollusks. There are other resources groups present in coastal settings that were frequently used in coastal human adaptations: cephalopods, crustaceans, fish, marine mammals, and other, lesser important groups. Some of these are present in archaeological contexts from very early on, across the world (Erlandson 2001; Erlandson and Scott 2006). Some of the more relevant aspects will be described below on each of those prey groups, fundamental for many coastal hunter-gatherers across time and space, including the Iberian Atlantic margin (e.g., Finlayson 2008; Finlayson 2013).

Mollusks

In some areas of the globe, the easiest marine foods to collect are mollusks, both bivalves and gastropods. Erlandson (2001: 293–294) argued that what shellfish lack in size make up in quantity and accessibility. On the other hand, Marean (Jerardino and Marean 2010; Marean 2011) has made a convincing argument that due to strong and fast oscillation of tides, mollusk shellfishing could have been dangerous, at least in the Indian waters of coastal South Africa. Nevertheless, another factor seems to have been an important and, perhaps, decisive element for the exploitation of these coastal resources—the fact that, unlike what was previously believed (e.g., Cohen 1977; Osborn 1977), mollusks fall within the group of high rank resources due to its reliability and productivity and efficient protein source (Erlandson 1988; Jones and Richman 1995; Hockett and Haws 2003) at both regional and temporal scales

(Stiner, Munro, and Surovell 2000; Parkington 2001; Bailey and Milner 2002; Mannino and Thomas 2002), but also due to the fact that their exploitation can be fully integrated in a system based on gender and age division of labor, resulting in high gathering productivity (Meehan 1977; Glassow and Wilcoxon 1988; Moss, 1993; Bird and Bird 1997; Claassen 1998; Bird and Bliege Bird 2000; Erlandson 2001).

Among the edible species across the world, limpets and mussels seem to have been frequently exploited, at least in early times; although with different intensities, it is the case of Pinnacle Point in South Africa (Jerardino 2010; Marean 2011) and Bajondillo in Southern Spain (Cortes-Sanchez et al., 2011). The interesting aspect is that these are the species that produce the highest levels of AA and DHA, at least during the spawning phases (Brazão et al., 2003; Jensen 2006; Milligan and Bazinet 2008), and they may have been important and the reason why they are present in various early coastal sites both in Africa and Europe

Mollusks, in general, are rich in protein and many essential minerals, but they are low in fat and carbohydrate. Proteins can be metabolized to produce energy, although theoretically a diet high in protein and low in fat and carbohydrates could have serious health consequences, producing the so-called protein poisoning (Noli and Avery 1988; Hockett 2012). Nevertheless, Buchanan (1988) surveyed a range of hunter-gatherer groups with high protein diets and found no evidence of any health effects due to the diet.

Iberian coastal mollusks are marked by a great diversity of species, many of which are edible. Humans, however, do not use all the edible available species, pretty much the same way as land hunter-gatherers do not rely upon all the terrestrial resources available to them (Lee 1968). Coastal people tend to focus, and even specialize, in a certain group of available species. The range of species gathered might be wider in same areas, depending on the local productivity as well as on the fact that both sandy and rocky shores are exploited. Looking at the available archaeological data from early sites (e.g., Waechter 1951; Clark and Straus 1983; Straus and Clark 1986; Antunes 1991; Zilhão et al., 2010; Brown et al., 2011; Colonese et al., 2011; Manne and Bicho 2011; Steele and Álvarez-Fernández 2011; Cortés-Sánchez et al., 2019; Zilhão et al., 2020) there are sometimes a fairly large group of shellfish species. Some of those are likely to have been accidently brought to the site as they frequently live either within the colonies of the edible species (e.g., mussels) or are attached to them. Another possibility is that, independently of the fact that they can be used as food they were also used for ornamental reasons (e.g., Álvarez Fernández and Jöris 2008, Álvarez-Fernández, 2011; Tátá et al., 2014).

Cephalopods

Cephalopods include three main groups of edible organisms, squids, cuttlefish, and octopus. While squid does rarely appear close to the intertidal shore, both cuttlefish and octopus are frequent users of the intertidal coastal band. Both species are very easy to fish, but they are present in different ecological settings: octopus is caught in the natural pools in the rocky shores during the low tide and is easily caught by hand without any specialized tools; cuttlefish come with the high tide into shallow coastal water lines to spawn during most of the year and while it is possible to catch by hand it is much easier to collect them with a sack of some kind. Today, at least in southern Portugal, it is very common to catch either species while shellfishing. From the archaeological point of view, remains are extremely rare, since the only hard part is the cuttlebone (in cuttlefish) and the gladius (in squid), as well as the rostrum present in all groups. These are all made mostly of chitin that, unfortunately, is prone to rapid erosion. Still, they were an easily gathered and available resource while looking for shellfish and likely exploited from very early. In addition to their dietary qualities, they are the origin for the so-called India-ink, potentially used for both human and clothing decoration.

Crustaceans

The crustacean subphylum (part of the arthropods) is composed by more than 67000 species, covering an incredible array of morphological diversity. For the matter at hand, the important organisms used by hunter-gatherers includes crabs, lobsters and crawfish, shrimp, and goose barnacles. The latter are exclusively marine, and tend to live in shallow and tidal waters, usually in erosive settings. During spring tides, they are easy to gather and appear in large colonies. They can be pulled out directly from the rock, although they tend to come out as single individuals. With the help of a wedge, they come out as a set with dozens of specimens. During neap tides, they may not be so easy to gather since they tend to live in an erosive wavy action zone of the lower intertidal zone, particularly on those areas where they have been exploited systematically. They are small but the fleshy stalks are edible and thought to be very tasty. Perhaps due to both of those facts (low productivity and considered to be very good), goose barnacles tend to be today rare as well as one of the most expensive shellfish types at least in southern Iberia.

Crabs, lobsters, and shrimp are also composed of many species, many of which are edible. These are frequently on the shore and live in the intertidal zone, both in rocky and sandy bottom contexts. They are very easy to gather by hand and they do not need any specialized tool, though the gathering productivity is usually fairly low. In many cases, this will rise fast if baited and or a net is used. Some species tend to live just below the intertidal zone and, thus, shallow diving is required. Crab and lobster exoskeletons are made of chitin and crystalline magnesium calcite. While some body regions (e.g., the claws) are strongly mineralized and very hard and dense, the shell of the body is less mineralized and thus more elastic (Boßelmann et al., 2007). These differences seem to be related to the mechanical requirements of each organ. The differences of hardness in the shell among various species seem to be related to the biological escape behavior of the animals (Boßelmann et al., 2007). This is very important because it might explain the differential preservation found in archaeological contexts, where claws are more common than the rest of the crab shell. Nevertheless, crab shells are very rare in Paleolithic sites, although the cave site of Figueira Brava has evidence of very early exploitation of crabs by Neanderthals south of Lisbon (Zilhão et al., 2020).

Echinoderms

Echinoderms includes various main classes, including starfishes, sea urchins and sea cucumbers. Only two of those classes are edible, the sea urchins and the sea cucumbers, but only the urchins have non-edible hard matter, the carapace, and the spines, to survive in the archaeological record. Still, these are very rarely present in Paleolithic sites because both parts are very delicate and break very easily if any force or weight is applied upon them.

Sea cucumbers can be prepared as food from either from raw or dried specimens, and everything is eaten. The sea urchin needs to be prepared, at least with the removal of the spines. The shell is then open from the ventral surface and the only the gonads are eaten, either raw or after the sea urchin has been boiled or grilled. This is perceived as a delicacy in many parts of the world, including Asia, South America and, of course, Iberia. There are over 950 sea urchin species, but in coastal Iberia the most common species is the common sea urchin (*Paracentrotus lividus*) found at least in the Middle Paleolithic site of Figueira Brava (Zilhão et al., 2020) as well as in the Gibraltar caves (Brown et al., 2011), as well as in Northern Spain the site of El Cuco (Gutiérrez-Zugasti et al., 2013, Gutiérrez-Zugasti et al., 2018).

Fish

There is an incredible range of fish species, from the tiniest specimen to extremely large animals (such as the tropical open sea 20 metric ton whale shark), of which many are edible. Fish schools are highly common and represent many species around the world, while some species follow a solitary type of behavior which is rarer.

Fish biomass and productivity can vary greatly, from ecosystem to ecosystem within a small region due to coastal morphology, geology, currents and winds, and the availability of each species' food. This fact is probably the basis for Kelly's statement of ". . . fish cannot be tracked—this is a particular problem in exploiting oceanic fish. The forager can only go to a likely place to find fish, then begin searching randomly. If there are no fish there, the forager could waste quite a bit of time before accepting this is likely" (Kelly 1995: 209). Although this is largely true, there are times when certain fish species can be easily exploited in large numbers with the help of simple technology at the shore. It is possible to catch fish by hand, and it is quite easily to do so in the cases of low tide pools where fish get trapped. This type of fishing, of course, can occur casually as a forager looks for shellfish or simply roams the shore for raw materials, including minerals and previously floating wood, more durable and harder for making utensils of all kinds. With technology, fish gathering productivity will rapidly and exponentially increase. Simple technology such as fish gorges, hooks, and nets can improve the fishing results tremendously, more so because in many instances the predictability of the results will also increase. These include longlining, nets and fishtraps. These are expensive gear, and its production is time-consuming, but they have high efficiency, not only in terms of the numbers of captured specimens but also because they do not need the constant presence of humans: they can go there at intervals from one to more days, removing and collecting whatever the gear caught. Both nets and fishtraps do not need any bait (but the latter will work better with some bait), but longlining needs a daily replenishment of bait for each hook. The great advantage of both the traps and the longlining is that fish stay alive while with the nets the fish tend to die after a few hours. Certain species such as the anadromous types, come to the river every year and are easily caught with or without the use of gear while others tend to spawn on the shore or estuary settings. They are, thus, highly predictable both in terms of location and season of the year and they can be mass harvested during those times.

Processing of the catch for storage and later consumption is easy, mainly at coastal environments: salt is naturally available and due to the frequent coastal wind regimes, drying is also an easy task. Although, in both cases the fish in many cases needs to be processed, that is, scaled and eviscerated. In addition, smoking is also a possibility that usually does not require any direct fish processing.

Very much like mollusks, fish also tends to be rich in protein, vitamins, and minerals and less so in fat and carbohydrates. Nevertheless, there are many fish species, from coastal environments that are fatty fish, such as the salmon or the tuna. Fish is in general easily digestible and metabolized by the human body (Erlandson 2001)

Archaeologically preservation of fish is rare in Paleolithic contexts, although is present in some sites during the Middle Paleolithic in Europe (Guillaud et al., 2021). Both vertebra and otoliths tend to preserve better than the rest of the skeleton, but in many cases the recovery of fish remains at an early site depends greatly on the excavation strategy used by the archaeologists. Small mesh size (no bigger than 3 mm and preferably 1 mm) and water screening are the main elements

FIGURE 1
Map of Iberia with the main sites discussed in the text. 1. Jaizkibel, 2. Altxerri, 3. Amalda, 4. Santimamine, 5. Toralete, 6. El Cuco, 7. El Pindal, 8. El Perro and La Garma, 9. El Juyo and Morín, 10. Altamira and El Salín, 11. La Riera, 12. El Castillo, 13. Tito Bustillo, 14. Las Caldas, 15. Pena Lliboi, 16. Xestido III, 17. Mira Nascente, 18. Praia do Pedrogão, 19. Lagar Velho, 20. Coelhos, Picareiro, and Anecrial, 21. Caldeirão, 22. Praia Rei Cortiço, 23. Furninha, 24. Suão, 25. Toledo, 26. Cabeço da Amoreira and Cabeço da Arruda, 27. Figueira Brava, 28. Vale Boi, 29. Companheira and Ibn Ammar, 30 Matalascañas, 31, Gorham's and Vangard; 32. Bajondillo, 33. Humo, 34. Nerja.

for the recovery of fish remains (Bicho et al., 2000; Bicho, Haws, and Hockett 2006).

Marine mammals

Although not nearly as diverse as shellfish, fish or crustaceans, marine mammals present a diverse array of species. These include cetaceans (whales and dolphins), pinnipeds (seals, sea lions, walrus), and sea cows (dugong and manatees), as well as smaller animals such as sea otters. On the other hand, they tend to be much larger than any of the other coastal resources, common weights are above the half metric ton and in the case of the biggest whales, as large as 100 tons. They are frequent biannual migrants, following pre-determined paths, easy to access in many cases. Due to their size (and in certain cases also due to their tusks and teeth) are dangerous preys and pursuit and encounter is frequently seasonal. Still, the amount of meat as well as subcutaneous blubber, other body parts (skin, bones, teeth, ivory) makes them a highly valuable asset after it is hunted and killed. Frequently, dead animals get stranded and end up dying on the shore. They can be then easily scavenged, and many parts of the body can be used if the animal has not died long before. The meat and organs of marine mammals are usually very rich in proteins, vitamins, and minerals, and, depending on the organ and on the species, also in fat. The blubber can also render oils and be stored for later use as fuel for both heating and lighting. The hard skeletal parts can be used for making fishing gears (as important as harpoons) as well as decorative and ornamental elements. The skin can be used not only for clothing as well as for constructing housing and boats.

Hunting of marine mammals can be costly, due to procurement of single individuals both on land and on sea. Technology, such as harpoons and boats, however, may greatly help to improve efficiency in many cases, although there are large, permanent, colonies of seals and sea lions that can be easily hunted down with little effort. In addition, there are also smaller colonies that are seasonal, usually with breeding or birthing locations, but tend to group always in the same spots across time—thus, at least pinnipeds offer a predictable and abundant resource that is usually on land (Muñoz 2011). Still, hunting gear as well as boating technology is frequently associated to pinniped and cetacean hunting. This type of technology is usually very costly in terms of production and maintenance, representing a significant investment of energy (Erlandson 2001).

The definition of "coastal adaptations"

Although apparently simple to understand the concept of human coastal adaptations, the reality is a bit more complex. This stems from the fact that there are many ways and many scales of adaptation to coastal environments and the use of its resources: from a very small scale, where, for example, one small group of foragers can accidently reach the shore and scavenge a dead cetacean laying on the sand, to a large-scale adaptation where a large society bases all its economic, dietary, social structure as well as its full daily lives on marine resources. If in fact, marine resources were decisive for human evolution and complex cognition (either/or for brain and social development), the main point of contention is to identify the scale in the use of coastal resources that might have had an impact in human evolution. Thus, as Marean (2014) stated, it is fundamental to clearly and unambiguously define and use concepts such as "coastal adaptation," "maritime adaptation" and "systematic use of coastal resources" and examine what archaeological sites truly fall in each category.

It seems reasonably, then, to argue that if the exploitation of coastal resources is one of the hallmarks of modern cognition, then the use of coastal resources had to have been recurrent and/or intensive enough to impact continuously the human diet. In turn, this had to have a direct outcome on the overall human health of which possibly the brain and retinal development promoted by DHA and AA were the most important for human evolution and the emergence of human cognition. In addition, a new human adaptation may have been borne out of the use of coastal resources: according to Marean (2014), the exploitation and harvesting of coastal resources, at least in certain regions such as South Africa, require a deep understanding of the relation between the tidal cycles and the astronomical calendar and the diverse impact that lunar phases have on resource accessibility and, thus, on its economical return. To know and to understand the correlation between astronomical events and the best time of spring tides to safely exploit the exposed rich intertidal zone reflects necessarily a context of complex developed human cognitive system.

The underlying assumption is that to be able to recognize the economic potential of marine resources it is necessary to have a stable and continuously use of the coastal environment. Thus, for Marean, the origin of a true coastal adaptation in South Africa represents a turning point in the hunter-gatherer hominin adjustment from the previous highly mobile, low density and non-territorial system to a denser and more packed demographic situation and also more permanent and longer settlement.

It is thus necessary to define the applicability of each term to archaeological contexts. While it seems that in the scientific literature the definition of *Maritime adaptations* is fairly consensual, that is not the case for *Coastal adaptations* and *Systematic use of coastal resources*. The former includes seafaring with boat technology and the regular use of boats for both travel and subsistence. In this case, travelling frequently placed hunter-gatherers-fishers away from the shores, while coastal and marine subsistence are a significant part of their diet (e.g., Erlandson and Scott, 2006; Marean 2014; Will, Kandel, and Conard 2019).

The definition of *Coastal adaptations* and *Systematic use of coastal resources*, however, is not nearly as consensual, mostly because both terms are frequently used very loosely in the literature. Meanings of *Coastal adaptations* range from the presence in a coastal area (without necessarily the use of any marine dietary resources) to those contexts where human life-way was transformed by the exploitation of the marine available resources (e.g., Beaton 1995; Bicho and Haws 2008; Marean 2014). It is, thus, necessary to define its meaning better and narrowly, to improve its application.

A few years back, in the inaugural paper of the Journal of Island and Coastal Archaeology, Erlandson and Fitzpatrick (2006: 8) defined coastal adaptations "as any subsistence lifestyle based along the margins of a large body of water that includes the regular use of foods from aquatic habitats." This definition seems clear enough, but nevertheless issues stem from the grainy definition of "regular use of resources".

Marean (2014) has proposed a three-level approach to mend the lack of scale and intensity of the "regular use of resources":

1) *Sporadic use of coastal resources* is when only a small part of the diet is derived from coastal resources and their exploitation is not regular and cyclic that is, daily or monthly. The result is that the mobility system is not organized around a local or regional mapping or schedule based on the cyclic nature and location of coastal environments.

2) *Systematic use of coastal resources* reflects a context where coastal resources were regularly and recurrently used, but economically they did not alter the regional adaptation, nor did they change the human settlement system.

3) *Coastal adaptation* implies an import transformation in the human adaptation directly related to the sea and its resources. Here, the main staple food is from animals that live along the shoreline, mostly from the intertidal zone, including marine mammals, fish, mollusks, crustaceans, birds, etc. Coastal foods, thus, are so important that the mobility strategy deliberate crosses the shore niche as part of the annual plan of landscape use, and in the limit becomes a year-round coastal settlement.

These definitions are straightforward, but still the main problem is their application to the archaeological record, that is how to identify and separate a systematic coastal resource use from its higher-level sister, the coastal adaptation. Marean proposed a simple and highly pragmatic approach to resolve the problem: the presence/absence of shellmiddens and shell remains. The presence of coastal adaptations is confirmed by the occurrence of a shellmiddens (defined as a context where sediment is shell supported, that is where shells are inter-fingered and the fine sedimentary matrix fills in the spaces

FIGURE 2
Examples of ornamental perforated shells in the Portuguese Upper Paleolithic. Top to bottom: *Littorina obtusata* from Vale Boi; *Trivia* sp from Vale Boi; *Theodoxus fluviatilis* from Vale Boi; *Antalis* from Vale Boi.

among the shells); a systematic use of a coastal niche is established by the presence of large amounts of shells, although not making up a midden, but present with regularity and recurrently through the sediments.

Recently, Will et al. (2019) have proposed a different approach, based on an evolutionary perspective: coastal adaptations are a multifaceted set of traits in a group that increases the reproductive fitness of that population through the incorporation of the consumption and use of marine resources during the occupation of coastal landscapes. In practical terms, this includes the expansion of settlements to coastal or near-coastal settings while regularly exploiting and consuming marine resources, such as mollusks, mammals, birds, or fish, independently of forming true shellmiddens.

Archaeological coastal proxies

The "shellmidden" variable suggested by Marean is without a doubt a valuable proxy for the definition of coastal adaptations and systematic use of coastal resources. Nevertheless, it is limited by various factors including shellmidden taphonomical alterations. Perhaps more importantly, is the use of marine coastal resources such as fish that may not be fully represented in the archaeological record due to poor preservation of the ichthyologic remains - their bone density is very low and destruction is usually fast, even if they were abundant at the time of occupation and deposition.

It is unequivocal that edible marine shell species are the main element considered representative of coastal economies. Those remains are highly visible in the landscape and because of that they help to pinpoint and find archaeological sites representative of coastal adaptations. They also accumulate fairly rapidly and, thus, create large middens easily seen in almost any landscape—it is the case of the Mesolithic Atlantic shellmidden, such as those from the Muge in central Portugal (Bicho et al., 2010; Bicho, Cascalheira, et al., 2013), the 3,000 year old "mega" shellmiddens from coastal South Africa (Jerardino 2010), the so called Sambaquis from Brazil (Gaspar 1998; DeBlasis et al., 2007; Villagran et al., 2010), or the present-day accumulations seen in both sides of the African continent, such as in Senegal (Hardy et al., 2016; Camara et al., 2017) or on the Indian side, as seen by one of us in the field work near Inhambane, central Mozambique. The visibility and the volume would suffice to consider them one of the most reliable indicators of coastal use.

TABLE 1 List of sites used for the PCA analyses (Serrano Lozano et al., 1995).

Code	Site/context	Phase	# Fish species	# Edible Mollusk species	# Non-edible Mollusk species	# Crustaceans species	# Bird species	# Marine Mammal species	# Perforated Shell species	# of Other Proxies	Distance in kms to present shoreline	References
1	Bajondillo 17	Middle Paleolithic		3						1	0,1	Cortés-Sanchez et al. (2011)
2	Bajondillo 18	Middle Paleolithic		1		1				1	0,1	Cortés-Sanchez et al. (2011)
3	Bajondillo 19	Middle Paleolithic		3	3	1				1	0,1	Cortés-Sanchez et al. (2011)
4	Benzu	Middle Paleolithic	1	1	1						0,1	Ramos et al. (2003)
5	Cabeço da Amoreira	Mesolithic	8	8	3	3	1		2	1	0,1	Bicho et al. (2013), Detry. (2007); Dias et al. (2016)
6	Cabeço da Arruda	Mesolithic	4	8	3	1	1		2	1	0,1	Bicho et al. (2013), Detry. (2007) Dias et al. (2016)
7	Caldeirão Gravettian	Upper Paleolithic		2	3				2		60	Zilhão, (1997)
8	Caldeirão Magdalenian	Upper Paleolithic	1		4				3		60	Zilhão, (1997)
9	Caldeirão Solutrean	Upper Paleolithic		2	7				3		60	Zilhão, (1997)
10	Coelhos	Upper Paleolithic	1						1	1	45	Almeida et al. (2004)
11	Figueira Brava	Middle Paleolithic	18	12	16	6	18	2			0,1	Antunes, (1991) Zilhão et al. (2020)
12	Furninha	Middle Paleolithic									0,1	Bicho et al. (2010)
13	Gorham's	Middle Paleolithic	1	6	5		1	2		1	0,1	Stringer et al. (2008)
14	Humo 3	Middle Paleolithic		3							0,1	Bicho (2015) Fernandez et al. (2011)
15	Ibn Ammar	Middle Paleolithic		4							2	Bicho (2004)
16	La Riera Magdalenian	Upper Paleolithic	1	4	4				1		2	Straus and Clark, (1986)
17	La Riera Solutrean	Upper Paleolithic		2	11				2		2	Straus and Clark, (1986)
18	Lagar Velho Gravettian	Upper Paleolithic							1		25	Zilhão and Trinkaus (2002)

(Continued on following page)

TABLE 1 (*Continued*) List of sites used for the PCA analyses (Serrano Lozano et al., 1995).

Code	Site/context	Phase	# Fish species	# Edible Mollusk species	# Non-edible Mollusk species	# Crustaceans species	# Bird species	# Marine Mammal species	# Perforated Shell species	# of Other Proxies	Distance in kms to present shoreline	References
19	Lagar Venho Solutrean	Upper Paleolithic			1				1		25	Zilhão and Trinkaus (2002)
20	Mira Nascente	Middle Paleolithic								1	0,1	Haws et al. (2010); Haws et al. (2011); Haws et al. (2020)
21	Nerja Magdalenian	Upper Paleolithic	5	5	25	2	2	2	5	2	1	Morales (1998) Izquierdo et al. (1995) Serrano Lozano et al. (1995)
22	Nerja Solutrean	Upper Paleolithic		5	6				5	2	1	Morales (1998) Izquierdo et al. (1995) Serrano Lozano et al. (1995)
23	Picareiro Madgalenian	Upper Paleolithic	1	3					2		40	Bicho et al. (2000); Bicho et al. (2006)
24	Praia do Pedrogão	Middle Paleolithic									0,1	Aubry et al. (2005)
25	Praia Rei Cortico	Middle Paleolithic									0,1	Haws et al. (2010); Haws et al. (2011); Haws et al. (2020)
26	Toledo	Mesolithic	17	14	9	5			3	2	4	Haws et al. (2010); Haws et al. (2011); Haws et al. (2020)
27	Vale Boi Early Gravettian	Upper Paleolithic		2					1		2	Bicho et al. (2004); Bicho et al. (2013); Manne and Bicho. (2011)
28	Vale Boi Gravettian	Upper Paleolithic	1	7	1	1		1	3	1	2	Bicho et al. (2004); Bicho et al. (2013); Manne and Bicho. (2011)
29	Vale Boi Magdalenian	Upper Paleolithic		2	1				1		2	Manne and Bicho, (2011)
30	Vale Boi ProtoSolutrean	Upper Paleolithic		2					1		2	Bicho et al. (2004). Manne and Bicho, (2011)
31	Vale Boi Solutrean	Upper Paleolithic		7	3				3	2		Bicho et al. (2004). Manne and Bicho, (2011)
32	Vangard	Middle Paleolithic	1	3	7		1	4		1	0,1	Brown et al. (2011) Stringer et al. (2008)

Still, the low number of known early sites with marine remains is due to the low data visibility—not all have shells, and in some cases these have not preserved well. As pointed above, this visibility has been partially a result of the bias in the theoretical paradigms of authors: the appearance of marine resources was just a “glitch” in the normal diet and those early humans as was site location. Site location, however, is likely a very important element in the issue of visibility. Many of these early sites with marine resources (or with indirect evidence for their use—Haws et al., 2011) tend to be located in very specific areas on or near the modern coast line. In general, and without any transportation technology such as horse riding, hunter-gatherers have a distance limit of 10 km for inland transportation of edible shellfish (Bigalke 1973; Meehan 1975), even if they process the shellfish and remove the shells (Bird and Bird 1997). If the distance is more than that between logistical and residential base camps, then the skeletons and shells of coastal dietary resources (shellfish, fish, and sea mammals) are left behind. The general consequence of that fact is that coastal resources will be found only within a 10 km radius from the ancient paleoshore. In any case, a study on zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*) coming from the Great Lakes region seems to indicate that at least the adult specimens of these two species may survive up to between 3 and 5 days of transportation (Ricciardi, Serrouya, and Whoriskey 1995), as long as they are not detached from the rock, when the survival to aerial exposure is limited to 24 h (Tucker et al., 1997).

For at least the last c. 100,000 years sea was lower that today, with the lowest peak some 20 ka ago during the Last Glacial Maximum (-120 m), and thus the continental shelf extended considerably the terrestrial landscape of Middle and Upper Paleolithic times. The present modern high sea-stand covered that platform used by Paleolithic hunter-gatherers, with continuous rise since the beginning of the Holocene, and thus submerged almost entirely the coastal archaeological record between the end of the Marine Isotope Stage 5e (MIS5e) and today (Flemming et al., 2017; Flemming, Harff, and Moura 2017). The same phenomenon took place before the previous sea highstand, the MIS5e. From a timeframe perspective, it is very clear that probabilistically the number of sites that should be underwater is incredibly high, since the amount of time is very long compared to the period when highstand settings took place (Bailey and Flemming 2008). Also, the submerged region is a very large area exceeding an estimate of 16 million km^2, or about 10% of the total current habitable land surface. However, since those moments were marked by a large ice cap cover and the Americas and Oceania were not occupied yet, that means than the coastal shelf of Africa, Asia, and Europe, now submerged, was even more important for early human adaptation, since apparently it was a well-watered land (Bailey 2004; Finlayson 2013) less arid than the inland regions. That is clear in the Iberian Atlantic coastal region, with physical massive transformation after MIS 5 (Moura, Gomes, and Horta 2017; Bicho, Infantini, and Marreiros 2020).

Coastal sites and data from Atlantic Iberia

The Atlantic Iberian coast is close to 2000 km long, starting on the French-Spanish border on the western edge of the Pyrenees, at the extreme north, and running westerly, south, and then easterly again to reach the Rock of Gibraltar, the divide between the open Atlantic Ocean and the Mediterranean (Figure 1).

From the geomorphological point of view, this coast is highly diverse with long stretches of flat sandy beaches, some as long as 100 km, high consolidated dunes dating from the Miocene to the early Holocene, and medium to high vertical rocky cliffs, standing more than 100 m tall. All these settings are cut through by rivers, from small streams to vary large-sized rivers such as the Tagus, occasionally related to underwater canyons (e.g., off Nazaré and Portimão). Another coastal feature of Atlantic Iberia is the presence of large barrier-islands, such as those present today in Aveiro, Faro, and Cadiz, all extremely rich in biomass and ecological diversity.

Another key element in the region is the presence of the upwelling system, that increases the biomass productivity, mostly in southern Portugal (Loureiro, Newton, and Icely 2005), and occurs at least since MIS5 times (Abrantes 1991, 2000). This phenomenon made the region particularly reach in coastal resources during the Late Pleistocene, even more than today.

Paleoenvironmental proxies seem to indicate that climate was fairly mild in the coastal regions of Portugal and southern Spain even during periods traditionally seen as more rigorous (Carvalho and Bicho 2021; Carvalho et al., 2021). Although terrestrial resources likely were never truly lacking, coastal resources due to their easy access and abundance were frequently exploited from very early on (Bicho and Haws 2008).

Another relevant aspect of the Atlantic coastal region in Iberia is the extent of the present submerged platform. This corresponds to the area above the -125 m bathymetric line, the likely maximum extent of the sea level during the Last Glacial Maximum in Iberia (Flemming et al., 2017; Moura, Gomes, and Horta 2017; Bailey et al., 2020). While this submerged landscape may be as much as 30 km away from the present coastline, in many places is much closer than that. This is due to a very steep bathymetry, mostly in areas where high cliffs are present such as at the Finisterra Cape, the Nazaré, Lisbon and Portimão Canyons, and the Espichel, Sines, Sagres, and Santa Maria capes (Moura, Gomes, and Horta 2017). Thus, it is very likely that this band was intensively used during the Paleolithic, and while many sites may have been destroyed, there should be submerged sites still today as suggested by a number of sites dating to the Late Pleistocence and early Holocene in Atlantic

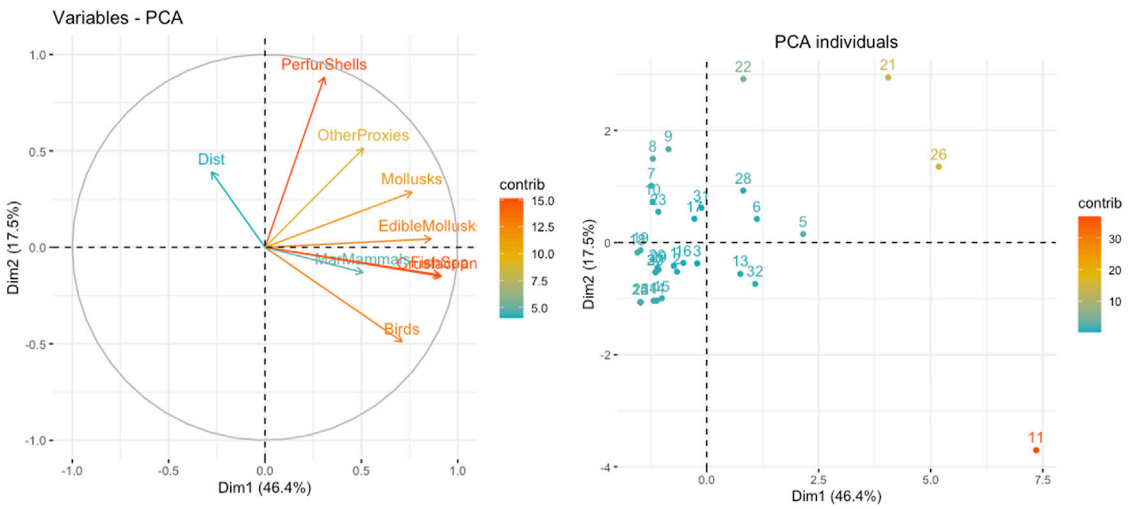

FIGURE 3
PCA Biplot of Dimensions 1 and 2. For site code, see Table 1.

coastal Iberia (Arias Cabal, 2020; Bicho, Infantini, and Marreiros 2020).

The earliest evidence for coastal Atlantic human occupation is dated to the MIS5, seen in a couple of sites in central Portugal. Two of those sites are securely dated, the cave of Figueira Brava (Zilhão et al., 2020) and the open-air site of Praia Rei Cortiço (Haws et al., 2011; Minckley et al., 2015). Praia Rei Cortiço is located just above the intertidal zone, although erosion is frequent due to strong wave action during winter storms. The site was located near a coastal lagoon, during a time of sea high-stand phase, and other than pollen there are no other organic remains. The pollen indicates a typical mixture of temperate and Mediterranean forests, with a series of shifts between cool-wet and warm-dry phase between c. 110–90 thousand years ago. The lithic assemblage is made mostly of quartzite and quartz with a few pieces in chert. From a technological point of view, the assemblage is marked by the presence of typical Levallois, with a few points and flakes, as well as cores (Minckley et al., 2015).

The site of Figueira Brava is located right on the present coast, on a cave open in the limestone cliff between the Tagus and the Sado rivers, just a couple of meters above present sea level. This is an area where the bathymetry is very steep and as a consequence Zilhão and colleagues (Zilhão et al., 2020) argue for a close distance to the contemporaneous shore, no more than 2 km away. Based on the abundant presence of limpets (*Patella* sp., including P. *vulgata*, *ullyssiponensis*, *depressa*, and *rustica*), mussels (*Mytillus galloprovincialis*), clams (*Calista chione*, *Ruditapes decussatus*, and *Scrobicularia plana*) and two types of large crabs (*Cancer pagarus* and *Maja squinado*), Zilhão suggests that there was a routine collection of shellfish. This intensive exploitation of coastal resources is also confirmed by the presence of a wide range of fish that includes European eels (*Anguilla anguilla*), congers (*Conger conger)*, morays (*Muraena helena*), sharks (*Squatina squatina*), sea bream (*Diplodus vulgaris* and *Sparus aurata*, among others), mackerel (*Scomber scombrus*), and sea bass (*Dicentrarchus labrax)*. In addition, there are also common dolphin (*Delphinus delphis*) and ringed seals (*Pusa hispida)*, as well as various types of marine birds (auks, gannets, shags, and cormorants—see Zilhão et al., 2020 for the complete list). The birds are likely to be natural depositions, but the presence of mallards and geese suggests human exploitation. The marine diet was complemented by a wide range of terrestrial sources that include not only mammalians (lagomorphs, red deer, horse, ibex, and aurochs), but also the intensive use of pine nuts. The lithic assemblage follows the normal standard for Mousterian technology in Portugal with the presence of centripetal technology as well as some Levallois. There are rare, retouched pieces, mostly denticulates and sidescrapers. Most of the assemblage is made on local quartz, but there are a few pieces of chert.

Although not dated, the open-air site of Praia do Pedrogão, futher north, is in a very similar geomorphological setting than that of Praia Rei Cortiço and it might have a similar chronology. While there are no preserved organic materials, the lithic assemblage is also similar: quartzite and quartz, with a very low number of formal retouched tools and the presence of Levallois (Aubry, Ribeiro, and Angelucci 2005; Benedetti et al., 2009).

There are other cave sites found on the coast of Portugal, namely, Furninha, (Portuguese Estremadura), Iban Ammar, and Companheira, both in Algarve in the estuary of the Arade river, near the city of Portimão. Unfortunately, there are no dates but

TABLE 2 Summary of results of PCA: Dimensions eigenvalues; variables correlations and contributions to dimensions; and individuals (Sites) contributions to dimensions.

		Eigenvalue	Percentage of variance	Cumulative % variance
	Dim 1	**4.1776**	46.418	46.4
	Dim 2	**1.5754**	17.505	63.9
	Dim 3	**1.1970**	13.300	77.2
	Dim 4	**1.0332**	11.479	88.7
	Dim 5	0.4455	4.951	93.7
	Dim 6	0.3044	3.383	97.0
	Dim 7	0.1659	1.843	98.9
	Dim 8	0.0772	0.858	99.7
	Dim 9	0.0238	0.264	100.0

Variables.

Correlation

	Dim.1	Dim.2	Dim.3	Dim.4
Fish spp	**0.907**	−0.1423	0.2230	−0.2369
Edible mollusks	**0.861**	0.0435	-0.0358	-0.3125
Mollusks	**0.763**	0.2865	0.0497	**0.4176**
Crustaceans	**0.915**	−0.1506	0.1726	−0.2525
Birds	**0.710**	**−0.4889**	0.3272	0.2073
Marine mammals	**0.507**	−0.1303	-0.3159	**0.7322**
Perfurated shells	0.307	**0.8812**	0.1630	−0.0144
Other proxies	**0.511**	**0.513**1	**−0.5432**	−0.1087
Distance	−0.278	0.3907	**0.7650**	0.2239

Contribution

	Dim.1	Dim.2	Dim.3	Dim.4
Fish spp	19.70	1.28	4.156	5.4303
Edible mollusks	17.75	0.12	0.107	9.4533
Mollusks	13.92	5.21	0.207	16.8815
Crustaceans	20.04	1.44	2.490	6.1713
Birds	12.08	15.17	8.944	4.1599
Marine mammals	6.16	1.08	8.338	51.8890
Perfurated shells	2.26	49.29	2.219	0.0201
Other proxies	6.24	16.71	24.648	1.1435
Distance	1.84	9.69	48.892	4.8511

Individuals (Sites)

Contribution

Site	Dim.1	Dim.2	Dim.3	Dim.4
1	0.4032	0.3424	2.76e + 00	8.81e−01
2	0.3304	0.5349	2.11e + 00	8.68e−01
3	0.0339	0.2743	2.08e + 00	7.09e−01

(Continued on following page)

TABLE 2 (*Continued*) Summary of results of PCA: Dimensions eigenvalues; variables correlations and contributions to dimensions; and individuals (Sites) contributions to dimensions.

		Eigenvalue	Percentage of variance	Cumulative % variance
4	1.0495	2.1327	1.09e–01	9.51e–02
5	3.4614	0.0449	5.40e–03	8.29e + 00
6	0.9380	0.3526	5.34e–01	3.63e + 00
7	1.1405	2.0330	1.17e + 01	1.08e + 00
8	1.0832	4.4311	1.37e + 01	1.88e + 00
9	0.5443	5.5185	1.32e + 01	2.42e + 00
10	1.0894	1.0621	1.51e + 00	8.86e–02
11	40.4387	27.2300	1.43e + 01	2.14e + 00
12	1.6317	2.2435	1.63e–01	3.78e–02
13	0.4201	0.6158	6.06e + 00	4.44e + 00
14	0.9248	2.1186	2.02e–01	4.32e–01
15	0.7532	1.9563	1.25e–01	6.00e–01
16	0.2026	0.2620	3.34e–03	1.24e–01
17	0.0566	0.3590	2.55e–02	9.27e–01
18	1.7891	0.0642	1.46e + 00	7.74e–02
19	1.6320	0.0375	1.49e + 00	1.69e–01
20	0.9038	0.3936	2.61e + 00	2.26e–01
21	12.2704	17.2326	2.85e + 00	1.38e + 01
22	0.4995	16.9143	3.76e + 00	6.38e–01
23	0.8736	0.5990	5.17e + 00	5.02e–08
24	1.6317	2.2435	1.63e–01	3.78e–02
25	1.6317	2.2435	1.63e–01	3.78e–02
26	20.0678	3.6419	5.73e–04	2.28e + 01
27	0.9770	0.5519	2.47e–02	2.33e–01
28	0.4962	1.7072	1.88e + 00	1.77e–01
29	0.8619	0.4666	2.06e–02	1.22e–01
30	0.9770	0.5519	2.47e–02	2.33e–01
31	0.0105	0.7657	1.98e–02	7.92e–01
32	0.8763	1.0749	1.18e + 01	3.20e + 01

The bold values highlight the dimensions (Dim) with eigenvalues >1 that are retained or the significant (p > 0.001) correlation coefficients between variables and dimensions.

some similarities with the assemblages and settings of the site described above, suggests that they are earlier rather than late Mousterian.

Furninha was excavated at the end of the 19th century by Nery Delgado (Delgado and Filipe, 1884; Cardoso and Bicho 2021). The cave, located on a low limestone coastal cliff, had a 4 m sequence, where Middle and Upper Paleolithic horizons were present (Bicho et al., 2010), overlaid by Neolithic and Chalcolithic deposits (Cardoso and Carvalho 2011). There are references to some shells in the sequence, but unfortunately, there is no unequivocal confirmation that those aquatic resources were associated with the Levallois and discoidal technology.

Ibn Ammar and Companheira caves are located just a few km from each other, on either side of the estuary of the Arade river, near the city of Portimão. They are both part of complex cave systems, and are both characterized by small collections, composed of stone tools, terrestrial and marine fauna, specifically different shellfish species (Bicho 2004; Rüther et al., 2022). Two human bones were found in Companheira, but no species has been yet assigned to either fossil (Rüther et al., 2022). The lithic assemblages are characterized by the presence of Levallois and discoidal technologies, made on quartzite, quartz, chert, and limestone. Terrestrial faunas include red deer, equids, aurochs, and rabbit.

Mira Nascente is an open-air location, dated to c. 41 ka ago. It can be found some 30 m above sea level, half-way upslope in a coastal dune (Haws et al., 2010; Haws et al. 2011; Haws et al. 2020), north of the town of Nazaré. This is a high-quality chert-rich country, and thus the lithic assemblage is composed mostly of a regional red chert with just a few pieces of quartzite. The technology includes classic Levallois for both flakes and points. Like in other Middle Paleolithic sites, formal tools are rare. Other than charcoal, no organics were preserved, but use-wear indicates the likelihood of fish consumption (Haws et al., 2011).

The Atlantic Spanish coast provided much elusive evidence for the use of coastal resources during the Middle Paleolithic. While no traditional archaeological sites are known from the southern section, the only northern examples are found close to the coast, on the narrow flat band between the sea and the hilly inland terrain of the majestic Cantabrian mountains. The main site is the cave site of El Cuco (Gutiérrez-Zugasti et al., 2013, Gutiérrez-Zugasti et al., 2018), where levels X through XIII have high numbers of individuals and a wide diversity of shellfish species as well as echinoderms and crustaceans associated with Levallois and discoidal technology. These are dated to c. 40,000 years ago. In addition to El Cuco, there are also a few other sites (Morín, El Castillo, or Amalda) with a few shells in Middle Paleolithic horizons (Gutiérrez-Zugasti et al., 2011). Perhaps the most interesting Middle Paleolithic location is that of Matalascañas, near Cadiz in the Doñana National Park. There, an important set of Neanderthal footprint track was documented, showing that our ancestors were using the coastal dune field over 100 thousand years ago (Mayoral et al., 2021), perhaps at the same time as other Neanderthal groups were visiting the Praia Rei Cortiço in central Portugal and eating shellfish in Figueira Brava.

At the far southern end lies the Rock of Gibraltar with its Middle Paleolithic caves (e.g., Finlayson et al., 2008; Stringer et al., 2008). Gorham's and Vangard caves lie today literally on the edge of the water at high tide. Even during past times of Neanderthal occupation, the shore was very close. Perhaps, that is the reason why those two sites offer such a diversity of shellfish, marine mammals, and marine birds dating back at least 60 ka (Stringer et al., 2008; Brown et al., 2011).

The Upper Paleolithic evidence is very different from the previous phase since its evidence in Vasco-Cantabrian Spain is extremely well documented. There are innumerous long sequences, generally with good organic preservation, including bones and shells, with art evidence, both in cave and mobile art examples (e.g., Straus and Clark 1986; Arias 2009; Arias et al., 2011; Straus 2015; Straus et al., 2015). The latter in sites such as El Pendo, La Garma, El Juyo, Jaizkibel, Santimamine, and Toralete, attest the connection to the coast and to the presence of marine resources available, and most likely exploited by those hunter-gatherers: there are there are pictorial and engraved references to marine elements both in cave and mobile art—it is the case of the caves of El Pindal and Altxerri, with the representation of pleuronectiform fish (Arias Cabal, 2020) or the image of a whale on a sperm whale tooth dating to the Magdalenian from the Las Caldas cave (Rivero 2015). Also, the presence of frequent ornamental marine shell beads is very common in most sites in the region (Álvarez Fernández and Jöris 2008).

The intensive use of coastal resources clearly started in the Cantabrian Gravettian, although there is some evidence that the exploitation of marine resources took place in the earlier phases of the Chatelperronian and the Aurignacian in the region. Mollusks, echinoderms, crustaceans (both crabs and barnacles), fish and even cetaceans and seals were consumed starting 30,000 years ago, from the Gravettian to the Azilian (Straus and Clark 1986; Straus 2005; Gutiérrez-Zugasti et al., 2011; Álvarez-Fernández, 2011; Straus 2018).

Mollusks are very abundant in many sites, mostly in caves, in the Vasco-Cantabrian region (Álvarez-Fernández, 2011) and include a wide range of edible species. Cuenca Solana was also able to identify their use as tools (Cuenca Solana 2012). Although the frequency and the number of shells is very high, there are no true shell middens during the Upper Paleolithic, despite the presence of thousands of shells at some of those archaeological horizons (Gutiérrez-Zugasti et al., 2011; Álvarez-Fernández, 2011). Their growing importance through time is the basis for the argument that during this period there was a continuous increase in human population and as a result, there was a change in the economy, based on intensification and diversification in the exploitation of the natural resources, including marine resources (Straus and Clark 1986). On northwestern Iberia, there are only a few sites known, of which the most important are Pena Lliboi and Xestido III (Villar Quinteiro, 1997). However, no fauna has been found at these sites, and only their location seems to be of importance since they are within a few kms of the present shore.

In the Portuguese coast, the scenario seems different from that seen in northern Iberia. While the coast in the west section of Iberia is much longer than in the north, it offers a much diverse range of settings and is not limited by a single, closed mountain range such as those found in the Vasco-Cantabrian Spain. Consequently, the landscape is much more open and it offered a wide range of ecological niches and topographical situations that allowed a more diverse human settlement—also a more difficult context to identity preserved Pleistocene archaeological sites, since caves are not as common as in Northern Spain.

The result is that there are only a handful of sites with marine resources found in Atlantic Portugal, that increases slightly if one includes ornamental shells. All sites are located between 10 and 50 km as the crow flies, from the present coastline to those cave sites where marine elements are present. These sites are Suão, Lagar Velho, Coelhos, Picareiro, Anecrial, and Caldeirão (Zilhão 1997; Almeida 2000; Zilhão and Trinkaus 2002; Almeida et al., 2004; Bicho, Haws, and Hockett 2006; Haws, 2012), all in Portuguese Estremadura, and Vale Boi in the Southern coast, in Algarve (Bicho, Stiner, and Lindly 2004; Bicho, Cascalheira, and Marreiros 2012; Bicho, Manne, et al., 2013). Most of these sites present long Upper Paleolithic stratigraphies, sometimes even with Mousterian at the base, and overlaid by Holocene deposits.

Marine resources include fish (more common during the Magdalenian), marine mammals (dolphin and seal), crustaceans (barnacles and crabs), all usually in very residual numbers, and shellfish (limpets, mussels, cockles, clams, scallops), that in the case of Vale Boi are present in high numbers forming thin midden layers, mostly during the Gravettian. The ornaments, that is, perforated shells (Figure 2) include a wide range of species (Chauviere 2002; Vanhaeren and D'Errico 2002; Tátá et al., 2014), more diverse during the Gravettian (Tátá et al., 2014) than during later phases. The main species used for bead production, however, are *Littorina obtusata/mariae*, *Trivia monacha/arctica*, *Tritia reticulata*, and *Antalis* (or the extinct *Dentalium*), all coming from the Paleolithic shores.

How to define which archaeological localities represent coastal adaptations

The main issue that remains is to understand when both coastal settings and marine resources were used in a systematic way and become part of the settlement system as well as of the diet and economy of those hunter-gatherers.

As discussed above, Marean (2014) suggested that the presence of shellmiddens was the only form that one could ascertain the presence of coastal adaptations in the archaeological record. Unfortunately, while this seems to be true, a large part of the Iberian sites (and those from many parts of the world) do now have enough information due to erosion and lack of preservation (both depositional structures and organic materials) to be integrated in this equation. Also, in many cases, publications, mostly old ones, do not offer full numeric data in terms of NISP or MNI on species, particularly on shellfish and fish. Thus, it is impossible to ascertain the quantity of marine resources that were effectively excavated and found at each site or layer. Only partial and proxy information is available in many cases because of those factors and this, in turn, makes it impossible to make comparisons and to ascertain the type of coastal adaptation that took place in each site. To surpass this issue, we have applied a simple statistical method (Supplementary information) to archaeological data coming from a range of Iberian sites dating to the Middle and Upper Paleolithic and the Mesolithic (Table 1) to verify if some variables are good proxies to infer the presence of coastal adaptations (*sensu* Marean). The variables we used are distance to present shoreline, the number of species of fish, non-edible mollusks, edible mollusks, crustaceans, birds, marine mammals, and perforated shells, as well as other potential proxies (e.g., use wear results in the case of the Middle Paleolithic site of Mira Nascente). The data were analyzed with principal component analysis (PCA). PCA is used in exploratory data analysis and for analyzing the structure of multivariate data. Commonly it is used for dimensionality reduction. This representation of data in a reduced number of dimensions as well as small sample size facilitates the observation of clustering in archeological data that might indicate distinct artifact types (Carlson 2017) or variables such as in the present case . The interest of implementing the PCA on these data was assessed using Bartlett's sphericity test and Keiser-Mayer-Olkin measure of sampling adequacy (KMO MSA). Components with eigenvalues >1 were retained. Analyses were performed in R version 4.1.3 (RCoreTeam 2022) using functionalities from the add-on packages FactoMineR (Lê, Josse, and Husson 2008), psych (Revelle 2015), and factoextra (Kassambara and Mundt 2020).

Our data set includes a total of 32 layers from 11 Middle Paleolithic, seven Upper Paleolithic, and three Mesolithic sites. The geographic provenance of the sites includes mostly the Atlantic coast, but we also have site from north Africa (Benzu) as well as relevant sites from the Mediterranean coast (Bajondillo and Humo from the Bay of Malaga, both Middle Paleolithic) and the Upper Paleolithic Nerja cave. Some of these have very little data, limited just to the location near the extant shore, others have full numbers of NISP or MNE per species. We used a set of nine variables: number of fish, edible mollusks, non-edible mollusks, crustacean, bird, marine mammals, and perforated shell species; number of the potential proxies (presence of art with marine elements, echinoderms, cephalopods, use wear showing fish use); and distance in km to the present shoreline.

The Mesolithic shellmiddens, Toledo, on the coast (Araújo 2012), and Cabeço da Arruda and Cabeço da Amoreira, in the Muge valley (Bicho et al., 2010) are clearly the result of coastal adaptations, confirmed by isotopic data on human skeletons where marine resources contributed to the diet up to 70% (Bicho 2012; Peyroteo Stjerna 2016; Bicho et al., 2017), as well as by the size of mounds (40x60 m and 3–5 m in height in the case of Muge), mostly composed of shells. These sites can be used as anchors or proxies for the determination of both which sites are resulting from coastal adaptations and which variables can be used for determining that status.

The results of the PCA for the variables and sites are shown in the plots in Figure 3 and Table 2 (and compiled in the Supplementary Material S1). PCA fairly represented the data (Bartlett's, $p<10^{-4}$ with 36 d.f., and KMO MSA=0.603). Distance to the shoreline is not a significant variable. Perhaps, if we had the true distance to the contemporaneous shoreline, the results were different but, unfortunately, it would be impossible to ascertain such distance with the present-day data and an estimate could potentially bring more errors than to use the extant shore. Nevertheless, we decided to include it in the study. There are four variables that are clearly significant in dimension 1 (46.6% of the variance): the number of species of crustaceans, fish, edible mollusks, and mollusks, with birds showing a lower contribution to the system. In dimension 2 (17.5%) there are three variables with strong contributions: the number of species of perforated shells and of birds, and the variable of other proxies.

Sites on the positive side of Dimension 1 are those that are likely representing coastal adaptations, and include in addition to the three Mesolithic shellmiddens, three Upper

Paleolithic assemblages, two from Nerja cave in the Spanish Mediterranean, and the Gravettian occupation in Vale Boi; and three Middle Paleolithic sites (Vangard, Gorham's and Figueira Brava). However, Dimension 2 separates the Mesolithic and the Upper Paleolithic sites from the Middle Paleolithic based on the presence of ornamental shells and the lack of bird species (in the Upper Paleolithic sites).

Discussion

The presence of coastal sites is heavily influenced by the fact that the Atlantic coast in Iberia has important submerged landscapes. In fact, the Pleistocene shore may rest, depending on the chronology, some 30–50 km away from the extant shore, corresponding to the -125 bathymetric line dating to the Last Glacial Maximum (Flemming, Harff, and Moura 2017; Harff and Flemming, 2017; Moura, Gomes, and Horta 2017; Bailey et al., 2020). Nevertheless, most areas present a very steep bathymetry, so the submerged zone is much narrow than that and the distance to present shoreline is within 10 km as the crow flies. Unfortunately, wave action and depth, as well as intertidal range are key elements that have had a strong impact on underwater archaeological preservation (Fa 2008; Arias Cabal, 2020; Bicho, Infantini, and Marreiros 2020) as well as that extent of underwater archaeology field work. The result is that underwater evidence is non-existent in Iberia and, thus, marine and coastal Pleistocene archaeology is coming from terrestrial settings, some very close to the intertidal zone.

The special upwelling conditions, particularly in the South, during Pleistocene times, may have provided a particular ecological coastal setting with high coastal marine productivity (Abrantes 1991, 2000) and because of that, coastal richness may have brought people to live and exploit the Iberian Atlantic shores since Middle Paleolithic times, as suggested by the presence of various sites located on the edge of the modern intertidal zone as well as by the presence of marine faunas where organic preservation exists.

The presence of edible marine species such as fish, marine mammals, and shellfish, many km inland in cave sites namely in Coelhos, Picareiro, or Lagar Velho, raises some interesting aspects. The distance likely precluded that inland populations exploited themselves coastal resources. This is due to the travelling time coupled with the fact that marine resources tend to have a short living time and spoil fast and are not able to endure a trip of a few of days as it would be the case for inland hunter-gatherers. However, there could have been a developed and systematic exchange network, where coastal populations would bring the marine resources halfway, and exchanged those for inland raw materials, including chert, with the inland groups. Otherwise, it would be hard to conceive a mobility system that integrated a round-trip of 100 km, that included both a whole day for shellfish gathering and fishing, followed by a rapid return to the residential campsite transporting those resources in a day, so they would not spoil. Of course, to this, one would have to add the knowledge of the tides, which, as we know inland people tend to ignore completely. Of course, travelling time would not be a concern in the case of ornamental shells, since spoiling was not a concerning factor. And that is likely why there are more inland sites with ornamental shells than with edible resources.

In the case of Vale Boi, there is a clear indication that distance to the contemporaneous shore was a key factor on the frequency of marine resources: while during the Gravettian, shells are present in high numbers, they decrease severely during the LGM, that is, when the coast line is furthest away (Manne and Bicho 2011; Bicho, Manne, et al., 2013).

Archaeological data from the Atlantic Iberian coast clearly shows that the seascape was used starting more than 100,000 years ago, possibly as long as in the Mediterranean world (Stiner 1994; Stringer et al., 2008; Cortes-Sanchez et al., 2011; Villa et al., 2020). For this chronology, site location seems to be the most important proxy, but in some cases (e.g., Figueira Brava) it is unequivocal that marine resources were key elements on the diet of those populations, perhaps in certain times and locations as important as the terrestrial resources. There also seems to be an increase through time on the importance of coastal settings and resources on the life of the Iberian Pleistocene hunter-gatherers.

Our PCA results show two relevant, but very different elements: the variables that can be used to potentially ascertain the sites/layers corresponding to systematic use of the coastal settings (the number of species of crustaceans, fish, edible mollusks, and non-edible mollusks); and the fact that this took place already during the Middle Paleolithic, but likely different from the Upper Paleolithic adaptations.

The intensity in the use of crustaceans, fish, edible mollusks, and mollusks are present in the Middle Paleolithic sites of Figueira Brava and the two-cave site in Gibraltar, as well as in the Upper Paleolithic site of Nerja and Vale Boi, although not all the layers show that. In the case of Vale Boi, only the Gravettian occupation is likely a systematic based coastal adaptation, while those in the latter periods are not—this suggests that the distance to the shoreline is the key variable here that changed the type of diet and economy of that human group. The main differences between the Middle and Upper Paleolithic seems to be the presence of birds in the Middle Paleolithic sites and ornamental shells in the Upper Paleolithic. This difference indicates an identical use of the natural marine resources, and thus a similar diet of those populations. On the other hand, the differences in the birds and perforated shells, suggest a different way of dealing with body ornamentation, with shells in the case of Upper Paleolithic, and feathers and potentially bird bones in the case of the Neanderthals populations, as seen in other areas of

Spain and Gibraltar (Finlayson et al., 2012; Rodríguez-Hidalgo et al., 2019).

Conclusion

This study shows that the Atlantic Iberian margins were used in a diverse form during the Pleistocene. Aspects such as the orography of the Vasco-Cantabrian world were an important variable in the human settlement during the Paleolithic, while the flat Portuguese coast, marked by a strong upwelling system provided a highly rich coastal environment that was frequently exploited from very early on, adding to the available terrestrial resources. It is also likely that coastal resources travelled inland, possibly as a part of a complex, but systematic mechanism of network exchanges, sending marine resources inland and bringing lithic resources to the coast. Potentially, this had a seasonal character, but no archaeological evidence can today confirm this hypothesis, neither it can confirm the likelihood that those regional networks were also a key factor on the exchange of people between groups increasing the genetic diversity at each group.

Also relevant is that a wide range of marine resources were exploited from very early on, including crustaceans, fish, mollusks, and marine mammals, some of which were also used for body ornaments. The latter apparently circulated a lot more than the edible resources, probably due to the spoiling effect of travelling inland of fresh marine resources.

Our study also suggests that there are a series of variables, that together, can be used to ascertain or as proxies for the presence of coastal adaptations (sensuMarean 2014). These are the number of species of crustaceans, fish, edible mollusks, and non-edible mollusks. Also, based on this work, it is possible that while coastal adaptations existed since the Middle Paleolithic in Iberia, the lack of perforated shells and the abundance of marine birds characterizing the Middle Paleolithic sites separate them from the Upper Paleolithic occupations. While the presence of ornamental shells in the Upper Paleolithic is a direct consequence of cultural activities related to social behavior, and the presence of birds in the Middle Paleolithic may just be a consequence of a semi-symbiotic relation between Neanderthals and birds as cavers, avoiding the presence of other larger predators. The evidence from various sites in Iberia seem to indicate that those birds were used by Neanderthals for both feathers and talons for body decoration. While the diet and economy were possibly similar between the two populations, apparently the human decorative form and, thus, the social and visual representation of both groups, were distinct.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

NB prepared the archaeological data and wrote the manuscript. EE prepared the statistics and wrote the manuscript

Funding

This study received Portuguese national funds from FCT—Foundation for Science and Technology through projects UIDB/04326/2020, UIDP/04326/2020, UIDB/ARQ/04211/2020, UIDP/ARQ/04211/2020, PTDC/HAR-ARQ/27833/2017 (Fundos FEDER through Programa Operacional Regional do Algarve - CRESC Algarve2020 for the project ALG-01-0145-FEDER-027833), and LA/P/0101/2020.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.957214/full#supplementary-material

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 01 September 2022
DOI 10.3389/feart.2022.869487

Thermo-microstratigraphy of shells reveals invisible fire use and possible cooking in the archaeological record

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The archaeological visibility of hearths related to shellfish cooking methods is limited, particularly in pre-ceramic shell midden contexts. Important evidence for use of fire is the thermal alteration of components, namely the identification of burnt shells. Mollusk shells that mineralize as aragonite are particularly indicative of burning due to the conversion of aragonite to calcite through recrystallization at known temperature thresholds. However, roasting temperatures needed to open bivalves, do not necessarily cause thermal alterations in the cooked shell. This complicates the significance of shell mineralogy by itself to recognize cooking, and discerning pre-depositional from *in situ* heating. To distinguish between cooking and burning, we combine micromorphological analyses with microscopic Fourier transformed infrared spectroscopy to investigate mineralogical thermo-alterations alongside microstratigraphic formation studies. Experimentally heated specimens of *Cerastoderma edule* and *Scrobicularia plana* are used to identify the temperature thresholds of biogenic calcium carbonate phase alteration at the micro-scale. These results are then used to interpret mineral alterations in deposits from two Mesolithic shell midden contexts from Portugal. Micro-stratigraphically controlled mineralogy proved to be particularly useful to distinguish between pre-depositional heating from *in situ* heating, configuring a novel methodology for recognition of traces of cooking shellfish versus traces of fire used for other purposes. Mapping the mineral phase conversion at a micro stratigraphic scale also allows us to identify instances of *in situ* fire events that were invisible macroscopically. This combined microstratigraphic and mineralogical methodology considerably increases our capacity of deciphering intricate shell midden stratigraphy and occupational events.

KEYWORDS

prehistoric cooking, shell midden, mesolithic, microstratigraphy, mineralogy, aragonite, calcite, palaeotemperature

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 04 February 2022
ACCEPTED 18 July 2022
PUBLISHED 01 September 2022

CITATION
Simões CD and Aldeias V (2022), Thermo-microstratigraphy of shells reveals invisible fire use and possible cooking in the archaeological record. *Front. Earth Sci.* 10:869487.
doi: 10.3389/feart.2022.869487

Introduction

Mollusk shells are common components in archaeological deposits and important indicators of paleoenvironment, coastal foraging ranges, and diet. While the use of shells to identify exploited resources and reconstruct coastal paleoenvironments in prehistory are relatively common (Mannino and Thomas, 2002; Mannino et al., 2007; Colonese et al., 2009; Andrus, 2011; Mannino et al., 2011; Prendergast et al., 2016; Canti, 2017; Prendergast and Schöne, 2017; García-Escárzaga et al., 2019), few studies have focused on how mollusks have been processed and potentially cooked in prehistoric settings, particularly in the absence of ceramic containers. This is relevant since most archaeological shells relate to dietary waste (Erlandson, 1988; Erlandson and Moss, 2001; Bailey and Milner, 2002; Craig et al., 2007; Diniz, 2016; García-Escárzaga and Gutiérrez-Zugasti, 2021). The evolution of cooking and associated pyrotechnology is a crucial behavioral trait that may vary in time and space (Wrangham and Conklin-Brittain, 2003; Wrangham and Carmody, 2010). Currently, to what extent fire was used to process shellfish in prehistoric times through roasting techniques is largely understudied.

Archaeological evidence for the use of fire relies on the recognition of combustion by-products and traces in the archaeological record. The identification of ashes, charcoal, burned components, and underlying thermally altered substrates (Mentzer, 2014; Aldeias et al., 2016; Goldberg et al., 2017; Mallol et al., 2017) are proxies for the presence of combustion. However, intact combustion features can be difficult to discern due to both post-depositional processes, such as dissolution, or preservation issues. This is particularly true for open-air shelly deposits where small components like ash can easily be blown away or migrate down the profiles due to the high level of sedimentary porosity (March et al., 2014). Furthermore, the construction of fires on top of sandy shelly deposits often do not present an indicative rubified substrate (Villagran, 2018; Aldeias et al., 2019). Another important aspect, however, is that fires used for shellfish roasting might not entail the preservation of intact combustion features–which are, at its simplest, an intact ash layer with charcoals and burned components overlying a baked substrate. This is because, as ethnographic records show, shellfish roasting fires frequently involving the removal of fire residues, since hearths can be done either above the shellfish or using rocks previously heated by fires (Meehan, 1975; Waselkov, 1987). In these cases, the ashes and charcoals are pushed aside to retrieve the thermally opened mollusks. Such activities entail the dismantlement of the combustion products, with the dispersion of ashes and charcoals, to retrieve the cooked mollusks, resulting in the loss of the stratigraphic signatures of intact hearths (Aldeias et al., 2019). Our ability to identify and differentiate these–function-related–syn-depositional disturbances from naturally reworked combustion residues is currently challenging. Even so, important evidence for use of fire is the thermal alteration of components, namely the identification of burnt shells. Mollusk shells that mineralize as aragonite are particularly indicative of burning due to the conversion of metastable biogenic aragonite to calcite through recrystallization at known temperature thresholds (Lécuyer, 1996; Pokroy et al., 2007; Parker et al., 2010; Toffolo, 2021).

Here we argue that burning and cooking should be differentiated not by simply identifying burned archaeological shells, but by assessing the associated burned components in their original sedimentary context. For this, we need to understand two related aspects: first, the identification of what are the traces left by roasting (not boiling) of shellfish in pre-ceramic contexts; second, the contextual association of burned shells and other components to differentiate the primary or secondary–potentially unintentional–burning of previously deposited shells.

This paper focuses on understanding burning in shells mineralized as aragonite. For that, we use experimentally heated specimens of *Cerastoderma edule* (common cockle) and *Scrobicularia plana* (peppery furrow) to discern biogenic calcium carbonate (CaCO3) phase alteration at the micro-scale. These results are then used to calibrate mineral alterations in deposits of two Mesolithic shell midden contexts from Portugal (Figure 1). Micromorphological analyses (Courty et al., 1989; Macphail and Goldberg, 2017; Nicosia and Stoops, 2017) of microfacies and their interpreted formation processes are combined with microscopic Fourier transformed infrared spectroscopy (microFTIR) (Goldberg and Berna, 2010; Berna, 2017) with twofold objectives: 1) to reconstruct the microstratigraphic histories of deposition in shell-rich contexts, and 2) to discern between microstratigraphic traces of fire for shellfish processing versus secondary, post-depositional, burning of shells, according to our expectations, synthesized in Table 1.

Materials and methods

Experimentally heated shells

We used the collection of modern shells of *C. edule* and *S. plana* that were heated in a muffle at controlled temperatures by Aldeias et al. (2019). The shells were inserted into ceramic crucibles and heated at increasing temperatures from 100 to 900°C, for 5 and 20 m heating durations. Mineralogical analyses reported by Aldeias et al. (2019) were done by hand grinding a portion of the heated shells and obtaining infrared transmission and ATR spectra on powdered shell material. The collected results showed that calcitic phases start to appear at slightly different temperatures in each species: 200°C in *C. edule* and only at 350°C in *S. plana*. They also observed that the complete

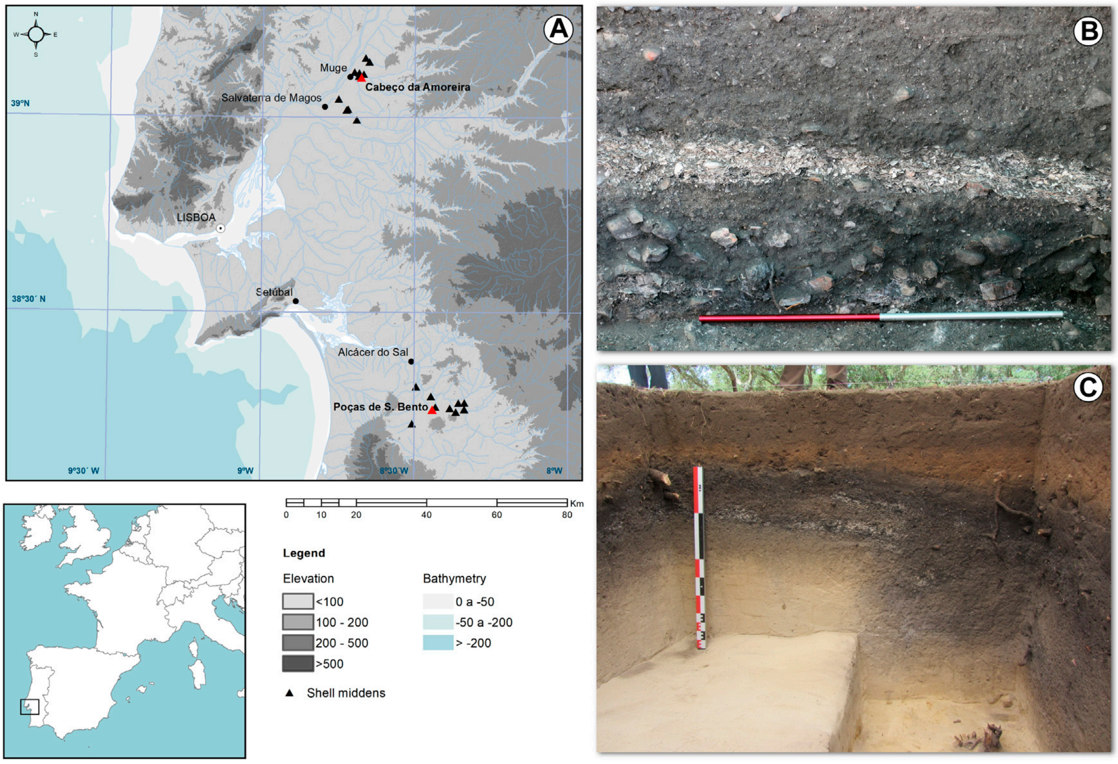

FIGURE 1
(A) Geographic location of the Mesolithic shell middens analyzed. **(B)** Aspect of the stratigraphy at Cabeço da Amoreira, in the Muge Valley. **(C)** Aspect of the stratigraphy at Poças de São Bento, in the Sado Valley.

TABLE 1 Expectations on preserved traces of cooking shellfish versus burning shells.

	Cooking (roasting)	Burning (hearths)
Combustion structures	Not likely to be preserved after use	Can be preserve after use
Combustion residues	Not *in situ* ash and charcoals, shells, burnt aggregates and thermoclasts	Thermal alteration of shell mineralogy, *in-situ* ash, charcoal and heated substrate (substrate not related to fire event)
Shell mineralogy	Aragonite, with rare calcite	Mainly calcite
Shell fragmentation	Less fragmented	More fragmented

transformation of the original biogenic aragonite to calcite occurred at slightly different temperatures for each species: at 500°C for samples of *C. edule* and at 400°C for *S. Plana* (Aldeias et al., 2019).

In the present study, we further expand on this previous work by using microFTIR on thin sections produced from the same shells of *C. edule* and *S. plana* used by Aldeias et al. (2019) heated for 5 min at the threshold of the transformation interval previously observed, that is, at 250, 350, 400, and 450°C (Figure 2). Since the carbonate phase conversion in *C. edule* was shown to start at lower temperature than *S. plana* (Aldeias et al., 2019), two specimens of *C. edule* heated at 200°C were also used, though one of them was heated for 20 min, a difference that Aldeias et al. (2019) observed to have no effect on the FTIR-ATR results. Two specimens of each shell species were heated to enable double tests at each temperature (repetition one and repetition two in Figures 2, 3), resulting in 18 individual experimental shell samples used in this study (10 samples of *C. edule* and eight samples of *S. plana*) (Figures 2, 3). The experimental shells were impregnated with a polyester resin, cut along their growth axis, and produced into 2.7 × 4.6-cm thin sections by Spectrum Petrographics (Vancouver, United States).

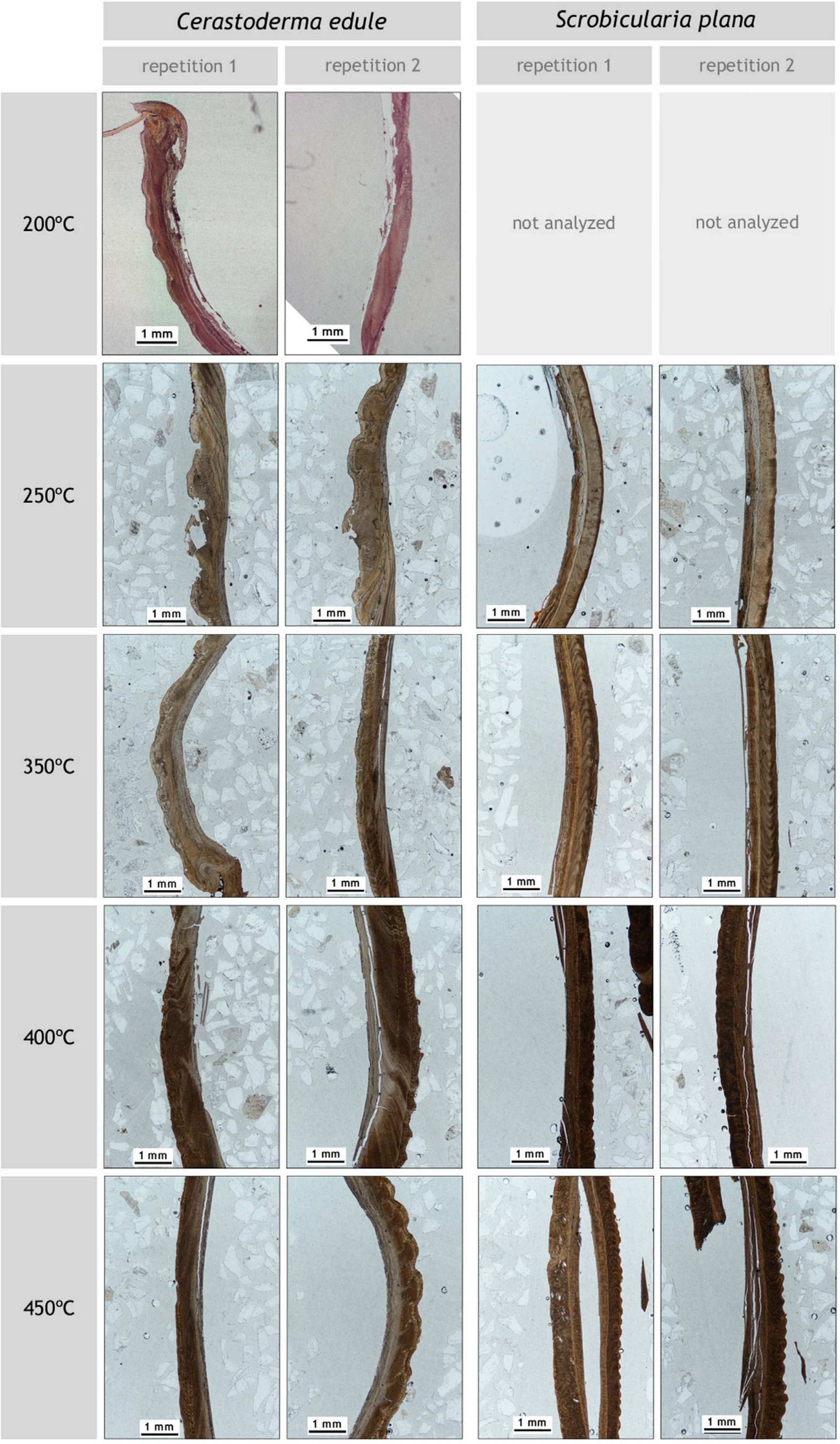

FIGURE 2
Petrographic images of the 18 thin experimentally heated shells used in this study, showing the observed effects of thermo-alteration: darkening and cracking increase with higher temperatures, though the crystalline structures are still visible.

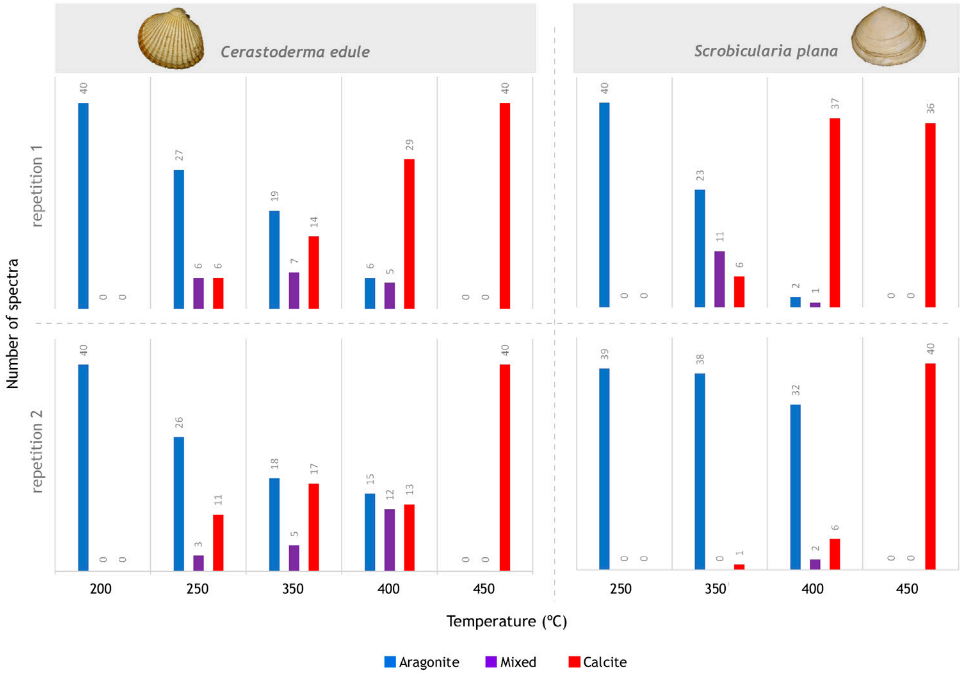

FIGURE 3
Aragonite-calcite conversion in the 18 experimentally heated shells; each individualized graph represents a single specimen of the two repetitions at each temperature; note the gradual conversion observed in *Cerastoderma edule* and the abrupt conversion in *Scrobicularia plana*. Shell species image credits: Natural History Museum Rotterdam, adapted from original file at WoRMS Database (https://www.marinespecies.org/index.php) under a CC BY-NC-SA license.

TABLE 2 Types of sedimentary microfacies identified in Cabeço da Amoreira and Poças de São Bento shell middens used in this work.

Microfacies type	General description in thin section	Interpreted formation process	Thin sections
Direct single tossing	Interconnected anthropogenic components, mostly shells, but occasionally also fishbones, stone knapping debris, charcoal and silty-clay aggregates occur. The shell valves, frequently complete, present a sub-horizontal arrangement and can have some interstitial finer material, such as comminuted organic matter, or excrements	Anthropic tossing event in primary position. Interpreted as a single moment of activity	CAM112; CAM109; PSB913
Reworked shelly sediments	These comprise a few slightly different subtypes in each site, but overall consist of variable amounts of randomly distributed and fragmented shells, bones, and fishbones. These components are supported by a matrix of sand with some pebbles of other local lithologies, sometimes rich in fine organic material, usually charred	Intentional dumping of shell-rich sediment loads. Anthropogenically reworked sediments which components are not in primary position	CAM109; CAM206; CAM210; PSB107; PSB913
Active layers	Few millimeter-thick layers where shells and other platy components (e.g., bones) are distributed in sub-horizontal stringers. These components show cracks typically associated with *in situ* crushing	Surface layer affected by repeated trampling, causing general compaction, and crushing of components	CAM109; CAM206; PSB107; PSB913

Archaeological thin sections from mesolithic shell middens

To assess the context of heated components in archaeological deposits, we investigate two Mesolithic shell midden sites from Portugal (Figure 1): Cabeço da Amoreira and Poças de São Bento. Both sites are among the largest shell middens in the Muge and the Sado valleys, respectively. These are two major paleoestuaries with brackish conditions formed during the Early Holocene sea-level rise (van der Schriek et al., 2007; Vis et al., 2008; Costa et al.,

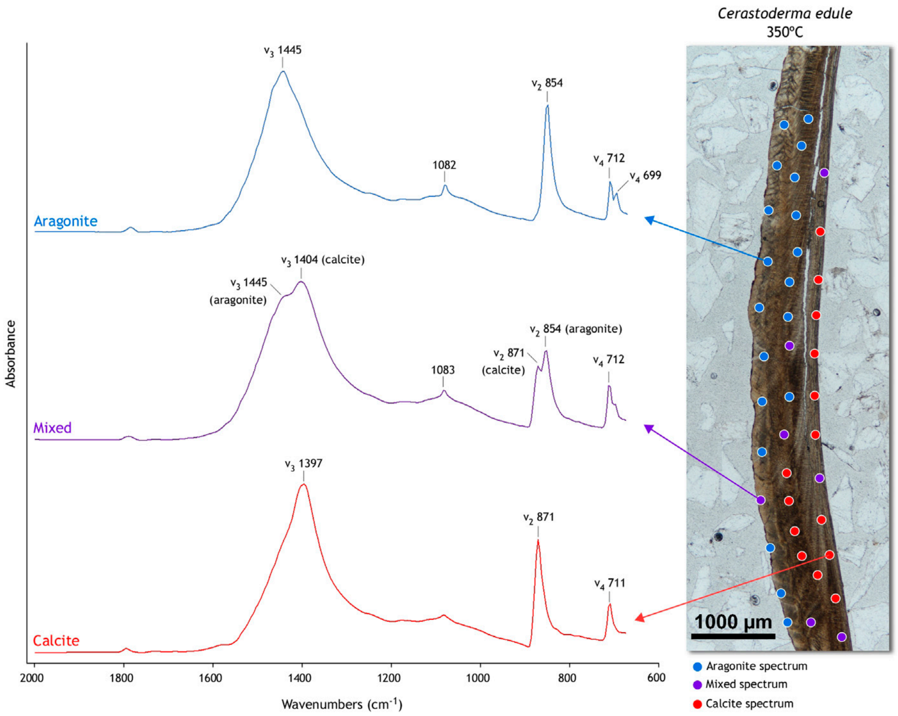

FIGURE 4
(A) Examples of microFTIR spectra of aragonite, calcite, and mixing both, obtained in experimentally heated specimen of *Cerastoderma edule*. **(B)** Petrographic microphotograph of the analyzed specimen with an example of the regular distribution of points to obtain microFTIR measurements; note the distribution of calcite spectra along the inner surface and aragonite spectra in the outer surface, showing a heterogenous conversion.

2019). The beginning of Mesolithic occupations of both the Muge and Sado valleys is characterized by the onset of human burials dated to 8,500–8,000 cal BP, in simple hollows opened in the sandy substrates of both sites (Bicho et al., 2010; Diniz and Arias, 2012; Bicho et al., 2013; Peyroteo-Stjerna, 2020; Arias et al., 2021). The following cumulative anthropogenic accretion of shelly deposits (and further human and animal inhumations) in several sites in the estuaries' margins spanned until *c.* 7,400 cal BP, when the first Neolithic farmers were populating the surrounding regions (Bicho et al., 2017; Diniz et al., 2021). In the case of Cabeço da Amoreira and Poças de São Bento, pit features and putative post-holes at times cross-cut the complex interbedded shelly deposits.

Previous micromorphological studies have focused on reconstructing the depositional histories and the range of activities leading to the formation of these shell middens of Cabeço da Amoreira (Aldeias and Bicho, 2016) and at Poças de São Bento (Duarte et al., 2019). These studies stressed human-driven accumulations as the main agents of deposition, with the identification of three main types of deposits (sedimentary microfacies): 1) deposits in primary position, related to single events of direct shell tossing, 2) reworked shelly sediments resulting from mass reallocation of previously discarded debris, and 3) active layers related to more stable occupation surfaces. Table 2 describes the characteristics of the microfacies based on the micromorphological studies of those sites, alongside the indication of the thin sections that are used in the current paper.

The experimentally heated shells can be directly compared to these archaeological sites since *C. edule* and *S. plana* are the predominant species at both sites. Micromorphological samples were collected at the two sites through the removal of undisturbed sediment blocks from the excavation profiles and carefully wrapped either with soft paper or with pre-plastered bandages. The blocks were then dried for several days and impregnated with a polyester resin mix. For Cabeço da Amoreira, large 5,7x13,5 cm thin sections were produced by the *Servei de Micromofologia i Anàlisi d'Imatges* at the University of Lleida (Spain). For Poças de São Bento, 5x7 cm thin sections were produced at the *Departamento de Ciencia y Engenieria del Terreno y de los Materiales* of the University of Cantabria (Santander, Spain). Thin sections from Cabeço da Amoreira are labelled CAM followed by an unique number identifier,

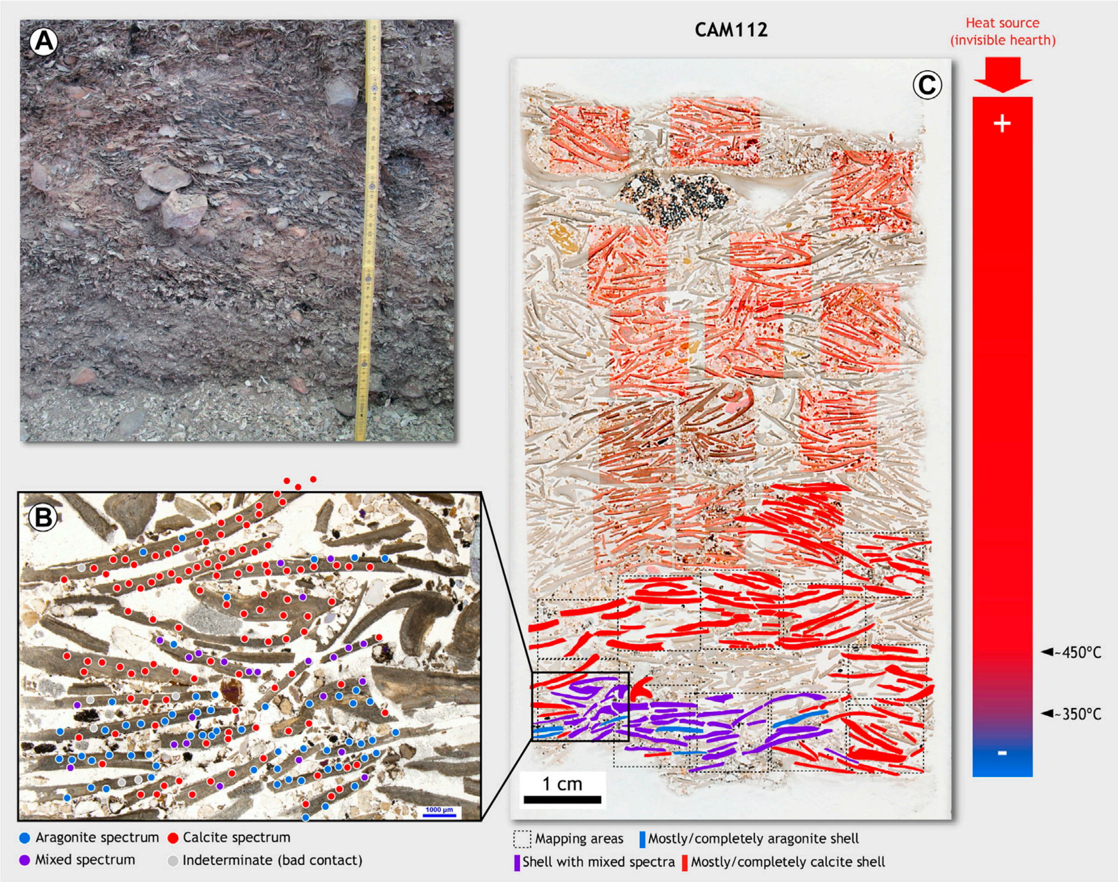

FIGURE 5
Sample CAM112. **(A)** Close-up of the field profile of the direct tossing deposits; note the absence of any evidence of structured combustion feature **(B)** Petrographic microphotograph showing an example of how the points to obtain FTIR measurements were distributed through the archaeological shells in the mapping areas; note the distribution of heated (calcitic) shells in the top of the image, while the shells in the bottom are not completely thermo-altered, with mainly aragonitic mineralogy, and the measurements of mixed mineralogy concentrate in the transitional area. **(C)** Thin section scan showing the mapping areas of ~1 cm^2 (dashed rectangles) and individual shells' mineralogy obtained; the not-dashed rectangle indicates the location of the microphotograph A, and the rectangles with reddish filter indicate mappings where all shells are calcitic; the vertical bar to the right shows the approximate paleotemperature gradient experienced by the shells when subjected to post-depositional fire placed on top of the deposit, and invisible at the macroscopic scale.

whereas thin sections from Poças de São Bento bear the label PSB, also followed by an unique number identifier (e.g., CAM112 or PSB107). The microscopic observations were carried out under petrographic microscopes with plane- and cross-polarized light at magnifications ranging from 20x to 400x in plane polarized light (PPL) and cross-polarized light (XPL).

Microscopic fourier transform infrared spectroscopy mapping

MicroFTIR spectra were collected directly on the thin sections (of both experimental shells and archaeological micromorphology samples) using a Thermo Scientific Nicolet iN10 MX microscope. Spectra were collected in attenuated total reflectance (ATR) mode using a germanium crystal tip at a 4 cm^{-1} resolution in 256 and 64 scans, for experimental shells and archaeological ones, respectively, both within the 675–4,000 cm^{-1} range, and were compared with available libraries. The germanium tip has 150 x 150 µm diameter, though the measured area can be less than 150 µm depending on the degree of contact between the tip and the thin sections.

In the 18 samples of experimentally heated shells, a standard number of 40 individual measurements were collected in each shell (39 in one of them–see Figure 3), equally distributed in the shells' thickness (Figure 4), resulting in 1,438 individual measurements (see Supplementary Material). In the archaeological thin sections, several mapping areas of 1 cm^2

were selected throughout the slides' surface (Figure 5) to analyze the shells that were visibly specimens of *S. plana* and *C. edule*. Depending on the preservation degree and size of the shell fragments, a variable number of measurements were placed in each shell within each map (Figure 5), in the most similar way possible as in the experimental shells, covering the specimens' thickness along their section. For archaeological shells in six thin sections, a total of 9,038 individual measurements were collected (see Supplementary Material).

Results

Experimentally heated shells

The microFTIR mapping on the oven-heated shells yielded the spectra correspondent to the CaCO3 polymorphs of biogenic aragonite and calcite (Figure 4). Biogenic aragonite spectra present the same peak position for shells heated above 200°C as reported by Aldeias et al. (2019) in ATR: the ν_3 asymmetric stretch at 1,445 cm^{-1}, the ν_1 symmetric stretch at 1,082 cm^{-1}, the ν_4 peak at 856 cm^{-1}, and the ν_2 doublet at 712 and 700 cm^{-1}. Calcite is represented by the ν_3 peak at 1,397 cm^{-1}, the ν_4 peak at 871 cm^{-1}, and the ν_2 peak at 711 cm^{-1}, in accordance with reference data (Weiner, 2010). A third type of spectrum exhibits mixture of both aragonite and calcite polymorphs in the specimens heated at the transitional temperature phases. In the mixed spectra, the peaks of both polymorphs in the same band overlap, usually with one appearing as a shoulder (Figure 4), depending on the relative proportions, as described elsewhere (Loftus et al., 2015; Toffolo et al., 2019).

We observed that the occurrence of all three types of spectra occur in a same shell during the mineral transformation temperature interval (Figure 3). The microFTIR mapping revealed a slightly different pattern between both species in the aragonite conversion to calcite. In *S. plana* the total conversion is faster since the shells remain mostly aragonitic at 250 and 350°C. At 400°C nearly all measurements provided calcite spectra, with only a few mixed ones, and exclusively calcite spectra at 450°C. In the case of *C. edule*, the conversion is more protracted, with mixed spectra already at 250°C, co-existence of aragonite and calcite spectra in similar proportions at 350 and 400°C, and only at 450°C all measured points correspond to calcite. These results generally match the trends identified by FTIR-ATR previously obtained by Aldeias et al. (2019).

Both shell species revealed similar petrographic transformations in terms of darkening and longitudinal fissures development with increasing temperature. At 250°C the shells are practically intact, and at 350°C the inner surface exhibits fissures along the different layers, that are progressively intensified at 400 and 450°C. In general, the effects of these alterations are more intense in *S. plana* than in *C. edule*. In Figure 2, it can be observed that at 450°C, *C. edule* exhibits only slightly darkened patches, following the carbonate growth lines, whereas *S. plana* is homogenously darkened, although the growth lines are still visible.

Archaeological thin sections

In CAM112 the areas mapped with micro-FTIR reveal that most shells are calcitic, except at the bottom, where they remain aragonitic or with a mixture of both polymorphs. This shift is progressive, and it is observed also within the mapping areas in the bottom of the thin section, where the totally calcitic shells are above, aragonitic shells are in the bottom, while mixed spectra occur in greater amounts the transitional middle area (Figure 5).

In CAM109, the bottom layer of single tossed shells reveals a totally aragonitic mineralogy in all mapping areas. In the overlying layer of reworked shells, the shells are predominantly aragonitic, except for rare random shell fragments that yielded mixed spectra and calcitic mineralogy, especially towards the top of the deposit. The microFTIR mapping in the active layer at the top of this thin section revealed also mainly aragonitic shells. Overall, in CAM109 the shells are not thermo-altered, being only the layer of reworked sediments that includes few thermo-altered shells (Figure 6).

In contrast to CAM109, in the thin section CAM206, the mapped areas in the active layer revealed completely calcitic shells (Figure 7). In the reworked deposits both under- and overlying the active layer, the shells in the mapped areas exhibit similar proportions of all mineralogical spectra (Figure 7). Thin section CAM210, a sample of reworked shelly sediments, revealed mostly aragonitic shells with rare calcitic fragments (Figure 8).

The sample PSB107 mapping exhibits mostly calcitic shells in the active layer and a mix of all mineralogical spectra in the underlying reworked deposit, though aragonitic ones predominate (Figure 9).

All of the thin sections produced from sample PSB913 provided a mainly aragonitic mineralogy of the shells in all represented layers (Figure 10). Rare fragments of calcitic shells were documented in the direct shell tossing deposit as well as in the reworked shelly sediments deposit (Figure 10).

As it can be observed in Table 3, these results reveal very diverse situations for each type of sedimentary microfacies identified micromorphologically, with several meaningful implications for the circumstances in which the thermo-alteration of shells and their discarding are related in the shell midden formation.

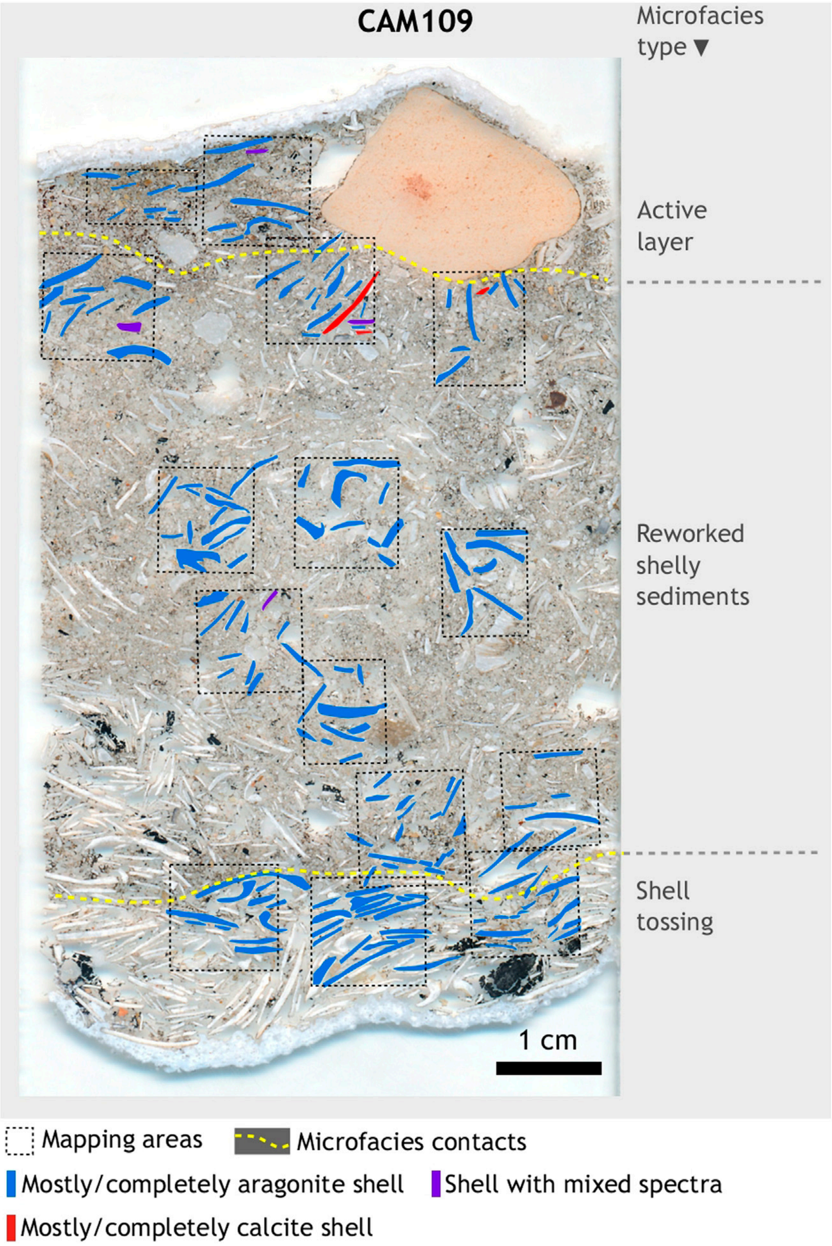

FIGURE 6
Thin section scan of sample CAM109 showing individual shells' overall mineralogy obtained through microFTIR.

Discussion

Burning of shells in the archaeological record does not exclusively equate to cooking, as it can occur simply because fire was used for any other purpose: for warmth, light, cooking or smoking of other food items besides shellfish. The construction of a fire on top of shelly deposits previously accumulated can also lead to (unintentional) thermal alteration of those shells (March et al., 2014). In such cases, the shells constitute previous debris unrelated to the fire event and not indicative of hearth use or function. One should be cautious, therefore, in relating shells burned at high temperatures (above 200°C) with shellfish cooking, since those higher temperatures imply the burning of the edible mollusk. How to recognize the intentional use of fire to cook shellfish has been challenging through analysis of thermal alterations of individual shells by themselves (Milano et al., 2016; Müller et al., 2017; Milano et al., 2018; Staudigel et al.,

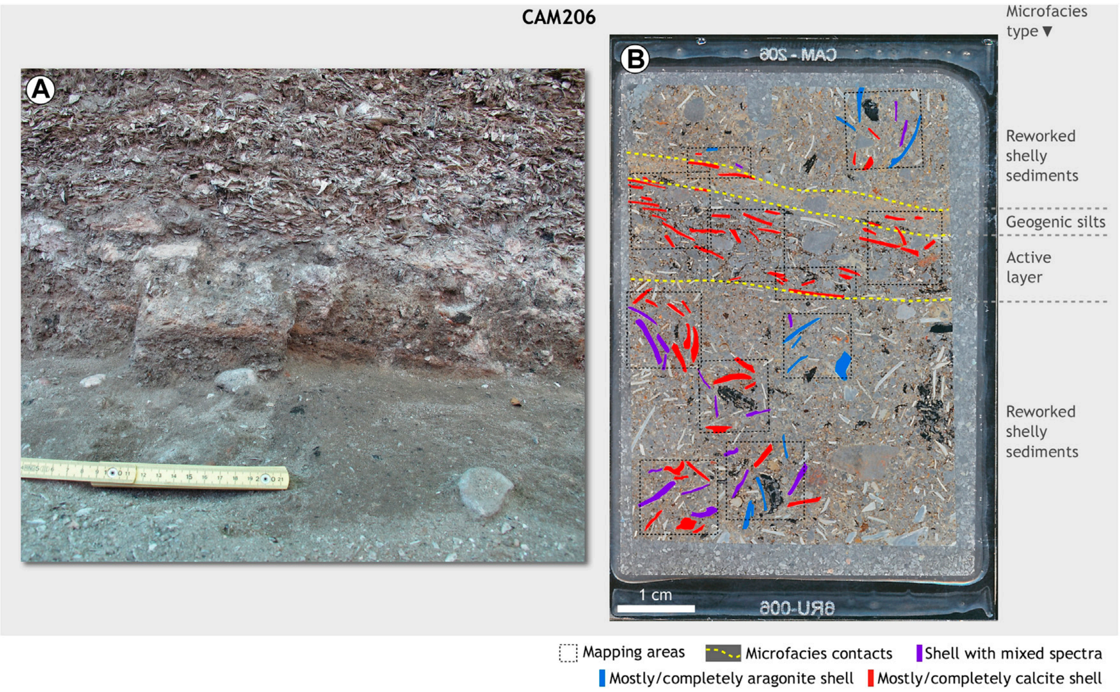

FIGURE 7
Sample CAM206: **(A)** Field photograph of the sample in profile, prior to block extraction. **(B)** Thin section scan of the samples showing individual shells' overall mineralogy obtained through microFTIR.

2019). Here we integrate the thermo-stratigraphic and contextual factors to build upon those previous attempts.

Mineral phase conversion and CaCO3 diagenesis

Like other bivalves, *S. plana* and *C. edule* are formed by two and three layers, respectively, composed of aragonite crystals that exhibit different crystalline microstructures and grow by precipitating incremental lines controlled by environmental conditions during the mollusk life (tides, temperature, stress) (Schöne, 2008). During shell growth, organic matter is also secreted, filling the space between the aragonite crystals and can represent 0.05–5% of weight (Weiner, 2010).

Milano et al. (2016) demonstrated a progressive microstructure expansion with increasing temperatures in *C. edule*, associated with the organic matrix loss. Heating is one of the possible causes for disappearance of mollusk shell's organic matrix pointed out in the literature, which has been recorded at temperatures >300°C and a total replacement of aragonite to calcite at around 500°C (Milano et al., 2016; Milano and Nehrke, 2018). Our results overall agree with previous studies but show that the aragonite to calcite conversion starts at slightly different temperatures in the different species (Figure 3), namely at 250°C for *C. edule* and 350/400°C for *S. plana*. However, the temperature of complete mineralogical recrystallization of the shells was recorded at 450°C for both *S. plana* and *C. edule*.

Biogenic aragonite is known to reprecipitate as calcite in chemically unstable archaeological contexts (Weiner, 2010; Toffolo, 2021), but not always through recrystallization as it occurs upon heating. Meteoric water induces dissolution of biogenic aragonite and subsequent neoformation of calcite, which means a progressive loss of shell material, eventually until complete disappearance of the shell (Toffolo, 2021). This phenomenon is observed at the Mesolithic shell middens analyzed here by the existence of pendants composed of calcite spar in the underside of components (shells and pebbles) which most probable source are shells in upper layers that were dissolved (Aldeias and Bicho, 2016; Duarte et al., 2019). Previous studies on the transformation of biogenic aragonite into calcite suggest that diagenetic recrystallization observed in the geologic record is likely to be a much slower process than the timespan occurred at the Mesolithic archaeological contexts under study (Curtis and Krinsley, 1965; Brand, 1989; Ritter et al., 2017; Peacock et al., 2020; Toffolo, 2021). The presence of aragonitic shells in the older layers of the studied shell middens further indicates that the alteration from biogenic aragonite to calcite is not time dependent at these sites.

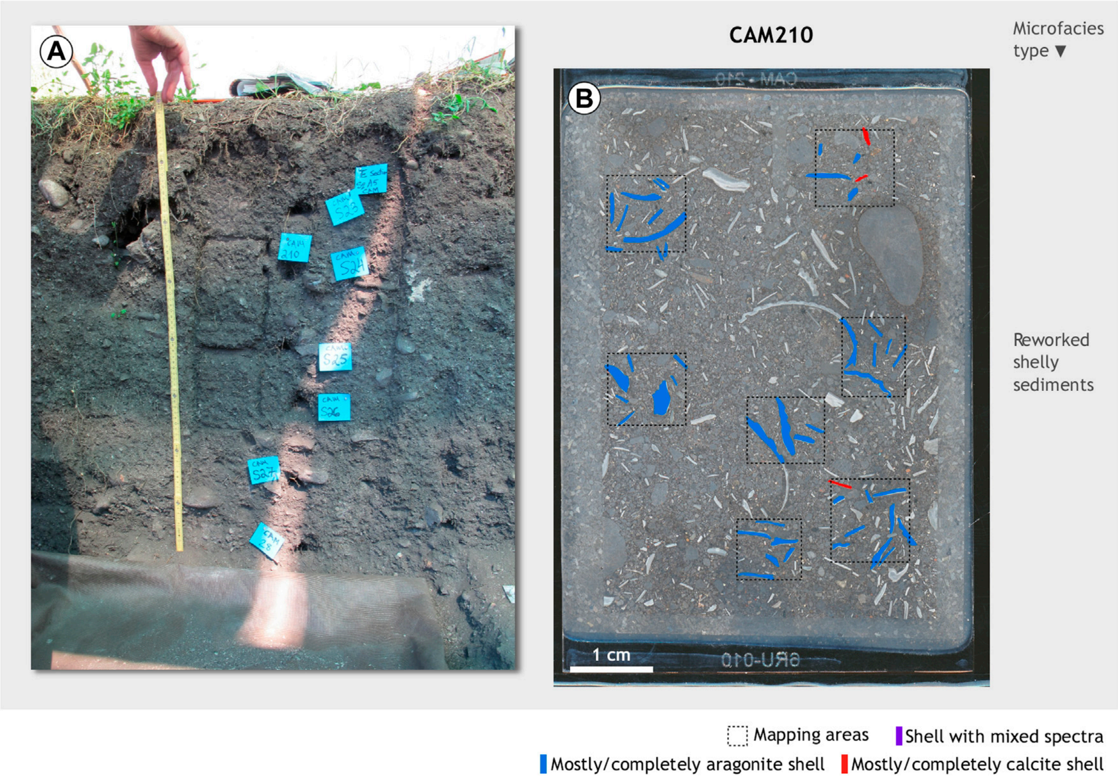

FIGURE 8
Sample CAM210: **(A)** Field photograph of the sample in profile, prior to block extraction. **(B)** Thin section scan of the samples showing individual shells' overall mineralogy obtained through microFTIR.

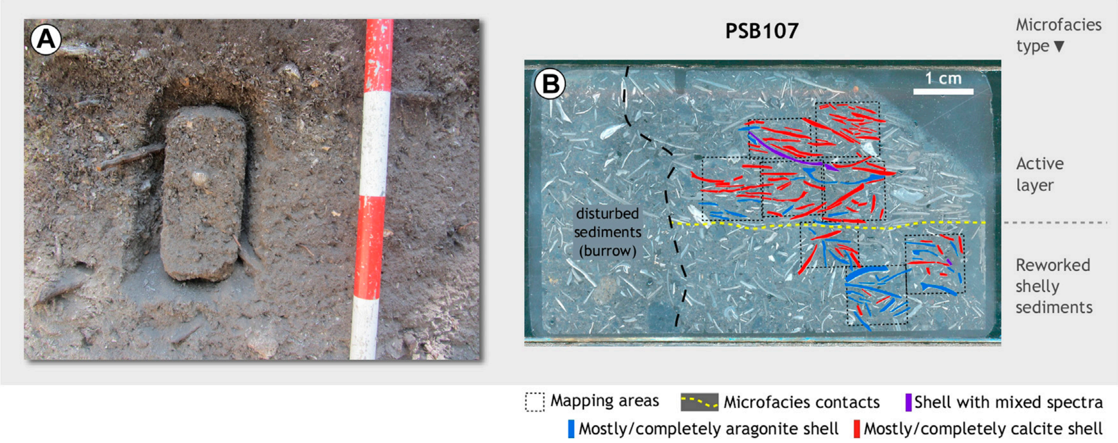

FIGURE 9
Sample PSB107. **(A)** Field photograph of the sample in profile, prior to block extraction; note the general homogeneity that the shelly deposit exhibits in the field, though different depositional and postdeposional events are revealed by microstratigraphy and mineralogy. **(B)** Thin section scan with individual shells' overall mineralogy obtained through micro FTIR.

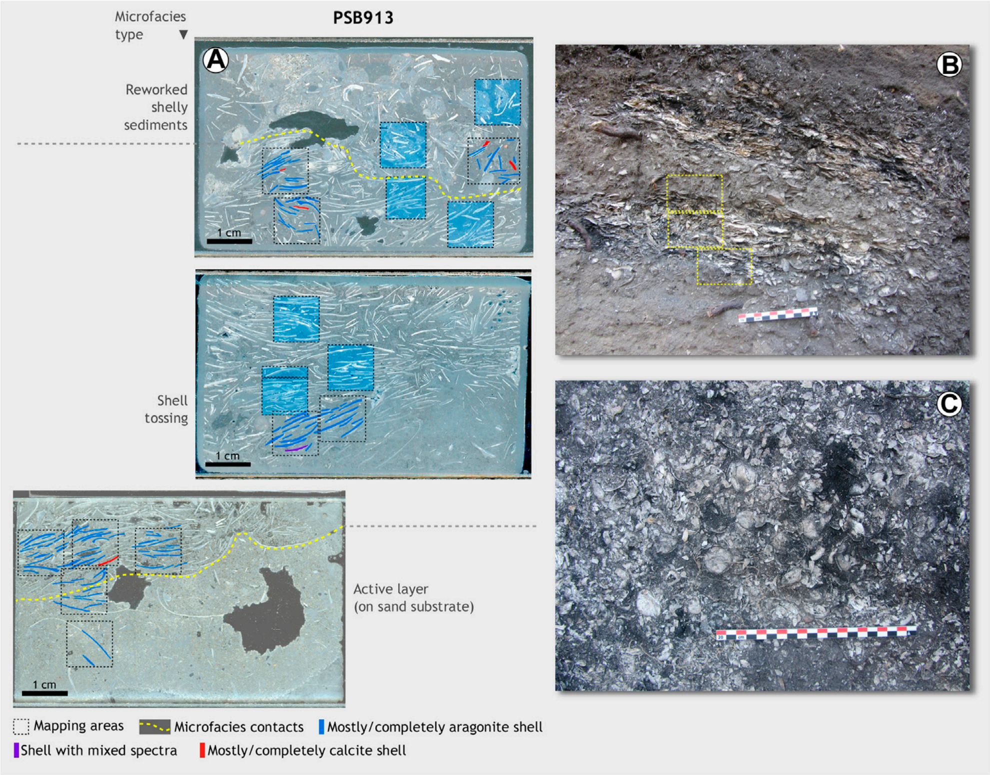

FIGURE 10
Sample PSB913. **(A)** Scans of three thin sections produced from the sample, showing individual shells' overall mineralogy obtained through micro FTIR; rectangles with bluish filter indicate that all shells in the map are aragonitic. **(B)** Close-up of the field profile with the direct tossing deposits and reworked deposits interstratified; note the absence of heated substrate or any containment features for combustion; the dashed yellow rectangles indicated the approximate provenience of the thin sections. **(C)** Plane aspect of the direct tossing deposit interpreted as immediate discard of roasting residues; note the abundance of charcoal and the integrity of shells that in general revealed no mineralogical thermal alteration.

Another cause for aragonite-calcite recrystallization in shells is biological post-depositional activity induced by microorganisms that feed on the shells' carbonate through micro-boring (James and Jones, 2015). These originate secretion of micritic calcite within micro-tunnels that, with time, replace entirely the skeletal clast microstructure. We can rule out this agent in our archaeological shells, since no micro-boring is observed in thin section, as shells preserve larger crystals in their different layers. Biologically induced calcite at both sites was observed too, in the form of alveolar septal and needle fabric cements hardening some layers, usually at the bottom of the shell mounds, where shells are still well preserved (Aldeias and Bicho, 2016; Duarte et al., 2019).

In our specimens experimentally heated between 250 and 450°C, microFTIR yielded aragonite, calcite and mixed spectra (Figure 3). The previous FTIR-ATR experiments by Aldeias et al. (2019) showed the existence of a mixed stage during the temperature threshold in powdered shell material. Here, the

TABLE 3 Shell mineralogy in each type of microfacies per thin section.

	CAM109	CAM112	CAM206	CAM210	PSB107	PSB913
Direct single tossing	Aragonite	Fully aragonitic at the bottom, grading into fully calcitic at the top	—	—	—	Aragonite, very few calcite
Reworked shelly sediments	Mostly aragonite, with very few calcite and mixed	—	Aragonite, calcite and mixed	Mostly aragonite, with few calcite and mixed	Aragonite and calcite	Aragonite, very few calcite
Active layers	Aragonite	—	Calcite	—	Mostly Calcite with few aragonite	Aragonite

coexistence of areas where aragonite remains unchanged and others where aragonite was completely converted to calcite in the same shell was revealed by microFTIR mapping. This evidence shows that the aragonite to calcite conversion within a same shell can be heterogenous (Figures 3, 4). The reason for this is unknown, but we can tentatively suggest that it might be related to the different aragonite crystal microstructures that constitute each layer of these bivalves. Different crystalline microstructures had been demonstrated to react differently to temperature increase (Milano et al., 2016). Our experimentally heated shells showed that the complete calcite conversion starts from the inner surface and progressively expands to the outer surface in all shells of both species, as exemplified in Figure 4. This suggests a correlation with the different microstructures in the shell layers but needs future targeted research to be confirmed.

Experimental studies on infrared spectra with aragonite and calcite shows that mixtures of both polymorphs is discernable in the ν_2 and the ν_3 peaks of CaCO3 where the relative intensities correspond to the predominance of one over the other (Loftus et al., 2015; Toffolo et al., 2019). We observed spectra with these different relative peak intensities in our experimental heated shells (e.g., Figure 4), indicating variable proportions of both aragonite and calcite phases in the measured point in the shell. Therefore, the aragonite-calcite conversion by heating occurs heterogeneously and at different temperatures in each species. The coexistence of aragonite, mixed aragonite-calcite, and calcite spectra in the same shell, was also observed in the archaeological thin sections (Figure 5), a correlation that strongly suggests a thermal cause for their CaCO3 phase conversion.

Thus, we assume that the recrystallization in the archaeological shell middens analyzed here was not cause by diagenetic processes. This is further supported by the preservation of shell's aragonite, which strongly indicates preservation of the original ontogenically precipitated aragonite, thus absence of major diagenesis (Weiner, 2010). Furthermore, a diagenetic cause for the conversion is incompatible with the existence of aragonitic and calcitic shells in deposits at different depths throughout the sites' lateral stratigraphies. All these factors strongly indicate that the aragonite-calcite conversion in the archaeological shells analyzed here is caused by thermal alteration related to fire use by humans at the sites.

Tracing depositional histories through mineralogical alterations

Previous micromorphological analysis of these shell middens distinguished several different deposition modes that include: direct single-tossing events of shells, reworked load-dumped shelly deposits, and active layers interpreted as occupational surfaces (see Aldeias and Bicho (2016) and Duarte et al. (2019) for details). In this work, we add data on shell's *in situ* mineralogical composition to the microfacies analysis.

Our results show that aragonitic shells predominate in microfacies related to reworked shelly deposits. These reworked deposits result, almost exclusive, from accumulation of *S. plana* specimens, thus indicating that most shells were not subjected to temperatures above 250°C. Therefore, it is more plausible to assume that most reworked deposits are composed by shells generally not subjected to high temperatures (i.e. above 250-350°C) before their deposition. Only in thin section CAM206 aragonite and calcite occur in similar proportions (Figure 7). In this case, about half of the measured shells were exposed to temperatures above 400°C prior to being reworked. The fact that heated shells are still in close association to each other, but not in their primary position, could be indicative of a low degree of mixing, or a reworking within smaller distances. The occurrence in the same microfacies of other components, namely large charcoals and pebbles (Figure 7), further supports this hypothesis, and is in contrast with the lack of charcoals associated with fully aragonitic shells in other reworked deposits analyzed. The fact that shells in CAM206 deposit are very fragmented can be a consequence of heating, which makes shells more brittle, and not necessarily intense reworking.

The microfacies interpreted as having functioned as surface active layers, thus subjected to physical pressure due to intense occupational activity and trampling, showed different cases of shell mineralogy. The shells within the active layer represented in CAM206 are fully calcitic and supported by a charcoal-rich matrix (Figure 7). In PSB107, the shells in a trampled layer are also fully calcitic (except rare aragonitic ones) (Figure 8), but here no charcoals are present in the matrix. These active layers, unlike reworked deposits, do not show mixing of aragonite and calcite polymorphs, indicating that heating in active layers might be syn-depositional, thus related to the occupation activities responsible for their formation. In turn, CAM109 and PSB913 represent occupational debris not affected by high temperatures, thus fire activity was more limited in its formation, as anticipated by the lack of other charred components.

Micro-stratigraphic shell mineralogy suggests that the trampled shell debris in CAM206 resulted from occupation activities involving fire, strong enough to burn shells, although not *in situ*, but resulting from short-distance dispersion originated by occupation actions such as trampling or sweeping. In sample PSB107, regardless of the microstratigraphic contact between the active layer and the reworked shelly deposit, the thermal alteration of the shells exhibits a gradual vertical pattern through that contact, better observed in CAM112, as discussed below.

Differentiating cooking from burning

Ethnographic accounts suggest that shellfish cooking does not require high temperatures or long exposures to fire, since the main goal is to open the valves and retrieve the eatable mollusk without burning it (Meehan, 1975; Waselkov, 1987). These sources describe that most techniques used for cooking shellfish imply roasting by simply exposing the shellfish to hot embers. The roasting experiments of Aldeias et al. (2019) basically generate aragonitic shells that experience temperatures always below 200°C, which agrees with other experiments (Müller et al., 2017). However, Aldeias et al. (2019) noticed some exceptions in the case of roasting with fire above or directly on embers. With these cooking methods, localized hot spots may entail the exposure of individual shells to temperatures higher than 200°C, producing spatially concentrated conversions to calcite. Still, most shells cooked this way remain aragonitic. Therefore, both ethnographic and experimental data point to low temperature exposure of shellfish, even when using roasting techniques. Thus, archaeological specimens cooked this way should retain their aragonitic structure. Archaeological assemblages of shells exposed to temperatures above 450°C, showing a complete conversion to calcite, are difficult to explain as resulting from cooking and require other explanations. In turn, this raises the question of how can we infer cooking shellfish in archaeological sites?

Contextual data from micromorphology helps in identifying deposits in primary position and is thus optimal to look for traces of activities that formed them. In our studied thin sections, examples of deposits in primary position consist in those formed by direct single tossing of shells and likely relate to the immediate discard of the shell right after the consumption of the mollusk. The mineralogy of tossing deposits analyzed by microFTIR mapping present twofold situations. In samples CAM109 and PSB913, shells within direct tossing deposits are fully aragonitic, with very residual calcitic ones in the latter (Figure 10). The bulk of these deposits are composed of *S. plana* specimens, with the retention of an aragonitic mineralogy clearly indicating that, when tossed away, the shells were probably not heated to temperatures higher than 350/400°C and definitely not above 450°C.

The deposit in sample CAM112 showed a completely different situation. Here, the mineralogical analysis revealed a gradient, with a progressive conversion of aragonitic to calcitic shells as we move upwards in the deposit (Figure 5). This suggests that the shells in the upper part of CAM112 were affected by homogenous heating at higher temperatures, that progressively decreased downwards. As this sample is composed almost entirely by *S. plana*, the palaeotemperature experienced by the shells in the deposit can be more precisely pinpointed (Figure 5). The mixed spectra of the lowest shells shows exposures to temperatures mainly below 350°C, with some shells heated to above 400°C. Above this area, all shells are calcitic (that is, heated to more than 450°C). This vertical gradient strongly suggests that the aragonite-calcite conversion occurred *in situ*. Since the integrity of the deposit has not changed, this evidence is better understood not as the result of cooking of that specific shellfish but interpreted as the effect of a later fire placed on top of the shell tossing deposit. Therefore, the sequence of events would have been an action of discarding shellfish followed by an unrelated fire activity in this locale. No significant charcoals are observed in CAM112, which supports the hypothesis of this deposit having functioned as a combustion substrate. A similar interpretation of burning–and not cooking–can be applied to the gradient conversion observed in PSB107 (Figure 9), where the burned shells were subsequently affected by trampling, causing structural compaction, and crushing.

Our expectations for prehistoric shellfish roasting in the archaeological record involve the presence of mainly aragonitic shells alongside combustion remains, such as abundant charcoals and ashes, which may not preserve the typical microstratigraphy of *in situ* fires (Table 1). A set of evidence such as this was identified in superimposed deposits represented in sample PSB913 (Figure 10). Spatially, this feature resembled an intact combustion feature, however, after micromorphological analysis, the components here were interpreted as related to direct single tossing event of abundant charcoals and well-preserved shells (Figure 10). The microFTIR mapping revealed fully aragonitic shells in these deposits, with residual exceptions. This led us to consider this context a result of immediate discard of debris directly from roasting activities. The occurrence of few shells that have experienced exceptionally higher temperatures due to localized hotspots occurring in roasting features confirms the expectation formulated in the experiments by Aldeias et al. (2016).

Implications for prehistoric shellfish cooking and archaeological site formation

In our approach, micromorphology coupled with microFTIR mapping allowed us to overcome two issues raised by previous works on shellfish cooking. The fact that aragonite-calcite conversion occurs above the burning threshold makes mineralogy by itself not suited to detect pre-depositional heating (Müller et al., 2017). Our investigation shows that, with contextual control and spatial and micro-stratigraphic precision, mineralogical alterations can be useful not only to infer pre-depositional heating, but also for distinguish it from *in situ* heating.

Staudigel et al. (2019) applied clumped isotopes to specifically distinguish boiling from roasting. They found that a "nonuniform distribution of Δ47 values between shell midden constituents suggests a nonuniform thermal history for shell midden constituents" (Staudigel et al., p. 4), in agreement with data obtained by Müller et al. (2017). Both studies conclude that this may be an effect of the technique used for cooking that consisted either in using only one of the valves or heating the entire bivalve from below, causing an uneven heating of valves, being the lower one significantly more affected than the top. Our results concur that boiling was unlikely and that roasting might have been a preferential cooking technique in the absence of hot stones or organic containers. This is suggested by the existence of some shells heated above 450°C, hence fully calcitic, among unheated shells and charcoals in the remains of interpreted roasting activity (Figure 10). With boiling, one would expect no mineralogical change at all in shells mineralogy (Milano et al., 2016; Milano et al., 2018). Staudigel et al. (2019) raise several effects specific of shell midden formation that hamper interpretation of pre-depositional heating, such as the discarding of uncooked shells, different thermal histories for different shells, or cooking techniques where heating is unevenly distributed. Our approach, by including micromorphological analysis that allow to study the thermal history of shells in their undisturbed archaeological context, considerably overcomes these limitations. We advocate for future integration of the contextual data from sedimentary microfacies to discern cooking from burning in the archaeological record.

Conclusion

Micro-stratigraphically controlled mineralogy proved to be particularly useful to distinguish between pre-depositional heating from *in situ* heating, configuring a novel methodology for recognition of traces of cooking shellfish versus traces of fire used for other purposes. One of the strengths of this approach was enabling the identification of *in situ* fire events that were invisible in the macroscopic archaeological record lacking structural features containing them, by mapping the mineral phase conversion stratigraphically. This advantage, combined with the potential of distinguishing between (primary and reworked) depositional events related to shelly sediments and post-depositional events related to fire use, considerably increases our capacity of deciphering intricate shell midden stratigraphy and occupational events.

Future work combining micromorphology and *in situ* mineralogy mapping would benefit from integrating other shellfish species and exploring contexts with evidence of *in situ* fires, such as features structured with pebbles, since ashes are rarely found in open-air shell middens and charcoals easily disperse. The combined micromorphological and mineralogical approach to originally aragonitic shells from such contexts would perhaps elucidate if the shells immediately below and above fire features are burnt or not, to infer pre-depositional heating of the combustion substrates. If it is only in the combustion-related layers that shells are burnt, it could perhaps relate to tossing shells to an active burning fire for other purposes than cooking them and correlate with the array of cultural activities documented in prehistoric shell middens. The application of the methodology we propose is not limited to shell middens, on the contrary, it has a high informative potential in any prehistoric context that contains shells mineralized as aragonite and subjected to burning to better characterize their depositional and pre-depositional thermal histories.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

VA designed the study, CS carried out the analysis and both equally contributed to data interpretation and writing the manuscript.

Funding

CS is currently funded by the European Union's Horizon 2020 research and innovation programme through a MSCA Widening Fellowship under Grant Agreement nr. SEArch–101003409, and during the early stages of this research by a doctoral fellowship BES-2012-053695 granted by the Spanish Government. VA is funded by the Portuguese Fundação paraa Ciência e Tecnologia (FCT), grant numbers PTDC/HAR 20 ARQ/29606/2017 and IF/01157/2015/CP1308/CT0002. Research at Cabeço da Amoreira was funded by FCT projects PTDC/HAH/64185/2006) and PTDC/HIS-ARQ/112156/2009 awarded to Nuno Bicho (University of Algarve). Research at Poças de São Bento was funded by the Spanish Government grants HAR2011-29907-C03-00 and HAR2014-51830-P, both awarded to PabloArias (University of Cantabria) and by FCT through grant PTDC/HIS-ARQ/121592/2010 awarded to MarianaDiniz (Universidade de Lisboa). Open Access to this article is financed by FCT—Fundação para a Ciência e a Tecnologia, within the scope of the project ICArEHB UIDP/04211/2020 IHC PROGRAMATICO.

Acknowledgments

We wish to thank Nuno Bicho, Mariana Diniz and Pablo Arias, the directors of the field research at the archaeological sites where the samples used in this study were obtained, for allowing us to use the field data and for comments on the manuscript; Raquel Maria for the training and helping CS in the microFTIR preliminary tests, conducted at the Max Planck Institute for Evolutionary Anthropology; and José Paulo da Silva for support in technical issues with the FTIR microscope at Algarve Centre of Marine Sciences (CCMAR) used to obtain the data presented in the paper. We would also like to especially thank Shira Gur-Arieh, who was involved in the shell experiments reported previously, and the reviewers whose comments helped improving the manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.869487/full#supplementary-material

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 01 September 2022
DOI 10.3389/feart.2022.941911

Soils and terrestrial sediments on the seafloor: Refining archaeological paleoshoreline estimates and paleoenvironmental reconstruction off the California coast

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On global, regional, and local scales, sea level histories and paleoshoreline reconstructions are critical to understanding the deep history of human adaptations in island and coastal settings. The distance of any individual site from the coast strongly influences decisions about the transport of coastal resources and has a direct impact on human settlement and resources procurement strategies. Our ability, then, to identify relic productive habitats, such as wetlands, that were subaerial during time periods relevant to human occupation, is critical to models of human settlement and resource patterning that guide our search to identify cultural resources. Accurate location of productive habitats becomes more critical when searching for terminal Pleistocene sites submerged by postglacial marine transgression. While paleoshoreline reconstructions and sea level histories can provide a baseline for identifying drowned and ancient coastal ecosystems, post-transgressive sediment deposited on the seafloor can skew accurate paleoshoreline location. To correct for this, we used sub-bottom profiling data from the southern California Coast to determine revised paleoshoreline locations and to identify sonar signatures indicative of paleogeographic contexts that may harbor wetland environments. These data were used to define core sample locations that resulted in the identification of submerged, preserved paleosols. The paleosols data, presented here for the first time, have provided information on ancient landscapes and relic habitats that were subaerial prior to postglacial sea level rise. In our study area on the continental shelf off the California Channel Islands archipelago, the paleosols correspond to a critical period of shifting

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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 12 May 2022
ACCEPTED 11 July 2022
PUBLISHED 01 September 2022

CITATION
Gusick AE, Maloney J, Braje TJ, Retallack GJ, Johnson L, Klotsko S, Ainis A and Erlandson JM (2022), Soils and terrestrial sediments on the seafloor: Refining archaeological paleoshoreline estimates and paleoenvironmental reconstruction off the California coast.
Front. Earth Sci. 10:941911.
doi: 10.3389/feart.2022.941911

habitats, evolving landscapes, species extinctions, and the arrival of humans into a rapidly changing ecosystem.

KEYWORDS

paleolandscape, paleoecology, marine archaeology, paleosol, terminal Pleistocene, Early Holocene

1 Introduction

The Pleistocene-Holocene transition and the preceding millennia were turbulent periods worldwide. The end of the last glacial cycle was ushered in ~20,000 years ago with a warming climate, melting glaciers and ice sheets, rising seas, and reemerging habitats adjusting to the thaw. Globally, the ten millennia following the Last Glacial Maximum was a time of human dispersal into, and adaptations to, new and changing landscapes. This was particularly true for the coastal regions of the Americas. Beginning at least 14,000 years ago, but potentially several millennia earlier (Dillehay et al., 2008; Dillehay et al., 2012; Erlandson et al., 1996; McLaren et al., 2018), *Homo sapiens* settled across these coastal regions, taking advantage of thriving marine and coastal ecosystems. That coastal habitats harbor some of the earliest evidence for habitation in the Americas should come as no surprise. Ocean and coastal ecosystems and the habitats and resources they support have been intertwined with the human story for over 100,000 years. Whether providing food for subsistence (Singer and Wymer 1982; Cortés-Sánchez et al., 2011; Marean et al., 2007; Steele and Álvarez-Fernández 2011), seagrasses and seaweeds for twine (Connolly et al., 1995), shells for artistic expression (Joordens et al., 2015), or dispersal routes into new lands (Erlandson 2001; O'Connor et al., 2011; Erlandson and Braje 2015), aquatic spaces have impacted both the biological and cultural development of our species (Henderson 2019). The deep time history of these spaces make them integral for understanding our past.

Clarifying the role that coastlines played in the millennia after the last glacial cycle is complex. As ice sheets melted and seas rose, over 9.5 million km^2 of land was inundated from 20,000–6,000 years ago (see Dobson 2014). In some regions not completely submerged, the amount of land lost to sea level rise is equal to or greater than the subaerial landscape of today; the islands in the Southern California Bight (SCB), a geographic region extending from Point Conception to San Diego in Southern California (Figure 1), are a prime example. The amount of inundated paleolandscape in this region is a key factor in considering coastal social science research focused on the time period during eustatic sea level rise. Rather than honing efforts only on the subaerial portion of the landscape, the regional seascape must also be considered an integral factor in coastal archaeological research. By integrating data from the land- and sea-scape, researchers consider a maritime cultural landscape (Westerdahl 1992), that deemphasizes a modern waterline divide that has shifted through time. The recognition that landscapes and seascapes shift over time and associated habitats are not static, is critical to understanding human-environmental dynamics and interactions (Ford 2011). The importance of maritime cultural landscape studies that consider submerged paleolandscapes is particularly salient in the SCB, which holds some of the earliest evidence for human use of coastal resources in the Americas (Erlandson et al., 2011; Gusick and Erlandson 2019), but has been significantly impacted by post glacial marine transgression.

The impact of postglacial submergence is acutely evident when considering Santarosae, a maritime cultural landscape located within the SCB. Santarosae includes the subaerial Northern Channel Island (NCI) landmasses and the continental shelf that surrounds them. Early human habitation on these islands is apparent in the 20 or so archaeological sites dating to 11,000 cal BP and earlier identified on the subaerial landscape (Gusick and Erlandson 2019). Directly after ~11,000 cal BP, there is evidence for a growing population on the islands (Braje et al., 2020), with over 120 sites dating to the Early Holocene (11,000–8,000 cal BP). The variation in number between the terminal Pleistocene and Early Holocene sites on Santarosae suggest that many more pre-11,000 cal BP sites are present on the more than 200 km^2 of land submerged after the Last Glacial Maximum. To search for evidence of a more extensive terminal Pleistocene occupation, and to clarify the timing of habitation in the region, researchers must consider the maritime cultural landscape of Santarosae and integrate what is known from the current subaerial portion of the landscape with the submerged paleolandscape. Important in this endeavor is identifying areas on the continental shelf that present preservation potential. While modelling can help focus research on areas that likely contain preserved sections of the terminal Pleistocene subaerial landscape, actual identification of preserved paleosols through sampling is critical to reconstructing past landscapes and environments and possibly identifying preserved terminal Pleistocene archaeological sites on the continental shelf. Because paleosols form on past landscapes, they can be analyzed to reconstruct the paleoenvironment present during their formation. Submerged preserved paleosols are also markers of sections of the ancient landscape that survived marine transgression intact. This is particularly important in areas such as the SCB where high tidal and wave energy erode the continental shelf, destroying any archaeological sites it may have contained.

The SCB, and Santarosae in particular, has been a primary focus of submarine mapping and coring efforts of the Archaeological and Biological Assessment of Submerged Landforms off the Pacific Coast project (Braje et al., 2021). Funded by the Bureau of Ocean Energy Management, this broad and multidisciplinary study occurred from 2012–2020 and included submerged landscapes around the

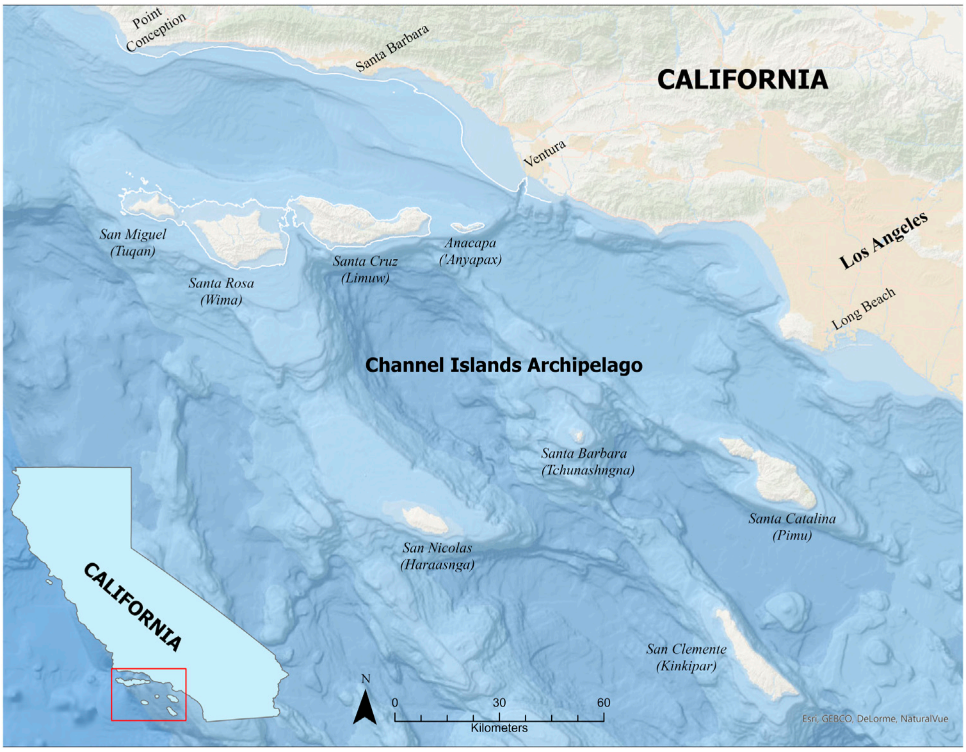

FIGURE 1
Map of the northern portion of the Southern California Bight and the Channel Islands archipelago showing both the southern and northern groups. White boundary around the NCI is the 70 m isobath showing the general extent of Santarosae and the adjacent mainland ~13,000 years ago.

NCI and off the coast of Oregon. Project partners included federal agencies, universities, museums and tribal nations and included a variety of specialists ranging from archaeologists to, marine geologists, marine biologists, marine geophysicists, and tribal knowledge caretakers. Designed to better understand the paleoenvironment and paleolandscape of Santarosae, this project included initial data synthesis of archaeological and environmental records combined with geological and geomorphic seabed data to develop a model to guide field research (Braje et al., 2021). Areas selected for the field investigation had a high likelihood of preservation of cultural material and/or may present paleolandscapes or paleohabitat data to help clarify the extent of land and the nature of terminal Pleistocene-aged Santarosae. Field investigations included broad-scale sonar survey for submerged paleolandscape characterization followed by tightly gridded sonar surveys from which core locations were selected. Twenty-six cores were collected from the submerged landscape of Santarosae and preserved paleosols were identified in three of the core samples. This is the first known collection of preserved paleosols from the submerged section of Santarosae and they have provided data to consider the evolution of the paleolandscape and the paleoenvironment that existed on the island prior to its partial inundation. The identification of the preserved paleosols is a critical development in the ongoing efforts to identify regions where archaeological sites may be preserved on submerged landscapes in the SCB.

2 Materials and methods

2.1 Study area

The NCI are part of the 257-km-long Channel Islands archipelago located in the SCB (Figure 1). The eight islands that form the chain are typically divided into two groups: the southern Channel Islands, Santa Barbara (Tongva name: *Tchunashngna*), San Clemente (*Kinkipar*), San Nicolas (*Haraasnga*), and Catalina (*Pimuu'nga*); and the NCI, San Miguel (Chumash Name: *Tuqan*), Santa Rosa (*Wima*), Santa Cruz (*Limuw*), and Anacapa (*'Anyapax*). These islands have the cool wet winters and warm summers typical of the Mediterranean climate in Southern California, which supports a surprising richness of vascular plants (Gill et al., 2019). The Channel Islands archipelago is in one of five world regions with Mediterranean-type ecosystems—California, Central Chile, the Mediterranean Basin, the Cape Region of South Africa, and

Southwestern and South Australia—that collectively cover only about 2 percent of the world's landmass, but comprise 20 percent of the world's vascular plant species (Esler et al., 2018). The marine ecosystems within these regions also tend to be rich, making them ecological "hot spots" that have long been attractive for human habitation. The waters surrounding the NCI contain a rich marine ecosystem supported by seasonal nutrient rich upwelling and extensive kelp forests (Graham et al., 2009; Erlandson and Braje 2015). This combination supports a biodiversity that is among the richest in the world (Steneck et al., 2002), where kelp forests support shellfish, fish, marine mammals, sea birds, and seaweeds. This region is part of the proposed "Kelp Highway" that extends from Japan to Baja California where the richness of kelp forest resources may have supported a terminal Pleistocene coastal migration of humans into the Americas (Erlandson et al., 2007).

The NCI are located in the western Transverse Ranges Province. This physiographic province is restrained on the west by the Big Bend in the San Andreas Fault, resulting in transpression and associated faulting and folding, and creating a structural orientation that is more east/west than the typical northwest/southeast structural trend of the Pacific-North American plate boundary (Atwater, 1987). While the landscapes of the four islands vary, coastal areas on the islands are characterized by rocky shores and sea cliffs, separated by sandy pocket beaches and dunes (Schoenherr et al., 2003). These coastal areas transition into emergent marine terrace and mountainous areas with varying topography among the islands. The marine terraces on the NCI have a long history of study, and formed through a combination of uplift and oscillating sea level through glacial and interglacial stages of the past two million years (Muhs et al., 2014). During periods of relative sea level stability, broad, and gently seaward dipping abrasion platforms were created by wave-base erosion at the coastline. On uplifting margins, the abrasion platforms created at sea-level highstands can be preserved above sea level, forming the step like landscape, with broad flat marine terraces that characterize the California coast and the NCI (Sorlien 1994; Dickinson 2001; Pinter et al., 2003; Muhs et al., 2014). Abrasion platforms created at times of lower sea level have been submerged by rising seas, but their morphology may be preserved (Klotsko et al., 2015), and several have been identified in geophysical data surrounding the NCI (Emery 1958; Chaytor et al., 2008; Laws et al., 2019). These submerged platforms can record the history of coastal landscape and paleoshoreline changes around the islands.

Around the NCI, there are five submerged abrasion platforms between ~15 and 130 m below sea level (mbsl) evident on bathymetric profiles (Emery 1958). More recently, Chaytor et al. (2008) used high-resolution multibeam bathymetry to map five submerged abrasion platforms at depths ranging from ~22 to 90 mbsl offshore from Santa Cruz Island. If ancient shorelines on these terraces are preserved, they can be identified by an increase in slope on the landward edge of the wave-cut abrasion platform. The base of the slope is known as the shoreline angle, and represents the location of a preserved ancient shoreline. The locations and dates of these paleoshoreline angles are critical in clarifying proposed relative sea level rise and uplift rates, which informs understanding of paleolandscape formation (Lambeck et al., 2002; Chaytor et al., 2008; Muhs et al., 2014; Laws et al., 2019). This is particularly important because sea level rise following the last deglaciation significantly transformed the offshore landmasses. Although never connected to the mainland, the NCI once formed a super island called Santarosae located ~7 km from the mainland continental coast at the end of the last ice age (Orr 1968). Chumash descendant and linguistic scholar Matt Vestuto has suggested a Chumash name for Santarosae, Shamalaḿa, meaning "it was one." As glacier meltwater poured into the oceans starting around 20,000 years ago, sea level rose 100–110 m until stabilization about 7,000 years ago (Clark et al., 2014). During this massive sea level rise, roughly 75 percent of the landmass of Santarosae was inundated, severing the land bridges between the islands and creating the four NCI present today. The inundation of the archipelago affected shoreline length and island size, greatly restructuring marine habitats, and significantly increasing the distance between the NCI and the mainland (Kinlan et al., 2005; Reeder-Myers et al., 2015). The timing of this inundation is significant as it occurred during a period relevant to human dispersal onto the island.

Human remains dated to approximately 13,000 years old were identified in 1959 on northwestern Santa Rosa Island in Arlington Canyon (Orr 1962; Johnson et al., 2002), and represent the oldest remains identified to date on the Pacific Coast of the Americas. Far from being an isolated case of early occupation, the subaerial remnants of the partially submerged Santarosae contain some of the most extensive evidence for Paleocoastal occupation (13,000–8,000 cal BP) in the Americas (Erlandson et al., 2011; Gusick and Erlandson 2019). More than 120 Paleocoastal sites have now been recorded on the NCI, including more than 11 that have material radiocarbon dated to 11,000 cal BP and older, and at least 19 additional sites that have no organic datable material, but contain diagnostic technology suggesting a probable terminal Pleistocene age (Braje et al., 2013; Braje and Erlandson 2008; Erlandson et al., 2008; Erlandson et al., 2016; Rick, 2008; Rick, 2009; Rick et al., 2005a; Rick et al., 2013; Rick and Erlandson 2012). The peoples who arrived on Santarosae prior to 11,000 years ago would have adapted to one large landmass with abundant pines and numerous streams and wetland environments transitioning into sandy beaches, rocky shores, and productive intertidal and subtidal habitats. As seas rose and inundated the land bridges between the islands during the Pleistocene-Holocene transition (Reeder-Myers et al., 2015) the changes to regional coastal ecology would have been significant with shifting intertidal to subtidal habitats, inundation of river valleys, and flooding and shifting of estuaries and lagoons (Masters and Aiello 2007:40). Today there are no extant estuaries on the NCI, but archaeological evidence suggests that estuaries were present during times of lowered sea levels and were exploited by island groups (Erlandson 1994; Erlandson et al., 2011; Rick et al., 2005b; Erlandson et al., 2019).

2.1.1 Santa Cruz Passage and Crescent Bay

The Santa Cruz Passage is the body of water between Santa Cruz and Santa Rosa islands. This portion of the drowned landscape of Santarosae has been a focus of efforts to document the paleolandscape and paleoecological transitions that occurred when rising seas inundated this region. The margins of this passage, represented by the currently subaerial landscapes of western Santa Cruz and eastern Santa Rosa islands, hold clusters of Paleocoastal sites (Gusick, 2012; Gusick, 2013; Erlandson et al., 2016; Erlandson et al., 2019; Gusick and Erlandson 2019; Gill et al., 2021). The entire roughly 15 km span between the current shorelines on the margins of the Santa Cruz Passage was subaerial until ~11,000 years ago, with broad plains traversed by several large drainages that likely formed a mix of wetland habitats and sandy beaches. The biological richness in these habitats are hot spots for human exploitation, replete with abundant shellfish, sea birds, waterfowl, and pinnipeds. Considering the paleogeography of this region along with the Paleocoastal sites led Erlandson et al. (2016) to identify a large south-facing, semi-protected paleo-embayment in this region that he dubbed Crescent Bay. Several of the largest drainages on Santarosae likely flowed into this large (~8 km wide) embayment and then into the large offshore Santa Cruz Submarine Canyon (see Figure 3). Recent research suggests that this area also contained a paleovalley (Maloney et al., 2017; Johnson 2020) and the semi-protected nature of Crescent Bay—protected from the dominant winds and swells that battered the north coast of Santarosae—provides a setting where submerged archaeological sites are most likely to have been protected from marine erosion as sea levels rose. It is clear that one or more estuaries existed around the margins of Crescent Bay, the only examples known from California's Channel Islands. Two shell middens (CA-SCRI-857 and CA-SRI-708) located above current sea level around the margins of the bay provide some of the earliest evidence for human harvesting of estuarine clams (*Chione* spp.) in North America, between ~11,400 and 11,200 cal BP (Erlandson et al., 2019; J. Erlandson, personal communication, 8 May 2022).

Aside from productive habitats, Crescent Bay may also have been the location of two tar seeps that have been recorded near the western Santa Cruz Island coastline (Roberts 1991; Braje et al., 2005). Asphaltum (bitumen/tar) is a natural substance that has been used by humans for 70,000 years (Boëda et al., 2008), and in this region, there is evidence of its use dating back more than 9,000 years (Erlandson et al., 2008; Hodgson 2004; McCawley 1996; Salwen 2011). Importantly, it was used as an adhesive in technologies, such as hafting projectile points to shafts, and as a water-proofing agent for woven water bottles and watercraft that were integral to the maritime hunter-gathers cultures in the region (Connan 1999; Fauvelle 2014; Oron et al., 2015). Some of the larger known tar seeps on the adjacent mainland have extensive archaeological sites near them (Moore et al., 2007; Gamble 2008), and archaeological sites on the NCI contain evidence of asphaltum use throughout human occupation of the islands (Braje et al., 2005; Brown 2016). Such tar seeps were another resource that made the Crescent Bay area attractive for groups settling the islands in the terminal Pleistocene and earliest Holocene.

The Santa Cruz Passage and Crescent Bay have been a focus of the Archaeological and Biological Assessment of Submerged Landforms off the Pacific Coast project, which to date has resulted in numerous publications and graduate theses (Braje et al., 2019; Braje et al., 2022; Gusick et al., 2021; Johnson 2020; Laws et al., 2019; Tahiry 2019), based off the data generated by both broad and tight-gridded sonar surveys conducted with an Edgetech 512i (0.5–16 kHz) Chirp system. Particularly relevant to the selection of core locations are three studies that clarified paleodrainage morphology and evolution (Tahiry 2019), locations of paleoshorelines and uplift rates (Laws et al., 2019; Braje et al., 2022), and extent of marine sedimentation (Johnson 2020). In the Crescent Bay area off the western coast of Santa Cruz Island, a wide paleovalley (up to ~3.5 km wide and ~16 m deep) was identified within the Chirp data (Figure 2) (Maloney et al., 2017; Tahiry 2019; Johnson, 2020). This paleovalley contained smaller, nested channel features, and was filled with an acoustic unit exhibiting unique signatures consisting of high-amplitude, wavy, sub-parallel, discontinuous reflectors with transparent to chaotic signature between reflectors. This unit was interpreted to be characteristic of fluvial-estuarine deposits, filling the paleovalley feature. Closer to shore the acoustic signature is more chaotic and stratigraphy is difficult to observe. This unique signature is predominately imaged within Santa Cruz Passage, with most of its distribution directly offshore from Santa Cruz Island.

Using these same Chirp data in the section of Crescent Bay near to Santa Cruz Island, Laws et al. (2019) mapped six paleoshoreline angles identified at 39, 40, 41, 59, 60, and 61 mbsl (rounded to the nearest whole number). The identification of paleoshorelines angles is significant as elevation and ages of preserved paleoshorelines on marine terraces can be used to reconstruct sea level, uplift, and deformation histories (Kern and Rockwell 1992; Kelsey and Bockheim 1994; Muhs et al., 2012; Muhs et al., 2014; Haaker et al., 2016), which are commonly used in marine archaeological (and other) research to focus survey where there is a high likelihood to recover target data. For example, based on a glacial-isostatic adjustment model, Clark et al. (2014) suggest the Last Glacial Maximum lowstand was 106 mbsl. Using this sea level curve, researchers may model the extent of Santarosae landmass at that time by identifying the 106 m isobaths that surround the NCI; however, isobaths measures distance from the current sea level to the sea floor. It does not account for post sea-

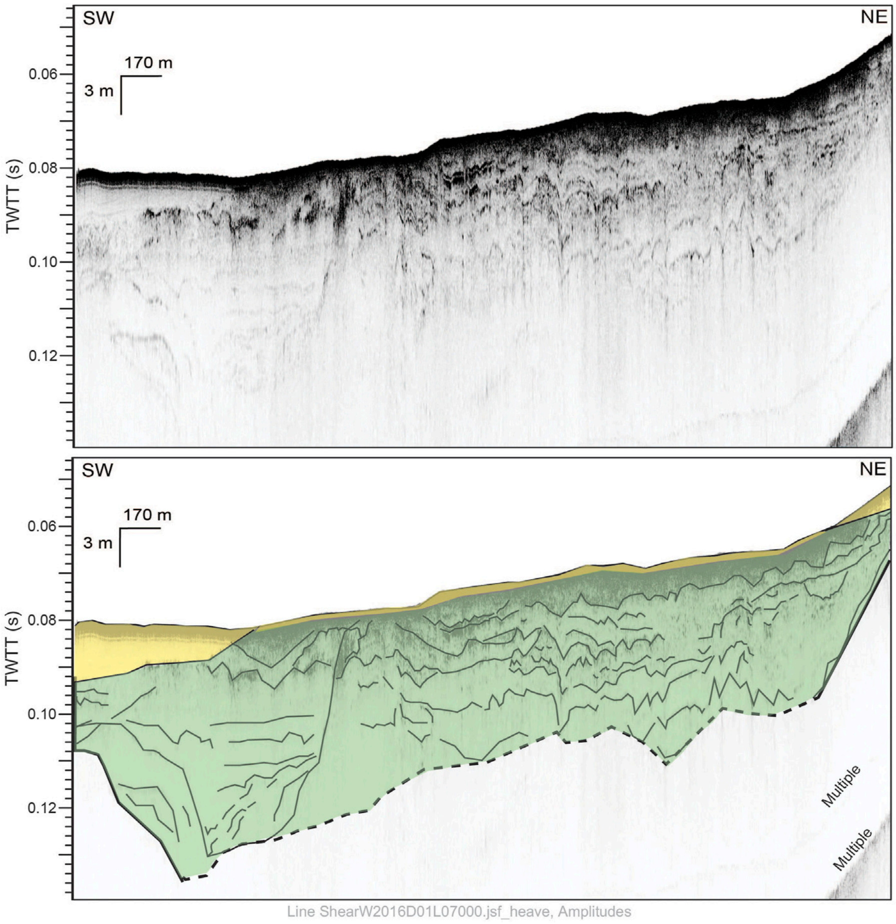

FIGURE 2
Uninterpreted (top) and interpreted (bottom) seismic line from area off Santa Cruz Island where Box 6 is located. Transparent yellow unit is interpreted as marine. Green unit with wavy reflectors is interpreted as terrestrial. High amplitude reflectors are traced in interpretation to show sedimentary structure. See Figure 3 for location (adapted from Johnson 2020).

level rise deposition of sediments offshore, which can be extensive in the SCB region (Erlandson 2021). The marine sediment that lies atop the actual exposed surface that existed during lower sea level (e.g., the subaerial surface) can impact the accuracy of modelled paleoshoreline depth. In fact, results from Laws et al. (2019) suggest that at the Last Glacial Maximum, Santarosae was not as large as predicted using paleoshoreline models from modern bathymetry.

The significance of identifying paleoshorelines angles to update models of paleoshorelines locations and their relevance to identification of submerged archaeological site location is highlighted in Braje et al. (2022). Using the Laws et al. (2019) paleoshoreline angles identified off Santa Cruz Island, Braje et al. (2022) recalculated distance to paleoshorelines, compared to bathymetric models, for sites occupied along the margins of the Santa Cruz Passage. Measuring distance from a cluster of Early Holocene-aged sites (CA-SCRI-547, -549, and -798) dated between ~9,000 and 8,500 cal BP, the 40 m bathymetric contour was 2.44 km further from the sites than the Chirp identified 40 m paleoshoreline angle (Braje et al., 2022; Figure 4C). This suggests that the shoreline during occupation of the sites was significantly closer to the sites than initially modelled. This significant difference in the two modelling methods is likely because this is a geologically complex area, where several large drainages empty into the ocean (Schumann and Pigati 2017). This context may have caused more extensive marine sedimentation that deeply buried the abrasion platform and paleodrainages. When considering archaeological histories and ancient land use in this region, distance to shoreline is significant. Proximity to coastal resources and adjacent productive habits is critical in estimating settlement and subsistence patterns and possible site locations (Erlandson 2001). A variation of 2.0–2.5 km could shift modelling efforts when considering prioritization of habitats, creating an inaccurate model for settlement patterns. When searching on the continental shelf for possible preserved archaeological sites, a

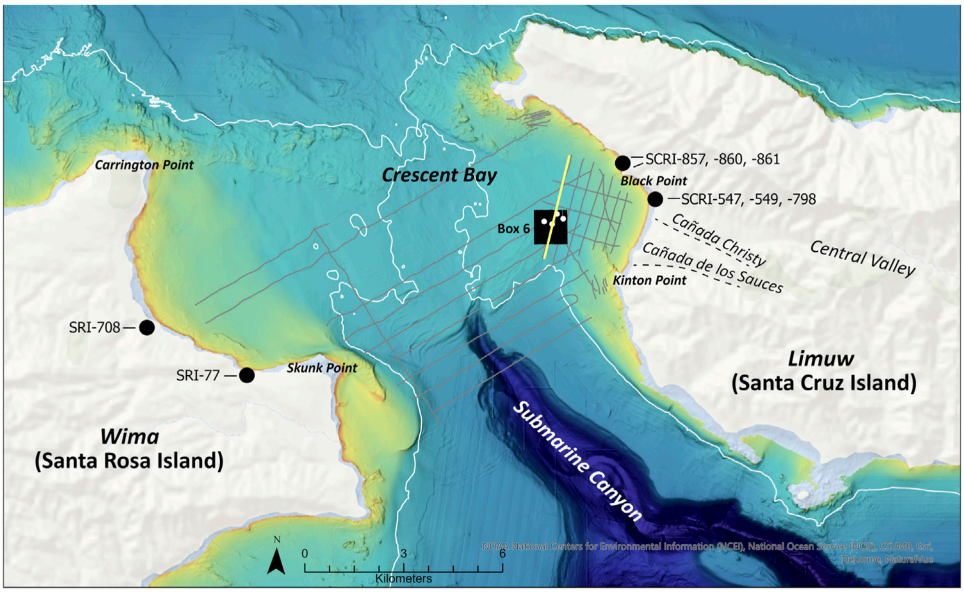

FIGURE 3
Santa Cruz Passage and Crescent Bay research area. Grey lines are transects from broad Chirp survey. Yellow line is the seismic line where the paleovalley was identified (shown in Figure 2). Black lines are the tight-grid spaced Chirp transect within the 1 km^2 box 6. White dots are the core locations within Box 6. Black circles are general locations of archaeological sites mentioned in the text. Dashed black lines indicate locations of canyons mention in text. White line is the 40 m bathymetric contour, showing assumed extent of Santarosae at ~9,000 years ago.

difference of 2.0–2.5 km may result in collection of data that was not subaerial during the time period of interest.

2.2 Methods

The Chirp data analyses described above were critical in selection of core locations. An initial broad landscape survey offshore of the NCI included collection of 65 regional survey lines over ~190 linear km, including 21 sonar lines collected over ~95 linear km within the Santa Cruz Passage. Data were collected from NOAA's R/V Shearwater towing an Edgetech 512i (0.5–16 kHz) Chirp with line spacing varying between 350 and 700 m. The Chirp subbottom profiler provided submeter vertical resolution and ~40 m sub-seafloor imaging. Chirp data were processed using SIOSEIS (Henkart 2006) and Seismic Unix software (Cohen and Stockwell 1999) to remove heave artifacts and adjust gains. Data were imported into IHS Kingdom and ESRI ArcGIS v. 10.5 (www.esri.com) for interpretation. Kingdom was used to calculate layer thicknesses and the depth to acoustic reflectors. A nominal sound velocity of 1,500 m/s was used to convert time to depth.

These initial broad geophysical surveys were used to investigate large swaths of the seafloor and identify features such as paleochannels, canyons, dune fields, paleoshorelines, faults, and terraces, as well as buried geological units. Based on these data, four 1 km^2 areas were selected for targeted, tight-grid spacing (25 m) geophysical surveys. Data were collected from the R/V Point Loma using an Edgetech 512i profiler at 1–15 kHz. These surveys focused on small sections of the landscape deemed to have high potential to yield paleolandscape and paleoenvironmental data during the sampling phase of the project. One of these 1 km^2 areas, identified as Box 6, was located just west of Santa Cruz Island, and was selected due to the interpreted paleovalley (Maloney et al., 2017; Tahiry 2019) and unique deposition (Johnson 2020) identified in the Chirp data and described above. Within Box 6, 41 survey lines were collected covering ~41 linear km (Figure 3).

2.2.1 Coring

The sampling phase of the project was conducted aboard the R/V Sally Ride using a Rossfelder P-5 vibracore system. Core tubes were 4.5 m long and 10 cm in diameter and were vibrated into the sea floor until an impenetrable geologic unit was encountered. Twenty-six cores were collected from the submerged shelf around the NCI. Selection of targets for the coring regime focused on four core locations within each of the 1 km^2 survey boxes. The locations of Box 6 cores were selected based on acoustic signals interpreted as high amplitude anomalies and/or laminations with a shallow buried transgressive surface (Table 1; Figure 4). These core locations were near to the larger paleovalley that appeared to contain shallow channel-like features and relatively thin marine sedimentation that could be penetrated by coring (Maloney

TABLE 1 Intended targets identified in the sonar data used to position four cores within Box 6.

Core #	Total core length (cm)	Water depth (m)	Intended target	Latitude (DD)	Longitude (DD)
CI-VC-6a	95	36	Transition from layered to chaotic reflectors, edge of channel/shoreline, high amplitude anomaly	34.022960	−119.909564
CI-VC-6b	148	35	Laminations	34.025780	−119.908103
CI-VC-6c	165	35	High amplitude chaotic anomaly, adjacent to paleochannel, thin to no Holocene sediment	34.023634	−119.912200
CI-VC-6d	153	34	Faulted, horizons near surface (no Holocene unit), laminated package folded up	34.024538	−119.906014

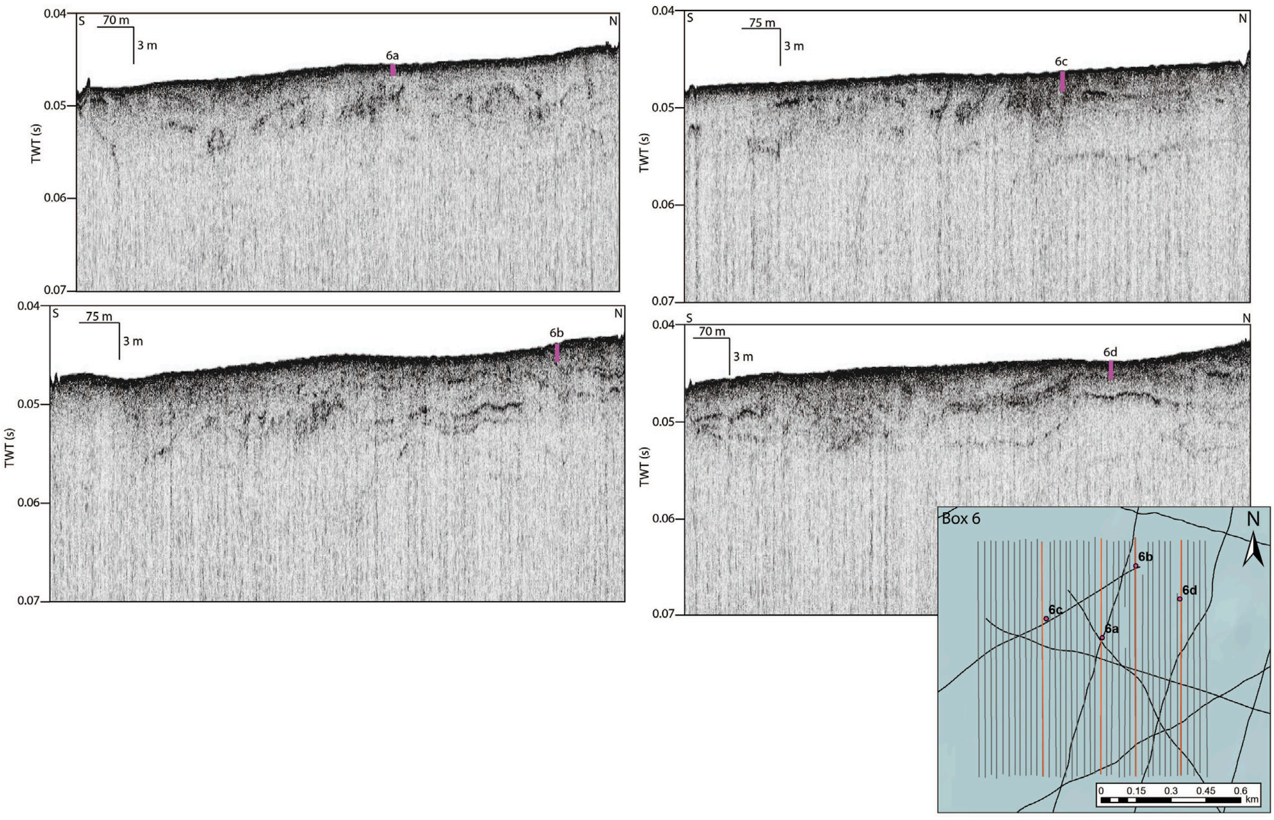

FIGURE 4
Chirp profiles within Box 6 showing locations of cores. Core locations and depth penetrated into the sea floor shown as pink bars overlain on the Chirp profiles. Inset box shows position of the cores within Box 6, and the corresponding Chirp profiles in orange. High-resolution Chirp data shown at 1 km scale to provide context for the depositional environment shown by the reflectors.

et al., 2017). Intended targets in the core locations were preserved sediments indicative of a wetland environment that likely existed prior to inundation of this section of Sanatrosae, and consistent with the early Holocene-aged sites located on the adjacent terrestrial portion of the island. Water depths at Box 6 coring locations were similar, varying from 34 to 36 mbsl. Based on relative sea level data, sea levels 35 m lower than today occurred at ~9,250 cal BP (Muhs et al., 2014).

After collection, all cores were transported to Oregon State University (OSU) Marine and Geology Repository core facility for processing and analysis. Core analyses included whole core computerized tomography (CT) scans using the OSU College of

Veterinary Medicine's Toshiba Aquilion 64 Slice medical CT scanner. The CT scans were viewed in 3D using OsriX Lite software and images from the center of each core were captured and saved as png files. Scale bars were fit to the CT scan images using Adobe Illustrator and the recorded total length of the cores. Cores longer than 1.5 m were sectioned due to instrument constraints. Core section images were stitched together using scaling, image overlay, and color corrections in Adobe Illustrator to create whole core images.

Once split, a geological description of each core, including sediment character, shell content, color, and stratigraphic features was completed. Marine shell samples were collected from cores that had stratigraphy suggestive of a change in depositional environment (e.g., changes in sediment characteristics down the length of the core). Shells were identified to the genus or species level and pre-treated for dating at the University of Oregon, Museum of Natural and Cultural History. Pre-treatment included etching in a 10% HCl solution and rinsing with deionized water. Some samples were powdered with a drill, but smaller samples were kept whole. All samples were sent to DirectAMS Radiocarbon Dating Services in Bothell, WA for analysis (www.DirectAMS.com). Samples were prepared and analyzed by DirectAMS using their National Electrostatics Corporation 1.5 SDH Compact Pelletron Accelerator Mass Spectrometer. Results were reported by DirectAMS as uncalibrated radiocarbon ages, corrected for isotopic fractionation with an unreported $\delta^{13}C$ value measured on the prepared carbon by the accelerator. The radiocarbon ages were calibrated using OxCal version 4.3 (Bronk Ramsey, 2009) and the Marine13 calibration curve (Reimer et al., 2013). All samples were also adjusted using a reservoir age of 261 ± 21 years (Ingram and Southon 1996).

3 Results

All four cores in Box 6 (6A, 6B, 6C, and 6D) penetrated past the transparent upper unit into the unit below with wavy, discontinuous reflectors (see Figure 4), at which point a stark change in sediment composition is observed from overlying gray sands with marine shells to distinct reddish, oxidized, angular sand, rocks, and mud that lack marine shells. In all four cores, just above the contact, the upper unit includes a high density of large shells, and subrounded-subangular pebbles. There were variable colors and dominant muddy grain size observed across all of the cores' lower units that were interpreted to represent possible deposition within a floodplain, as the sinuosity of the area's rivers changed with changing base levels.

All of the cores were capped with green marine sands or muds containing marine or estuarine molluscs, representing subtidal sands. Eight radiocarbon samples were collected from the Box 6 cores, all from the upper marine unit. The dates range from ~9,900 to 5,800 cal BP (Table 2). The ages from near the base of cores 6A and 6C are consistent with the model of relative sea-level for the islands, but dates from the base of cores 6B and 6D are younger than expected for their given depths (Figure 5).

The lower portions of all cores include terrestrial sediments, with deposits in cores 6A, 6B, and 6D identified as sequences of preserved paleosols (described below). These paleosols were recognized primarily from carbonaceous root traces, tapering and branching downward, as well as rhizomes of sedges. Good examples of these features are noted in the paleosol images in Figures 8, 9. Paleosol intervals had distinctive soil structures, such as crumb peds and a sharp top under sedimentary cover, with organic A-horizons gradational downward to B-horizons with high chroma mottles. Munsell color was measured on each horizon and testing with dilute (0.1 M) HCl showed that all horizons were non-calcareous. The individual paleosols were compared with the closest modern soil series (Table 3) mapped on the Channel Islands (United States Department of Agriculture, Natural Resources Conservation Service, 2007). Cores from Box 6 were examined in the Marine Geology Repository of OSU. A graphic log was taken of the cores containing paleosols (Figure 6) and individual paleosols photographed.

3.1 Core 6A

Core 6A was located at what was interpreted as the edge of a channel feature in Chirp data. The 27–28 cm of marine sediments capping a Xeroll (Ahoy) soil (Figure 7) produced single fragments of two discrete butter clam (*Saxidomus* spp.) shells at 11–15 cm below core surface that date to ~9,600 cal BP. These appear to have been articulated clam shells in a thin and discrete lens, suggesting no reworking and a likely age for the underlying soil of >9,600 cal BP. The Xeroll soil has high organic content in the surface (A) horizon which also has distinctive crumb ped structure. Root trces and root mottle was apparent in the subsurface (Bg) horizon. This was a grassland soil comparable with the modern Ahoy Series of the Channel Islands (United States Department of Agriculture, Natural Resources Conservation Service, 2007).

3.2 Core 6B

The location of core 6B was chosen to reach the acoustic unit with wavy, laminated reflectors. There is 18 cm of marine sediments overlying three stacked Ochrept (Fiale) and Fluvent (Riverwash) soils between 18 and 150 cm (Figure 8). Fluvent soils are more or less freely drained Entisols that form in recent water-deposited sediments on flood plains, fans, and deltas along rivers and small streams. They show little alteration of the parent sediment other than penetration by roots. Most Fluvents are frequently flooded, and stratification of the materials is normal. The Ochrept profiles have more organic matter, minor leaching in the surface (A) horizon, and clay enrichment in the subsurface (Bw) horizon that falls short of the amount needed for an argillic horizon. All three paleosols showed

TABLE 2 Radiocarbon dates from Box 6 cores.

DirectAMS no.	Sample name	Sample description	Core	Depth (cm)	^{14}C age (yrs BP)	Calibrated age (yrs BP) (1 sigma)
D-AMS-37338	6A_11-15	CA butter (*Saxidomus* sp.) clam shell	CI-VC-6a	11–15	9,031 ± 37	9,445.5 ± 39.5
D-AMS-37339	6A_11-15	WA butter (*Saxidomus* sp.) clam shell	CI-VC-6a	11–15	9,267 ± 38	9,658 ± 83
D-AMS-37340	6B_10-20	CA cone (*Conus* sp.) snail shell	CI-VC-6b	10–20	6,303 ± 32	6,453 ± 53
D-AMS-37341	6C_17-22	CA frog (*Crossata* sp.) shell	CI-VC-6c	17–22	8,498 ± 35	8,757 ± 95
D-AMS-37344	6C_2729	Tusk (*Dentalium* sp.) shell	CI-VC-6c	27–29	9,395 ± 41	9,893.5 ± 112.5
D-AMS-37345	6D_42-45	Prickly cockle (*Trachycardium* sp.) shell	CI-VC-6d	42–45	5,698 ± 29	5,815 ± 55
D-AMS-37346	6D_45-49	Slipper (*Crepidula* sp.) shell	CI-VC-6d	45–49	5,889 ± 30	6,029.5 ± 64.5
D-AMS-37347	6D_68-69	Horse (*Modiolus* sp.) mussel shell	CI-VC-6d	68–69	7,437 ± 32	7,633 ± 40

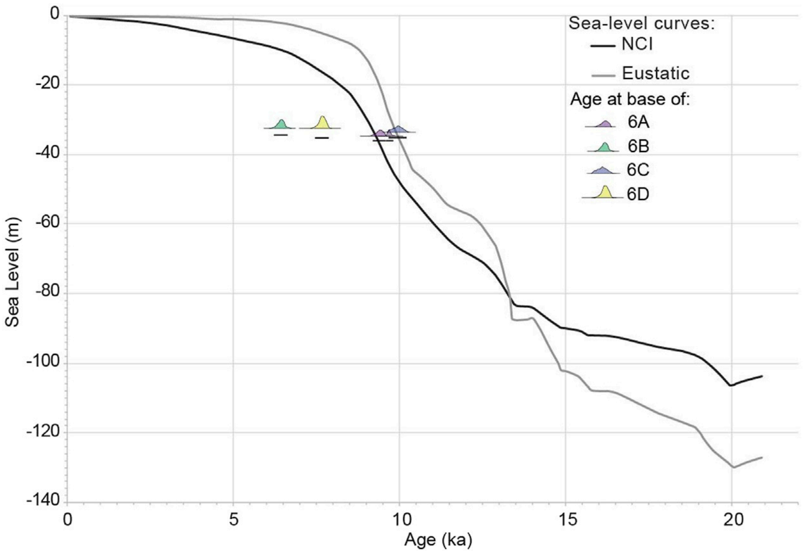

FIGURE 5
Dates closest to the base of the upper marine unit for each core plotted on a sea-level curve showing Age (ka) vs. Sea Level (m). NCI sea level curve based on Clark et al. (2014).

TABLE 3 Soil series recognized from paleosols in cores between Santa Cruz and Santa Rosa Islands.

Comparable soil series	Soil taxonomy	Vegetation[a]
Abaft	Psamment	Dune-binding grasses and forbs
Ahoy	Xeroll	Coastal terrace grassland
Fiale	Xerept	Coastal shrubland
Riverwash	Fluvent	Coastal scrub and marsh

[a] The vegetation listed is typical for the comparable soil series found currently on the Northern Channel Islands.

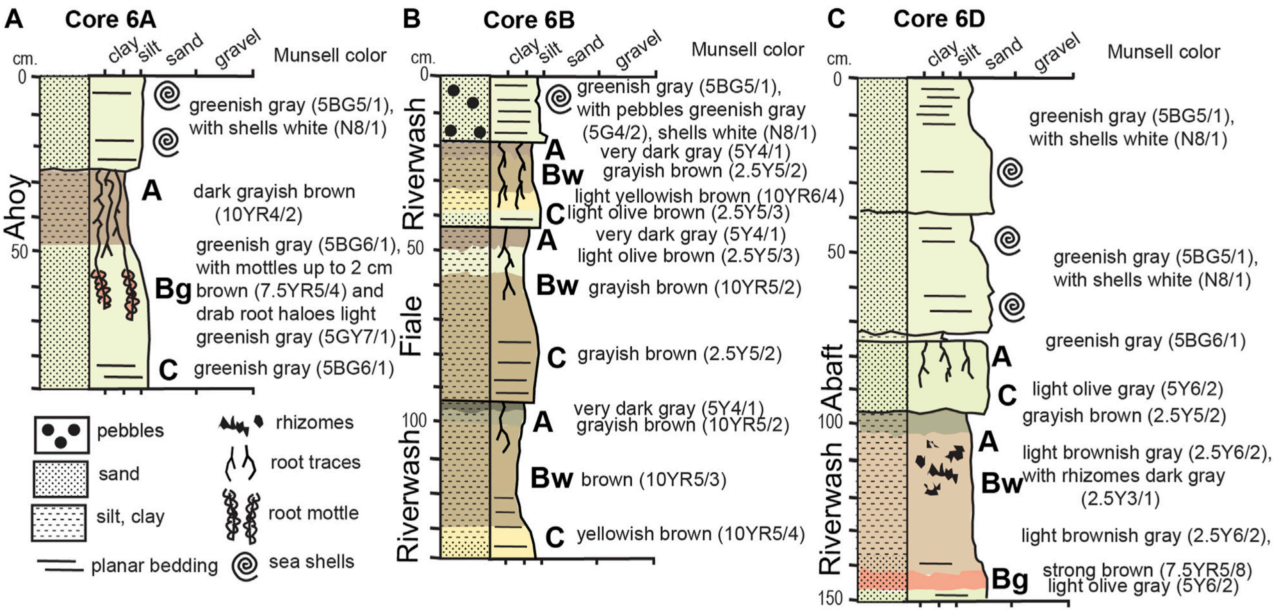

FIGURE 6
Graphic log of cores 6A, 6B, and 6D showing positon and type of paleosols in each core and the location of features such as root traces, root mottle, and rhizomes.

root traces in the surface (A) horizons continuing into the subsurface (Bw) horizons. A California cone (*Conus californianus*) shell fragment at 10–12 cm in marine sand above the paleosols dated to ~6,450 cal BP. The Ochrept is a coastal shrubland soil comparable with the modern Fiale Series of the Channel Islands and the Fluvent is a coastal scrub and marsh soil comparable with the modern Riverwash Series of the Channel Islands (United States Department of Agriculture, Natural Resources Conservation Service, 2007).

3.3 Core 6D

Core 6D was located where the wavy, laminated unit appeared uplifted toward the seafloor by faulting and folding. This allowed for sampling of deeper units that were unreachable in other locations. In the core, 72 cm of marine sediments are overlying two stacked Psamment (Abaft) and a Fluvent (Riverwash) soils between 72 and 150 cm (Figure 9). Three single fragments of *Trachycardium*, *Crepidula*, and *Modiolus* shell at 42–45 cm were AMS dated to ~5,800, 6,050, and 7,650 cal BP, respectively. The Psamment profiles are eolian sand with root traces like the modern Abaft Series of the Channel Islands which form under dune binding grasses (United States Department of Agriculture, Natural Resources Conservation Service, 2007). In the lower Fluvent soil comparable with the modern Riverwash Series (United States Department of Agriculture, Natural Resources Conservation Service, 2007), dark tubular masses appear to be carbonaceous plant rhizomes (perhaps Tule reed).

4 Discussion

Crescent Bay has become a critical submerged landscape to consider for defining the paleolandscape and paleoecological evolution of Santarosae, and in the search for preserved cultural heritage on the sea floor. Together with the adjacent subaerial potion of western Santa Cruz Island between Black Point and Kinton Point (see Figure 3), there is an archaeologically sensitive landscape that shows terminal Pleistocene through Early Holocene archaeological evidence around what may have been a sizable floodplain with adjacent wetland habitats. Geologically this is a complex area located at the western end of the flat Central Valley where two major island drainages, Cañada de los Sauces and Cañada Christy, terminate at the ocean. The Santa Cruz Island Fault also runs just north of Cañada Christy, adjacent to Black Point. The canyons in this area are strongly controlled by changes in sea level, as this constitutes the local base level for the island's river systems. When this base level lowers, the streams incise and erode upland areas, carrying sediment to the shoreline, creating a "lowstand delta" from the upland sediment (Schumann and Pigati 2017:522). With rising seas, streams aggrade and create sediment build up from the shoreline into the canyons. The effects of this sediment transfer during sea level changes alters coastal and shelf morphology,

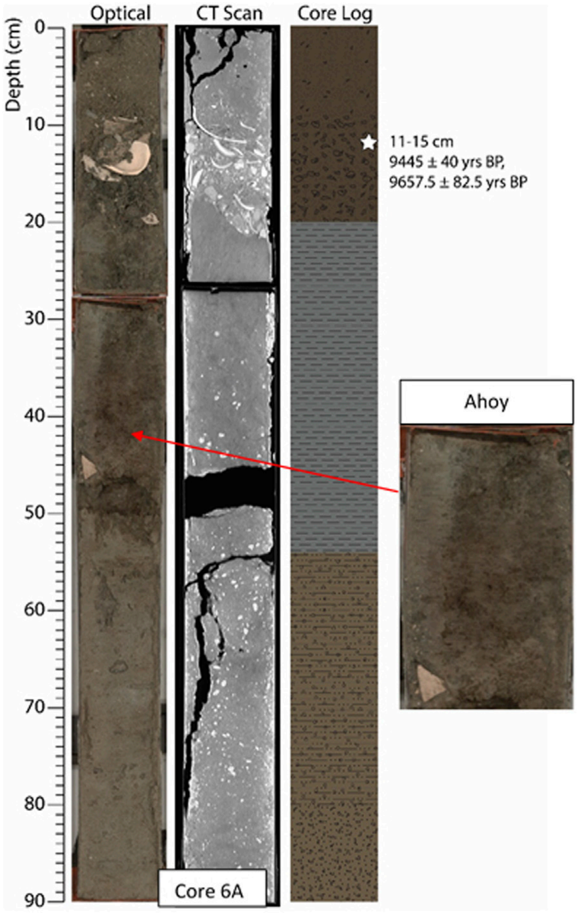

FIGURE 7
Optical, CT, and core log images of Core 6A with photograph inset of Ahoy (Xeroll) paleosols identified in core. White star on core log shows location of radiocarbon sample and depth and age are noted. Red arrow shows location of paleosol.

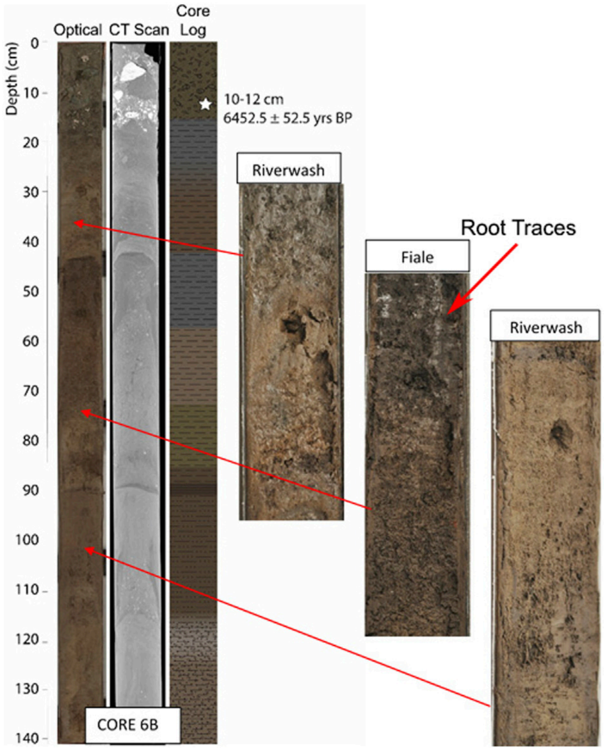

FIGURE 8
Optical, CT, and core log images of Core 6B with photograph insets of two Riverwash (Fluvent) and one Fiale (Xerept) paleosol. White star on core log shows location of radiocarbon sample and depth and age are noted. Red arrow shows location of paleosol. Distinct root traces are noted in the Fiale.

making identification of terminal Pleistocene land surfaces and habitats that have survived marine transgression difficult; however, accurate locations of preserved paleosols can aid in defining the spatial and diachronic evolution of terminal Pleistocene habitats that may have been foraging and habitation locales for Paleocoastal peoples. The locations of resources rich habitats, such as floodplains and wetlands, strongly influenced human settlement decisions and archaeological sites tend to cluster on landscapes with easy access to fresh water and wetland resources. These habitats are known from archaeological evidence to have existed on Santarosae (Erlandson et al., 2011; Erlandson et al., 2019; Rick et al., 2013), and research from the California mainland suggests that Paleocoastal habitation focused on rich wetland habitats, as well (Erlandson 1994; Byrd 1996; Reddy and Byrd 1997; York et al., 1999; Byrd and Raab 2007; Wahoff 2012; York 2012). Additionally, estuary deposits in particular are rich in organics and can provide data for understanding regional paleoecology (Watson et al., 2011). Estuaries contain rich biological resources that continually adapt to changes in environments and are ideal for helping interpret shifting climatic conditions (Cole and Liu 1994).

Due to their importance in paleoenvironmental modelling and data potential, the preserved paleosols identified as part of the current research are a significant step forward in the goal to understand and define the paleoenvironment of Santarosae and better understand where on the continental shelf cultural resources may be preserved. Although pollen analyses are needed on the paleosols, based on the closest modern soil series mapped on the Channel Islands (Table 3), the paleosols identified in cores 6A, 6B, and 6D represent a mosaic of shrubland, grassland, marsh, and dune-binding vegetation of a coastal plain. Cores 6B and 6D both had Riverwash (Fluvent) soils, which occur on flood plains, fans, and deltas along rivers and small streams. Although there were no peaty paleosols characteristic of permanently waterlogged wetlands, localized wetland patches are expected on a coastal plain. In fact,

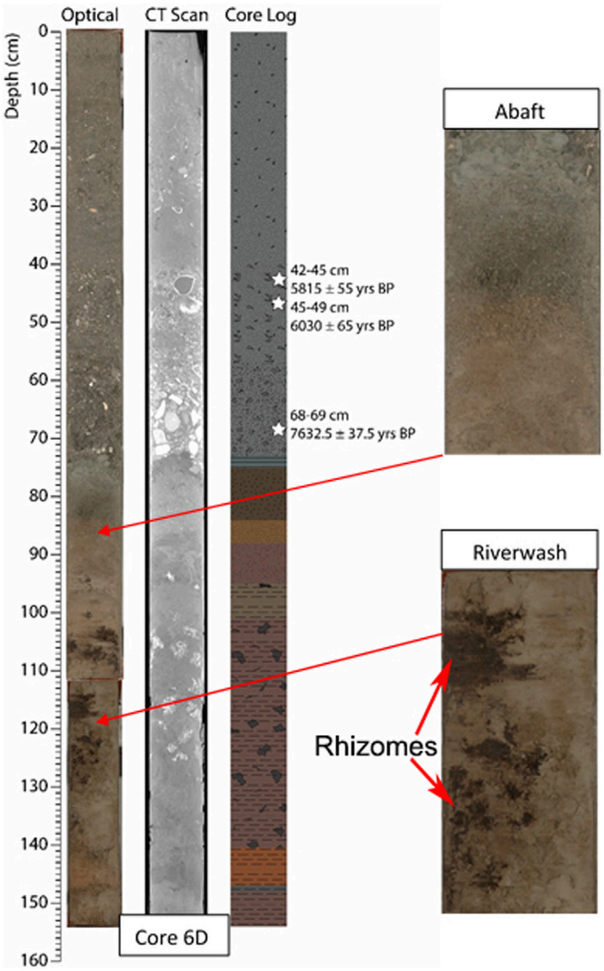

FIGURE 9
Optical, CT, and core log images of Core 6D with photograph insets of Riverwash (Fluvent) and Abaft (Psamment) paleosols. White star on core log shows location of radiocarbon sample and depth and age are noted. Red arrow shows location of paleosol. Rhizomes features are noted in the Riverwash.

localized wetland patches are currently present at the mouths of several of Santa Cruz Island's canyons, including Cañada de los Sauces, which is directly onshore from the coring site. The Riverwash paleosol in core 6D has stout carbonized rhizomes comparable with those of tule reed (*Schoenoplectus californicus*), which colonizes shallow lakes and river banks, suggesting that localized areas of wetland habitat were present prior to ~7,600 years ago, the minimum age for the paleosols in 6D based on radiocarbon dating of the upper marine unit. Core 6D also has an Abaft (Psamment) paleosol that overlays the Riverwash. Abaft soil are found in dune fields with a typical vegetation of beach and dune plant communities. On the Northern Channel Islands, Abaft soils are common on the stabilized dunes on the eastern shore of Santa Rosa Island, directly across the passage from Santa Cruz Island and on the western edge of Crescent Bay. Core 6A contains an Ahoy (Xeroll) paleosol, which forms on stable marine terraces and supports native and nonnative grasses. These coastal terrace landforms with grassland vegetation are prominent features on Santa Rosa and Santa Cruz islands (Schumann et al., 2014), and can be seen directly onshore from the coring site on the western sector of Santa Cruz Island. The fourth identified palesol, Fiale (Xerept), is an Inceptisol common on side slopes of hills and interfluves. This soil is common on the eroded slopes of the river cut terraces on the western sector of Santa Cruz Island. One Fiale series paleosol is between two Riverwash paleosols in Core 6B and additional analysis is needed to determine the temporal relationship between these three units. The Abaft, Ahoy, and Fiale paleosols had high chroma mottles indicating a seasonally high water table, but were well drained for most of the year.

As the base of the upper marine units in Cores 6A, 6B, and 6D represent the initial transgression and rise of sea level, the underlying surface is the wave transgressive surface, which was subaerially exposed prior to flooding (Laws et al., 2019). Therefore, although only the bases of the upper marine units were dated, we can determine minimum ages for the underlying paleosol sequences and infer the paleogeographic processes that allowed the soils to form. The base of the marine unit in Core 6A is dated ~9,600 cal BP. Below this unit is the undated Ahoy Series, suggesting a subaerial coastal plain was present prior to 9,600 cal BP. This older date for a subaerial terrace landform is supported by models of the Santa Cruz Passage beginning to form around 9,000–10,000 years ago, as sea level rise began separating Santa Cruz and Santa Rosa islands (Clark et al., 2014; Reeder-Myers et al., 2015). The Riverwash Series with possible tule reed rhizomes and the Abaft Series in Core 6D developed prior to 7,650 cal BP. These soils that form along waterways and among dunes, respectively, show the environmental shift in this section of Santarosae as seas continued to rise, creating rapidly changing shallow water environments and drowning river mouths, encouraging evolution of estuary systems (Graham et al., 2003). This paleogeographic process has been identified on the western section of the Passage, where a small paleoestuary on eastern Santa Rosa Island (Cole and Liu 1994; Anderson et al., 2010) attracted people throughout much of the terminal Pleistocene and early Holocene (Rick et al., 2005b). Coastal dune fields are also present on eastern Santa Rosa Island, most extensively at Skunk and Carrington points (see Figure 3). These dune fields formed during glacial periods when seas were lower, exposing the large submarine shelf, allowing the prevailing northwest wind to deflated carbonate sand from the shelf, and blow them on the land surface (Schumann et al., 2014). While the dune fields on Santa Rosa Island stabilized when sea level rose and inundated the shelf (Muhs et al., 2009), dunes did form in other localized areas across the now submerged shelf (Gusick et al., 2019: 152–153). The Abaft Series paleosol identified in Core 6D provides an indication of a localized area where dunes formed on the eastern section of

Crescent Bay. Lastly, Core 6B also contains two Riverwash paleosols that formed earlier than 6,450 cal BP, and provides additional data with which to define spatial and diachronic evolution of localized wetland patches within Crescent Bay as marine transgression continued to flood the lowland terrace.

While gently sloping nearshore shelves, such as those within the Santa Cruz Passage, may have encouraged development of estuarine and marsh ecosystems at the mouths of larger streams, their full development and productivity may have been halted by rapid changes in sea level (Reeder-Myers et al., 2015). Although more analyses are needed on the paleosols to understand the development of coastal and intertidal ecosystems along the margins of Crescent Bay, the baseline paleosol data indicating there were areas of localized dune and wetland patches can be considered with Paleocoastal habitation data known from the subaerial portion of the island. This combination can help determine if the shifting wetland habitats suggested by the preserved paleosols were present during habitation and a target for subsistence strategies during the Paleocoastal period.

Archaeological and paleoecological data show that an estuary existed on eastern Santa Rosa Island between 8,500 and 5,000 years ago (Anderson et al., 2010; Rick et al., 2005a), but Venus clam (Chione *undatella*) shells dating to ~11,000 and more than 600 birdbone fragments from waterfowl (geese/ducks) recovered from SRI-708 show that another, earlier estuary existed likely near to this site on the western margin of Crescent Bay (Erlandson et al., 2019). Associated with these faunal remains were chipped-stone crescents, transverse projectile point technology used for hunting birds and found primarily in sites dated to 11,000 cal BP and older, commonly adjacent to wetland environments (Erlandson et al., 2011; Rick et al., 2013; Sanchez et al., 2017). Another nearby site, SRI-77, also produced a *Chione undatella* shell dating to ~7,450 cal BP (Rick 2020), suggesting that estuary deposits were forming and sustaining resources on this western section of Crescent Bay during the postglacial marine transgression that was flooding the lowland terrace connecting Santa Cruz and Santa Rosa islands.

Across Crescent Bay on western Santa Cruz Island, and near to the core locations, there are two Paleocoastal site clusters (see Figure 3). On a high southwest-facing bluff at the mouth of Black Point Canyon and on the bluff across Black Point Canyon lie two lithic scatter sites (CA-SCRI-860 and CA-SCRI-861) that have produced chipped stone crescents, similar to SRI-708, that are suggestive of a terminal Pleistocene or earliest Holocene occupation and bird hunting (Erlandson et al., 2016; Sanchez et al., 2017). The position of CA-SCRI-860 and CA-SCRI-861 with hunting technology high above Crescent Bay suggests they may have been “look out” sites (Rick et al., 2013), possibly for tracking waterfowl in wetlands or pinnipeds hauled out on sandy beaches. Near to these lithic sites is one recently identified terminal Pleistocene site (CA-SCRI-857) dated to ~11,400 cal BP from which an estuarine calm was recovered (J. Erlandson, personal communication, 8 May 2022) suggesting an estuarine habitat in the region. Further south in the curve between Black Point and Kinton Point is a cluster of sites dating to the Early Holocene (CA-SCRI-547, CA-SCRI-549, and CA-SCRI-798) located above what is now Christy Beach. A total of five radiocarbon dates derived from well-preserved California Mussel (*Mytilus californianus*) shells provide a date range of 8,660–8,015 cal BP for the three sites. All are single thin shell lenses located down an erosional face of a coastal grassland terrace, and buried under 6–8 m of alluvium. In contrast to the terminal Pleistocene Black Point sites, these Early Holocene sites are mainly comprised of California Mussel and Black Abalone (*Haliotis cracherodii*) shells with a small amount of Pismo clam (*Tivela stultorum*) and Littleneck clam (*Protothaca staminea*), sandy shore species that are not widespread on the islands (Gusick, 2012; Gusick, 2013). The 3,000-years timespan and the varying technology and mollusks present in both clusters of Paleocoastal sites, likely reflect a rapidly evolving littoral ecosystem impacted by rising seas.

The dates and constituents of these sites support the core data that indicate wetland ecosystems were present across Crescent Bay. The ages of the known onshore sites and the cores show the wetland habitats within Crescent Bay were a target for exploitation from the terminal Pleistocene through the Early Holocene. The terminal Pleistocene sites on the western edge of Crescent Bay (Santa Rosa Island) have yielded estuarine shell as well as technology and faunal material indicating wetland bird hunting. Considered together, the terminal Pleistocene-aged Black Point sites on the eastern edge of Crescent Bay (Santa Cruz Island)—and closest to the core locations—also contained estuarine shell and the same bird-hunting technology as the contemporaneous sites across the bay. Though not on the margins of Crescent Bay, another terminal Pleistocene-aged site, CA-SRI-512, on the north coast of Santa Rosa Island produced crescents and hundreds of waterfowl bones indicating estuary and marsh exploitation during this same terminal-Pleistocene time period (Erlandson et al., 2011; Erlandson et al., 2019). The wide spread consistency of site constituents during this early habitation period suggests that wetland habitats were likely present in various areas around Santarosae and a draw for Paleocoastal peoples during the terminal Pleistocene on the island. The early Holocene-aged (~8,800 cal BP) sites on Santa Cruz Island yielded sandy beach species and no crescents, perhaps indicating a shift in availability or productivity of local wetland habitats as seas continued to rise and flood lowland areas. The search for terminal Pleistocene and early Holocene-aged sites on the subaerial portion of Santa Cruz Island has not been as extensive as on Santa Rosa Island and there may be more Paleocoastal-aged sites on this eastern edge of Crescent Bay that have not yet been identified.

5 Conclusion

While additional research and analyses are needed, the discovery of intact terrestrial soils preserved beneath the transgressive marine sediments on the current floor of the Santa Cruz Passage provides a "proof of concept" that: 1) terrestrial soils survived the effects of rising seas and active transgression that included strong submarine currents and an often turbulent Northeast Pacific surf zone; and 2) the south-facing Crescent Bay area that was a focus of settlement by Paleocoastal peoples and contains preserved terrestrial soils, likely contains intact submerged terrestrial sites of Early Holocene and terminal Pleistocene age. This is an important step in the search for submerged cultural material on the maritime cultural landscape of Santarosae. By focusing on features that were attractive to early maritime hunter-gatherers, such as wetland environments, we can narrow search parameters to identify archaeological "hot spots" on the continental shelf. These data are crucial in our ability to identify sensitive maritime cultural landscapes and eventually identify, document, and preserve underwater cultural heritage resources. Our current research has increased our understanding of the long-term ecology of Santarosae, of which little is known (Anderson et al., 2010), and expanded our knowledge of the paleolandscape in relation to the terminal Pleistocene peopling of the Americas. The seismic and core data have also contributed to the broad scale mapping of the Northern Pacific continental shelf and definition of regional archaeological and biologically sensitive landscapes (Braje et al., 2016; Braje et al., 2021). Collectively, these efforts help to understand how Pleistocene landscapes in the SCB evolved during rising seas, tectonic activity, and the regional shift to a drier climate that occurred during the Pleistocene-Holocene transition. This evolution has implications not only for early human habitation of the area, but also for addressing key questions in the ecological, biological, and geological disciplines.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

AG participated in all data collection and analysis and wrote the manuscript. JM participated in sonar and core data collection and analysis and manuscript writing. TB participated in all data analysis and manuscript writing. GR analyzed core data and contributed to manuscript writing. LJ participated in sonar and core data collection and analysis and manuscript writing. SK participated in sonar and core data collection, processing and analysis, and manuscript writing. AA participated in archaeological site data collection, analyzed faunal material, prepped samples, and contributed to manuscript writing. JME participated in archaeological site data collection, analysis of all data, and contributed to manuscript writing. All authors contributed to manuscript revisions, and read and approved the submitted version.

Funding

This work was supported by a Bureau of Land Management Cooperative Agreement Awarded (No. M15AC00012) to San Diego State University.

Acknowledgments

We would like to express our gratitude to our home institutors and the Bureau of Ocean Energy Management for supporting this research. We would like to recognize Neal Driscoll at Scripps Institution of Oceanography and the crews of the R/V Shearwater and R/V Sally Ride who were critical in helping us collect geophysical and core data. We also thank the Oregon State University (OSU) Marine and Geology Repository staff for assistance curating the cores. Thank you to the editors for inviting us to participate in this special issue, along with reviewers and editorial and production teams at Frontier in Earth Science for their constructive feedback and help with the publication of our manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 03 October 2022
DOI 10.3389/feart.2022.982694

OPEN ACCESS

EDITED BY
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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 30 June 2022
ACCEPTED 12 September 2022
PUBLISHED 03 October 2022

CITATION
Faulkner P, Sarathi A, Crowther A, Smith T, Harris M, Ali AK, Haji O, LaViolette A, Norman NL, Horton M and Boivin N (2022), Human-ecodynamics and the intertidal zones of the Zanzibar Archipelago.
Front. Earth Sci. 10:982694.
doi: 10.3389/feart.2022.982694

Human-ecodynamics and the intertidal zones of the Zanzibar Archipelago

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The intertidal zone, covering the nearshore fringe of coasts and islands and extending from the high-water mark to areas that remain fully submerged, encompasses a range of habitats containing resources that are as important to modern populations as they were to humans in prehistory. Effectively bridging land and sea, intertidal environments are extremely dynamic, requiring complexity and variability in how people engaged with them in the past, much as they do in the present. Here we review and reconsider environmental, archaeological, and modern socio-ecological evidence from the Zanzibar Archipelago on eastern Africa's Swahili coast, focusing on marine molluscs to gain insight into the trajectories of human engagement with nearshore habitats and resources. We highlight the potential drivers of change and/or stability in human-intertidal interactions through time and space, set against a backdrop of the significant socio-economic and socio-ecological changes apparent in the archipelago, and along the Swahili coast, during the late Holocene.

KEYWORDS

archaeomalacology, intertidal foraging, marine subsistence, human-environment interactions, eastern Africa

1 Introduction

Coastal areas, and by extension the intertidal zone, are of high environmental significance. From an ecological perspective, the coastal zone represents a transitionary area between terrestrial and marine environments, providing the physical connection between land and sea. The intertidal zone represents dynamic and complex systems, largely due to long- and short-term variability in tidal range and amplitude, wave energy, fluctuating salinity levels and temperature, and the effects of high-energy storm activity. Although nearshore coastal habitats present a unique set of challenging conditions for human exploitation as a result of these factors, importantly, the intertidal zone often comprises highly productive ecosystems. This is particularly the case for eastern Africa, which is characterised as containing highly productive coastal habitats and rich biodiversity (Richmond, 2011; Nordlund et al., 2014). Often forming one of the most prevalent groups of taxa inhabiting the intertidal zone, molluscs fill crucial roles within marine ecosystems, being carnivores/predators and herbivores/detritivores operating at all trophic levels. They serve as primary consumers, increase habitat complexity, and improve water quality through filtration.

Human engagement with intertidal habitats extends back minimally 160,000 years in southern Africa. Intertidal foraging and mollusc harvesting are pivotal elements in ongoing debates about human evolution, adaptation to dynamic marine environments, and behavioural modernity (Klein and Bird, 2016; Marean, 2016; Will et al., 2019). Although there is ongoing debate over the timing and nature of initial coastal resource use, when people became coastally adapted, and transitioned to fully maritime societies (Marean, 2014; Fleisher et al., 2015; Jerardino, 2016), of key importance when considering the nature of human engagement with marine environments is that the intertidal zone connects the land, and therefore people, to the sea. Intertidal foraging is thus an important component of marine resource use through time, with intertidal resources providing critical evidence in understanding past human-ecodynamics in coastal settings. Molluscs therefore play a potentially important role in disentangling key elements of human interactions with nearshore environments. This is particularly true on eastern African coasts and islands, where our understanding of intertidal foraging and molluscan resource use is less well developed.

Msemwa (1994) noted in his foundational ethnoarchaeological study of mollusc harvesting on the Tanzanian coast that the literature on shellfish collection across the eastern Africa intertidal zone was particularly limited. While archaeological research has grown substantially since then, archaeomalacology has not significantly progressed in the region, a point echoed in several recent studies. In their review of zooarchaeological evidence from the coast and islands of eastern Africa, for example, Quintana Morales and Prendergast (2018) comment on the richness and productivity of the intertidal zone, but note that their consideration of molluscan evidence is limited due to the lack of regional systematic archaeomalacological analyses. Although their focus is on wild and domesticated terrestrial fauna and fish evidence, they indicate the diversity of economic strategies apparent on the coast and islands, including mollusc gathering, fishing, hunting and animal husbandry.

Greater emphasis has been placed on the archaeological analyses of terrestrial vertebrate fauna and marine fish since the 1980s, with research undertaken in various areas between the Lamu Archipelago on the north Kenyan coast to southwest Madagascar (e.g., Mudida and Horton, 1996; Quintana Morales and Horton, 2014; Prendergast et al., 2016; Prendergast et al., 2017; Douglass et al., 2018; Quintana Morales and Prendergast, 2018; Quintana Morales et al., 2022). Molluscs were little mentioned in the ethnographic and ethnohistoric records on foraging on the eastern African islands as reviewed by Walsh (2007), where emphasis is on terrestrial fauna. To date, systematic assessment of molluscan assemblages is restricted to the ethnoarchaeological work of Msemwa (1994) and Ichumbaki (2014) on the mainland Tanzanian coast, and a handful of studies on Unguja (Zanzibar) Island (Faulkner et al., 2018, 2019a; Sarathi, 2018, 2020), Mafia Island (Christie, 2013; Faulkner et al., 2019b), and southwest Madagascar (Douglass 2017).

Perspectives on the role of molluscs in past economies vary, from a dietary staple to supplementary or starvation food (Erlandson, 2001). Similar interpretations of the relative importance of these resources have occurred in eastern Africa, where they have also been viewed as fallback or starvation food (e.g., Msemwa, 1994; Fleisher, 2003). Although broader syntheses of the molluscan evidence have been hampered by different analytical standards and incompatible data presentation (Fleisher, 2003), recent analyses of specific site assemblages in the Zanzibar and Mafia Archipelagos indicate that the economic importance of molluscs varied greatly through time and space (i.e., Faulkner et al., 2018; Faulkner et al., 2019b; Sarathi, 2020; Rødland, 2021). This suggests that how people engaged with the intertidal zone also changed considerably, and not necessarily unidirectionally, with long-term transitions from hunting and gathering to urban economies.

Extending from this point of view, here we present the first detailed, comparative analyses of molluscan assemblages from the Zanzibar Archipelago. By broadening the spatial and chronological scope within a defined region, we aim to investigate the nature of human interactions with nearshore environments, to identify change or stability in how people foraged and made decisions when engaging with the intertidal zone. We take an ecologically oriented approach to understanding human ecodynamics (following Fitzhugh et al., 2019), considering the nature of palaeoenvironmental shifts and contextualised within patterns of socio-economic/cultural changes, to provide a baseline understanding of intertidal foraging and decision-making through time.

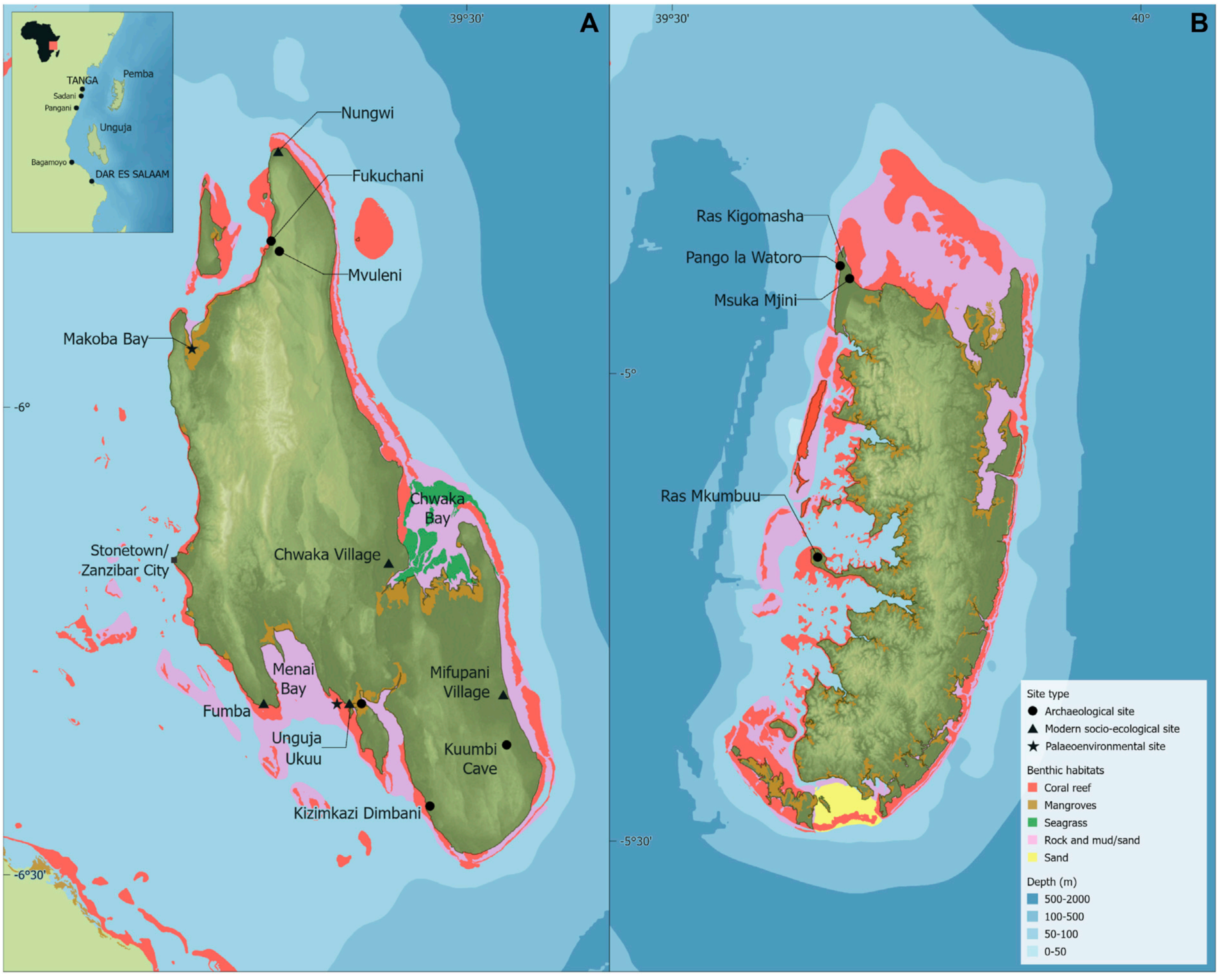

FIGURE 1
The Zanzibar Archipelago study area, showing locations mentioned in the text on Unguja Island **(A)** and Pemba Island **(B)** with the distribution of the dominant benthic habitats (Spalding et al., 2010; Khamis et al., 2017 [with permission from Elsevier, order no. 5338180474815]; UNEP-WCMC, WorldFish Centre, World Resources Institute, The Nature Conservancy, 2021; UNEP-WCMC and Short, 2021). Map created using ArcGIS Pro 2.9.1. Bathymetric data from GEBCO Compilation Group. (2021), administrative boundaries from GADM (2022).

2 Background

2.1 Unguja and Pemba Islands, Zanzibar Archipelago

The Zanzibar Archipelago, adjacent to mainland Tanzania (Figure 1), consists of c.50 islets and two large islands: Unguja at 1,670 km^2 and 119 m above sea level, and Pemba at 990 km^2 and 96 m above sea level. Unguja is separated from continental Africa by 25–30 km of shallow ocean (Zanzibar Channel, c.35–65 m deep), whereas Pemba sits c.55 km from the mainland surrounded by deeper waters, being separated from the continent by the c.400–800 m deep trench of the Pemba Channel (Agnarsson and Kuntner, 2012; Khamis et al., 2017). Higher precipitation occurs on the western sides of both islands, with deeper soils in these areas being more favourable for agriculture compared with the coral rag and shallow soils of the eastern coasts (Arthurton et al., 1999; Khamis et al., 2017). The vegetation of the coastal lowlands and islands of eastern Africa forms the Zanzibar-Inhambane regional mosaic, containing grassland, shrubland, and a mix of dry and moist forests (Burgess et al., 1998). At present, natural forest areas are largely restricted to protected areas, such as Jozani-Chwaka on Unguja and Ngezi-Vumawimbi on Pemba (Khamis et al., 2017).

The Unguja and Pemba coastlines are characterised by intertidal fringing platforms, commonly extending more than 1 km (in some areas up to 3 km) from the shore, with associated muddy flats, sand flats and beaches, and coral reefs. The northwest and eastern coasts of Pemba, and south and northwest coasts of Unguja, have narrow intertidal zones, with sandy-muddy shores dominating the west coasts. Much of the intertidal platform supports a cover of unconsolidated sediments that form the substrate of seagrass meadows. The platforms and fringing beaches on both islands' eastern coasts are flanked by sandy beach-ridge plains, the seaward edges of which are marked by prominent storm ridges (Arthurton et al., 1999; Arthurton, 2003; Khamis et al., 2017). In sheltered, shallow embayments, such as those on the south, west and northern coasts of Pemba, and north and southwest coasts and in Chwaka Bay of Unguja, extensive mangrove and seagrass habitats with deeper sand/mud substrates are common. Some of these areas have developed more recently due to ongoing sedimentation and processes of progradation (Arthurton et al., 1999). Unguja's reefs support a large proportion of regional and global reef-coral diversity (Zvuloni et al., 2010). Living corals cover c.90 km^2 across the archipelago, although corals are primarily distributed around the two main islands. Corals form continuous reefs on the eastern coasts, with a patchier distribution on the west, particularly on Unguja (Khamis et al., 2017).

2.2 Archaeological and historical overview

The Zanzibar Archipelago evidences human occupation dating to 20,000 BP at Kuumbi Cave on Unguja. Kuumbi's pre-Holocene occupation corresponds with a land bridge that connected Unguja to the mainland. Occupation at Kuumbi disappears with the submergence of that connection at the start of the Holocene. Kuumbi was not reoccupied until the mid-first millennium CE (Chami, 2009; Kourampas et al., 2015; Shipton et al., 2016), when ironworking, farming communities expanded from the mainland onto the Zanzibar Archipelago. These communities are associated with a regional ceramic tradition known as Early Tana Tradition/Triangular Incised Ware (ETT/TIW) that marks the Middle Iron Age (MIA, c. 600–1,000 CE) (Fleisher and Wynne-Jones, 2011). Contemporaneous with Kuumbi's reoccupation included the appearance of small villages across the archipelago such as Fukuchani in north Unguja, and trading ports such as Unguja Ukuu in the south (Juma, 2004). This period was characterised by the rise of Indian Ocean trade on the Swahili coast, linking it with China, South Asia, and the Middle East (e.g., Juma, 2004; LaViolette, 2008; Wood et al., 2016), as well as the introduction of Islam (Crowther et al., 2015; Fitton and Wynne-Jones, 2017; Sarathi et al., 2022).

The abandonment of Unguja Ukuu in the early second millennium CE (Juma, 2004) coincided with new economic and political growth on the coast. The period from c.1000 to 1500 CE saw the emergence of urban centres at localities such as Msuka Mjini, Ras Mkumbuu, and Mvuleni (Horton and Middleton, 2000). These sites, often referred to as "stonetowns", were marked architecturally by the construction of stone and coral houses, mosques and tombs and housed a merchant elite that controlled trade along the coast and between coast and interior. Some stonetowns, such as the UNESCO World Heritage site of Kilwa off the central Tanzanian coast, gained sufficient wealth and power to function as autonomous city-states (Kusimba, 1999).

The 1500s saw the beginning of the colonial period, when foreign powers sought to dominate the Swahili coast. The Portuguese arrival in the Indian Ocean in the late 15th century was matched by Ottoman expansion into the Red Sea in the 16th century. While the Ottomans claimed theoretical sovereignty over much of the Swahili coast, the Portuguese set up factories and fortresses in some major ports to project power in real terms. On Unguja, the Portuguese period is represented by sites such as one located beneath the Old Fort in Stone Town, and Mvuleni in the northwest. Portuguese-period sites suggest a shift in trade networks as new coastal settlements were established and older ones were abandoned. The great Swahili city of Kilwa, for example, was abandoned after it was attacked by the Portuguese. The decline of Portuguese power in the 18th century coincided with the rise of Omani dominance over much of the Western Indian Ocean. Ultimately, the Omani Empire was partitioned, leading to the establishment of the Sultanate of Zanzibar (1856-1964) which itself became a British protectorate in 1890 (Glassman, 2011).

The year 1964 brought revolution to the archipelago and eventual merger with the Tanganyikan mainland to form modern Tanzania. Since its independence from the Omanis, Zanzibar has modernised in a variety of ways. As a result, modernity and its social, cultural, and economic contexts represent a rupture from the past in many respects. The tourist industry, with its enormous international investments, has severely disrupted traditional modes of subsistence—more so on Unguja than Pemba—with the rise of industrial fishing and increasing availability of motorised boats affecting how fishing and shellfish gathering take place. Traditional modes of subsistence persist, however, in places such as Mifupani on Unguja.

2.3 Study site locations, descriptions and chronology

2.3.1 Northern Pemba: Pango la Watoro and Msuka Mjini

North Pemba supports coral reefs, mangroves, intertidal and subtidal flats with seagrass beds and algal growth. Some areas contain rocky cliffs and intertidal rock flats while others have long sandy beaches. On the western side, numerous embayments are characterised by shallow water, sand banks, seagrass, and mangrove forests. The northern tip (Ras Kigomasha) has a wide intertidal zone with vast seagrass meadows. Fringing coral reefs surround Ras Kigomasha with some interruptions due to input from freshwater channels. Reefs on the western side are similar to that described below for southern Pemba, with reefs on the east having a steep slope and low coral cover due to strong wave action (Richmond, 2014). To Ras Kigomasha's southeast is a relatively large area of mangroves within Ngezi Forest and at the mouth of a creek and estuary.

Pango la Watoro, the northernmost site in our study, is a small limestone cave that fronts directly onto a sandy beach on the western side of Ras Kigomasha. Excavations in the cave (1 × 2.5 m) by the Sealinks Project in 2012 uncovered low densities of cultural remains throughout the deposits, including c.17th-18th century pottery, fragments of iron implements, charred millet grains, and terrestrial vertebrate faunal remains, as well as a large molluscan assemblage. Although analyses of the non-molluscan excavated components are ongoing, the available evidence suggests that the cave was used only intermittently over the last few hundred years.

Msuka Mjini is a large settlement located at the southeastern end of Ras Kigomasha, c.300 m west of its eastern shoreline. The site covers c.2ha and is known primarily for the ruins of a large, well-preserved 15th century mosque situated at its centre. The mosque famously bears an inscription of the date AH 816 (1413–4 CE) on the inside of its mihrab (Horton, 2017). East of the site is a long sandy beach with a large and expansive sand/mud and rocky intertidal zone fringed by an uninterrupted coral reef. A single 1 × 1 m test trench was excavated at the site in 2016 by the Sealinks Project, uncovering a series of rapidly formed midden deposits. These contained c.13th–15th-century pottery including Middle Eastern and Chinese trade wares, terrestrial vertebrate faunal remains, and fish bone, with analyses of these materials in progress.

2.3.2 Southern Pemba: Ras Mkumbuu

The site of Ras Mkumbuu is located at the end of a long, narrow and low-lying peninsula on the western side of Pemba. Covering 10ha at its zenith, the site boasts one of the most extensive and best-preserved set of ruins on Pemba, and has attracted archaeological attention since the 1930s. Survey and excavations by Kirkman (1959) and Horton (2017) established the presence of two main settlement phases: 10th–12th centuries CE (c.1,050–750 BP) focused on the site's eastern ridge, and 14th–16th centuries CE (c.550–350 BP) at the site's western end. Ras Mkumbuu is rich in cultural materials, including diverse imported pottery, glass and stone beads, and metal objects, attesting to its important role as a Swahili trading port and stone town. In 2012, the Sealinks Project excavated four small (1 × 1 m, 2 × 1 m) test trenches at the eastern end of the site. Three of these targeted an area adjacent to the beach at the base of the eastern ridge, where midden material was located. The fourth was placed into the side of a mound on the top of the ridge, which cut through a shallow sequence of compacted house floors. A range of cultural materials, c.10th–12th century in date, were recovered.

Southern Pemba supports coral reefs, mangroves, intertidal and subtidal flats with seagrass beds and algal growth. The continental shelf is narrow and deep waters lie close to the shore. This combination of characteristics has resulted in high coastal species diversity. Around Ras Mkumbuu, the peninsula is surrounded by expansive sand and mudflats fringed by coral reef and containing areas of patch reef. Mangroves are common around the mouths of rivers and creeks and in the sheltered bays of this area. There are rocky outcrops and headlands with small isolated sandy beaches in small bays and rocky inlets. The expansive intertidal sand and mudflats backed by mangrove forests support high taxonomic diversity (Richmond, 2014).

2.3.3 Northern Unguja: Fukuchani and Mvuleni

The northern coast of Unguja is characterised by expansive sand flats and rocky platforms, seagrass beds, patch, and fringing reefs, with little representation of mangrove communities (Richmond, 2014).

The site of Fukuchani is situated on the northwest coast of Unguja, opposite Tumbatu Island. It comprises ten mounded midden deposits (c.2 m × 10 m) running parallel to the coastline and the remains of daub structures (Horton and Middleton, 2000; Horton and Chami, 2018). Three trenches excavated by the Sealinks Project in 2011 (FK10, FK11, FK12) revealed Middle Iron Age occupation evidence, with radiocarbon dates and diagnostic ceramics indicating site use in the 7th–8th centuries CE (c.1,350–1,450 BP). In addition to substantial midden deposits, wild terrestrial vertebrate fauna, near-shore marine fish (primarily reefs and estuarine), Middle Eastern trade wares, Early Tana Tradition/Triangular Incised Ware (ETT/TIW) ceramics, shell and glass beads, and charred millet grains were recovered (Crowther et al., 2016; Prendergast et al., 2017). Fukuchani's molluscan assemblages were presented in Faulkner et al. (2018), with the initial analyses suggesting a primary focus on rocky habitat taxa akin to reef sweeping. The Fukuchani assemblages are reanalysed here, combining data from the three trenches and reassessing taxonomic composition and habitat at a higher resolution.

Mvuleni is a late 16th–17th-century Portuguese site located at the foot of an escarpment c.750 m inland from Fukuchani with evidence for commercial farming (e.g., tobacco). The site was investigated through detailed mapping and photogrammetry, shovel-test pit (STP) survey, and test and block excavations to identify activities and implications for Portuguese-Swahili interactions in a rural setting (LaViolette and Norman, 2023). A large central house/warehouse dominates, built by Swahili craftsmen of mortared coral-rag, surrounded by a loopholed coral-rag wall. The walling extends north around space where the coralline substrate is at ground surface and a staircase with access to a shallow limestone cave with brackish water; there is local memory of fresh water there. The walling extends south around a 2ha plot of farmland, evidence for earth-and-thatch structures, and latrines and washing spaces. Inside, a small bastion juts out from the seaward wall. STPs and excavations around the bastion revealed the highest density of midden materials at the site, including locally made and European ceramics, a game token and marble, iron knife, crossbow bolt, animal bone (analysis of which is ongoing), and many kgs of burned mussel and crab shell. On the escarpment are 170 m of unmortared coral-rag walls which provided an extraordinary view of activity in Tumbatu and Zanzibar Channels.

2.3.4 Southern Unguja: Unguja Ukuu, Kuumbi Cave and Mifupani

Unguja Ukuu is located on Menai Bay, on the southwest coast of Unguja. Menai Bay is characterised by extensive algal flats and seagrass beds, with patch reefs in deeper parts of the bay, and fringing reefs on the seaward edge of the rocky platforms and small islets. The eastern shore of Menai Bay is a back-reef shoreline, or intertidal shelf, containing incised tidal channels, and extending up to 2 km offshore to the fringing reef system. Mangroves occur in the northern, western, and eastern margins of the bay, with dense forests associated with Uzi Creek and Channel (Berkström et al., 2013; Punwong et al., 2013b; Yahya, 2013; Kotarba-Morley et al., 2022).

Unguja Ukuu is a large proto-urban centre and significant trading port. Based on numerous radiocarbon dates and presence of diagnostic ceramics, occupation there dates to the Middle Iron Age, 7th–10th centuries CE (c.1,350–1,050 BP) (Crowther et al., 2016). Earth-and-thatch structures are associated with significant vertebrate assemblages and middens, as well as evidence for a mix of industrial (lime burning, iron slag) and domestic activities. Similar to Fukuchani, ETT/TIW ceramics and shell and glass beads were recovered, in addition to bead grinders, local and imported trade wares, and African and Asian crops. The vertebrate evidence indicates caprine herding, wild animal exploitation, and the remains of fast-swimming fish (tuna, potentially shark) from deeper waters alongside the reef and estuarine taxa (Juma, 2004; Crowther et al., 2016; Prendergast et al., 2017; Culley et al., 2021). Geoarchaeological evidence from two trenches (UU11, UU14) provide a c.200–350-years sequence of geomorphological change and coastal progradation, combined with increasing human occupation, deposition of anthropogenic debris and potentially land clearance for agricultural activity (Kotarba-Morley et al., 2022; see also Fitton, 2017). Molluscan remains from four of five trenches excavated by the Sealinks Project in 2011–2012 (UU11, UU13, UU14, UU15) were published by Faulkner et al. (2018), focusing on establishing basic assemblage structure and an initial understanding of the mollusc exploitation there. As with Fukuchani, data from the four trenches are combined and reanalysed here to enable robust comparisons with the other assemblages.

Kuumbi Cave is in the Jambiani district of southwest Unguja, c.2.5 km from the present coastline. One of a series of solutional limestone caves within marine limestone terraces of Pleistocene age (Kourampas et al., 2015), from c.20,000 BP the site would have been no more than 7–8 km from the shore due to the steep continental shelf off eastern Unguja (Prendergast et al., 2016). The excavations, stratigraphy, and chronology from the 2012 Sealinks Project excavations have been previously detailed (e.g., Kourampas et al., 2015; Prendergast et al., 2016; Shipton et al., 2016; Faulkner et al., 2019a). The terrestrial and marine molluscan assemblages reported in Faulkner et al. (2019a) focused on the role of these resources in long-term coastal economic adaptations. Highlighted was the use of different intertidal habitats through time relative to postglacial sea level rise, with people using a generalised, sweeping strategy of habitat foraging. Here we restructure and re-analyse the Kuumbi marine molluscan assemblages, with these data falling within four main chronological phases: a late Pleistocene occupation (combining the previously identified Phases 3 and 4) that spans c.20,000–17,000 BP; terminal Pleistocene-early Holocene (Phase 2: c.13,000–11,000 BP); and separating the Phase 1 layers reported in Faulkner et al. (2019a) into the Middle Iron Age (as 1B: c.1,350–1,000 BP) and Late Iron Age (as 1A: c.1,000 to 500 BP) following Prendergast et al. (2016).

On the southeastern coast of Unguja, northeast of Kuumbi Cave, research undertaken in Mifupani village provides a robust sample of modern mollusc harvesting. The people of Mifupani gain their livelihood participating in the tourist industry, fishing, mollusc gathering, horticulture, raising livestock, and some hunting. Sarathi (2020) conducted a 12-months subsistence study of fish and invertebrates gathered there for comparison with archaeofaunal datasets; the marine vertebrate data are not considered in the analyses below as our focus is on intertidal foraging and molluscan assemblages. People can forage along the sandy beach, across the intertidal platform comprised of rock, sandy substrate and seagrass, and onto subtidal reef fringing the intertidal zone c.2–3 km from shore. Although people forage for bivalves (*Donax incarnatus*) by digging through sand, most mollusc gathering occurs on the intertidal reef flat or just beyond it (Sarathi, 2020). The Mifupani study complements socio-ecological research in Nungwi, Chwaka Bay and Menai Bay (Nordlund et al., 2010; Yahya, 2013; Fröcklin et al., 2014), but is more longitudinal and comprehensive, providing a modern baseline that can be used alongside archaeomalacological datasets on Pemba and Unguja.

2.4 Palaeoenvironmental context

Assessment of relative sea levels in the southwestern Indian Ocean has indicated a high degree of regional complexity in the timing and nature of post-glacial sea levels. Variability in relative sea levels across this broad area is likely due to glacio-isostatic processes, tectonic movement, and changing oceanographic conditions (e.g., Pirazzoli, 1991; Camoin et al., 1997; Woodroffe et al., 2015; Prendergast et al., 2016). Regionally, there appear to be two broad types of relative sea level patterns

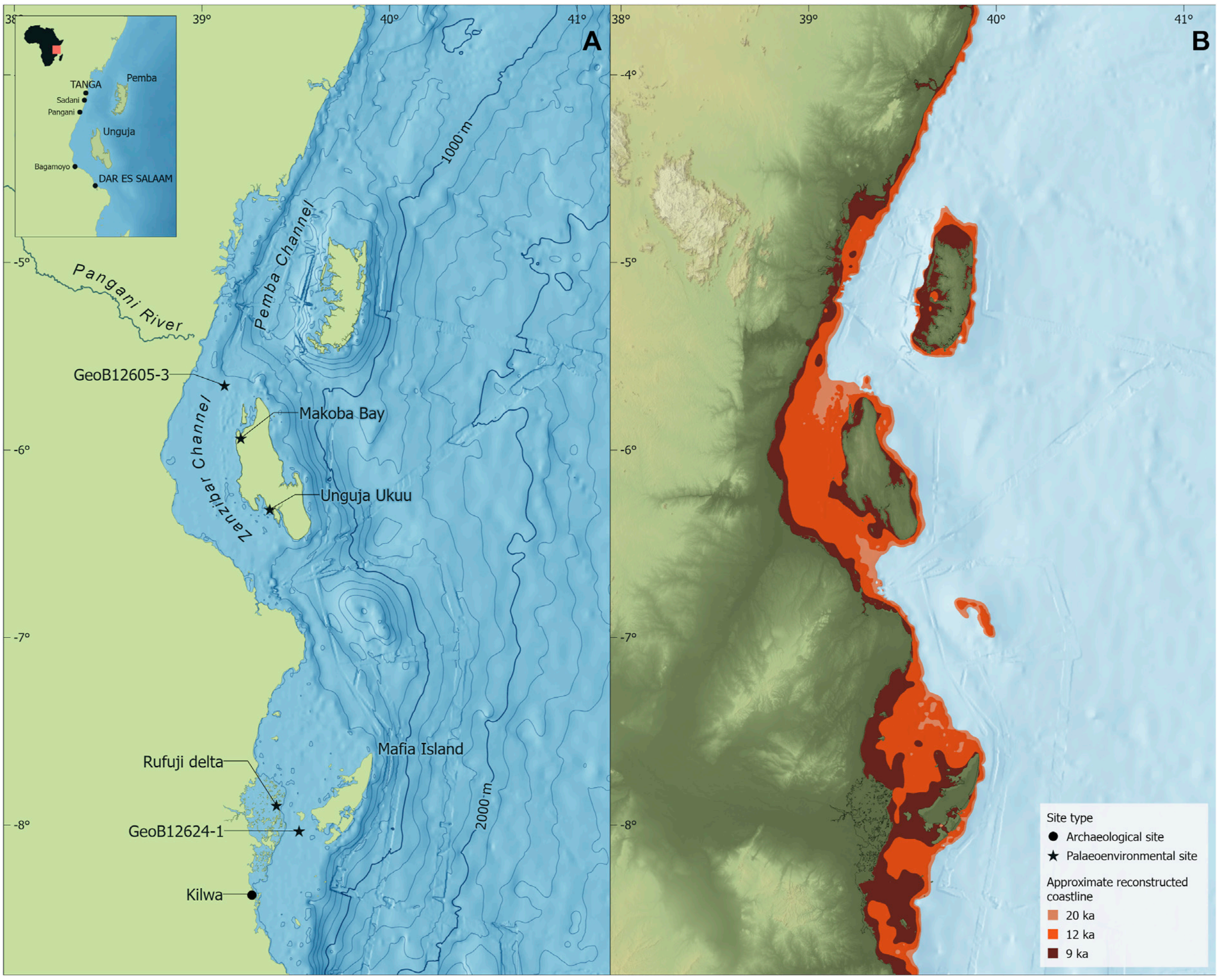

FIGURE 2
Bathymetry of the Tanzanian coast and Zanzibar Archipelago, including the location of the marine sediment cores for sea level and palaeoenvironmental reconstruction **(A)**. Reconstructed sea levels at c. 20,000, 12,000 and 9000 BP **(B)** after Prendergast et al. (2016). Map created using ArcGIS Pro 2.9.1. Bathymetric data from GEBCO Compilation Group. (2021), administrative boundaries from GADM (2022).

(Camoin et al., 2004; Woodroffe and Horton, 2005). The first represents a constant rate of sea level rise to 3,000–2,000 cal BP without evidence for a mid-to late Holocene highstand. This pattern appears prevalent on offshore volcanic and coral islands, e.g., Réunion, Mauritius, Mayotte, and the Seychelles (Colonna et al., 1996; Camoin et al., 2004; Woodroffe et al., 2015). The second pattern, following a rapid rise during the terminal Pleistocene-early Holocene, indicates a highstand in the order of 2.5–3 m above present c.6,000 cal BP, with a subsequent slow regression to present levels in the late Holocene. This second pattern has been identified in Madagascar, and on the Kenyan and Mozambican coasts (Camoin et al., 2004; Woodroffe et al., 2015; Accordi and Carbone, 2016).

The recent reconstruction of relative sea levels presented by Prendergast et al. (2016) provides a localised sea level curve for the Zanzibar Archipelago over the last 20,000 years. As Pemba Island effectively lies off the continental shelf, it was isolated during the Last Glacial Maximum (LGM) (and since the early Pliocene; Rowson et al., 2010) due to lower sea levels and the 800 m deep Pemba Channel (Stagna et al., 2022). The Prendergast et al. (2016) model indicates that Unguja was connected to the mainland until c.9,000 BP, with a phase of more rapid sea level rise between c.12,000–9,000 BP (Figure 2; Figure 3A). This accords well with two pulses of rapid sea level rise recorded in Mayotte in the Comoros, dated between 12,800 and 12,400 BP and between 10,100 and 9,600 BP, followed by a gradual increase to roughly present levels from c.7,000 to 1,500 BP (Colonna et al., 1996). The sea level model is also largely supported by mangrove observational data from the Rufiji Delta (Punwong et al., 2013a) on the southern mainland Tanzanian coast, as well as in Unguja Ukuu and Makoba Bay (Punwong et al., 2013b, 2013c; Woodroffe et al., 2015) in the

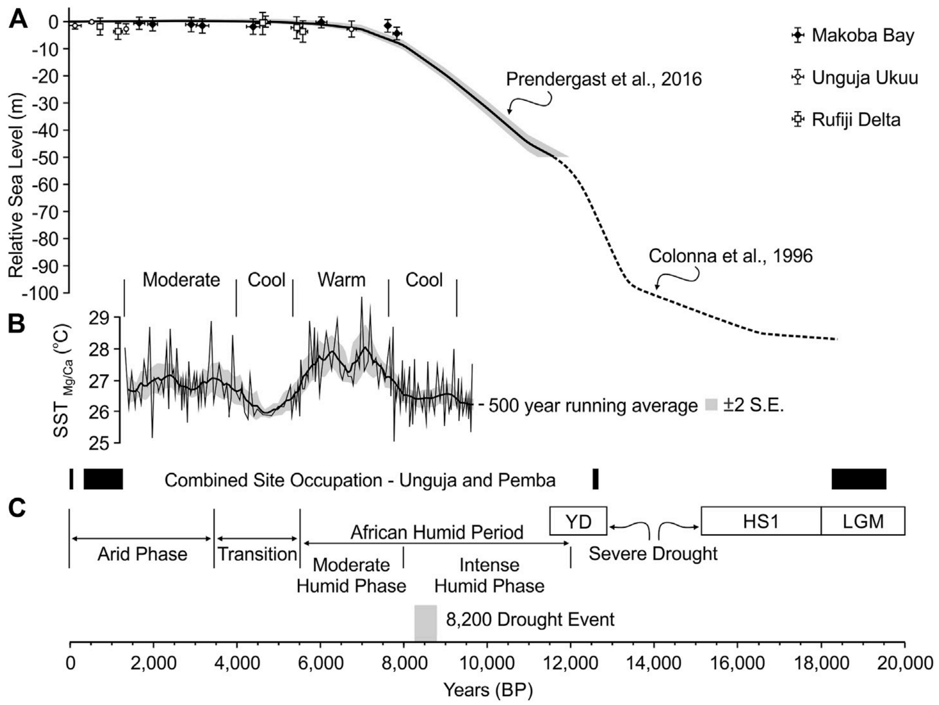

FIGURE 3
Composite sea level curve spanning 20,000 BP to present **(A)** adapted from Colonna et al. (1996) with permission from John Wiley & Sons (order no. 5334670340538); Prendergast et al. (2016); high resolution SST record, Pemba/Zanzibar Channel **(B)** adapted from Kuhnert et al. (2014) with permission from Cambridge University Press (order no. 5334730499127); combined site occupation chronology for Unguja and Pemba (see Table 1 for further site-specific chronological and assemblage details) and major climatic phases since the LGM in eastern Africa **(C)** based on information in Liu et al. (2018).

southwest and northwest of Unguja Island. Sea surface temperature (SST) varies through time, with cooler periods from 9,700 to 7,800 cal BP and 5,600–4,200 cal BP, interspersed with warm (7,800–5,600 cal BP) and moderate (4,200–1,350 cal BP) temperatures (Figure 3B). Within these overall trends are high-frequency SST variations at centennial scales (Kuhnert et al., 2014).

Importantly, these mangrove data also indicate a phase of early to mid-Holocene sea level rise and late Holocene sea level fluctuation, with sea levels potentially higher than present at c.4,700–4,600 cal BP. Although variable in the rate and timing of sea level rise, it appears that sea levels possibly increased to 0.5–0.6 m above present at Makoba Bay and Unguja Ukuu. This minor increase above present levels is partly supported by the observations of maximum erosional notches on undercut limestone cliffs on Unguja (Arthurton et al., 1999), estimated to approximate that of contemporary higher water levels at spring tides. Mangrove development continued after the mid Holocene, with lower sea levels around c.4,000 cal BP and c.2,000 cal BP, albeit with variability in the nature of fluctuations between locations attributed to local mangrove response to sedimentation and/or erosion (Punwong et al., 2018). For example, at Makoba Bay, sea levels rose after 1,550–1,450 cal BP, whereas at Unguja Ukuu, the mangrove observational and archaeological data suggest sea level was 0.5–1 m below present levels between c.1,300 and 1,000 cal BP, followed by a more recent transgressive episode (Mörner, 1992; Punwong et al., 2013b, 2013c; Prendergast et al., 2016; Punwong et al., 2018). Although mangrove communities have been a feature of the Unguja and Pemba coastlines from c.8,000–7,000 years ago, there is evidence for a reduction in the extent of mangroves (e.g., around Unguja Ukuu) since c.530 cal BP. This reduction has been linked to increasing use of mangrove wood as construction material and fuel (Punwong et al., 2013b).

Modern development of the expansive reef systems fringing Unguja and Pemba was likely initiated in the early Holocene based on sea levels, with reef accretion tracking sea level rise (albeit with a time lag between sea level rise and reef growth) until the reefs reached their near-surface position by the mid-Holocene (Camoin et al., 1997; Camoin et al., 2004). By that time, rising sea levels would have breached the ocean-facing fringing reefs to cover the limestone platforms noted above. The flooding of these platforms would have significantly increased reef system development and intertidal/shallow subtidal habitats around the islands (Arthurton et al., 1999; Arthurton, 2003). In combination with these processes, relatively low sedimentation rates identified for Unguja Ukuu and Makoba Bay (0.3–6.6 mm cal yr^{-1}) on Unguja indicate minor progradation effects in the archipelago (Punwong et al., 2018), at least until the latter half of the first millennium CE with increased anthropogenic impacts associated with coastal settlements (e.g., Fitton, 2017; Kotarba-Morley et al., 2022).

Palaeoclimatic evidence from eastern Africa indicates temporal and spatial complexity since the LGM (Figure 3C). As summarised by Liu et al. (2018) in comparing broader climatic records with a marine sediment core extracted 40 km offshore, from the mouth of the Rufiji River (GeoB12624-1), the LGM is broadly characterised by arid conditions, with two distinctive dry-wet periods (at 15,000–14,500 BP and 11,500–11,000 BP). The latter mark the transition into the African Humid Period of the late Pleistocene-early Holocene. Severe drought would have been experienced in the area north of 8–10°S during the Heinrich Stadial 1 (c.18,000-14,600 BP) and the Younger Dryas (c.12,800–11,500 BP), which includes the Zanzibar Archipelago. The African Humid Period represents a significant phase of climate change across the continent during the Holocene. Based on analyses of marine sediments and benthic foraminifera extracted from an offshore core located c.20 km from the Pangani River mouth, at the western transition between the Pemba and Zanzibar channels (GeoB12605-3), the African Humid Period is represented by two regional phases. The first is an intense humid period from c.12,000 to 8,000 cal BP (with an abrupt drought event around c. 8,200 cal BP), with a second, moderate humid phase from 8,000 to 5,500 cal BP. These humid phases were followed by a transitionary period between 5,500 and 3,500 cal BP and a broad late Holocene arid phase (Romahn et al., 2015; Liu et al., 2017). Evidence of sedimentation rates from this core supports these broad climatic phases, with continuous sedimentation between 9,700 and 1,350 BP, although at a decreasing rate from the core base to the top. The higher sedimentation rates between 9,700 and 8,000 cal BP are attributed to lower sea levels and increased precipitation in the Tanzanian hinterland, followed by a decrease in sedimentary input due to increasing aridity and higher sea levels in the mid to late Holocene (Kuhnert et al., 2014; Liu et al., 2016). More recent climatic fluctuations occur across eastern Africa, with increased aridity from c.950-680 BP, wetter conditions from c.680 to 100 BP, and persistent drought conditions spanning the late 18th and early 19th centuries (Lane and Breen, 2018).

There are gaps in the known occupation sequences for Unguja and Pemba, and critically between c.12,000 and 1,500 BP which represents a period of significant environmental change connected to sea-level rise, separation of Unguja from the mainland and broad climatic fluctuations. Nonetheless, reviewing the baseline paleoenvironmental data provides a clear frame of reference for the available archaeological evidence. Importantly for the late Holocene phases of occupation in the archipelago, even accounting for fluctuating sea levels and associated habitat reconfiguration, the nearshore environments around the islands were largely established by c.3,000–2,000 years ago.

3 Materials and methods

3.1 Identification and abundance

All archaeological molluscan assemblages were analysed at the House of Wonders Museum (Beit-el-Ajaib) or the Peace Memorial Museum (Beit-el-Amani) in Stone Town, Zanzibar, between 2013 and 2019. Identifications were made to the lowest taxonomic level possible (family, genus, or species) based on published keys, descriptions, specimen photographs (e.g., Spry, 1964, 1968; Abbott and Dance, 1998; Carpenter and Niem, 1998; Robin, 2008, 2011; Richmond, 2011), and in comparison with the physical reference collections housed at the University of Sydney. Shell modification was also noted, including burning, damage by marine sponges and polychaete worms, drilling and boring, presence of vermetids (sessile gastropods which may attach to other shells), hermitting by crabs, root etching, and dissolution of the shell (chalkiness). Where they do occur, evidence of burning (2.6%–7.2%), hermit crab alteration (0.1%–0.2%) and predatory modification/epibiont adhesions (0.1%–1.7%) are minimally represented across the assemblages. Evidence of water rolling is also minimal, ranging between 0.1 and 3.0% of assemblages, although there is the possibility of these kinds of taphonomic indicators being obscured by the effects of shell dissolution in these sites. No anthropic modification of the shell (i.e., for ornament production or tool use) was recorded for any of the assemblages. Quantification is based on the calculation of the Minimum Number of Individuals following Harris et al. (2015) and Giovas (2009), using a range of taxon-specific non-repetitive elements (outlined in Faulkner et al., 2018; 2019a). Previously published molluscan data from Unguja Ukuu and Fukuchani (Faulkner et al., 2018) and Kuumbi Cave (Faulkner et al., 2019a) have been reviewed, the taxonomic attributions revised where required, and additional habitat data compiled. Similarly, modern molluscan assemblage data has been compiled for the village of Mifupani in the Jambiani district (Sarathi, 2020). The taxonomic attributions for all archaeological and modern assemblages were checked using the World Register of Marine Species (WoRMS Editorial Board 2022) to ensure that the most up to date nomenclature was recorded.

The following methods are applied to the data at genus and species levels separately to investigate variability in foraging at different taxonomic levels. We do not differentiate between taxa identified as economic or incidental taxa. Economic taxa include those species incorporated into the diet and for the production of tools and ornaments, with incidental taxa defined as those likely to represent harvesting by-products (e.g., juveniles, small-bodied taxa) or natural incorporations into the deposit. As our focus is on investigating the nature of intertidal foraging strategies, we view all taxa as representing the intertidal habitats from which they originated regardless of whether they were harvested incidentally, and as such are considered to provide important information linked to foraging across the intertidal zone. The exceptions to this are the small Batillariidae (mudcreepers) and Vermetidae (worm shells) gastropods, as these taxa largely reflect storm surge deposition or are cemented to other mollusc shells (such as *Pinctada* spp.). These taxa have the potential to skew results of the habitat analyses as a result and are therefore excluded. The Polyplacophora (chiton) are included as separate categories within each of the analyses as these taxa have been attributed to class level only within each dataset (and are therefore independent categories).

3.2 Richness, nestedness and taxonomic composition

Taxonomic richness is defined as the number of species or other taxonomic category (family, genus) in a sample, and represented as NTAXA (Grayson, 1984; Lyman, 2008). This is a simple and effective measure of assemblage richness, provided that the taxonomic categories identified for analysis are independent, although it can be adversely affected by sample size and may conceal variability in assemblage evenness/ dominance. As such, it is important to combine species richness with the measures of heterogeneity focused on dominance and/or evenness discussed further below (Magurran, 2004; Santoro et al., 2017).

In ecology and biogeography, nestedness analyses have been used to investigate species composition, distribution, and interactions across continental and island ecosystems (Ulrich and Almeida-Neto, 2012). First described for insular faunas, such as those found on many islands, nestedness has been related to patterns of colonisation and extinction. Therefore, the general expectation is for an ordered pattern of species presence and richness, where the species composition of a small assemblage is a nested subset of a larger assemblage. Similar trends have been identified at the meta-community level, with strong nestedness reflecting species traits and environmental conditions (Bascompte et al., 2003; Ulrich et al., 2009; Ulrich and Almeida-Neto, 2012). In archaeology, nestedness has been used to complement assessment of the relationship between taxonomic composition and sample size. In these analyses, smaller assemblages with low richness should nest within larger assemblages if they have been derived from the same community (e.g., Wolverton et al., 2015; Faulkner et al., 2021). This also has the potential to shed significant light on past human behaviours, such as foraging strategies, selection, and transportation. This is especially true when considered alongside the available environmental and archaeological contextual information to test whether a series of assemblages distributed through time and space may be derived from similar palaeoecological communities (Peacock et al., 2012; Wolverton et al., 2016).

Nestedness analyses are based on species presence-absence data derived from a site or sampling location. The presence-absence matrix is ordered by the most common species (to the upper rows) and locations with the greatest richness (to the left columns), with nestedness indicated by the concentration of species present in the upper left matrix corner (Ulrich and Almeida-Neto, 2012). The most typically used method of quantifying nestedness is the matrix temperature measure (T), with values ranging between 100° (no nestedness) and 0° (perfect nestedness) (Atmar and Patterson, 1993; Ulrich et al., 2009). As it appears unclear whether the temperature metric should be applied to networks of interacting species (Bascompte et al., 2003), as is effectively the case in investigating archaeological assemblages derived from the interaction of humans with other species of interest, the NODF metric is also calculated (Almeida-Neto et al., 2008; Ulrich et al., 2009). This measure is based on the standardised differences in column and row fills, combined with the overlap of presences in adjacent columns. The NODF values range from 0 (no nestedness) to 100 (perfect nestedness). Nestedness matrices, metrics and significance (Z-scores and *p*-values) are calculated using the NeD (http://purl.oclc.org/ned) online interface (Strona et al., 2014).

Correspondence analysis and chord distance analysis are used here to explore similarities and differences in the taxonomic composition of the assemblages (e.g., Faith and Lyman, 2019; Harris et al., 2016; Semken and Graham, 1996). Correspondence analysis is a method of ordination that displays the rows and columns of a data matrix as points in corresponding low-dimensional space, such as a bivariate scatterplot. As such, assemblages will plot closer together when similar in taxonomic composition, with taxa plotting closer to those assemblages to which they are more strongly associated (Faith and Lyman, 2019). Chord distance is a metric used for abundance data (as a measure of Euclidean distance between normalised vectors), useful for assessing dissimilarity between samples or assemblages (Legendre and Gallagher, 2001). Chord distance provides a useful measure of dissimilarity as taxa are not heavily weighted when represented by single individuals (Harris et al., 2016). The values derived from chord distance analyses range between 0 (no difference in relative abundance) and $\sqrt{2}$ (no taxa in common) (Faith and Lyman, 2019). Chord distance is calculated as:

$$CD_{jk} = \sqrt{2 - 2\frac{\sum x_{ji}x_{ki}}{\sqrt{\sum x_{ji}^2 \sum x_{ki}^2}}}$$

where $x\,ji$ is the abundance of taxon i in assemblage xki and i is the abundance of taxon i in assemblage k.

The correspondence analyses and chord distance analyses were performed using the PAST Paleontological Statistics Package Version 4.10 (Hammer et al., 2001).

3.3 Diversity indices

Heterogeneity measures can be divided into Type 1 indices that are affected by the occurrence of rare species (richness), and Type 2 indices sensitive to the abundance of the most common species (dominance). Evenness and dominance refer to the distribution of specimens across taxonomic categories. An even assemblage is one where all species are similarly abundant, and an uneven assemblage one where one or few taxa dominate in combination with a high number of rare species (Faith and Du, 2018). The best-known and widely used examples of Type 1 and Type 2 measures in archaeological research are the Shannon (H') and Simpson ($1\text{-}D$) indices respectively (Lyman, 2008; Magurran, 2004).

The Shannon index (H′) measures diversity based on the relationship between species richness (NTAXA) and the relative abundance (MNI) of each taxonomic category. Using taxonomic richness and abundance, this index calculates the likelihood of predicting the taxonomic affiliation of the next individual drawn from a population, assuming that individuals are sampled randomly from an infinitely large population (Magurran, 2004; Gifford Gonzalez, 2018). The Shannon index is calculated from the equation:

$$H' = -\Sigma pi\ (ln\ pi)$$

where pi is the proportional abundance of taxon i.

Shannon index values usually fall between 1.5 and 3.5 (reflecting lower to higher diversity), rarely increasing beyond 4.0 (Magurran, 2004), and as a measure of heterogeneity, this index is sensitive to both richness and evenness (Faith and Du, 2018).

The Simpson index ($1\text{-}D$) represents the probability that two randomly samples individuals will belong to the same taxon. For zooarchaeological assemblages, which are classified as finite samples (Magurran, 2004; Lyman, 2008; Faith and Du, 2018), the unbiased option of the Simpson index is calculated as:

$$D' = \frac{\Sigma ini\,(ni - 1)}{N\,(N - 1)}$$

where ni is the abundance of taxon i and N is the total number of individuals.

Simpson index values fall between a minimum of 1/NTAXA (where all taxa are equally abundant) to approximately equal to one where an assemblage dominated by a single taxon. The Simpson index is usually expressed as $1\text{-}D'$ so that larger values are associated with greater evenness (Magurran, 2004; Faith and Lyman, 2019). Importantly, the Simpson index is less sensitive to variations in richness and sample size effects, has high efficiency, has the greatest discriminatory power for uneven communities, and appears to be less sensitive to inter-site differences than the Shannon index (Magurran, 2004; Faith and Du, 2018).

As with the correspondence and chord distance analyses, the diversity analyses were undertaken using the PAST Paleontological Statistics Package Version 4.10 (Hammer et al., 2001). Confidence intervals at 95% for the Shannon and Simpson indices were generated via bootstrapping (9,999 iterations), with diversity permutation tests (9,999 random permutations) used to assess significant differences in each measure (Hammer and Harper, 2007; Harris et al., 2016; Santoro et al., 2017).

3.4 Molluscan zonation and benthic habitat attribution

Recent investigations of molluscan habitats linked to human foraging undertaken by Harris and Weisler (2017) and Rogers and Weisler (2022) in the eastern Pacific Islands form the methodological basis of the analyses of zonation and benthic habitats on Unguja and Pemba. These authors applied hierarchical classification schemes for marine benthic habitats, with mollusc taxa assigned to discrete environmental/geographic zones and habitats. Environmental zone refers to the location of the benthic community (e.g., shoreline intertidal, reef), with habitat referring to the geomorphological structure (e.g., coral, rock/debris, sand). As a similar, detailed classification scheme has not yet been developed for eastern African coastal and island areas, a modified and simplified scheme is applied to the assemblages from Unguja and Pemba. Simplification of the hierarchical classification scheme also suits the geographical and chronological scale of these analyses, providing an opportunity to develop baseline comparative data across the two islands. It also suits the resolution of the information available for molluscan taxa of the Western Indian Ocean, which demonstrates an extremely high degree of species diversity. For example, there are numerous genera of Polyplacophora with c.40 species from more than three families, c.400 gastropod families with at least 2,500 species, and c.50 bivalve families comprised of more than 800 species (Richmond, 2011). While not all these taxa occur within the Zanzibar Archipelago, it highlights the taxonomic complexity of the region.

We use the major tidal areas of the intertidal zone, moving along the gradient from the shoreline to sublittoral as the initial environmental zone designation. Three broad intertidal zones are defined following Richmond (2011): supralittoral (or supratidal), eulittoral and sublittoral (or subtidal). The supralittoral zone is largely dry, being inundated for only a few days a year. The littoral fringe at the seaward edge of the supralittoral zone is only covered by the sea during spring high tides. The eulittoral zone, falling between mean high and low water neap levels, is exposed on every tide. Finally, the sublittoral zone is permanently submerged,

TABLE 1 Assemblage structure per site, showing richness (NTAXA) and relative abundance (MNI) values. Note: Polyplacophora are included in each taxonomic level as an individual category.

Phase[a]	Approx. Age (BP)	Site	Code	Family level		Genus level		Species level	
				NTAXA	MNI	NTAXA	MNI	NTAXA	MNI
LSA	19,400	Kuumbi Cave 3/4	KC3/4	21	392	18	378	17	340
LSA	12,500	Kuumbi Cave 2	KC2	17	434	17	424	18	364
MIA	1,400	Fukuchani	FK	41	1,363	47	1,044	45	467
MIA	1,200	Unguja Ukuu	UU	41	5,174	62	4,901	64	3,730
MIA	1,200	Kuumbi Cave 1B	KC1B	26	1,200	27	1,167	26	1,110
LIA	750	Kuumbi Cave 1A	KC1A	17	96	15	87	16	78
LIA	700	Ras Mkumbuu	RM	28	1894	33	1873	31	1798
LIA	650	Msuka Mjini	MMJ	24	217	26	206	24	113
Colonial	350	Pango la Watoro	PLW	43	997	64	892	67	726
Colonial	350	Mvuleni	MVU	46	4,167	62	4,059	71	3,512
Modern	0	Mifupani	MFP	47	70,497	93	70,497	124	70,156
Total				76	86,431	151	85,528	208	82,394

[a] LSA, later stone age; MIA-Middle Iron Age; LIA, later iron age.

with the sublittoral fringe bordering the eulittoral on the landward edge only exposed during or near spring low tides. Geomorphic structures, or substrate characteristics, are designated based on the definitions provided in Harris and Weisler (2017). Taxa are also categorised according to their benthic organism type, either as infaunal (those that live and burrow within the substrate) or epifaunal (those that live on or attached to the outer surface of their environment or other organisms).

The compilation of habitat data was undertaken with reference to Abbott (1959, 1960, 1961), Abbott and Dance (1998), Carpenter and Niem (1998), Cernohorsky (1984), Dekker (2018), Harasewych and Moretzsohn (2017), Harris and Weisler (2017), Healy et al. (2011), Lamprell and Healy (1998), Lamprell and Whitehead (1992), Richmond (2011), Shefer et al. (2012), Willan et al. (2015), and Wilson (1993). Data collection was restricted to taxa at genus and species levels, excluding family-only level taxonomic attributions (11 bivalve, 17 gastropod families) in line with the range of analyses outlined above. Reliable habitat information could not be determined for several taxa, with one bivalve genus (8 MNI), three gastropod genera (4 MNI), and 11 gastropod species (combined 378 MNI). The habitat information and coding per taxon are provided in Supplementary Material S1.

4 Results

4.1 Assemblage characteristics

The characteristics of the molluscan assemblages from the eight sites outlined above are presented in Table 1, with the full list of species per site assemblage provided in Supplementary Material S1. The data from Kuumbi Cave are separated into the distinct chronological phases noted above, with all other sites recorded as individual assemblages (i.e., aggregating data into a single site-based assemblage). The assemblages are listed in Table 1 in approximate chronological order, providing details on the number of taxa and relative abundance (MNI) at family, genus, and species levels. The number of taxa and MNI vary considerably across the assemblages, with the highest MNI and/or NTAXA values irrespective of taxonomic level consistently derived from the modern Mifupani dataset, and lowest values from Kuumbi Cave 1A.

To investigate potential sample size effects on assemblage structure and richness, NTAXA values are plotted against MNI at genus (Figure 4A) and species (Figure 4B) levels. At both genus and species levels, the positive relationship indicated by the linear trendline appears to be driven by the large sample size and high richness at Mifupani, although the strength of these relationships is moderate (genus and species R^2=0.499). There is little change when removing Mifupani, with a similarly moderate strength of relationship between NTAXA and MNI (genus R^2=0.506; species R^2=0.519). That said, although individual assessment of the Msuka Mjini, Ras Mkumbuu, Pango la Watoro and Mvuleni assemblages is not currently possible, previous assessment of species area curves for Unguja Ukuu and Fukuchani (Faulkner et al., 2018), and for each chronological phase at Kuumbi Cave (Faulkner et al., 2019a), indicates these assemblages were sampled to redundancy. These results may be seen to indicate that approximately 50% of the variance in NTAXA is explained by sample size, however the degree of data dispersion combined with the differences in site context and chronology (see section 2.3) indicates that a range of human behavioural and environmental factors are likely strong contributors.

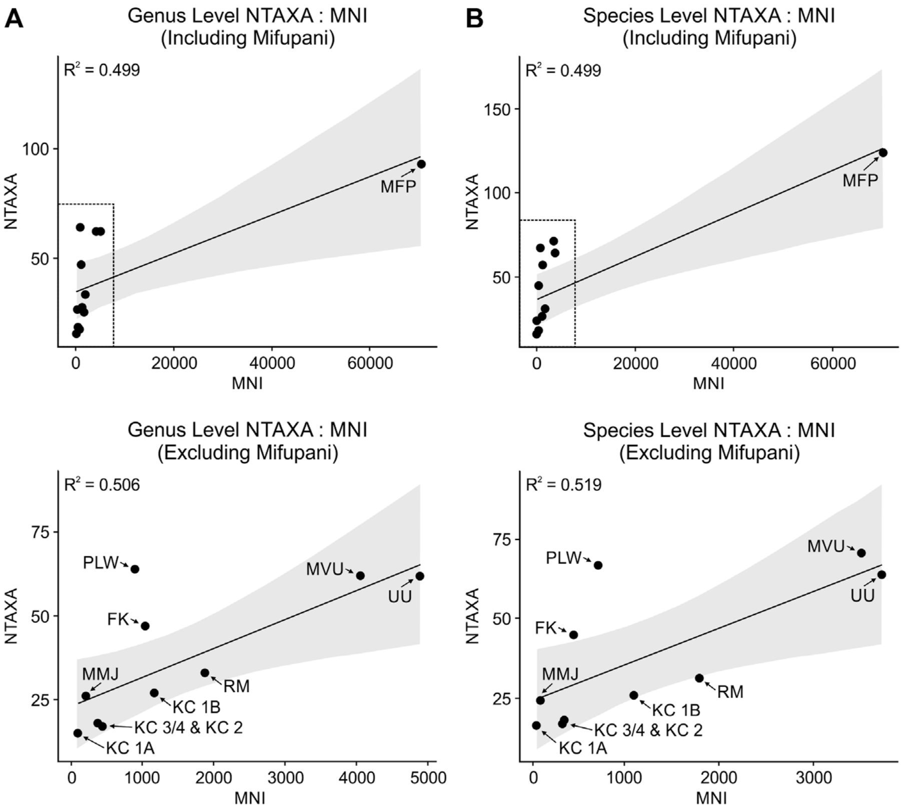

FIGURE 4
NTAXA: MNI plots at genus level **(A)** and species level **(B)**, with linear regression lines and standard error (grey shading). KC 3/4, Kuumbi Cave 3/4; KC 2, Kuumbi Cave 2; FK, Fukuchani; UU, Unguja Ukuu; KC 1B, Kuumbi Cave 1B; KC 1A, Kuumbi Cave 1A; RM, Ras Mkumbuu; MMJ, Msuka Mjini; PLW, Pango la Watoro; MVU, Mvuleni.

4.2 Richness and nestedness

The nestedness results at genus and species levels are relatively similar. The nestedness metrics and significance statistics for the assemblages at both levels are presented in Supplementary Material S2, with the Z-scores and *p*-values (all at $p < 0.001$) for each measure indicating that the assemblages with lower NTAXA values nest within those with higher NTAXA. The nestedness temperature values are low for genus (16.935°) and species (15.532°), indicating a high degree of nestedness for all assemblages. In comparison, the combined NODF values of 57.359 (genus) and 49.611 (species) indicate a moderate rather than high degree of nestedness. These overall NODF values are confirmed by the separate row and column values.

Visual inspection of the genus and species nestedness matrices (Figure 5; with matrix data provided in full in Supplementary Material S3 at genus level and Supplementary Material S4 at species level) provides support for the moderate NODF nestedness results. There is a clear concentration of taxonomic representation in the upper left of each matrix, representing a core group of genera and species common to all assemblages; 27 genera and 25 species occur in 50% or more of the assemblages. The overall distribution of taxa, with what can be described as unexpected absence and presence above and below the diagonal reference lines respectively, indicates imperfect nestedness. This is a result of 124 genera and 183 species being represented in less than 50% of the assemblages. The matrices provide a relative indication of assemblage grouping, with Mifupani separated from Pango la Watoro, Mvuleni and Unguja Ukuu. Fukuchani, Ras Mkumbuu, Kuumbi Cave 1B (MIA) and Msuka Mjini cluster together, with the LSA (KC 3/4 and KC 2) and the LIA (KC 1A) assemblages from Kuumbi Cave falling together.

4.3 Taxonomic composition

Consideration of taxonomic composition provides an indication of similarity and difference between assemblages, effectively building on the nestedness results. The contribution of key taxa (at ≥5% by MNI to one or more of the assemblages) at genus level per assemblage is presented in Figure 6.

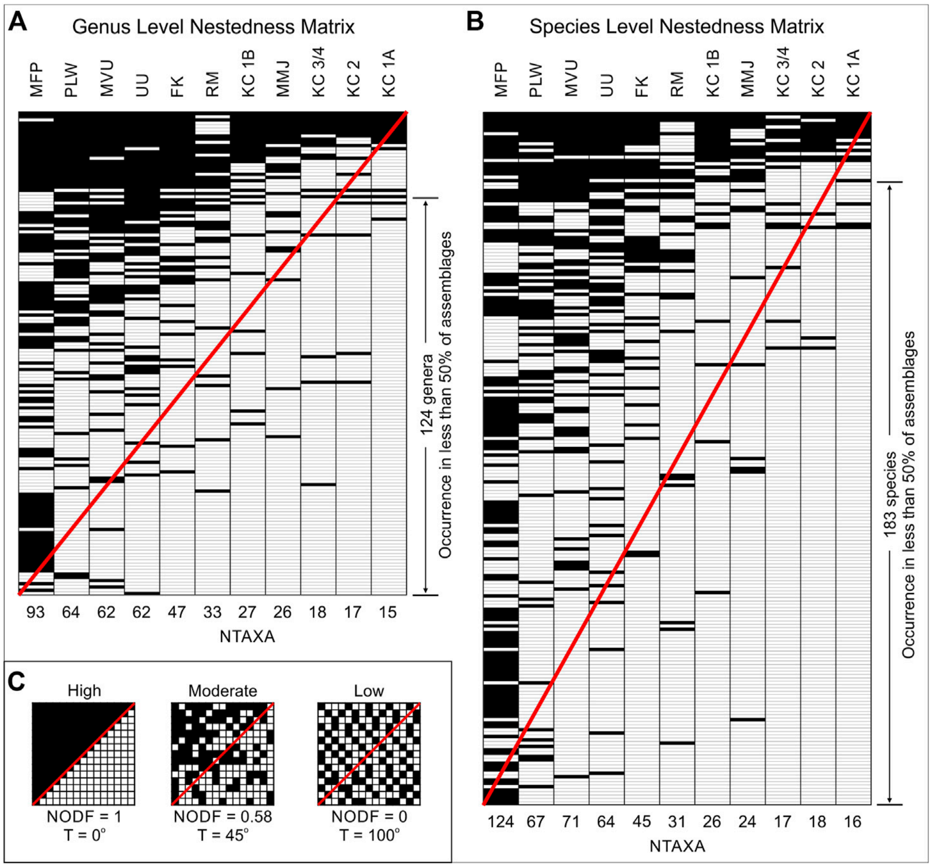

FIGURE 5
Nestedness matrices for the assemblages at genus level **(A)** and species level **(B)**. Red diagonal lines used for visual reference. Example matrices **(C)** showing high, moderate, and low nestedness with associated T and NODF values (adapted from Johnson et al., 2013). MFP, Mifupani; PLW, Pango la Watoro; MVU, Mvuleni; UU, Unguja Ukuu; FK, Fukuchani; RM, Ras Mkumbuu; KC 1B, Kuumbi Cave 1B; MMJ, Msuka Mjini, KC 3/4, Kuumbi Cave 3/4; KC 2, Kuumbi Cave two; KC 1A, Kuumbi Cave 1A.

The four Kuumbi Cave assemblages are dominated by gastropods, primarily by *Nerita* with minor contributions of *Turbo*, *Lunella*, the Polyplacophora and *Monodonta*. Fukuchani and Msuka Mjini have a greater proportional representation of the bivalve *Pinctada*, with variable but comparatively minor contribution to each assemblage by both bivalve and gastropod taxa. Unguja Ukuu has a similar composition, albeit with an increased proportional representation of the bivalves *Anadara* and *Atactodea*, and a lower contribution of a range of other bivalves and gastropods. Pango la Watoro and Mvuleni are dominated by *Nerita*, with minor contributions from *Gibberulus*, *Vasum* and *Saccostrea* at Pango la Watoro. At Mvuleni, a mix of bivalves and gastropods, including *Vasum*, *Pinctada*, *Arca*, *Cerithium* and *Tucetona*, are also strongly represented. In contrast, Ras Mkumbuu is heavily dominated by *Anadara* (c.80%), and Mifupani exhibiting a more even distribution for *Anadara* and *Gibberulus*, followed by *Anodontia*, *Volema* and *Gafrarium*. All other taxa are minor, but more evenly represented in comparison with the other assemblages.

The trends at genus level are largely replicated by species level taxonomic representation (Figure 7), although exclusion of the genus level data forces some reordering depending on level of identifiability. For example, while *Pinctada* was the dominant genus at Fukuchani, species level attributions for this genus were unattainable for this assemblage. As a result, the contribution of several bivalves (*Anadara antiquata*, *Arca ventricosa*, *Atactodea striata*, *Saccostrea cuccullata*) and gastropods (*Pleuroploca trapezium*, *Nerita balteata*, *Lunella coronata*) becomes more apparent.

The chord distance results at both genus and species levels highlight similarities and differences in taxonomic composition between these assemblages (Supplementary Material S2). At genus level, there is minimal dissimilarity noted for some site pairs; between all Kuumbi Cave assemblages, between Pango la Watoro and Kuumbi Cave 3/4, 1B and 1A, and between

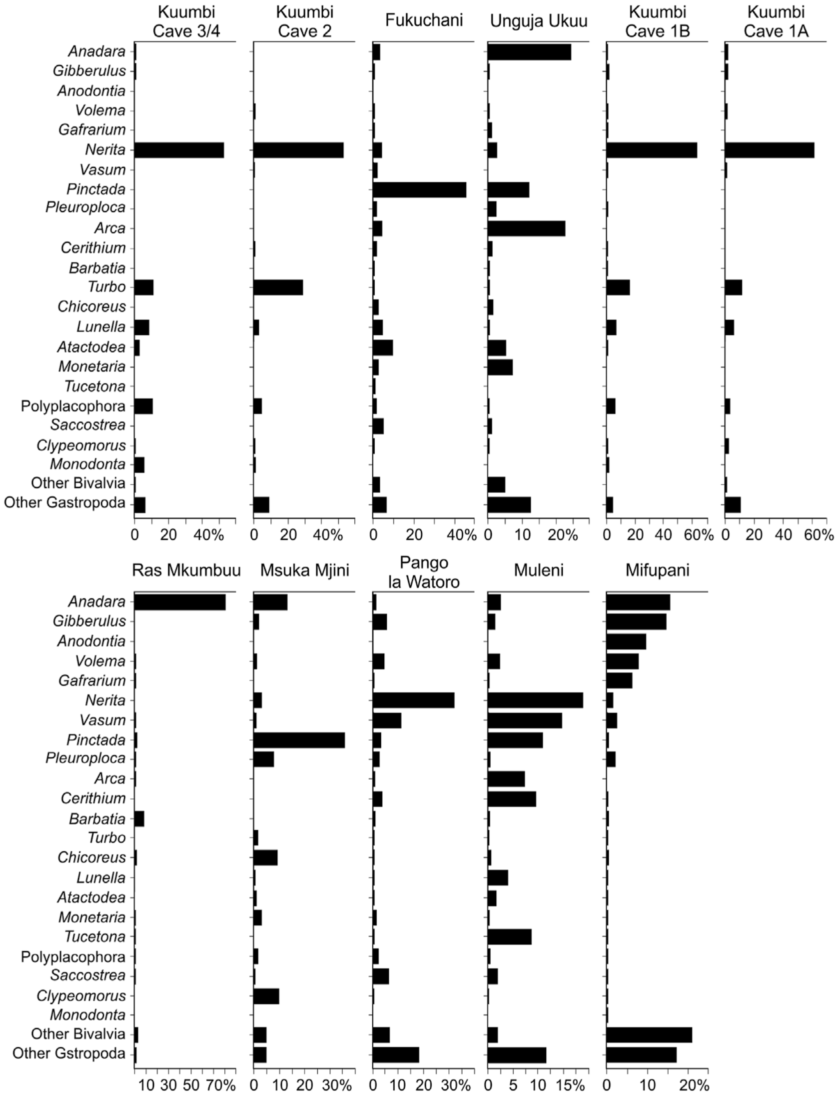

FIGURE 6
Contribution of key taxa (%MNI) at genus level to each assemblage. Each taxon listed contributes ≥5% by MNI to one or more assemblage.

Fukuchani and Msuka Mjini. There is moderate dissimilarity between Mvuleni and all Kuumbi assemblages, as well as Mvuleni and Pango la Watoro. Kuumbi Cave 2 exhibits moderate dissimilarity to Pango la Watoro, as does Unguja Ukuu with both Ras Mkumbuu and Msuka Mjini. Moderate dissimilarity is also exhibited between Kuumbi Cave 2 and Pango la Watoro, and between Ras Mkumbuu and Mifupani. All other assemblage pairs indicate moderate to high dissimilarity at genus level. At species level, only the comparisons between the Kuumbi Cave assemblages indicate minimal dissimilarity. Moderate dissimilarity is exhibited between Pango la Watoro and the Kuumbi Cave assemblages, between Unguja Ukuu and both Ras Mkumbuu and Msuka Mjini assemblages, and between Ras Mkumbuu and both Msuka Mjini and Mifupani. As with the genus level data, most assemblage pairs exhibit moderate to higher levels of dissimilarity.

Correspondence analyses exploring the relationship between taxonomic composition and assemblage variability at genus and species levels reinforce the data presented above (Figure 8). For the genus level correspondence analysis (Figure 8A), axes 1 and 2 account for 37.2 and 25.3% of the variance in taxonomic abundance respectively. Mifupani falls close to the origin, indicating that it is less differentiated or distinct relative to the other assemblages based on taxonomic composition. This is highlighted by the clustering of taxa close to the origin, including *Anadara*, *Barbatia*, *Anodontia*, *Gafrarium*, *Gibberulus* and *Vasum*, which occur across several assemblages but are less discriminating. The Kuumbi Cave

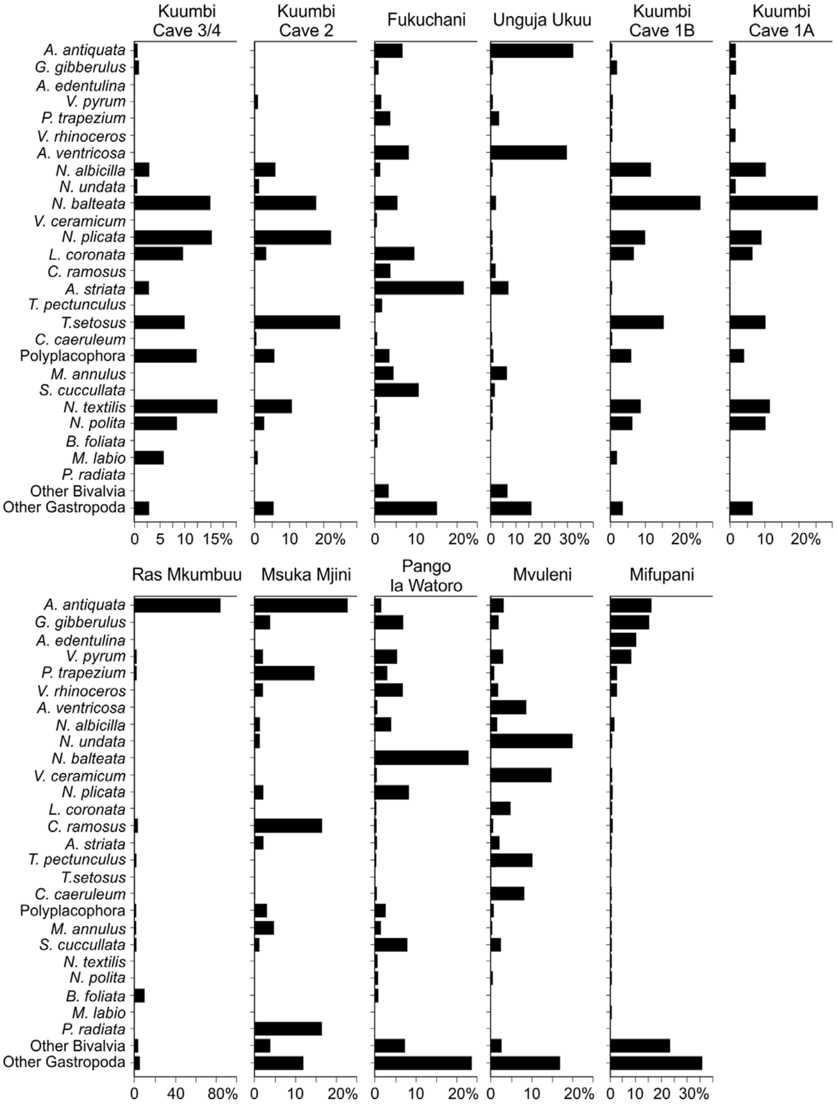

FIGURE 7
Contribution of key taxa (%MNI) at species level to each assemblage. Each taxon listed contributes ≥5% by MNI to one or more assemblage.

assemblages fall positively on axes 1 and 2, cluster closely together, and are more strongly associated with *Monodonta*, *Turbo* and *Nerita*. Similarly, Pango la Watoro and Mvuleni exhibit positive axis 1 and 2 scores, but with Mvuleni falling closer to 0 on axis 2. These assemblages are largely discriminated by *Nerita*, *Lunella* and *Tucetona*, although to a lesser degree than Kuumbi Cave. Somewhat similarly, Ras Mkumbuu falls at 0 along axis 1 and is negatively scored on axis 2. This site sits in closer proximity to Mifupani as it is dominated by *Anadara* and *Barbatia*. Msuka Mjini, Unguja Ukuu and Fukuchani all score positively on axis 1 and negatively on axis 2, and sit within relative proximity indicating greater similarity (particularly between Msuka Mjini and Unguja Ukuu). These sites are associated with *Pinctada*, *Atactodea*, *Arca* and *Monetaria*, with other dominant taxa such as *Anadara* being less discriminating for these assemblages.

For the species level correspondence analysis (Figure 8B), axes 1 and 2 account for 28.9 and 24.9% of the variance in taxonomic abundance respectively. Mifupani retains its position close to the origin, with both Ras Mkumbuu and Msuka Mjini now shifting to fall closer to the origin. This indicates greater similarity in assemblage structure and less discrimination by taxonomic composition at species level. The Kuumbi Cave assemblages retain their discrete cluster and association with *Turbo setosus*, *Monodonta labio* and several *Nerita* species, with Pango la Watoro also falling within a relatively similar position to

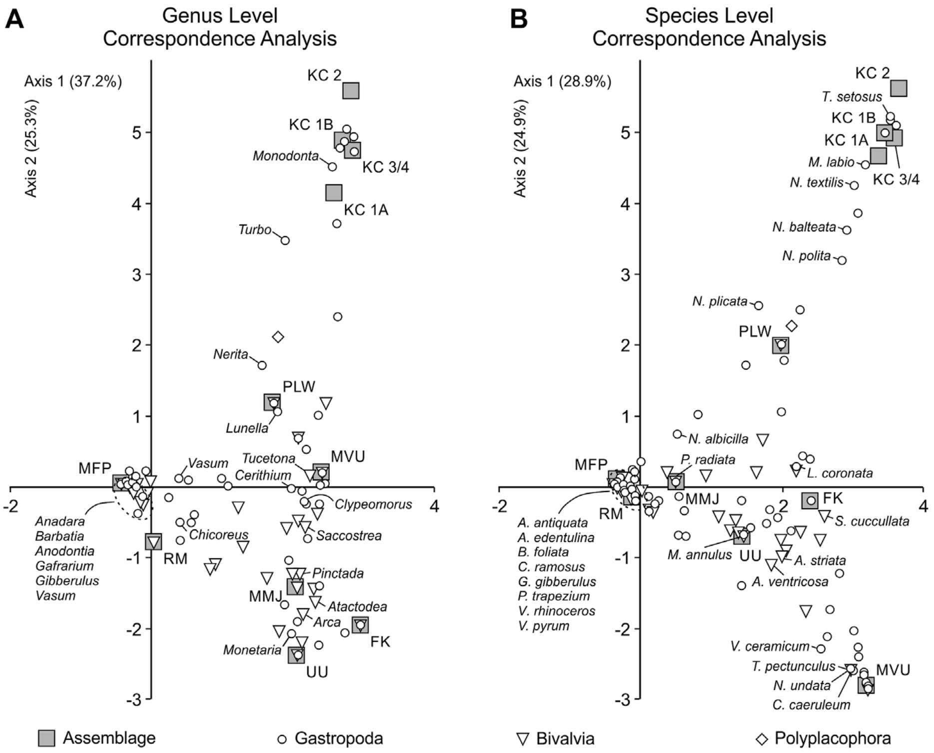

FIGURE 8
Correspondence analysis of taxonomic abundance at genus level **(A)** and species level **(B)**. Key taxa for the combined and individual assemblages (contributing ≥5% by MNI) are labelled. KC 3/4, Kuumbi Cave 3/4; KC 2, Kuumbi Cave 2; FK, Fukuchani; UU, Unguja Ukuu; KC 1B, Kuumbi Cave 1B; KC 1A, Kuumbi Cave 1A; RM, Ras Mkumbuu; MMJ, Msuka Mjini; PLW, Pango la Watoro; MVU, Mvuleni; MFP, Mifupani.

that observed at genus level. The three assemblages that score positively on axis 1 and negatively on axis 2, Unguja Ukuu, Fukuchani and Mvuleni, are associated with different taxa, with Unguja Ukuu falling closer to Msuka Mjini and Ras Mkumbuu (and therefore closer to the origin). Both Fukuchani and Mvuleni are highly differentiated from each other and the other assemblages, with Fukuchani associated with *Lunella coronata*, *Saccostrea cucullata* and *Atactodea striata*, and Mvuleni associated with (and discriminated by) *Vasum ceramicum*, *Tucetona pectunculus*, *Cerithium caeruleum* and *Nerita undata*.

4.4 Assemblage diversity

The Shannon H' and Simpson 1-D values are presented in Table 2, along with richness (NTAXA) and MNI values for each assemblage. The NTAXA, H' and 1-D values are graphed in Figure 9 for visual comparison, with the assemblages in approximate chronological order from the oldest to most recent (left to right).

At genus level (Figure 9A), the H' and 1-D values parallel each other to a large degree. These data indicate a higher degree of diversity for Fukuchani, Unguja Ukuu, Msuka Mjini, Pango la Watoro, Mvuleni and Mifupani, with moderate to high diversity recorded for the four Kuumbi Cave assemblages. Ras Mkumbuu shows the lowest values for both measures of diversity. The results of the diversity permutation tests at genus level (Supplementary Material S2) indicate significant differences for both H' and 1-D between the majority of assemblages. Kuumbi Cave 1A, 1B and 2 are not significantly different, with Kuumbi Cave 3/4 not differing significantly from 1A alone. For H', Fukuchani and Unguja Ukuu are significantly different from each other, but neither are significantly different from Msuka Mjini. For 1-D, only Fukuchani is not significantly different from Msuka Mjini. Across both measures of diversity, Unguja Ukuu, Ras Mkumbuu, Pango la Watoro, Mvuleni and Mifupani are significantly different from all other assemblages.

Both diversity index values are consistently high at species level (Figure 9B), although the H' values show greater variability than those calculated for 1-D. With these data, Fukuchani, Pango la Watoro, Mvuleni and Mifupani demonstrate higher diversity, followed by Kuumbi Cave and Msuka Mjini. For both measures, as with the genus level data, Ras Mkumbuu exhibits substantially lower values in comparison with all other assemblages. The diversity permutation test results at species level (Supplementary Material S2) again indicate significant

TABLE 2 Genus and species level richness and diversity values by assemblage for Shannon H' (upper) and Simpson 1-D (lower) indices.

	KC 3/4	KC 2	FK	UU	KC 1B	KC 1A	RM	MMJ	PLW	MVU	MFP
Genus											
NTAXA	18	17	47	62	27	15	33	26	64	62	93
MNI	378	424	1,044	4,901	1,167	87	1873	206	892	4,059	70,497
H'	1.69	1.42	2.39	2.50	1.44	1.65	0.96	2.37	2.90	2.77	3.06
1-D	0.69	0.63	0.77	0.86	0.58	0.62	0.35	0.83	0.87	0.90	0.92
Species											
NTAXA	17	18	45	64	26	16	31	24	67	71	124
MNI	340	364	467	3,730	1,110	78	1798	113	726	3,512	70,156
H'	2.34	2.12	2.95	2.22	2.27	2.44	0.78	2.57	3.16	2.89	3.14
1-D	0.89	0.84	0.91	0.80	0.86	0.89	0.29	0.88	0.92	0.91	0.93

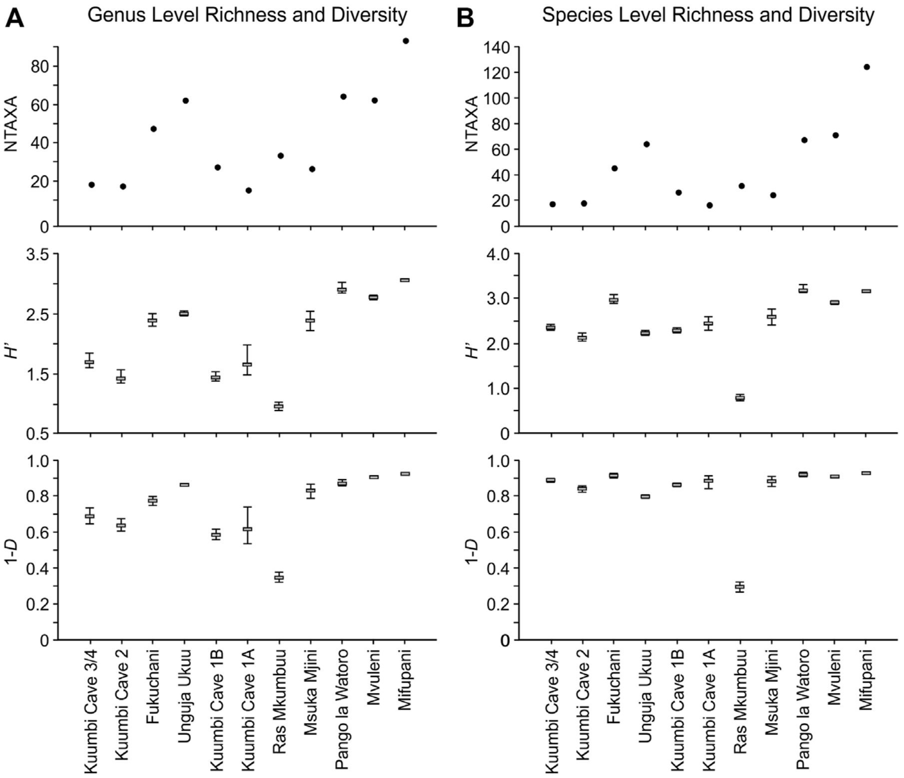

FIGURE 9
Plots of richness (NTAXA) and diversity indices (H' and 1-D) for each assemblage at genus level **(A)** and species level **(B)**. Confidence intervals for each measure are the percentiles bootstrapped at 9,999 iterations.

differences for both H' and 1-D between most assemblages, although these data are more complex than indicated at genus level. For both measures, Kuumbi Cave 3/4 is not significantly different from Kuumbi Cave 1A and Msuka Mjini, and both Fukuchani and Msuka Mjini are not significantly different from Mvuleni. Kuumbi Cave 1A and 1B do not differ significantly from each other, and Msuka Mjini is not significantly different from Kuumbi Cave 1A. At species level, Ras Mkumbuu and Mifupani are consistently significantly different from the other assemblages.

The diversity index values and results of the permutation tests at both genus and species level indicate, for the most part, lack of a clear, directional chronological trend in richness and diversity. Irrespective of assemblage richness, these data largely indicate a moderate to high or high level of diversity, with a degree of variability apparent across assemblages. Regardless of

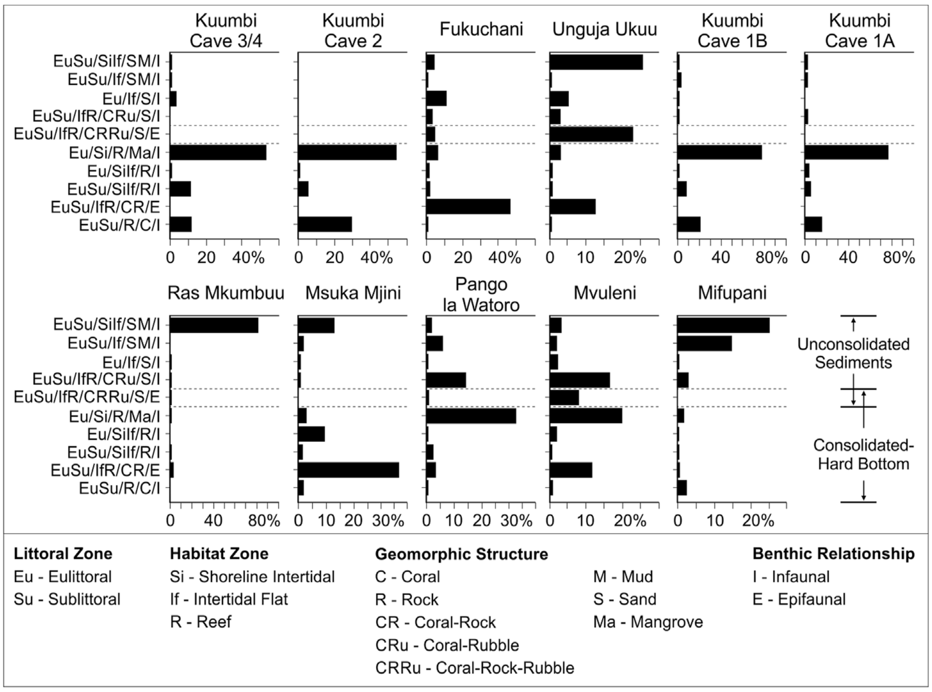

FIGURE 10
Contribution of dominant habitat zones (%MNI) at genus level to each assemblage. Each habitat listed contributes ≥10% by MNI to one or more assemblage. See Supplementary Material S1 for further information on habitat code definitions.

taxonomic level and diversity measure, Mifupani and Ras Mkumbuu are consistently separated from all other assemblages; Mifupani for its high richness and diversity, Ras Mkumbuu for its low richness and significantly lower levels of diversity.

4.5 Zonation and benthic habitat analysis

Habitat categories identified for taxa at genus and species levels are presented in Figures 10, 11. In both cases, the dominant habitat areas that represent ≥10% by MNI of one or more assemblage are included. At genus level, 10 habitat categories represent between 47% (Mifupani) and 88% (Kuumbi Cave 2) of the total assemblages, and at species level 16 habitat categories represent between 65% (Mifupani) and 99% (Kuumbi Cave 3/4) of the total assemblages.

At genus level (Figure 10), Kuumbi Cave shows a consistently high representation across all occupation phases of taxa from mangrove, rock and coral substrates across shoreline intertidal to intertidal flat habitats (76%–88% MNI), with minimal representation of taxa from sand and/or mud substrates from shoreline intertidal, intertidal flat and reef habitats (2%–4% MNI). Kuumbi Cave 2 only contains taxa from consolidated/hard substrates. Fukuchani (46% MNI) and Msuka Mjini (37% MNI) are both dominated by taxa from coral and rock substrates in intertidal flat-reef habitats, with molluscs from a range of habitats and soft substrates comprising 21 and 17% MNI at these sites respectively. Pango la Watoro and Mvuleni exhibit similar distributions, with both containing proportionally higher intertidal flat-reef coral and rubble taxa (14 and 16% MNI respectively) and shoreline intertidal rock/mangrove taxa (32 and 20% MNI respectively). Unguja Ukuu contains a higher proportion of shoreline intertidal-intertidal flat sand and/or mud taxa (26% MNI), intertidal flat-reef coral, rock, rubble and sand taxa (23% MNI), and intertidal flat-reef coral and rock taxa (12% MNI). Ras Mkumbuu and Mifupani exhibit very different patterns of habitat representation. Mifupani contains a combined 40% MNI of taxa from shoreline intertidal-intertidal flat sand/mud habitats, with a lower proportional representation across all other habitat categories. Ras Mkumbuu contains 81% MNI of taxa from shoreline intertidal-intertidal flat sand and/or mud substrates, being the assemblage most skewed towards a single habitat zone.

As with the results of taxonomic representation above, the trends in proportional habitat designations at genus level are largely reproduced at species level (Figure 11). The exclusion of the genus only level data shifts the proportions of some habitat zones, as well as expanding on the range of identified habitat

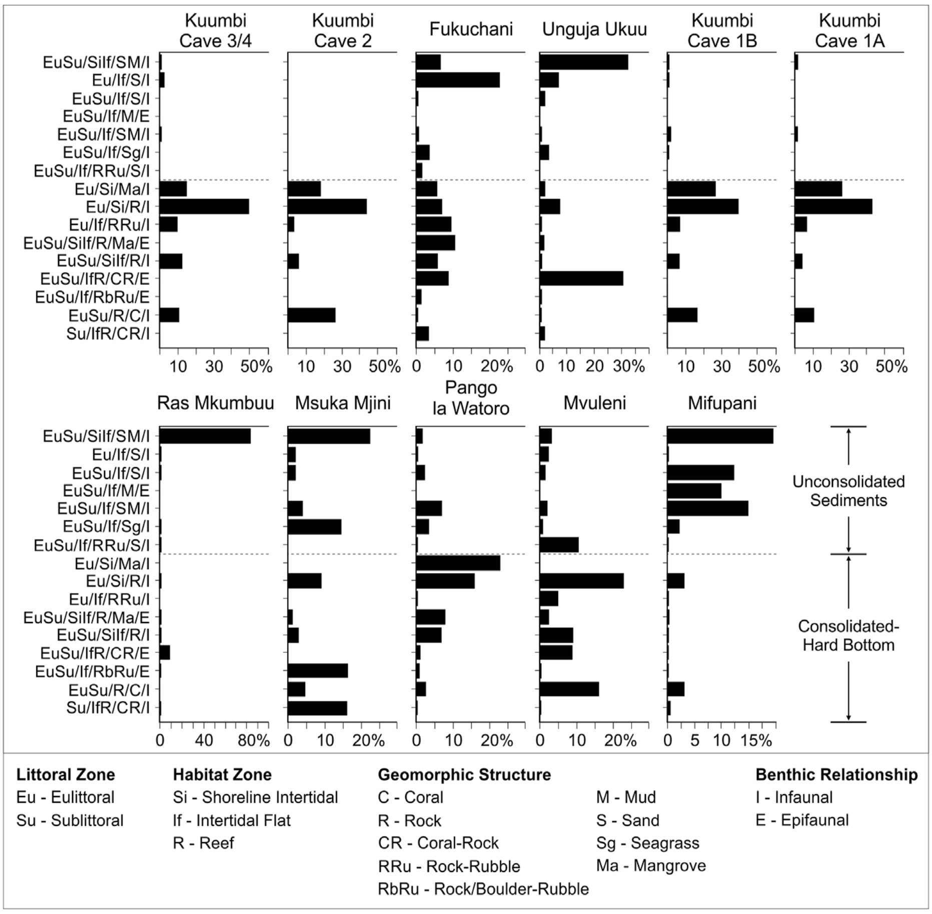

FIGURE 11
Contribution of dominant habitat zones (%MNI) at species level to each assemblage. Each habitat listed contributes ≥10% by MNI to one or more assemblage. See Supplementary Material S1 for further information on habitat code definitions.

categories, moving from more inclusive genus to more exclusive or explicit species categories. That said, the distributional patterns are similar across the taxonomic levels. This is particularly the case with the degree of skew in the data from the four Kuumbi Cave occupation phases, Ras Mkumbuu, and Mifupani. The habitat distributions from Fukuchani, Msuka Mjini, Pango la Watoro, and Mvuleni are still concentrated within particular habitat areas, but there is now a slightly flatter distribution, with the peaks observable in the genus level data being slightly reduced or redistributed. In contrast, the species level habitat distribution for Unguja Ukuu now shows a greater proportional representation in the shoreline intertidal-intertidal flat sand and/or mud habitat (33% MNI) and the intertidal flat-reef coral/rock habitat (30% MNI), with all other habitat zones being substantially reduced.

The chord distance results for habitat representation highlights several key similarities (Supplementary Material S2). Kuumbi Cave demonstrates minimal dissimilarity between all occupation phases regardless of whether habitat representation is viewed at genus or species level. Similarly, there is moderate dissimilarity when comparing Unguja Ukuu with Fukuchani, Ras Mkumbuu and Msuka Mjini. Moderate dissimilarity is noted between Pango la Watoro and Mvuleni, and between both sites relative to all Kuumbi Cave phases. Mifupani exhibits moderate dissimilarity when compared with Unguja Ukuu, Ras Mkumbuu and Pango la Watoro. The main differences in chord distance are slightly increasing values from genus to species when comparing Mvuleni with both Fukuchani and Unguja Ukuu, with slightly decreasing values exhibited from genus to species when comparing Msuka Mjini with both Ras Mkumbuu and Mifupani. The major difference in habitat representation occurs between Fukuchani and Msuka Mjini, increasing from minimal to moderate-high dissimilarity from genus to species. All other comparisons present moderate to higher levels of dissimilarity.

5 Discussion

In their review of the Swahili coast zooarchaeological record, Quintana Morales and Prendergast (2018) highlight a chronological trajectory in the exploitation of terrestrial and marine fauna. The earliest coastal records indicate a focus on wild terrestrial game, fishing and mollusc harvesting, with marine resource use continuing with the incorporation of food production while wild terrestrial hunting reduced through time. Between the first and second millennium CE, as socio-economic structures shifted concomitant with increasing urbanism, social changes and long-distance trade, people focused more intensively on domesticated animals and offshore marine environments. Interestingly, this perspective connects to terrestrial vertebrates and marine fish resources more than mollusc foraging (Quintana Morales et al., 2022), as any shift away from the shoreline and broader intertidal zone is not reflected in the archaeological or modern socio-ecological data. Although available data indicate the maintenance of intertidal foraging as an economic activity in the Zanzibar Archipelago, as people engaged with the intertidal zone in complex ways, key differences in nearshore marine foraging occur through time and space.

The Kuumbi Cave data indicate different behaviours to those seen in the other assemblages from Unguja and Pemba. Across the four occupation phases there is a pattern of low richness and moderate to high diversity in assemblage structure, representing a small number of key taxa harvested from across the intertidal gradient, but with an emphasis on mangrove, rock, and reef hard-substrate gastropod species (e.g., *Nerita* spp, *Turbo* spp. And *Lunella coronata*). Interestingly, these characteristics are consistent across all occupation phases irrespective of chronology, changing sea levels or climatic fluctuation, being evident in the two LSA phases at c.19,400 (KC 3/4) and 12,500 BP (KC 2), and in the MIA and LIA phases at c.1200 (KC 1B) and 750 BP (KC 1A). This indicates accessibility of shoreline, intertidal flat and reef habitats on Unguja's eastern coast before separation of the island from the mainland c.9,000 BP, and into the late Holocene. Due largely to the steep bathymetry off the eastern Unguja coast, in a broad sense there has been comparatively minimal change in the structure of the dominant coastal habitats through time. Environmental composition and availability of taxa, however, are not the primary determinants of the Kuumbi Cave assemblage characteristics, as we would expect a range of intertidal flat habitats to have been accessible throughout the last 20,000 years. As *in situ* processing of harvested molluscs on the coast is likely, followed by differential transportation (sensu Bird et al., 2002; Meehan 1982), the nature of intertidal foraging during the LSA and prior to island formation cannot be easily identified, although the MIA/LIA assemblages give some indication of likely foraging behaviours that connect to the two late Holocene Kuumbi Cave occupation phases. The re-analyses of the Kuumbi Cave data and comparison with other Unguja/Pemba assemblages reinforce the initial interpretation of Faulkner et al. (2019b), that these assemblages primarily reflect a combination of foraging and transportation, with the latter being the key driver explaining the high similarity in assemblage structure and composition through time. Similar issues were flagged in South Africa (e.g., Plug, 2006; Steele and Klein, 2013) and at Panga ya Saidi in Kenya (Faulkner et al., 2021). The Kuumbi Cave assemblages therefore reflect selectivity for transportation, with the movement of key taxa from the coast in the order of 7–8 km during the Pleistocene, and c.2.5 km over the last 2,000 years.

Ethnographic data collection at Mifupani (Sarathi 2020) took place between June 2018 and June 2019 and involved the direct observation of shellfish and fish harvested by c.30 male and female informants on individual gathering trips. Mifupani represents a true generalised foraging strategy (Szabó, 2009; Harris et al., 2016; Harris and Weisler, 2017), with the assemblage characterised by high richness and high diversity, and although there is a proportionally greater representation of species from a variety of nearshore unconsolidated substrate habitats, people access all available intertidal habitat areas from the shoreline to fringing reef. Canoe use combined with wadable shallow waters created by the fossil reef system allows for the exploitation of multiple habitats. Significant factors absent in the archaeological past influence marine faunal exploitation at Mifupani, including the major impact of the tourist industry on maritime subsistence activities. The participation of Mifupani's residents in a market economy also greatly affected their subsistence decisions, e.g., the availability of meat for purchase having impact on how fishing and shellfish gathering took place in the village.

On Unguja, recent socio-ecological studies in Nungwi (Nordlund et al., 2010), Chwaka Bay (Fröcklin et al., 2014), and Menai Bay (Yahya, 2013) have focused on understanding critical elements of intertidal foraging primarily by women, and the increasing impacts of human predation pressure, anthropogenic habitat disturbance and climate change. These studies highlight differences in species abundance, richness, and diversity between areas under intensive collection and those subjected to minimal harvesting. Interestingly, 224 harvested species were identified by respondents at Nungwi in the qualitative interviews, however only 10 taxa were recorded during the biological field sampling (Nordlund et al., 2010). This is similar to data from Menai Bay, albeit to a lower degree, with 26 taxa recorded during the biological surveys and 34 taxa from the catch assessments (Yahya, 2013). In contrast, at Chwaka Bay the higher numbers of taxa were recorded during the biological surveys (39 taxa) compared to 21 taxa from the catch assessments (Fröcklin et al., 2014).

On the mainland, Msemwa (1994) focused on areas encompassing protected embayments with fringing reefs or coral islands, with areas of straight coastline excluded based on stronger wave action. Ethnographic observation was restricted to September-October, combining informal and formal interviews with first-hand observation. Emphasis was placed on collection during periods of spring tides, which correlate with productive fishing. The nature of harvesting and the taxa being collected were largely determined by shoreline characteristics and habitat structure, which were associated with species diversity and availability. Based on these data, it is suggested that mollusc collection around Dar es Salaam is a secondary activity used to cushion periods of fish scarcity. In this context, Msemwa (1994) recorded only 17 commonly harvested taxa, including six bivalves and 11 gastropods, with collection driven by factors including subsistence, use as bait, and commercial sale. Although most taxa could be collected year-round, *Anadara antiquata* was the dominant taxon harvested due to meat yield and accessibility, with individuals concentrated/clustering within the intertidal zone.

The full Mifupani study revealed the exploitation of many fish and invertebrate taxa totaling 281 individual species and incorporating 126 mollusc taxa. Most fishing and foraging took place in the shallows created by Mifupani's fossil reef, with minimal influence from tool use or modes of transportation. Collection was for subsistence, with no clear seasonal pattern of harvest for most taxa, although future analyses may reveal seasonal variation in exploitation patterns. Unlike Msemwa (1994), Sarathi (2020) concludes that fishing and mollusc gathering served as important sources of meat rather than as "crisis" foods. The most important factor affecting what was harvested is the availability of taxa, although this is now influenced by increased touristic activity in the intertidal area, climate change, and levels of human predation.

Fukuchani, Unguja Ukuu, Msuka Mjini, Pango la Watoro and Mvuleni exhibit similarities and differences across the range of comparative analyses. Fukuchani, Unguja Ukuu, Pango la Watoro and Mvuleni are all characterised by moderate species richness and moderate to high diversity, with Msuka Mjini also demonstrating moderate to high diversity but low species richness. There is variability in the diversity metrics, and which assemblages are significantly different from each other, depending on the taxonomic level being assessed. Evaluation of taxonomic and habitat representation using chord distance indicates a generally moderate to high distance value in comparing each of these five assemblages, although again these results vary depending on whether the assessment is at genus or species level. Correspondence analysis indicates greater similarity between Msuka Mjini, Unguja Ukuu and Fukuchani at species level, with Mvuleni and Pango la Watoro falling separately, but in closer proximity to these three assemblages than to Kuumbi Cave, Ras Mkumbuu or Mifupani. In both taxonomic and habitat representation there are broad similarities, but in many respects these are moderate. What draws these assemblages together is the proportional distribution of taxa and habitats, with broadly similar patterns loosely grouping the MIA-LIA assemblages from Fukuchani, Unguja Ukuu and Msuka Mjini, and grouping the colonial period Pango la Watoro and Mvuleni assemblages. The Fukuchani and Unguja Ukuu assemblages were previously interpreted as reflecting generalised foraging influenced by local habitat structure linked to species richness and diversity within the environment (Faulkner et al., 2018). The higher resolution analyses undertaken here reinforce this interpretation, with Msuka Mjini demonstrating similar trends. All three sites therefore reflect a general foraging pattern as one component of a broad-based economic structure that encompasses hunting and trapping, fishing, and food production to greater or lesser degrees. Pango la Watoro and Mvuleni are somewhat similar, but indicate a higher degree of selectivity and focus on hard substrate habitats across the intertidal gradient. This is unlikely to be purely determined by environmental factors and habitat distribution, particularly given the proximity of Mvuleni to Fukuchani and Pango la Watoro to Msuka Mjini, and the nearshore characteristics of both locations. In these cases, foraging strategies may be influenced by broader socio-economic transitions on the coast associated with the colonial period. As such, all sites exhibit somewhat generalised foraging strategies with variability mediated by the nature of their physical and social environmental contexts.

Extending from this last group of assemblages, Ras Mkumbuu provides evidence for a different set of foraging behaviours, deviating substantially from the other MIA-LIA assemblages in the archipelago, as well as the modern Mifupani data. Located on a long narrow peninsula, the site represents an urban complex bordered to the north and south by expansive intertidal sand and mud flats, patch and fringing reefs. These habitat zones are interspersed with patches of sandy beach and rocky headlands, indicating a mosaic of environments that would have supported a rich and diverse fauna. The reef systems in this area are particularly productive, supporting high taxonomic diversity. The molluscan assemblage, however, is characterised by a moderate degree of richness and very low diversity, being overwhelmingly dominated by the shoreline intertidal-intertidal flat sand/mud infaunal bivalve *Anadara antiquata* (84% MNI). Although the intertidal flats are prominent, the focused gathering of *A. antiquata* to the exclusion of all other taxa and available habitats indicates that foraging strategies and species selection were not determined by environmental structure. In addition, the fish assemblages, although small, indicate a focus on coral, rocky and outer reef taxa, with less exploitation of estuarine and inshore zones, and no sandy/muddy floor species (Quintana Morales and Horton, 2014). The Ras Mkumbuu evidence appears to conform more to Msemwa's (1994) modern urban foraging data, as well as the predictions proposed by Fleisher (2003) for the nature of mollusc foraging in complex urban sites. At Ras Mkumbuu, intertidal foraging and mollusc harvesting appears to reflect a strategy of highly focused gathering of an accessible and abundant species as a supplementary resource.

6 Conclusion

The longitudinal, multi-site comparative analyses of the Zanzibar Archipelago molluscan assemblages clearly highlight that the environment, habitat configuration, taxonomic distribution and density all provide the parameters for foraging across the intertidal zone. Complex relationships between these factors vary spatially and chronologically, dependant on broader environmental processes and how these manifest locally. This does not mean, however, that there is a simple, deterministic relationship between environment and human foraging behaviour, with the nature of intertidal foraging mediated by human choice embedded within specific socio-economic contexts. Given the complexities in the ways people engage with the dynamic conditions of the intertidal zone, it is not surprising that there is no single pattern of foraging behaviour across Unguja and Pemba.

The available data for the Zanzibar Archipelago have limitations, principally the lack of evidence for occupation between the terminal Pleistocene and mid to late Holocene, as well as our ability to incorporate broader economic data for each of the sites discussed here. For example, while high-resolution terrestrial and marine vertebrate data and archaeobotanical evidence are currently available for Kuumbi Cave, Unguja Ukuu and Fukuchani, further detailed analyses are required (or are ongoing) for the other archaeological sites incorporated into the analyses above. That said, in approaching the available data in a systematic manner, incorporating archaeomalacological and ecologically oriented modes of analysis across multiple archaeological contexts, we are able to move beyond interpretations constrained to individual sites. The analyses and results presented here provide robust baseline data for future investigations of human-ecodynamics on the coast and islands of eastern Africa, highlighting combinations of stability and variability in foraging behaviours that effectively argue against a single trajectory of foraging behaviour within the intertidal zone.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding authors.

Ethics statement

The studies involving human participants were reviewed and approved by the University of Madison-Wisconsin Institutional Review Board (2016-1353). The patients/participants provided their written informed consent to participate in this study.

Author contributions

PF, AS, and AC contributed to conception and design of the study. PF, AS, TS, MH, AA, and OH collected the assemblage data. PF performed the analyses and wrote the first draft of the manuscript. AS, AL, NN, and AC wrote sections of the manuscript. MH produced Figures 1, 2. PF, AS, AC, TS, MH, AA, OH, AL, NN, MH, and NB contributed to manuscript revision, read, and approved the submitted version.

Funding

PF was funded by a Faculty of Arts and Social Sciences Research Support Scheme grant and Tom Austen Brown Research funding (University of Sydney), and by the Max Planck Society. PF is an Australian Research Council Future Fellow (FT200100464). AS was funded by grants from the Fulbright-Hays Program (award#P022A170037), the National Geographic Society (award#EC-227-18), the Department of Anthropology at the University of Wisconsin-Madison, and the University of Wisconsin-Madison Graduate School. AC is an Australian Research Council Future Fellow (FT200100179) and was funded by postdoctoral fellowships from the British Academy and The University of Queensland. AL and NN were supported by Springer/Nature and the British Institute in Eastern Africa. NB was funded by a European Research Council grant for the SEALINKS Project (grant no. 206148). Radiocarbon dates for the Sealinks Project were provided by a UK Natural Environment Research Council grant (NF/2012/2/4).

Acknowledgments

We are grateful to the Zanzibar Department of Museums and Antiquities and the Office of Chief Government Statistician (Zanzibar Research Committee) for supporting our archaeological fieldwork and providing permission to conduct the research. PF, AC, MH, and NB extend their appreciation to the local communities on Pemba and Unguja, particularly in Makangale, Fukuchani, Unguja Ukuu, and Jambiani. AL and NN thank PF for his invitation to contribute to this paper. They are deeply grateful to AA for his magnanimity in all aspects of this research; the student crews for their many contributions, and the communities in Nungwi, Fukuchani and Mvuleni for their gracious assistance. AS is especially grateful to the people of Mifupani for sharing their subsistence activities with researchers daily for more than a year. Special thanks are due to Muhidini Mgana and Ameir Jecha for facilitating research at Mifupani. Finally, we thank the guest editorial team of Manuel Will, Andrew Green, Jon Erlandson, Ximena Suarez Villagran and Antonieta Jerardino for their invitation to contribute to this special issue.

Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.982694/full#supplementary-material

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 11 October 2022
DOI 10.3389/feart.2022.939214

OPEN ACCESS

EDITED BY
Jon McVey Erlandson,
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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 08 May 2022
ACCEPTED 11 July 2022
PUBLISHED 11 October 2022

CITATION
Dillehay TD, Tham TR, Vázquez V, Goodbred S, Chamberlain E and Rodríguez G (2022), Emergent consilience among coeval fishing and farming communities of the middle holocene on the North Peruvian coast.
Front. Earth Sci. 10:939214.
doi: 10.3389/feart.2022.939214

Emergent consilience among coeval fishing and farming communities of the middle holocene on the North Peruvian coast

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Coasts are dynamic, constantly changing ecosystems offering rich and varied foods and other resources. Compared with the monistic structure of crop production in many terrestrial parts of the world, some coastlines reflect a dualistic structure with complementary maritime and agricultural economies beginning in early prehistoric times. In particular, the Pacific coast of the Central Andes offers one of the world's most abundant and diverse supplies of marine resources. The late Pleistocene to middle Holocene (~14,500–4,000 BP) cultural sequences from south Ecuador to north Chile vary appreciably from one region to the next, but all reveal varying degrees of mixed diets of maritime and terrestrial foods. By at least ~7,000 BP, a diversity of seafood and domesticated crops were mutually exchanged to form varied specialized and unspecialized economies in a few Andean areas. This study reports on interdisciplinary data from a complex of archaeological sites with mixed economies along the desert coast of the Chicama Valley in north Peru, specifically the Huaca Prieta area dating between ~14,500 and 3,800 BP. Around 7,500–7,000 BP, intensified maritime and agriculture economies developed simultaneously with social differentiation between public ritual monuments and outlying domestic support sites in an environment of rich marine resources and fertile estuarine wetlands in the valley. This and other coastal areas played an important and persistent early role in human population growth, community formation, and the consilience of different but complementary technologies and principles of socio-economic organization to establish the foundations for later state development along the Central Andean coast.

KEYWORDS

huaca prieta, paredones, dual economy, peruvian coast, early complexity

Introduction

Coastal and marine ecosystems are unique habitats formed by animals and plants that thrive at the borders between ocean and land. Throughout human history these ecosystems have offered a wide range of resources and services, many of which have provided material benefits such as reliable and abundant food supplies and human dwelling habitats and benefits of a non-material nature that affected people in their spiritual, social, and cultural dimensions (Barbier et al. 2011; Blair 2016). By supporting spiritual and religious values, and providing a wide variety of food and non-food resources, including food production in fertile wetlands, coastal ecosystems substantially contributed to the sustainability and well-being of both past and present peoples and to the convergence of different resources, technologies and organizational principles of early sedentary and later proto-state societies in parts of the world (Bailey and Milner 2002).

Arguably one of the most impacting events in world history—food production and its consequences—led to economic surpluses and significant changes in landscapes, eventually supporting human population growth, the spread of sedentism and the rise of diverse social complexities. Yet, food production was more than just a matter of subsistence and landscape changes (e.g., Bender 1993; Hayden 1995; Graham and Goucher 2015; Redman 2019). It also led to dramatic shifts in social, ideological and demographic practices, including challenges such as the maintenance of cohesion in the face of variable community formations, increased social scale and differentiation, agency and identity, new technologies to meet new economic demands, and the need for different ways of developing new institutions to manage the changing nature of uncertainty and risk (e.g., Sterelny and Watkins 2015; Sanz 2018). Food technologies, mortuary patterns, domestic and public sites, burial patterns, organizational strategies, and symbolic iconographies reflect much of the archaeological evidence of the initial practices and institutions that were formed to deal with those challenges. Managing these changes through growing collective actions, coalescing technologies and knowledges, new strategies and "communities of practice" (e.g., Wenger 1998; Knappett 2013; Bogaard 2015; Dillehay 2019) may have been as problematic as arriving at successful food production, especially when societies combined different food strategies (i.e., fishing, animal husbandry, agriculture), which required different means of negotiation and organization to deal with challenges beyond those of a primary mode of production (i.e., agriculture). In recent years, there has been a renewed interest in examining these challenges and their consequences, especially the relationship between mixed food strategies and multiple pathways of emergent community development (Costin 2011; Robb 2013; Graham and Goucher 2015; Scarry et al. 2022).

While we can document the challenges and consequences of new developments in the archaeological record and acknowledge that in broad terms social interaction, symbols, ideas, and ritual practices had some role in shaping mixed or primary food producing communities, it is harder to find specific databases to explain how and why they succeeded or failed (e.g., Yoffee 2019). Although much more is known of the differing community lives of early agriculturalists (e.g., Bowles and Choi 2013; Graham and Goucher 2015; Spataro and Furholt 2020), less is known of closely interacting communities of farmers and herders and even less of co-existing coastal farmers and maritime fishers (e.g., fishing, shellfish and seaweed gathering) and their distinct or shared experiences. Reported here is a synopsis of an ongoing, long-term interdisciplinary research on the emergence of social complexity and the consilience of coeval Preceramic sedentary communities of specialized and unspecialized farmers and fishers in the Huaca Prieta area (Figure 1) of the lower Chicama Valley on the north coast of Peru from ~7,500 to 3,800 BP (All ages are radiocarbon calibrated). This area consists of two neighboring public mounds or ritual centers at Huaca Prieta and Paredones and their outlying, sustaining domestic sites (Dillehay and Bonavia 2017a-b; Dillehay 2017). Although different in size and purpose, with Huaca Prieta (Figure 2) mainly associated with a maritime economy and Paredones primarily with farming (Figure 3), the two mounds are contemporaneous and their activities complementary. The outlying domestic sites supporting these mounds reflect a mixture of different specialized and unspecialized food strategies. This research examines the people who occupied the mounds and domestic sites in the dynamic littoral and wetland habitats of the lower valley and their food strategies, boundary and identity formations, domestic and public activities, social differentiation and inequality, and economic organizations. Also examined is the long-term relationship between the "dominant culture" (Lohse 2007) of early ritual centers and their support communities. In the Andes, there is a long tradition of believing that if we understand ritual or ceremonial centers as the perceived apex of society, then by extension, we comprehend their subordinate sectors, the outlying domestic communities, which is not necessarily the case. We place this early coastal society within the conceptual space of complementary food producing communities and their joint multi-complex socio-cultural practices and seek to better understand the interaction among Preceramic fishers, wetland hunter-gatherers, and incipient agriculturalists, based on their respective uses of a changing Pacific seascape and the coastal landscape subject to shifting sea

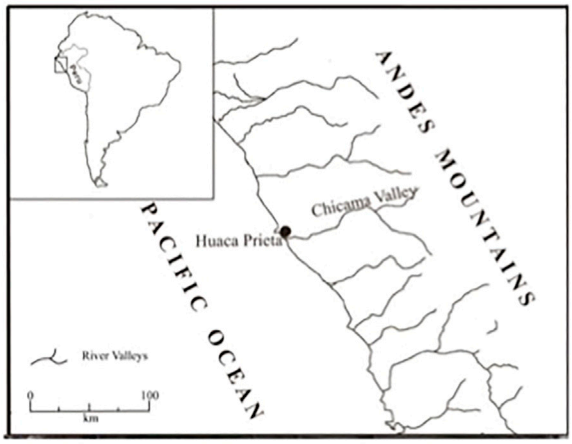

FIGURE 1
Location map showing northern Peru and major coastal river basins and the Huaca Prieta study area near the mouth of the Chicama River.

levels and major tsunami, El Nino and other physical events (Goodbred et al. 2017, 2020). It was the consilient linking together of different, technologies, foodways, community patterns, and ritual practices that contributed to the emergence of social complexity in this area of north coastal Peru.

To address the changing dynamics of these interactions and the relationship between communities and changing environments, our research focused primarily on three research questions. First, what was the nature of the shared or separate domestic communities of fishers and agriculturalists in the study area? That is, to what extent did these communities differ by food procurement, diet, isotope, dental, settlement, technology, mortuary, artifactual, and other patterns? Were there physical boundaries formed within and across them and socio-economic identities defined between them? Although the burial, dental and isotope data from the Huaca Prieta and Paredones mounds indicate a dual population of fishers and farmers, respectively (Tung et al. 2020), there also are indications of an unspecialized mixed dietary orientation in a few domestic communities, with some groups equally exploiting all resource habitats. Second, how different or similar are the co-existing communities of fishers and farmers, not only with regard to each other, but with respect to their ritual and burial practices at the ritual mounds and domestic sites? Did ritual activity at the mounds promote parity among specialized and possibly unspecialized domestic communities and foster a sense of harmony? Or was cohesion and harmony expressed primarily at the mounds and not in the domestic communities, which would suggest marked social distinctions between the public and domestic sectors? And three, how did these communities adapt to the changing coastal ecosystem over time?

Materials and methods

The methodology applied to these research questions is a combination of paleo-ecological research, archaeological survey and multi-site excavation in ritual and household sites across different maritime and terrestrial habitats, and a wide variety of

FIGURE 2
The Huaca Prieta mound situated on the south tip of the Sangamon Pleistocene terrace. Note excavation areas underway. The Pacific Ocean lies approximately 150 m west of the mound.

FIGURE 3
The Paredones mound in the foreground located about 600 m north of Huaca Prieta. In the background is a large Moche pyramid dated from ~1,500 to 1,200 years ago.

other interdisciplinary techniques including isotope, dental and genetic analyses. In studying different fishing and farming communities, we focused on several variables: 1) household and community variability in site organization in different locations along the littoral and in the immediate interior; 2) networks within and across sites and communities, especially in comparison to burial contexts and offerings, to quantification and qualification of food remains from different house and community forms, and to isotope and genetic data of human skeletons (Dillehay 2017; Tung et al. 2020); 3) new technologies evidenced by the appearance and diversification of weaving and decorative techniques in textiles and baskets, symbolic motifs on gourds and painted stones, irrigation canals and raised agricultural fields, and their differential associations with various site types; and 4) reconstruction of the paleo-ecology through time.

In specific regard to the present study, the research involved an interdisciplinary group studying the development of coastal and riverine landscapes and the change of ecological and environmental dynamics through time. Among the specific methods used in the work, the application of stable isotopes on diverse sample sets (e.g., carbonate shells and sediments, organic and carbonate plant remains, and human and animal bones and teeth) allowed common links between the human, environmental, and climatic records preserved in the lower Chicama Valley. Newly studied sedimentary deposits in wetlands have yielded high-resolution climate records from the littoral and deltaic lowlands, which have helped to constrain what the climate was like at the coast where early farming and maritime communities existed, and when coupled with the archaeological data, has permitted a direct correlation with human activities including culture, diet, and economy. In addition to the use of stable carbon and nitrogen isotopes to help interpret human diets, dental microwear analyses have allowed human diets to be analyzed using three-dimensional texture analysis.

Lastly, the relative frequency data for faunal and floral food remains at ritual mounds and domestic sites shown in Figure 14 are skewed toward marine food remains due to sampling procedures. All excavated cultural deposits at all sites (totally more than 1280 cubic meters excavated) were screened through three mesh sizes, including 1.0 cm, 0.5 cm and 0.2 cm. During both excavation and screening, visible macro-floral remains were retrieved. As a result, approximately 98% of all faunal remains (e.g., bone, shell) were recovered. Given the cubic meters excavated, it was logistically impossible to float all cultural sediments, thus only ~5% were floated, which resulted in a skewed sample favoring marine remains. Also studied were starch grains and phytoliths from hearth and other features, yet the results of these studies added only a few new floral species. Based on these results, Figure 14 shows approximate ratios of 10.0:0.1–0.2 of faunal to plant foods, respectively, for all site types. If all excavated sediments had been floated, these ratios likely would be closer to 9:1 to 8:2. Although the data are slightly skewed, the comparative frequencies of marine to plant foods between ritual mounds and tiered-domestic sites and among the different domestic sites is relatively accurate.

Results

Central Andean seascapes and landscapes

The offshore waters of the Pacific coast from Ecuador to Chile provide some of the most diverse and abundant marine resources in the world due to the cold Humboldt Current and major upwelling (Miloslavich et al. 2011). The region is one of the most appropriate places to study the socio-economic challenges and interactions that developed between early fishing and farming communities from ~10,000 to 4,000 BP. It is the only place in the world where maritime, agricultural, and pastoral economies coalesced to lay the foundations for the later development of pristine urbanism and state societies (e.g., Quilter 1991; Moore 2005; Piperno and Dillehay 2008; Moseley 1975, 1992; Patterson 1983; Sandweiss 1996). Moseley (1975, 1992) was one of the first archaeologists to conceptually articulate the importance of Preceramic maritime resources along the coast of Peru and how the abundance and predictability of seafood led to early sedentism and increasingly complex societies. He argued that people in large permanent communities, likely managed by part-time leaders, carried out large-scale corporate activities, focused primarily on constructing non-domestic, communal mounds that served as ceremonial centers in establishing the pre-state foundations of Andean coastal civilization. Since Moseley's initial publication, additional research has revealed that both marine foods and crops were important dietary elements in these early societies (Richardson 1981; Patterson 1983; Quilter 1991; Dillehay et al. 2007, 2009; Sandweiss 2009; Lavallee and Julien 2012; Marquet et al. 2012; Dillehay 2017; Beresford-Jones et al. 2018a, 2022).

Some of the most elaborate Preceramic maritime societies in the Central Andes include the Chinchorro culture of north Chile and south Peru (~8,000–4,500 BP; e.g., Arriaza 1995), and the slightly later mound cultures from southern Ecuador to central Peru that subsisted on mixed economies, whether fishing and farming or maritime and terrestrial foraging (e.g., Huaca Prieta, Paloma, Huaynuna, Aspero, Alto Salaverry, Los Morteros: see Alva Meneses 2008; Benfer 1984; Bird et al. 1985; Bonavia 1982, 1993; Cárdenas 1999; Dillehay et al. 1999; Feldman 1985; Fung 1988; Lanning 1963; Lavallée and Julien 2012; Llagostera 1992; Maldonado 1992; Mauricio et al. 2021; Moore 2007; Pearsall 2008; Power et al. 2021; Pozorski and Pozorski 1977; Quilter 1989; Shady 1983; Stothert 1985). These societies developed during the Central Andean "Neolithic" or "Andean Boom" (*sensu* Lavallee 2000) when social networks and resource sharing of small-scale maritime fishers and foragers adjusted to new organizational and institutional needs to deal with increased adoption of crops, co-residency with farmers, monument building, new community duties, competition and cooperation, social cohesion and occasionally economic and occupational specialization. Besides sites like Huaca Prieta and Paredones, many of these developments are featured at other places along the Peruvian coast, for instance, Bandurria on the north-central coast, where Chu (2011) excavated a public platform mound and a sedentary domestic area dated to ~5,200 BP. The domestic component was associated with a broad-spectrum economy focused on fishing, cultivation, and the exploitation of reeds in wetlands for manufacturing balsas, mats, walls, baskets, and others. Fishing, capturing of birds and collection of their eggs were practiced as well as cultivation of cotton, pepper, and gourds. In the delta wetlands of the Chao Valley on the north-central coast, the Los Morteros site was occupied between 7,000 and 3,100 BP (Cárdenas 1999; Mauricio et al. 2021). From ~5,700 to 3,900 BP, in particular, the site is characterized by public and domestic sectors with a mixed diet similar to contemporaneous localities elsewhere along the Peruvian coast. Farther south in the coastal areas of the Ica and Nazca valleys, Beresford-Jones (Beresford-Jones et al. 2018; 2022) analyzed lomas vegetation (in the Andean foothills) and shell middens, discovering increased sedentism between 7,000 and 5,000 BP. In addition to marine foods, he documented a wide variety of roots and fruits of wild plants from the lomas. In the nearby Palpa Valley at the Pernil Alto site (Gorbahn 2020), an alleged diversity of food crops was introduced between 5,900 and 4,800 BP, with hunting and gathering appearing as minor subsistence practices. These and other Preceramic sites represent various aspects of the socio-cultural "boom" from roughly 7,500 to 4,000 BP that established some of the basic socio-economic organizational principles that eventually led to greater cultural complexity in the Central Andean region.

Environmental setting

The physical setting of the lower Chicama Valley at ~14,500 BP, the earliest known period of human occupation along the littoral, was a broad, shallowly incised alluvial plain of sand and gravel sediments delivered by the Chicama River. These deposits are not unlike those found in the modern braided river channel or the exposed channels or washes to the north. The shoreline at ~14,500 BP was located ~16 km seaward and transgressed to ~10 km seaward by ~10,000 BP (Dillehay et al. 2012; Goodbred et al. 2017; Iriarte and Watling 2017). There is no evidence for persistent, aggrading wetlands at this time, although small, ephemeral ones probably existed along the alluvial corridor.

Beginning ~7,500 years ago, coastal plain sediments began to accrete over the sandy alluvial surface as the rising base level and groundwater table intersected incised areas of Chicama Valley. These flooded depressions formed the first persistent lagoons and wetlands near Huaca Prieta and the Sangamon terrace (Figure 4). The development of dunes and gravel beach ridges under the slowing sea-level rise further trapped surface runoff and groundwater in the back-dune areas, extending the lagoons and wetlands along the coast. The emergence of such habitats is widely recorded in valley-wide stratigraphic profiles by a 1–2 m thick sequence of interbedded fluvial muds, fine sand, peat, and freshwater carbonates (Goodbred et al. 2017). These early Holocene lagoon deposits have been mapped to at least 200–300 m in width and to have extended at least 12 km north along the coast from the modern river past the Sangamon or El Brujo terrace (Figures 4–6). Radiocarbon ages from the upper parts of these lagoon deposits average ~6,500 BP, after which the extensive peats and carbonate sediments associated with these settings disappear, or at least considerably contract in their extent.

Ephemeral (paludal) wetlands persisted from ~6,500 to 5,000 BP. The interpretation as ephemeral wetlands is consistent with the lack of peat formation or macro floral remains, as seasonal drying allowed plant matter to be remineralized and thus not well preserved. Beginning ~4,500 BP, a second phase of wetland and lagoon expansion took place and persisted to ~3,500 years ago (Goodbred et al. 2017). Renewed formation of peats and freshwater carbonates, interbedded with fluvial muds, reflects a return to active river discharge and sediment delivery, presumably driven by a wetter highland climate. These soil characteristics reflect diagenesis

FIGURE 4
Annotated Google Earth® image of the coastal system adjacent to Huaca Prieta and Paredones and extended to the Chicama River mouth. Stratigraphy of the coastal succession shows that the inland dunes lie on the gravel shoreface berm at the ~3,700 BP maximum transgression (dark blue line), at which time the shoreline would have been at the base of the Huaca Prieta mound. This is consistent with intercalated beach deposits and mound colluvium as the base of the mound dated to this time. Following maximum transgression, the shoreline prograded to the late Holocene shoreface (purple line), before a relative sea-level fall between 0.5 and 1 ka that forms a stranded shoreface and the new shoreline platform of the modern coast (aqua line). These shoreline boundaries are readily traced to the river mouth, where the stratigraphy is well exposed along the river cutbank.

and slow sediment accretion (0.2–0.5 mm/yr) in a vegetated but saturated environment, one perhaps intermittently flooded by surface water but with a very shallow groundwater table. In the area around the Sangamon terrace and the Chicama River mouth, these second-phase lagoons and wetlands were still large at ~100 m wide and 0.5–1.0 km long, but not as expansive as the earlier environments (see Figures 5, 6). Although reduced in size after ~3,500 BP, stratigraphic data reveal that wetlands persisted, as revealed by dense, dark-colored muds cemented by highly developed calcic horizons overlying lagoon deposits.

Another distinction of the second paludal phase is that new wetland habitats appeared well north of the Sangamon terrace. These wetlands were not the linear back-dune features that formed along the Chicama coast, but rather formed in the numerous, shallow inland quebrada outwash channels that are interspersed along the 20 km of coast north to Milagro (Figures 5, 6). Because these ephemeral outwash channels are not deeply incised (<2 m), these wetlands are only thin veneers of organic-rich sand or mud. A more positive water budget and higher groundwater table allowed wetland vegetation to become established, with ephemeral open-water environments (Goodbred et al. 2020). The shallow stratigraphy preserves alternating aeolian and wetland deposits, indicating that these wetlands were not as persistent as the larger, deeper features closer to the main Chicama river valley. Limited age dating suggests that many of the northern wetlands do not appear until the late Preceramic (~4,500–4,000 BP), but persist intermittently through Colonial and modern times.

The persistence of these shallow, ephemeral wetlands contrasts with the lagoons and wetlands south of the Chicama River, which, as before, infilled with river sediment after about a millennium and largely disappeared by ~3,500 BP. This time, however, they do not disappear because of aridification; rather, the delivery of fluvial sediment continues after 3,500 BP to form an incipient floodplain that is elevated above the water table. This expanding deposition of floodplain silts created new, arable landscapes in the lower Chicama Valley, which hallmarks the cultural transition from local wetland horticulture associated with Preceramic Huaca Prieta to the increasingly larger-scale agriculture of the ceramic-age Cupisnique to Gallinazo cultures (beginning ~3,500 BP; Goodbred at al. 2020). The environmental transition was driven by enhanced river discharge from the increasing strength and frequency of ENSO-driven precipitation (e.g., Moy et al. 2002). After millennia of coastal transgression since the early Holocene, the Chicama shoreline began to prograde after 3,500 years ago through the construction of gravel shoreface ridges, indicating large river discharge and transport capacity.

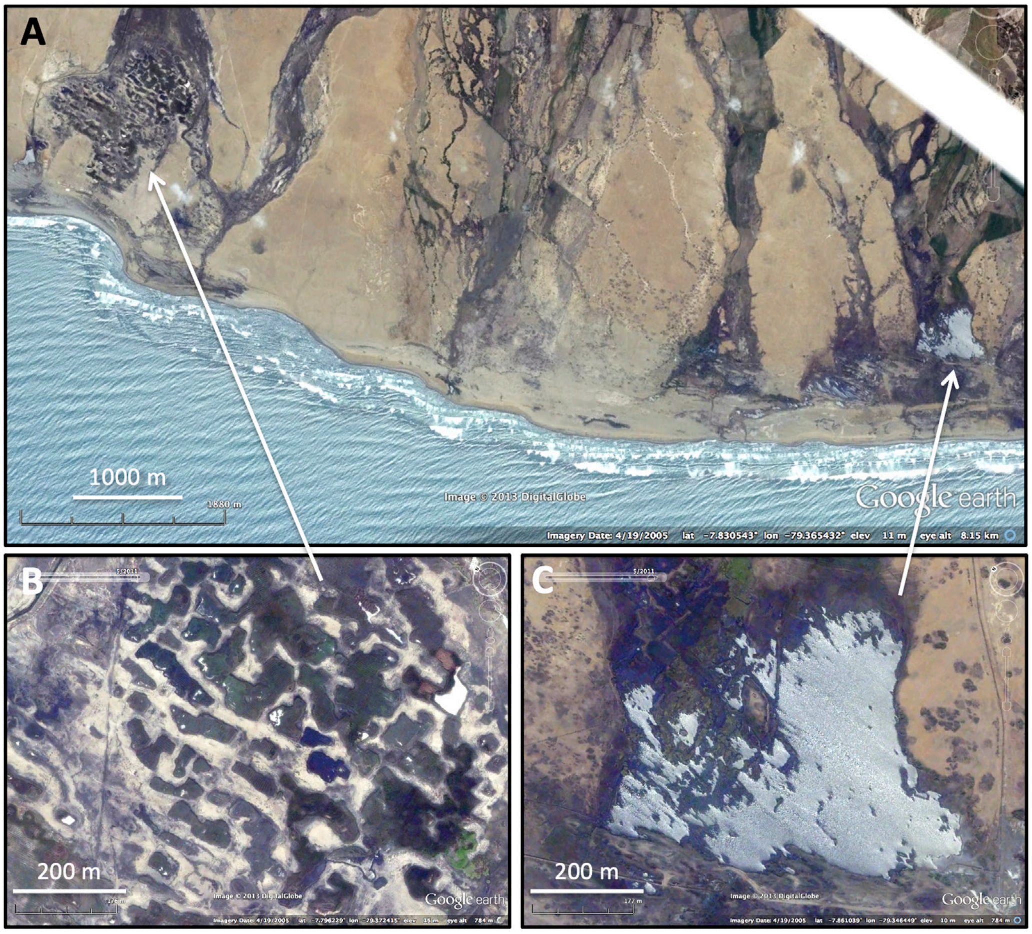

FIGURE 5
Google Earth® images of the alluvial plain north of the Chicama River valley. **(A)** The alluvial plain comprises gravelly, barren interfluves alternating with the outwash channels that define shallow depressions close to the water table and vegetated with wetland plants and desert scrub. **(B)** Close-up image of the vegetated area on the left (north) side of **(A)**, showing the area that comprises a cultural landscape organized into terraces and *camellones* (raised fields) for agricultural production, which were initially constructed ~5,000 BP. **(C)** Close-up image of the area on the right (south) side of **(A)** showing a small open-water lagoon and wetland fringe that locally form where channel scour has been especially deep during El Niño floods.

Also, after 3,500 years ago, the fluvial silts that infilled coastal wetlands and developed a new floodplain were increasingly dispersed across the middle Chicama Valley, where they began to blanket the region's typical alluvial sand and gravel surface. This deposition of arable sediments across the middle and upper valley continued to expand the agriculture landscape, with floodplain aggradation accelerating after ~2,500 BP and with increased frequency of wet-phase ENSO cycles (Goodbred et al. 2020). The expansion of arable lands was also facilitated by the increasingly extensive network of irrigation canals and coincides with the peak Moche and Chimu civilizations in the Chicama Valley between ~1,600 and 500 years ago. Changing shorelines and wetland environments in the area did not determine but certainly influenced settlement location and the density and availability of economic pursuit of marine or terrestrial resources.

The Huaca Prieta area

The earliest known human presence in the study area is characterized by intermittent cultural deposits below the Huaca Prieta mound, which along with Paredones and later ceramic-age mounds, were built on the remnant Sangamon Pleistocene terrace (see Figures 3, 5). These early deposits date from ~14,500 to 10,000 BP and are associated primarily with maritime and secondarily with terrestrial foragers. The terminal Pleistocene materials are buried in the upper 1–2 m sediments of the terrace, which at the time of human occupation was about ~16 km from the sea. Later, ~10,000–9,000 BP, maritime and inland foraging continued, with incipient horticulture probably introduced in estuarine wetlands (Dillehay et al. 2012a-b). The early Holocene period

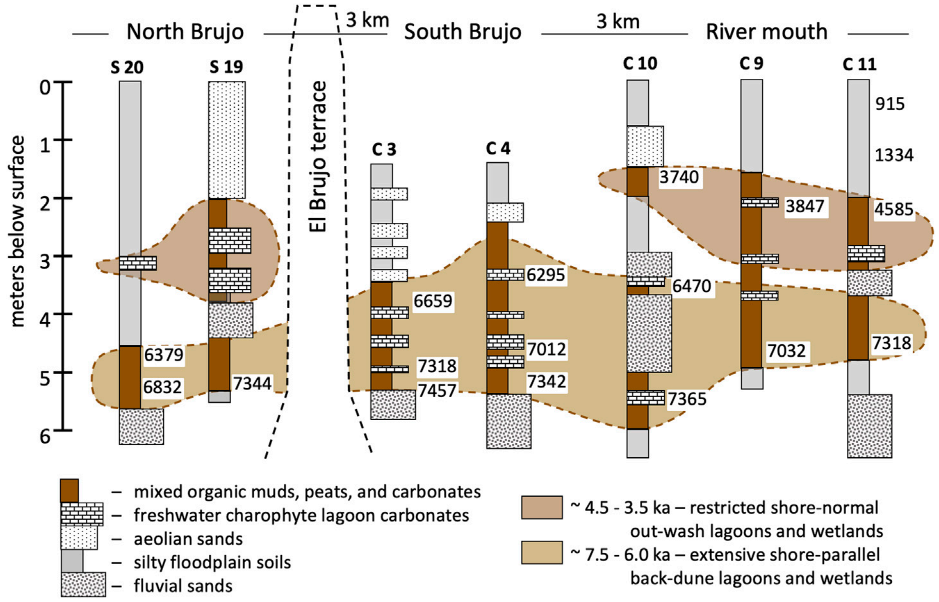

FIGURE 6
Simplified lithologs showing major sediment types and their associated depositional environments and ages (after Goodbred et al. 2017). Highlighted in brown are the organic muds, peats, and carbonate sediments that define the age and extent of paleo-lagoon and wetland systems from approximately 7,500–6,000 BP and 4,500–3,500 BP. Site locations shown in Figure 8. North Brujo refers to north of the Sangamon terrace. South Brujo refers to south of the terrace. River mouth refers to the Chicama River delta.

(9,500–8,000 BP) is represented by small-scale settlements with mixed economies. During this pre-mound period, people at Huaca Prieta focused primarily on the sea but also grew a few wild food crops, including avocado (*Persea* sp.), squash (*Curcurbita moschata*), chili pepper (*Capsicum* sp., and gourd (*Lagenaria* sp.; Dillehay et al. 2012; Vazquez et al. 2017). Faunal materials from both the late Pleistocene and early Holocene cultural deposits indicate a wide variety of shellfish, fish and other marine products, sea lion and water fowl, with deer and other mammals and wild plant foods from wetlands making up a smaller portion of the diet.

As mentioned earlier, around 7,800–7,500 BP rising sea levels led to back-flooding and the development of inland lagoonal deposits associated with the initial rise of the Huaca Prieta mound and some of the earliest domestic sites along the coastline of the Chicama Valley. Beginning around 6,500 BP, the lagoons disappeared and ephemeral paludal wetlands and the Chicama floodplain began to form (Goodbred et al. 2017). The paludal environment was almost exclusively associated with narrow, shallow inland washes where most incipient agriculture developed (Figure 5). Also appearing around 6,500 BP is the mound at Paredones, located ~600 m north of Huaca Prieta, and more numerous domestic sites along the washes to the north. It was at this time that the separate but complementary ritual communities of fishers and farmers at Huaca Prieta and Paredones more clearly developed, respectively (Dillehay 2017; Tung et al. 2020). Despite their residential and socio-economic separateness, these two groups exchanged foods and shared ritual spaces and feasting practices at Huaca Prieta and food preparation at Paredones. Although large quantities of marine and limited amounts of crop foods were consumed at Huaca Prieta, there is no clear evidence in the form of seed grinding stones, cutting blades and other crop-related lithics, hearths, and storage pits to suggest the preparation and consumption of plant food on a scale comparable to marine food. Instead, Huaca Prieta was used to occasionally perform rituals and to bury special individuals, to make bundled dedicatory offerings of coca leaves, textiles, marine shells (Figures 7A,B) and other items (e.g., feathers), and to continuously perform numerous ritual burnings of *palo santo* branches (*Bursera graveolens;* today shamans or *curanderos* still use the mound to offer coca leaves and *palo santo* sticks in bundles to cleanse ritual spaces and ward off bad spirits). These activities were bounded by hundreds of individual stone-lined structures and prepared floors (relatively clean compared to domestic house floors), probably used for small, private rituals. At Paredones, there are fewer burials, no stone-lined or other structures, prepared floors, textile bundles and similar offerings, yet numerous grinding stones, hearths, and

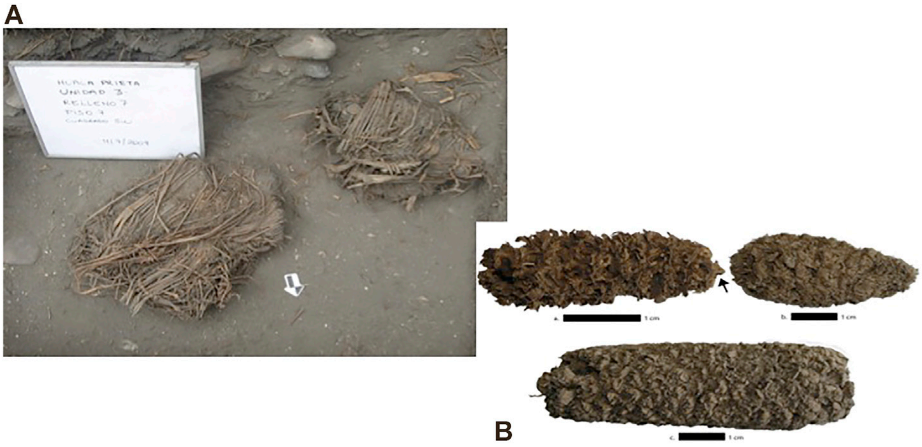

FIGURE 7
(A) Two tied- and -wrapped reed bundles containing coca leaves, marine shells, and fragments of textiles that were offerings placed on a pathway to the top of the Huaca Prieta mound and dated ~5,500 BP; **(B)** Maize cobs dated to ~6,500–6,000 BP from the Paredones mound (Grobman et al. 2012).

cutting tools indicative of food preparation, primarily plants.

Research on human skeletons, especially dietary assessment based on stable isotopes, dental, and mortuary patterns at Huaca Prieta and Paredones reveal an integrated economy of the two primary socio-economic sectors (fishing and farming, albeit minor foraging in estuarine wetlands for wild plant and animal food such as tubers and water fowl), with increased economic and occupational specialization and exchange and probably gender-based occupation by at least 6,000 BP (DeSantis et al. 2017; Dillehay 2017; Tung et al. 2020). Isotope studies of children's skeletons from the two mounds show dietary specialization deeply embedded in food customs early in life (see DeSantis et al. 2017; Tung et al. 2020). Specialization related to maritime and farming practices, with some groups focused on specific resources (e.g., salt, fish, shellfish, seaweeds), on specific resource zones (e.g., wetlands, shoreline and sea), and on agricultural raised fields in lagoons and canal-fed fields in washes (Goodbred et al. 2017, 2020; Vasquez et al. 2017; Tung et al. 2020). The distinct diets of some of these early farming and fishing communities apparently were a key factor in structuring their socio-economic and political organization.

In summary, the collective artifact, isotope, dental and burial data indicate that Paredones was the food preparation and occasional burial mound of farmers and Huaca Prieta was the ritual feasting and burial mound of fisherfolks. These two socio-economic segments appear to have resided peacefully side-by-side in separate shoreline and beach ridge-oriented and inland wetland- and wash-oriented household communities engaged in social and economic exchange. There is no weaponry or skeletal trauma in burials recovered from the public mounds (Bird et al. 1985; Titelbaum and Verano 2017) and domestic sites to suggest tension between the segments. If there had been conflict over competitive access to or exchange of resources, then inter-community ritual activities at Huaca Prieta and probably Paredones likely would have posed a powerful mitigating counterpart, emphasizing community-wide social cohesion and a long-term cooperative effort.

Specialized ritual centers and domestic sites

At both Huaca Prieta and Paredones, there is little to no convincing evidence of habitational debris, although it is likely that a few individuals occasionally resided on or at the base of the two mounds. The outlying domestic communities are believed to be the residencies of people who participated in rituals and/or were buried at Huaca Prieta and Paredones, as indicated by overlapping chronologies, similar diagnostic tool kits, exotic items, food remains, textiles, decorated gourds and other cultural features. It is possible that not all domestic sites were linked to the ritual mounds but current evidence suggest a strongly integrated settlement and socio-economic system along the valley littoral zone.

To reiterate, in the Huaca Prieta area subsistence and community changes were accompanied by communal constructions in the form of the large ritual and mortuary mound at Huaca Prieta (~32 m high and 182 m long; ~7,500–3,800 BP) and the associated smaller food preparation and mortuary mound at Paredones (~6 m high and 50 m long; ~6,500–3,800 BP). Chronological and construction evidence shows that both mounds were built in multiple phases over several millennia by thousands of individual ritual spaces, probably by small kin groups from residential communities

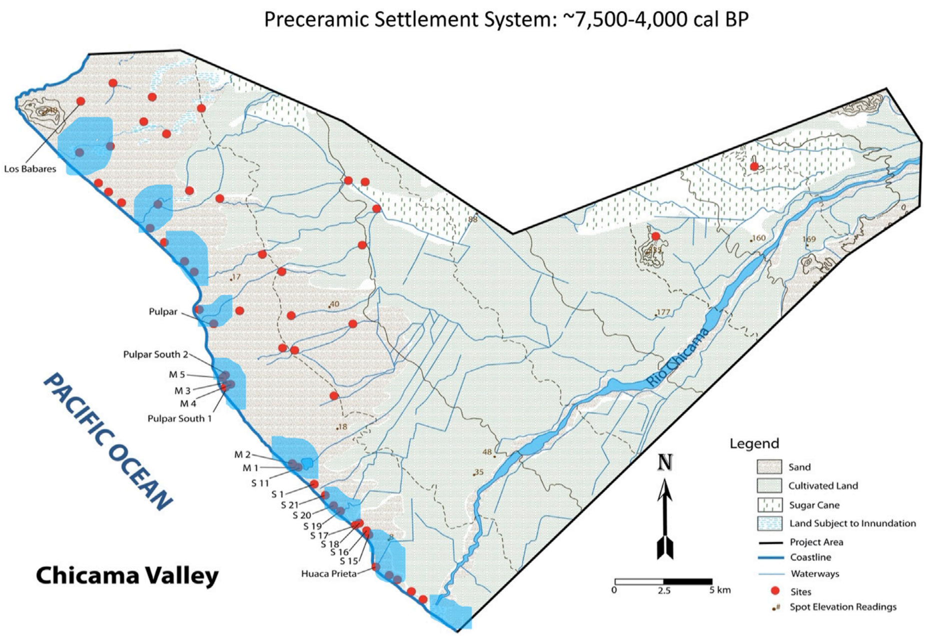

FIGURE 8
Location map of domestic sites (red dots), lagoons and wetlands (blue), narrow washes, geological coring and profiling sites (red dots and wetlands), Huaca Prieta and the Chicama River. Red dots represent clusters of domestic sites.

located on distant beach-ridges and along the terraces of wetlands and washes (Dillehay 2017). There is no evidence of corporate labor or permanent authorities at either mound. Although the mounds are separated by a short distance, as noted above, people buried in Huaca Prieta primarily ate marine foods and those in Paredones primarily consumed maize and other crop foods, suggestive of direct linkages with their corresponding outlying residential communities. Current genetic and isotope evidence suggests that there are no non-local individuals buried at either mound, indicating that interment probably was reserved for important local community members only. Burial evidence also suggests gender-based occupational roles. For instance, the current data from Huaca Prieta (Dillehay 2017) show that most females were buried primarily with weaving kits, gourd fragments, and/or textiles with distinct weaving and decorative traits, and that most men were interred primarily with fishnets, pelican feathers, shellfish, and/or other items indicative of sea-related activities. At Paredones, women were buried with grinding stones or without offerings and men had offerings of digging sticks, stone hoes, prismatic blades and/or other stone tools (starch grains of maize and other crops were recovered from cutting edges). Isotope and dental data also show that a few individuals interred in the mounds had mixed diets, suggesting, for reasons presently unknown, a few persons and/or households were not fully specialized and were more generalized food consumers (Tung et al. 2020). Additional data from households might reveal that a larger portion of the population was unspecialized and that the burial of fishing and farming specialists in the mounds might suggests that economic and occupational specialization held a privileged position in society, one that granted practitioners interrment in the mounds.

In regard to domestic communities, they are located on littoral beach-ridges and inland on low terraces of lagoons and narrow washes from 2 to 20 km north and 0.5–5 km south of Huaca Prieta (Figures 8, 9). A total of 88 Preceramic house mounds have been recorded (Figure 8). These mounds are generally oval in form, contain oval and rectangular houses, and vary in size from ~8–18 m in length, ~1–2.3 m in height (with portions often below-ground), and ~7–15 m in width. Littoral house mounds are located on beach-ridges and generally contain fishnets, seafood remains, and only a few small grinding stones (<15 cm in diameter) and were used by fishers. Inland house mounds are about the same size, contain semi-rectangular to rectangular houses, are located around shorelines of wetlands (0.5–1 km inland) and farther inland (1–5 km) on low terraces of narrow washes, and after about 5,500 BP often associated with raised and canal-fed agricultural fields. In some washes, there are 3–6 clustered house mounds: in one cluster there are 15–20 house mounds that form a semi-circular arrangement and in others there are 3–4 house mounds positioned on opposite terraces of washes. Inland mounds often are associated with small stone-lined

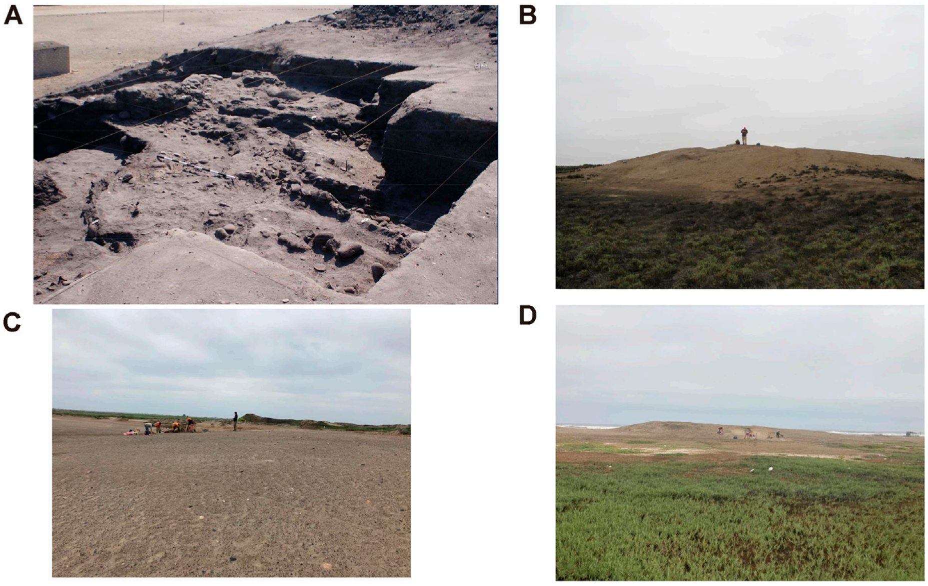

FIGURE 9
(A) Stratigraphically sequenced and superimposed oval-shaped, stone-lined Preceramic houses in Unit 16 located on the western edge of the Sangamon terrace near the Pacific Ocean and proximal to the Huaca Prieta mound; **(B–D)**: Domestic mound sites located along littoral beach ridges and inland washes and wetlands north of the Sangamon terrace (see Figure 8). An increasing number of these sites are being destroyed by modern-day residential and agricultural expansion.

FIGURE 10
Cotton textiles dated to ~5,800–5,500 BP at Huaca Prieta.

feeder ditches leading to small agriculture plots and often with large seed grinding stones (20–40 cm in diameter) and food preparatory lithics (e.g., prismatic cutting blades, stone hoes, scrapers). Current data suggest that the inland agricultural sites are associated with slightly more crop than marine foods, all suggestive of farming. Analyses of food remains (Bonavia et al. 2017; Vasquez et al. 2017), tool kits (Dillehay 2017), and preliminary isotope and dental studies on human skeletons (Tung et al. 2020) from beach-ridge and inland sites suggest that households closer to the shoreline specialized primarily on seafood and those in the interior focused primarily on farming. The differential forms and settlement patterns of households are generally consistent over time from roughly 7,500 to 4,000 BP, but probably increased in

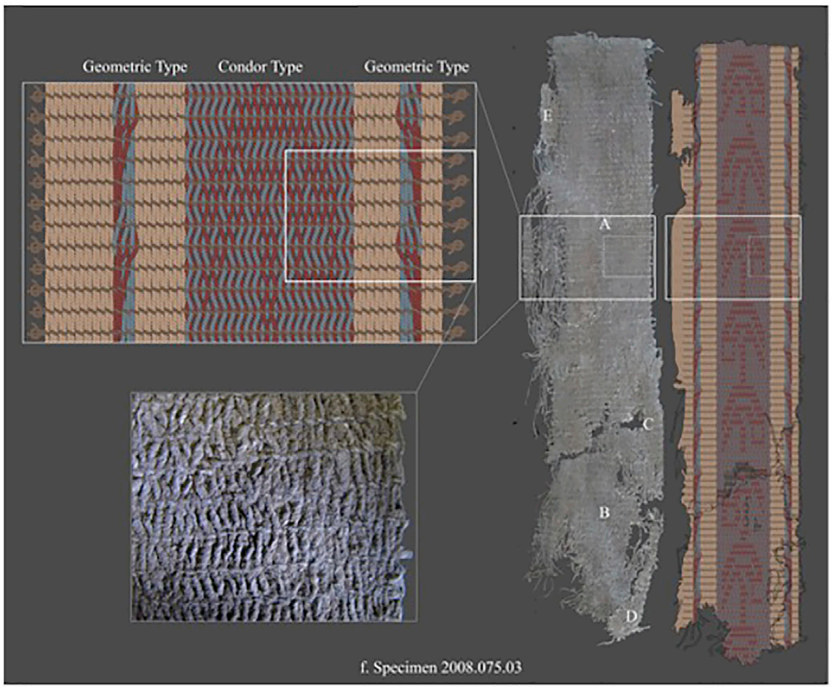

FIGURE 11
Schematic reconstruction of cotton textile with tightly woven design dated to about ~5200 BP.

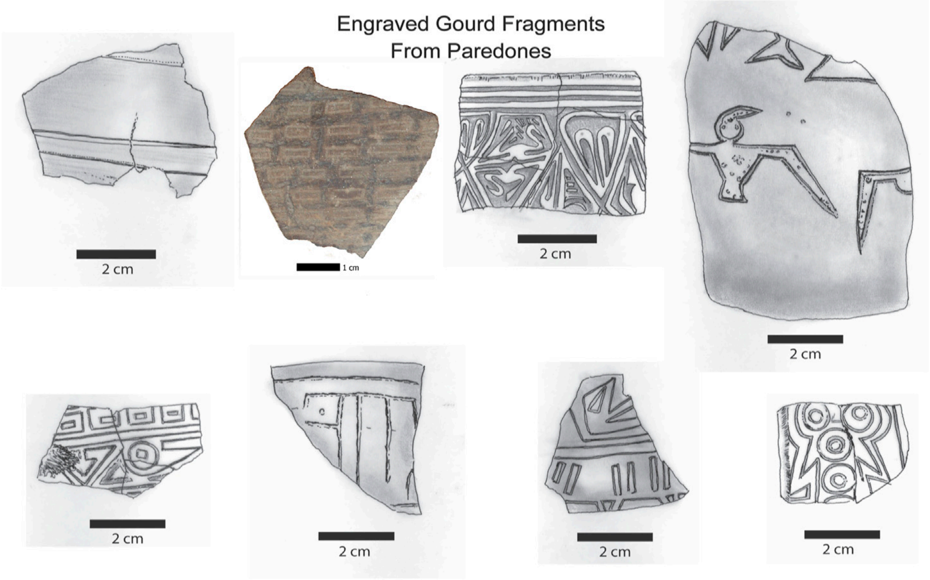

FIGURE 12
Etched gourds with various geometric and natural designs (e.g., human figures and birds) from the Paredones mound dated to ~5,800–5,000 BP.

number and density when wetlands and washes expanded in the interior areas between ~6,200 and 5,000 BP. There is no evidence to suggest that littoral and beach-ridge populations were significantly influenced by environmental changes except marine transgression and regression over time and perhaps during specific major El Nino and tsunami events (Goodbred et al. 2020), and then settlements probably adjusted their location accordingly. The micro-stratigraphy in several littoral and inland house mounds also reveal occasional abandonment for reasons not presently understood.

When viewed from a long-term perspective, by ~7,500–7,000 BP, during the primary lagoonal phase in the valley, household clusters increased in number and intensified exploitation of both marine and crop resources (Dillehay 2017). Other changes occurred between 6,500 and 5,500 BP, including the transition from oval to rectangular houses along interior washes, an increase in site size and increased production of textiles (Figures 10, 11), etched gourds and other symbolic artifacts (Figure 12), as suggested primarily by greater frequency in women's tombs and in ritual spaces at Huaca Prieta. Although some degree of cultivation existed earlier (~9,500–8,000 BP: see Vasquez et al. 2017), as evidenced by the presence of wild squash, avocado, chili peppers and beans, new and more intensified farming households eventually formed as the population expanded between ~7,000 and 6,000 BP in the interior wetlands and washes. By 5,500–5,000 BP, more than 350 marine species and 45 domesticated cultigens (especially maize) and wild plant species formed the local diet. By at least 5,000 BP, increased economic specialization is indicated by new agricultural techniques, that is, raised platforms in lagoons and canal-fed fields in washes (Dillehay 2017).

Once more crops were introduced and agriculture intensified ~5,500–4,500 BP, the local population increased, as indicated by a greater number and cluster of domestic sites during this period, moving farther inland along washes to access more land. Larger, presumably older residential sites are located on beach-ridges and around wetlands and washes: smaller, more shallow mounds are more inland, perhaps representing more recent households that expanded into the interior in later times. Rather than outsiders moving in to establish farming, current skeletal, isotope, dental and preliminary genetic evidence suggests that a portion of the existing population converted from a maritime to an agricultural economy. (Based on the intermittent presence of exotic items from southern Ecuador and extreme northern Peru (i.e., green stones and fragments of *Strombus* sp., *Spondylus* sp. and *Pocillopora* sp.) in a few littoral sites throughout the period under study, it is possible, however, that migrants from warm water areas farther north moved into the Huaca Prieta area. These exotics also may have been procured through exchange.). Given their location, the interior wetlands and washes were primary attractions for expansion, nucleation, and agriculture specialization, which probably increased resource competition and complementary exchange between fishers and farmers, especially with the continuous addition of more food crops (Vasquez et al. 2017). There also is some evidence of animal husbandry or exchange with farther inland pastoralists, as suggested by the presence of camelid wool fibers in textiles and bones around 5,500 BP, but this element of the local economy is currently poorly understood. Presumably, not only did small, specialized farming sectors continuously emerge after ~5,000 BP to complement marine food production and prior farming sectors, as well as exchange with more interior valley populations, but also new settlements were likely catalysts for technological innovation, such as the continuous addition of new weaving and twining techniques on textiles and nets (Splitstosser 2017), decorating gourds, raised and canal-fed fields, and food storage.

Location, location, location: tiered communities and mixed or specialized foodways

To date, our data indicate a three-tiered socio-economic community pattern based on location, site type and subsistence. The first and highest ranked tier is the location of the Huaca Prieta and Paredones mounds on the remnant Pleistocene terrace (Figure 4). The second highest ranked tier is stone-lined dwellings with prepared floors (e.g., Unit 16) located on the Sangamon terrace near Huaca Prieta and Paredones (Figure 8A). The third and lowest tier is pole-reed thatched oval dwellings and later wattle-daub semi-rectangular to rectangular huts in low house mounds located on the outlying littoral beach ridges and along the shorelines of inland wetlands and washes (see Figures 8B–D). From ~7,500 to 6,000 BP, current evidence indicates that houses in all locations initially were oval (~9–12 m^2) in form, with unprepared floors (Figure 13A), and that later from ~6,000 to 5,500 BP they either remained oval or changed to slightly larger semi-rectangular to rectangular forms (~12–15 m^2) either with unprepared or prepared floors: see Figure 13B). (A similar shift from oval to rectangular houses dates slightly later in the Nanchoc area located approximately 100 km northeast of Huaca Prieta on the lower western slopes of the Andes (Dillehay 2011). Moore reports a similar shift in house forms occurring later in far northern Peru (Moore 2010)).

There are three major archaeological indicators of food procurement, preparation and/or consumption associated with the three tiered-community pattern: 1) dental and isotope data from human skeletons (DeSantis et al. 2017; Tung et al. 2017; Tung et al. 2020; T. Tung personal communication, 2022); 2) activity areas associated with the presence or absence of seed grinding stones and lithic cutting and scrapping tools (with starch grains, phytoliths and/or fish scales on their use-edges) and storage pits or fishing nets and

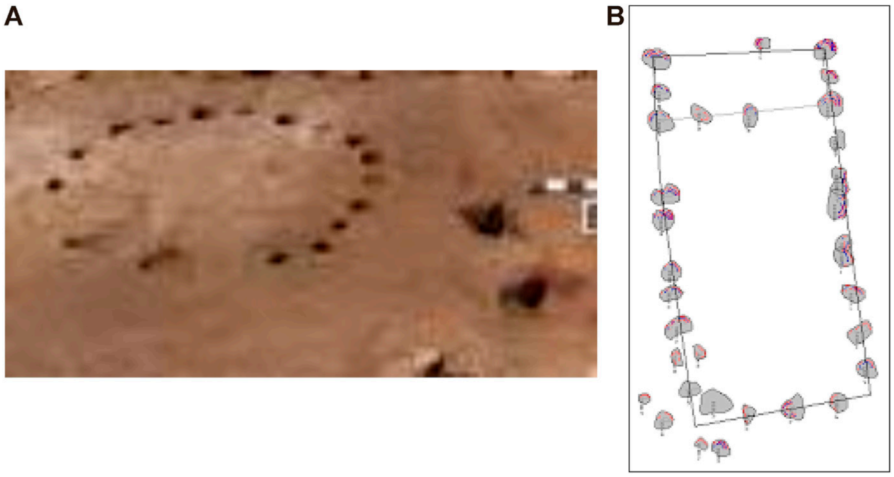

FIGURE 13
(A) Postholes of oval-shaped hut at domestic Site S-11 on a beach ridge ~5 km north of Huaca Prieta; **(B)** postholes of rectangular hut located at M-32 domestic site on the terrace of a narrow inland wash.

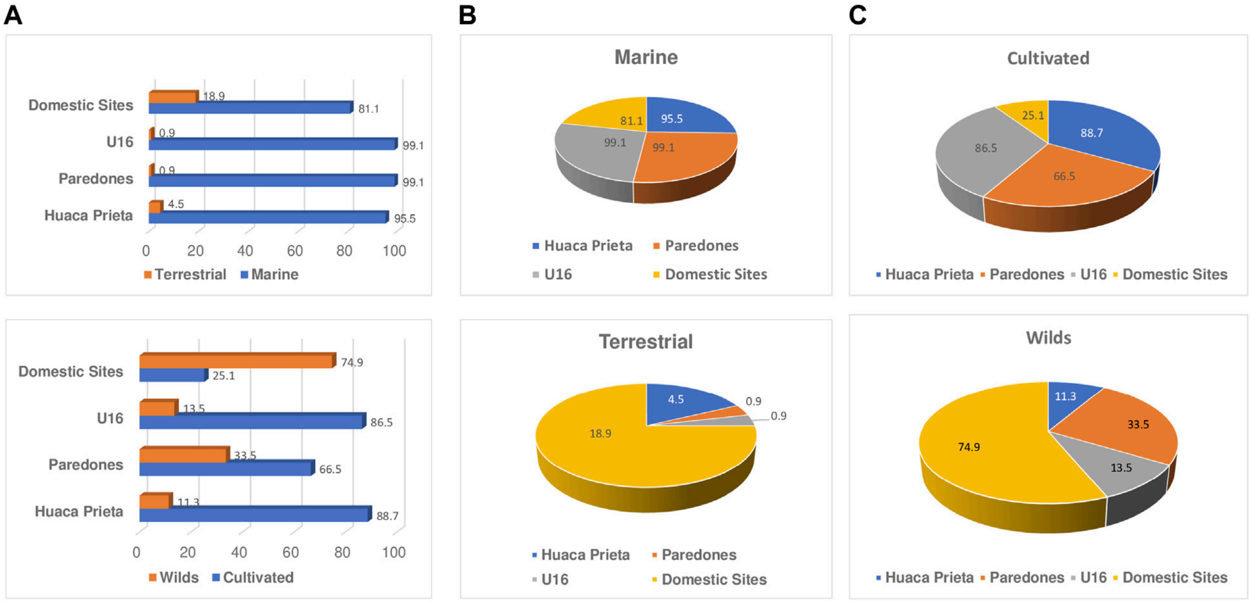

FIGURE 14
Bar-graphs and pie-charts showing percentages of marine, terrestrial (wild plants and animals in wetlands) and cultivated crops at ritual mounds (Huaca Prieta and Paredones) and domestic sites (Unit 16 or U16 near Hiuaca Prieta and outlying domestic sites).

other marine food-related implements (e.g., stone sinkers and gourd floats; Dillehay 2017: Bird et al. 1985); and 3) the frequency and type of food remains in sites (Bonavia et al. 2017; Vasquez et al. 2017). Based exclusively on data for indicator 3, Figure 14 shows the schematic relative frequency of maritime, cultivated and terrestrial wetland (i.e., tubers and other wild plants, water fowl, deer) foods recovered from ritual mounds and domestic sites, the latter divided into tier-2 residential sites (i.e., Unit 16: Figure 9A) located proximal to Huaca Prieta and tier-3 domestic localities situated in outlying areas. Results show that marine foods dominated at tier-3 sites (81.1%) and that wetland resources

(74.9%, mainly plants) were consumed more than cultigens (25.1%). In these sites, food remains probably reflect local procurement, preparation and consumption and inter-household and -community resource exchange between beach-ridge and inland communities. Marine foods were primary and cultigens were secondary food sources at tier-1 and -2 sites, the ritual mounds and Unit 16 households (i.e., U16 in Figure 14) near Huaca Prieta, respectively. At Paredones, marine resources constituted 99.1% of the food remains while at Huaca Prieta it was 95.5%. More cultivated foods were found at Huaca Prieta than at Paredones.

Data for indicators 1 and 2 disagree with evidence for indicator 3. That is, indicator 2 at the Paredones mound and its off-mound activities, which are primarily associated with seed grinding stones, lithic cutting tools (with phytolith, starch grains and fish scales on used edges; Dillehay et al. n. d.) and related activity areas (i.e., small storage pits, cooking hearths, food waste) indicate the preparation of large amounts of marine foods (99.1%) and much smaller quantities of plant foods (0.9%). Moreover, indicator 1, dental and isotope data from human skeletal remains, on and off the Paredones mound, indicate primary consumption of cultigens, mainly maize (Tung et al. 2020). It is doubtful that the high percentage of marine food revealed by indicator 3 was consumed by occupants or workers at this site. Based on indicators 1 and 2, it is most probable that workers prepared fish, shellfish and plant food at Paredones, mainly cultigens, probably for Huaca Prieta or eslewhere. At outlying domestic sites, 81.1% of the food remains were marine resources and 74.9% of the plant foods were wild plant species, the latter of which is not surprising since these sites are located adjacent to wetland areas. Although not detailed in Figure 14, indicator 3 data for households on beach ridges near the sea show a mixed diet primarily based on marine foods (98.2%) and secondarily on plants (1.8%), both cultivated and wild. Indicator 3 data for inland households along washes suggest 82.2% marine foods and 17.8% plant foods, mainly wild species. Although activity area, burial, dental and isotope data on recently excavated outlying households are currently under analyses, preliminary findings based exclusively on indicator 3 suggest primarily marine food specialization for beach-ridge households and primarily wetland resource specialization for inland households. There also is evidence from a few households to indicate mixed diets equally based on marine and terrestrial foods. At Huaca Prieta, the indicator 3 data reveal primary consumption of marine foods (95.5%) and secondary consumption of mainly cultigens with a few wild foods (4.5%). There are no grinding stones and only a few cutting tools and no activity areas (e.g., storage pits and cooking hearths) indicative of significant plant food preparation at Huaca Prieta, although there is widespread evidence of ritual feasting associated with food consumption, mainly marine foods (Dillehay 2017). Human dental and isotope records from Huaca Prieta confirm primary consumption of marine foods (Vasquez et al. 2017; Piperno 2017; Tung et al. 2020). All three indicators are generally in agreement for Unit 16, which is a cluster of tier-2 households located on the Sangamon terrace near Huaca Prieta (Figure 9A). In these households, marine food dominate the diet (99.1%). In summary, based on indicators 1 and 2, it appears that Paredones was the primary location of food preparation and Huaca Prieta was the place for ritual feasting and the consumption of a wide variety of foods. We currently do not have sufficient data to evaluate gender differences in food consumption among site types.

To conclude, caution is urged in collectively or singularly applying the different indicators of food preparation and consumption patterns at these types of sites. It appears that the frequency of food remains recovered from different site types primarily relates to different and changing settlement, occupation exchange, and foodway patterns, with some groups mainly focused on procurement, others on preparation, others on local and non-local exchange and others on consumption, all of which seem to invariably account for the low or high frequency of food types found in sites. In this case study, it appears that the exchange of different foods among specialized (and perhaps unspecialized) communities located in different habitats and the economic specialization of communities preparing and/or consuming foods partially account for the frequency of food types found in sites. Based on our current evidence, it seems that the most reliable indicators, of local food consumption are human isotope and dental records, that is, indicators 1 and 2. Also, to accurately reconstruct the socio-economic relationships among communities, several different types of domestic and ritual sites need study, not just one or two, and this approach requires a long-term research committment.

Social differentiation

Previous research suggested that there was little social differentiation expressed in house forms and burial patterns, respectively, at domestic sites and ritual mounds (Dillehay 2017; Dillehay and Rosales Tham 2022). More recent evidence, however, indicates that there is greater social differentiation than previously inferred and perhaps incipient stratification. As a result of obtaining more data, especially from domestic sites, differentiation now is evidenced by diversity in burial patterns, and particularly in the location of domestic sites and the types of house forms in them. Space does not permit a detailed explanation here, but in general social differentiation and probably marked inequality were defined by a combination of three variables: 1) tier-1, 2 and 3 settlement location; 2) smaller oval and larger semi-rectangular to rectangular house forms, with the latter later in time and likely associated with larger and perhaps more highly ranked social groups (e.g., extended family); 3) burial placement, whether in the ritual mounds and households proximal to them (i.e., Unit 16) or in outlying domestic sites, albeit status-linked patterns of body treatment and elaborate offerings (e.g., shells, colorful stones, decorated textiles, etched gourds) seem to not have been a major distinguishing social factor among the dead; and 4) type and frequency of food and food preparation implements present in different site types.

Recent research also suggests the existence of other social patterns: that is, particular households and groups of households seem to have persisted more than others in the same location through time, especially on beach ridges and lagoons near the shoreline, possibly associated with continuing ancestry and, for farmers, possibly of inheritance of land use rights, as inferred from uninterrupted refurbishing of house floors in the same house mounds and by stratigraphically continuous house floors (n=15–38) over a long period dating from ~7,000–4,000 BP. (A few house mounds reveal occasional abandonment for unknown reasons.) House mounds of fishers show the same patterns but perhaps more related to access rights to the sea. Overtime, a response to increased growth of the human population and probable increased pressure and selectivity on local resources and preferred habitats possibly brought about more intergroup competition and exchange and household and individual community (and possibly gender) identity-marking, although wider inter-community social integration is expressed in the expansion and use of the communal ritual mounds of Huaca Prieta and Paredones. Significant is that by at least ~6,200–5,500 BP symbolic artwork on textiles, baskets, gourds, and painted stones appeared in greater quantities at Huaca Prieta and Paredones (Dillehay 2017: Creamer et al. 2013; Bird et al. 1985). During this period, the most elaborate and innovative material culture was expressed in various decorative and weaving techniques on textiles and baskets found in only women's tombs and selected ritual spaces at Huaca Prieta. These developments are interpreted as probable increased identity-making among local communities, including gender-based identity, and as markers of social differentiation.

Splitstoser (2017) study of textiles from Huaca Prieta and Paredones indicate at least two separate weaving technologies and various subtypes associated with two different community sectors, each respectively representing the identity technologies of fishers and farmers. The same pattern holds for twining of baskets, which shows two major techniques and five to eight subtypes at the same time (Illinsgworth and Adovasio 2017). Variations in weaving and decorative techniques is not simply a function of time whereby new technologies were gradually learned and developed, because several different techniques are found together as offerings in the same female tombs and across contemporaneous tombs. Such variation offers no presently known technological or economic advantage, but likely were more symbolic in nature, that is, identity-markers associated with economic and occupational specialization and exchange, probably female occupation roles, and social cohesion.

Although more data are required to better understand these patterns, perhaps competitive farming and increased exchange with fishers (and probably other farmers, for instance, in the more interior areas of the valley after ~5,000 BP) eventually resulted in an increased demand for social distinction and identity-marking between individual households and communities, which different weaving and decorative techniques would have met for local women, if not men. If so, then the different techniques might be associated with distinct farming and/or fishing household groups on beach-ridges and along wetlands and washes. Varieties in weaving and decorative techniques documented at domestic sites, in turn, are linked to the same varieties found in female burials at Huaca Prieta.

Specialized communities of fisherfolks and farmers

The types of early ritual and domestic mound construction, specialized complementary economies and technologies (including raised agricultural platforms, canal agriculture, decorated textiles and gourds) suggest certain forms of supra-household and community-level collective practices. The social life of farming implies communities variously associated with affiliated household clusters in estuarine wetlands and interior washes, limited land clearance for cultivation plots, planting, harvesting and food processing, and probably shared water rights. Not only does farming require high inputs of labor and group collaboration, but farmers are tied generally to the land they cultivate and, thus, to more fixed communities. A challenge in developing an early farming life that has been widely acknowledged is the potential link between agricultural production cycles and the appearance of land use and property rights (e.g., Engel 1981; Shennan 2011; Bowles and Choi 2013; Becker 2014; Economou and Kyriazis 2017). In this regard, both the early raised field and small, scale, canal-fed farming in the study area might reflect long-term investments in land that probably would have created household- and community-based management, social and group identity-marking, use rights, and eventually ownership and inheritance.

In some ways, the same may be the case for fishers living together on beach-ridges near the Pacific shoreline and perhaps coming together to build reed boats or produce cotton nets, yet laboriously perhaps to a lesser extent than agriculture because the sea requires no preparation for food extraction the way land does. In contrast, a fishing community presumably would have less concern over resource use and property rights perhaps because the Pacific Ocean was probably defined as an open "commons" area, over which there is no, or less, strict ownership or jurisdiction (D'Altroy 2003; Dillehay and Navarro 2003; Lozada et al. 2009; Tellenbach 1986).

Archaeological and ethnohistorical evidence from the Andes suggests that later maritime communities were tightly affiliated and particularly specialized (e.g., Lizárraga 1908; Rostworowski 1999:170–171). This is the case in coastal Peru today and perhaps the same in the middle Holocene (although caution must be exercised in projecting from more recent times to the deeper past). Based on Spanish documents, we know that late pre-Hispanic and colonial fishers inhabited economically specialized communities (Lizarraga 1908; Rostworowski de Diez Canseco 1977a-b, 1989). Fishers did not till the land; by exchanging fish, they acquired a wide variety of marine and agricultural produce. In turn, neighboring farmers exchanged crops for marine foods. There were exceptions to these occupational divisions, and some fishing populations were not spatially isolated from other occupational groups (Lozada and Buikstra 2002; Lozada et al. 2009). However, whether these groups co-resided or lived separately, fishing and farming communities exchanged products, albeit primarily consuming seafood, thereby tying them together in bonds of reciprocity informed by resource sharing and other forms of cooperation. Maritime communities were particularly specialized, engaging in fishing, hunting sea lions, and collecting seaweed, shellfish, and marshy plants, activities that required specialized tools, sea craft, and deep knowledge of littoral and ocean ecologies. This occupational specialization also extended into other forms of difference. For example, maritime specialists often used their own types of pottery (Lozada et al. 2009), worshipped their own gods and temples, used different artistic symbols and identity-markers, and, in some cases, spoke their own dialects (Rostworowski de Diez Canseco 1977a; Mannheim 1991).

Although we have learned more about the lifeways and types of interactions between farmers and fishers, other questions and lacunae exist. For instance, not known is the extent to which changes in the local economy and the development of separate, neighboring agricultural groups between ~7,500 and 5,500 BP might have led to open sharing of maritime and terrestrial resource zones or to the drawing of fixed boundaries (e.g., walls, canals) and identity-marking (e.g., textiles, other artwork) between farmers and fishers. The geomorphological setting of the study area itself defines natural boundary conditions, spatially and sequentially, from shoreline to beach-ridges to inland wetlands and washes (all within a distance of 0.5–2.5 km), but still there might have been overlapping claims. Also not known is whether the development of cultivation and the production of an ever-increasing variety of food crops raised concerns over land use rights and land produce, and over social and gender status linked to these activities, if not between farmers and fishers, then perhaps between different subtypes of specialists or between specialists and non-specialists.

These scenarios lead us to ask what are the social and spatial consequences when one group, agriculturalists, for instance, required land use rights and the other, fishers with open access to the sea, perhaps did not? Did competition, boundary-making, and identity-marking occur between these co-existing communities and between gender-based occupations within and across them, the latter suggested by distinct weaving and decorative techniques in cotton textiles placed as offerings with only female burials at Huaca Prieta and Paredones (Splitstoser 2017)? Are these practices mirrored in the contemporaneous, outlying domestic fishing and farming communities, or are they different within and across them? In other words, do the ritual mounds or centers at Huaca Prieta and Paredones and the domestic sites differ in terms of their communities of socio-economic practices despite their interdependence, or can we presume that if we understand the centers, we understand their supporting domestic components, which seems not to be the case here. Why were more outlying community members not buried at the ritual centers but interred in domestic communities? Do individuals buried in the centers represent preeminent individuals, families, households, lineages or ritualized occupational or other associations cross-cutting local communities within and across the fishing and farming communities? Or were they simply representing household groupings of segmented, economically and environmentally (e.g., beach-ridges, lagoons, washes) specialized and perhaps unspecialized communities? More burial, isotope and genetic data are required from domestic sectors to answer these and other questions. More archaeological data also should refine the contextual differentiation between the different parts and scales of connectivity between centers and domestic sites. Especially needed is a better understanding of the socio-economic and demographic relationships between ritual centers and their associated domestic sites, which requires more focus on the latter. As noted earlier, in the Central Andes, archaeologists tend to concentrate on the centers, generally believing that if you understand their function and meaning, then, by extension, you invariably comprehend the domestic sites.

Discussion

The findings reported here focused on people residing in household clusters in varying littoral and wetland habitats and practicing rituals and burials at Huaca Prieta and Paredones, on their access to individual resource zones, and on the symbolic expression of their identities with specialized food production, individual communities, and gender identity-marking. Although an understudied theme in Andean studies, this research has shed new light on the long-term relationships between the traditionally perceived "dominant culture" of ritual centers and the generally perceived subordinate culture of domestic sites (Lohse 2007), and whether they equally expressed the same socio-economic practices and privileges. These data also offer a specific database to identify the various co-dependent domestic and public parts that conciliated to form increased and different venues of social complexity and interacting fishing and farming communities during the lengthy middle Holocene period under study. The coalescing of various institutions and activities passing into larger, interconnected ritual and specialized economic units had to have resulted from a changing combination of multiple, forming communities of fishers and farmers that learned new technologies, organizational strategies, and other practices with and from each other. As the communities developed and coalesced over time, they formed and became dependent upon the wider Huaca Prieta network and constellation of co-dependent communities. In turn, some members of this wider symbiotic community probably became more specialized in terms of interacting habitats, whether they were the sea, littoral, lagoons or washes. These early formations, especially between ~7,500 and 5,500 BP, were highly localized and largely confined to the wider littoral zone of the lower Chicama Valley, although contact with distant groups to the north is south Ecuador and to the east farther upvalley and in the Andean highlands is suggested by the presence of exotic shells, stones and cultigens, respectively.

Co-dependent maritime and agricultural activities involved different habitat locations organized by different communities beginning by at least 7,000 years ago. Although co-dependent, these communities were not necessarily coalescing as one unified society, at least not at the outset. When increased sedentism at this time brought people together into a locus of dense habitation along the littoral and specialized economies, neighboring inland habitats also experienced a settlement restructuring. At its most basic level, this must have included exchange of resources and mutual social relations operating within the specialized (and perhaps unspecialized) economies evidenced in these habitats. Exchange relations between these groups also probably consisted of exchanging goods for status rather than strict goods-for-goods exchange. More complex relationships of co-dependency could also have evolved, as when the littoral and more inland-based sites exchanged maritime and agricultural produce, respectively, to each other in transactions that depended on mutual exploitation of cycles of social and probably ceremonial debts.

Throughout the period under study, human populations grew significantly in the Huaca Prieta area with at least three socially, demographically, ecologically and economically differentiated tiers. In addition to different mixed and specialized economies, tiered settlement and community patterns, varying types of house forms and public mounds, other impressive features of this period are decorated cotton textiles and gourds, artworks in the form of sculptured stones and painted stones, all suggestive of communication with the cosmological and spiritual world. The type of political system represented by these societies is difficult to estimate. Several Andeanists believe that during the late Preceramic period there was a group-level of decision making due to the absence of elaborate houses and burials (Burger 1992; Dillehay 2017; Quilter 2022), but this thinking may change as more early sites are studied.

In north Peru, the Huaca Prieta area does not stand alone in its early socio-cultural complexity. It is probable that other ceremonial centers dating around or prior to 6,000 years ago exists along the coast and in the highlands, but they have not yet been discovered or their remains lie under later Preceramic or early Formative mound sites. Around 7,500 BP, the mound at Huaca Prieta was much smaller, estimated ~4-5 m high and 25-30 m long and associated with impermanent to permanent campsites of fishers and gardeners (Dillehay et al. 2012; Dillehay 2017). A similar case occurred at the Cementerio de Nanchoc site on the western slopes of the Andes in north Peru ~7,000 BP, where a small ceremonial mound (~2 m high and 25 m long) was flanked by outlying residential sites engaged in a mixed economy of long-distance exchange, hunting-gathering, and small-scale farming (Dillehay et al. 1989; Dillehay 2017).

To conclude, the scale and scope of socio-cultural complexity and mixed fishing and farming economies expanded greatly throughout the Central Andean coastal area (and farming and camelid husbandry simultaneously in the highlands) in the middle to late Preceramic period (7,500–4,000 BP). Archaeological knowledge of emergent socio-economic integration, technological exploration, innovation and development, and the antecedents and consequences of these activities are becoming clearer in the region, with different pathways to sociocultural and economic complexity depending on the local environmental and historical circumstances. The period of ~7,500 to 4,000 years ago is a critical time, representing the spread and evolution of sedentism, incipient occupational specialization, labor demands and lifestyle, dependence on domesticated plant and animal food sources, climate fluctuations, symbolic material expressions, perhaps more formalized ideological foundations, and population growth in several pre-state settings along the Pacific coast of the Central Andean region. The early dual maritime and agricultural society in the wider Huaca Prieta area was one of the most intense and complex coastal adaptations in the region during this period. Our long-term study of the area has elucidated some of the primary mechanisms that led to the inception and growth of this complexity and to a better understanding of the coalescing processes that fostered the development of non-centralized, incipient non-egalitarian communities in the area, economic specialization, gender-based occupational roles, social and labor division, technological innovation, and symbolic artwork. Other areas of the Central Andes may reveal similar or dissimilar socio-cultural transformations during the time period under study here.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Funding

National Science Foundation grants BS-200761 and BS-20197. National Geographic Society 2009-45. Vanderbilt University.

Acknowledgments

We wish to thank the Ministry of Culture in Peru for granting us permission to carry out research in the study area. We also are grateful to the National Science Foundation, National Geographic Society, Vanderbilt University, and the Universidad Nacional de Trujillo, Peru, for supporting our research. And above all, we are thankful to the local people living in and around the lower Chicama Valley for working with and supporting us. We deeply appreciate the warm and friendly reception and hospitality the project has received from local communities in the valley.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 26 October 2022
DOI 10.3389/feart.2022.988111

OPEN ACCESS

EDITED BY
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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 08 July 2022
ACCEPTED 21 September 2022
PUBLISHED 26 October 2022

CITATION
Holmes K, Lepofsky D, Smith NF, Crowell TD and Salomon AK (2022), Ancestral sea gardens supported human settlements for at least 3,800 years on the Northwest Coast of North America. *Front. Earth Sci.* 10:988111.
doi: 10.3389/feart.2022.988111

Ancestral sea gardens supported human settlements for at least 3,800 years on the Northwest Coast of North America

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The relationships between clam gardens and human settlement throughout the millennia reflects the inseparable links among human demographics, marine management systems, and the social-ecological contexts in which they are embedded. However, it can be difficult to assign causation between the initiation and development of eco-cultural innovations like clam gardens and the proliferation of human societies due to the temporal uncertainties associated with both. Here, we bring together data on the shape of the local relative sea level curve, clam garden wall elevation as determined by GIS and drone imagery, radiocarbon dates of clam garden walls, and ecological and archaeological field observations, to assign proxy ages for the clam garden walls of different tidal heights in Kanish and Waiatt Bay on northern Quadra Island, British Columbia, Canada. These data, combined with our mapping and dating of settlement sites, demonstrate a temporal relationship between clam garden building effort and the densification of human settlements. In Kanish Bay, where we have high resolution data, clam gardens begin to be constructed in significant numbers at least 3,800 years ago; this corresponds to a time of increased establishment of large human settlements. The corresponding increase in settlements and clam gardens reflects both the need to increase sustainable food production and the larger number of people who could sustain the ecological and social foundations of the production system. The correlation between number and area of clam gardens and the number of new, large settlements continues until ~2000 years ago. After this time, existing settlements increase in size, but no additional large settlements were established. New clam gardens continue to be built but in seemingly lower numbers. This shift in settlements and clam gardens suggest that a threshold in social-ecological carrying capacity may have been reached in this land- and seascape. In the last few centuries, there is a dramatic decline in the number of clam gardens and evidence of human settlement, corresponding to social and ecological changes associated with European colonization. Taken together, these data demonstrate the strong linkages among Indigenous peoples, their lands and seas, and resilient food systems over the millennia.

KEYWORDS

clam gardens, Northwest coast, traditional marine management, GIS, relative sea level, dating methods

Introduction

Over the past decade, there has been increasingly widespread recognition of the pervasiveness of ancestral marine resource and environmental management systems among coastal Indigenous Peoples worldwide (Pacific Sea Garden Collective 2022; Reeder-Myers et al., 2022). Details of past marine management systems vary among locations, but most encompass a diversity of actions and beliefs that allow sustainable and resilient harvests of marine resources over generations. While our collective knowledge of these systems arises from a range of types of evidence, much of what is currently known comes from observations and memories of relatively recent practices (e.g., Ruddle and Johannes 1989; Mathews and Turner 2017). In contrast, there is limited archaeological evidence for how these practices developed and how they were situated in past social-ecological systems (but see, for example, Mannino and Thomas 2002; Rakov and Brodianski, 2010; Lepofsky and Salomon, Forthcoming; Grone 2020; Reeder-Myers et al., 2022; Thompson et al., 2020). To some degree, this gap in evidence stems from the inherent difficulties in tracking traditional management practices in the more distant past (Fowler and Lepofsky 2011).

Clam gardens are rock-walled terraces built at the lowest intertidal zone by Indigenous peoples of the Pacific Northwest coast (Figure 1) to enhance the production of butter clams (*Saxidomus gigantea*) and Pacific littleneck clams (*Leuconoma staminea*) as well as other marine taxa (Deur et al., 2015; Lepofsky et al., 2015). The making and tending of these ancestral maricultural features are part of a suite of terrestrial and marine management practices used by Indigenous people from coastal Alaska to Washington State to increase food production (Caldwell et al., 2012; Turner 2014; Jackley et al., 2016; Lepofsky and Salomon, Forthcoming; Mathews and Turner 2017). Ecological studies demonstrate that clam gardens are two times more productive today than unwalled beaches because they create growing conditions that especially benefit juvenile clams (Groesbeck et al., 2014; Jackley et al., 2016; Salter, 2018). They also provide habitat for a range of other marine organisms that directly and indirectly benefit humans (Cox et al., 2019). Today, clam gardens are important not just because of their clear ecological benefits, but also because they are places of Indigenous learning and reconnecting to ancestral management and teachings (www.clamgarden.com).

Unlike many other traditional management practices, clam gardens provide material evidence that allows the study of variety of aspects of past management systems, including age. Radiocarbon dates from excavated clam gardens on northern Quadra Island in British Columbia, Canada (Figure 1)—the focus of this paper—suggest coastal peoples began building clam gardens at least 3,500 years ago (Smith et al., 2019). Archaeological and paleoecological data from Quadra Island demonstrate that clam gardens enhanced clam growth and thus, food production, for millennia (Groesbeck et al., 2014; Toniello et al., 2017).

While the efficacy of collecting radiocarbon dates from various spatial contexts within clam gardens has been demonstrated as a valid method for determining clam garden age (Smith et al., 2019), the logistics associated with excavating clam gardens limits the utility of this approach at broad spatial scales. This is because in most parts of the Northwest Coast, clam gardens can only be excavated during the extreme low tides (i.e., <60 cm above chart datum, Lower Low Water Large Tide [LLWLT])–which occur for a total of only about 50 daylight hours in May - August. The challenges in timing are further compounded by the difficulty of finding datable material when excavating a rock wall (Smith et al., 2019). Thus, even though the clam gardens of northern Quadra Island are among the most intensively studied on the coast, extant inferences about these features in past social systems are based on a small sample of only 35 radiocarbon dates from nine excavation units spanning a total of 15 km of rock-walled terraces (i.e., 0.0006% of available walls; Smith et al., 2019; Lepofsky et al., 2020).

Here, we use a novel approach that builds on previous paleoecological, ecological, and archaeological research in this region that focused on Holocene relative sea levels (Crowell 2017; Fedje et al., 2018), distribution and age of clam gardens (Lepofsky et al., 2015, 2020, Neudorf et al., 2017; Smith et al., 2019), and the past and present productivity of clam gardens for clams and other organisms (Groesbeck et al., 2014; Salter, 2018; Cox et al., 2019; Toniello et al., 2019). In particular, we combined the shape of the relative sea level curve, clam garden wall elevations as determined by GIS and drone imagery, and our field observations, to assign proxy ages for the clam garden walls of different tidal heights in Kanish and Waiatt Bay on northern Quadra Island (Figures 1, 2). These data, combined with our previous mapping and dating of settlement sites, allowed us to examine the relationship of this ancient marine innovation to local settlement histories. Together, this analysis provides insights into the central role that cultivating clams in clam gardens played in past food systems and their potential to do the same in current and future contexts.

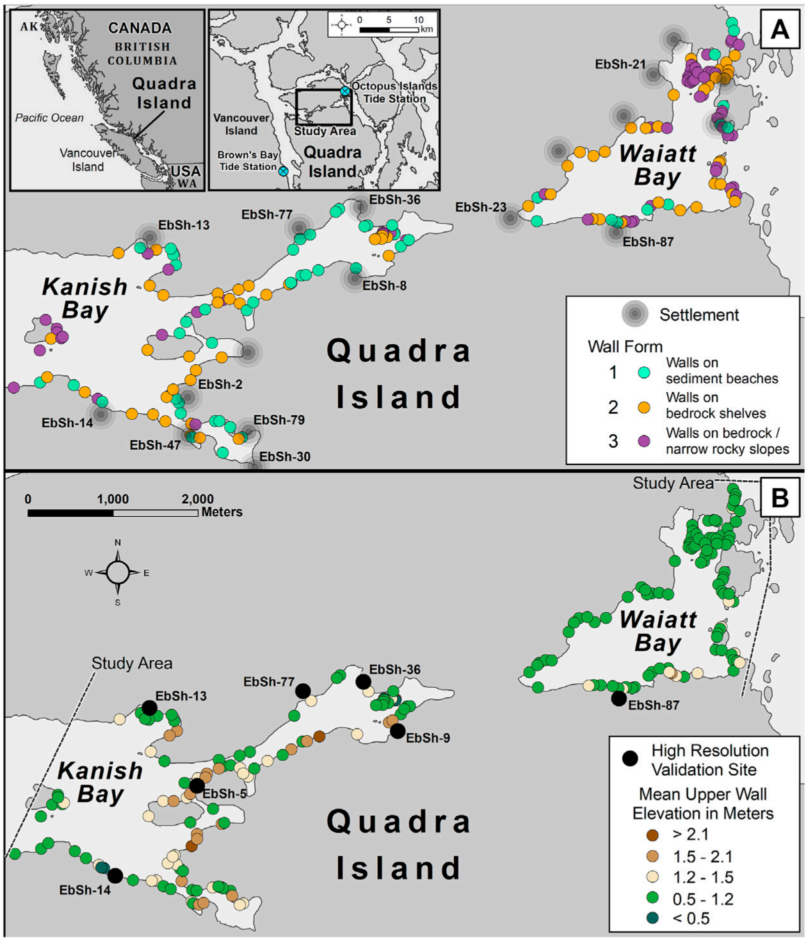

FIGURE 1
Clam gardens are found throughout the Pacific Northwest coast, from Alaska south to northern Washington State (A, left inset). Some areas like Kanish and Waiatt Bays on northern Quadra Island, British Columbia, have exceptionally high densities of clam garden features along the foreshore **(A)**. The three forms of gardens (see text for further explanation) are interspersed with many archaeological settlement sites, reflecting a densely occupied landscape (Radiocarbon dated settlements used in this study are designated with their site number.) **(B)** The tops of the clam garden walls are at different tidal heights (meters above chart datum (Lower Low Water Large Tide [LLWLT]) that can be used to infer relative age. Locations of high resolution validation sites are shown in black dots with associated archaeological site numbers.

Study site

Kanish and Waiatt Bays lie today within the traditional territories of the Northern Coast Salish and Laich-Kwil-Tach peoples. These large bays encompass many small bays and inlets that would have provided ideal locations for settlement (Figure 1A). The coastline is densely populated with large archaeological sites characterized by terraces formed from shell midden. These settlements shifted their locations seaward as sea levels dropped through time creating multi-terraced landscapes with the older occupations often in the back of the site (Crowell 2017). Except in extreme storms, all settlements within each bay could be easily accessed via canoe, while people living in the two bays were likely in frequent contact via a short overland trail or portage. Entering Waiatt Bay requires passing through narrow passages that experience rapid and dangerous tidal currents. Because of these narrows, the timing and magnitude of the tidal cycles differs between the two bays. As we explain below, these differences in tidal regimes, as well as our limited validation surveys in Waiatt Bay, precludes us from doing detailed analyses of wall elevations through time in Waiatt Bay or from making detailed temporal comparisons with Kanish Bay.

The archaeological context

Little is known about the culture history of Quadra Island and neighbouring islands. The area received a small amount of attention in the 1980s (Mitchell 1988, 1990; Mitchell and Donald 1988) which was not enough to establish a specific regional

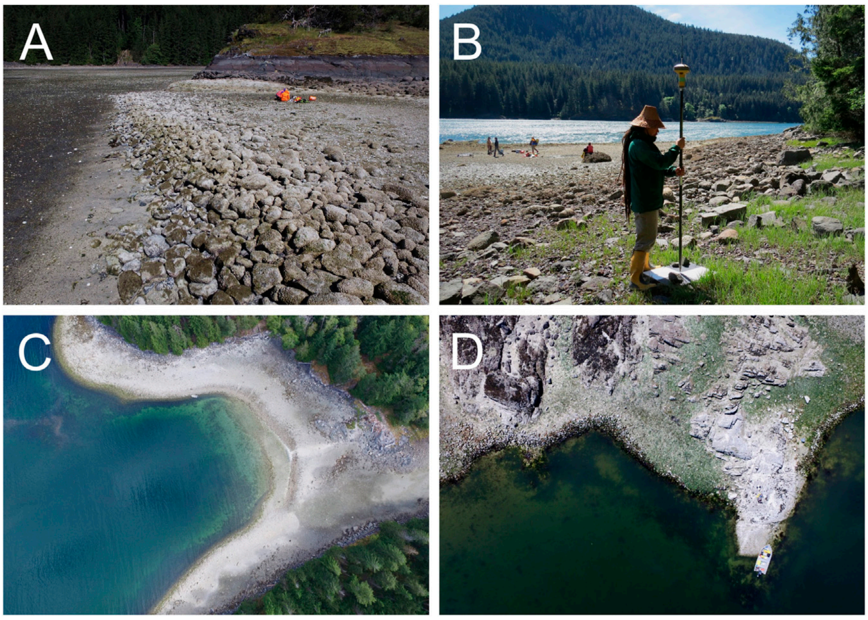

FIGURE 2
(A) Form one clam garden with terrace wall built on already existing clam habitat. **(B)** Real time kinematic survey prior to drone based imagery collection **(C)** High level survey view of a clam garden feature at settlement and clam garden site EbSh-5 in Kanish Bay, showing entire shore lined by clam garden rock walls. **(D)** Low level survey of a Form two clam garden in Waiatt Bay.

sequence. Quadra Island falls between two areas with better known sequences, the Salish Sea to the south which is relatively well documented, and the Johnstone-Queen Charlotte Strait region to the north which is more sparsely known. Given the specificity of local histories, and the differences in the documented culture histories for these two neighbouring regions, we cannot extrapolate from them to the archaeological record of the study area.

In addition to the clam garden and settlement research presented here, the main focus of research in the study area has been on the early post-glacial to mid-Holocene with a particular focus on modelling of paleoshorelines in search of early sites (Fedje et al., 2021a,b; Lausanne et al., 2021). In general, that research shows that people were settling on northern Quadra Island ~13,000 years ago (Fedje et al., 2018, 2016). Technologically, these people used a prepared core and bifacial technology that is similar to elsewhere on the Northwest Coast as a whole (Fedje et al., 2021b).

The archaeological record of the mid-to late Holocene is less well known. Like the rest of the Northwest Coast, the current shoreline is dotted with shell middens of various sizes, with the larger ones sculpted by human-created terraces and depressions that were the foundations for houses and other structures. Intertidal surveys elsewhere in the broader region have revealed numerous wooden fish traps which—together with the clam gardens reported here—reflect the extent and continuity of marine resource management through time and its importance in past social-ecological systems. Importantly, the limited zooarchaeological analysis for shell middens from Quadra (unpublished data) demonstrate that on Quadra Island, like much of the Northwest Coast, butter clams and Pacific littleneck clams—the focus of cultivation in clam gardens—by far dominate the invertebrate zooarchaeological record. The data on settlement patterns presented here significantly augments our understanding of the long-term social and ecological relationships among the ancestral people of Kanish and Waiatt Bays and their land- and seascapes.

The clam gardens of Northern Quadra Island

Quadra Island, like most parts of the British Columbia coastline, has experienced dramatic area-specific changes in relative sea level since the beginning of the Holocene due to eustatic and tectonic processes (Crowell 2017; Fedje et al., 2018); these changes can be used as the foundation for determining proxy ages for clam gardens. When clam garden technology was initiated some 4,000 years ago in Quadra Island, sea level continued to drop significantly until about ~1700 years ago. After that time, sea level declined gradually until it reached current levels in the last several hundred years (Figure 3A). Thus, clam gardens built 4,000 years ago at the lowest intertidal

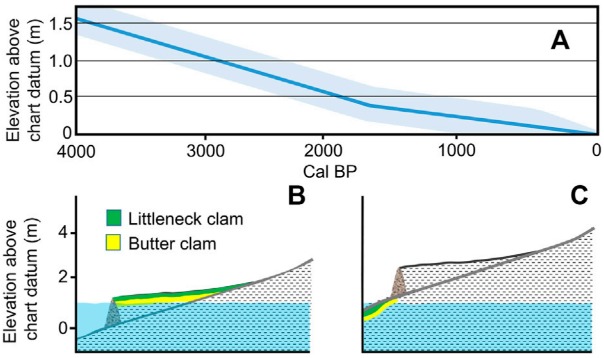

FIGURE 3
(A) Late Holocene sea level curve for northern Quadra Island, British Columbia, Canada presented with 25 cm error band around the mean to reflect errors introduced by the method of measurement and wall auto compaction (refer to Crowell 2017 for details). Note the change in slope roughly 1,700 years ago. **(B)** 4000-year-old clam garden during a 1.0 m tide 4,000 years ago showing the zone in which butter clams (yellow) and littleneck clams (green) could have been harvested. **(C)** Today, because of dropping sea levels in the study area, this same garden sits well above the zone in which clams grow. The height of the terrace wall above chart datum is a relative indicator of its antiquity.

zone are today situated well above the zone in which clams survive (Figures 3B,C).

The shorelines of Kanish and Waiatt Bays contain among the highest density of clam gardens on the Northwest Coast, with over 15 km of clam garden rock walls (~33% of the total shoreline; Lepofsky et al., 2020). The ancestral peoples of these bays built a walled clam garden terrace in any area that could be transformed (i.e., is not a bedrock cliff or a fine sediment beach at the mouth of a significant stream). The garden walls have three forms which often occur in combinations along a bay or stretch of shoreline (Figure 1A; Lepofsky et al., 2015; Smith et al., 2019): those built on soft sediment beaches that already supported clam habitat (Form 1; Figure 2A); those built on bedrock shelves with little to no prior clam habitat (Form 2); and those built on steep eroding boulder slopes also with little to no prior clam habitat (Form 3). The extent to which the Kanish and Waiatt Bays landscapes have been transformed by clam gardens reflects the importance of these innovations not only in past food security, but also the governance systems that managed these systems over the generations, and the knowledge embedded within these ancestral management practices.

All gardens were built by placing rocks at the lowest intertidal at the time of construction until they formed a rubble wall behind which sediment was deposited via wind and waves. The deposition of sediment and broken shell was also augmented by people (Hul'q'umi'num' Treaty Group 2011). Our understanding of these walls, based on our excavations, optical dating (Neudorf et el. 2017), and traditional knowledge (e.g., Deur et al., 2015), is that walls were built gradually over generations. Over time, as people continued to place rocks at the lowest intertidal, a wall and terrace was created that was near the optimal tidal height for growth and survival of littleneck and butter clams [~1.0–1.6 m (Groesbeck et al., 2014; Jackley et al., 2016)]. As we discuss further below, the current height (i.e., from base to top of wall) of some the walls today supports the notion that wall height increased slowly through time. Through time, as sea levels dropped and clam habitat moved seaward, people would have had to refurbish and move the walls seaward, or build entirely new walls, to maintain access to zones of optimal clam habitat.

Our previous archaeological investigations demonstrated that clam gardens started being built at least 3,500 years ago in Kanish and Waiatt Bays (Smith et al., 2019). While we had retrieved dates suggesting the walls could be centuries older, we assigned ages to individual gardens based on conservative criteria that we felt would not overestimate age. These criteria included giving primacy to the most recent shell date found below a wall, even though we often had older samples from other excavation trenches within the same wall. As demonstrated by our on-going work, including that presented here, wall transects can have different taphonomic histories and ages and thus this criterion alone is not sufficient reason to discount a date. Also, our conservative criteria did not consider the broad and overlapping error ranges of the radiocarbon calibrations on the shell samples, which vary from 350–495 years. To avoid imposing false precision on data that has broad error ranges, and in recognition of the fluid nature of clam garden construction, use, and maintenance, we include all radiocarbon dates here from below single walled gardens.

Methods

Field survey of wall heights

To estimate ages of the clam gardens in our study area, we used high precision aerial mapping to determine wall heights in meters above Canada chart datum, lowest low water large tide (LLWLT). We conducted aerial surveys of the 44 km of shoreline in Kanish and Waiatt Bays during the daylight low tides, on May 7th–ninth, 2016 and August 22nd-23rd, 2017. Imagery was collected using a DJI Phantom three Pro drone (i.e., a Remotely Piloted Aerial System [RPAS]) when the tide was <80 cm above chart datum. Two RPAS survey types were conducted: high-level surveys at 250 m altitude, which resulted in data with a resolution of 8–10 cm across the entire study area; low-level surveys at 40–75 m altitude, which provided 1–3 cm resolution data for seven smaller study locations (Figure 1; Figures 2C,D). The high-level surveys were used to capture clam garden wall data to ensure consistency across all areas, and the low-level surveys were used to validate and ground truth our findings.

In preparation for the RPAS survey, 60 cm square checkered ground control targets were dispersed throughout the study areas (Figure 2B). Thirty-one ground control targets were used for the high-level surveys and 67 ground control targets were used for the low-level surveys. The ground controls were surveyed using a Topcon GR5 real-time-kinematic global navigation satellite system. Vertical measurements used the HTv2.0 geoid and horizontal coordinates in NAD83 (CSRS) reference frame. Root-mean-square-error of vertical accuracy was calculated to be less than 1.5 cm for all surveys conducted. The high altitude RPAS survey followed the shoreline with two offset flight lines along the entire Kanish and Waiatt Bays shore, resulting in 4,056 images collected. The seven low altitude study areas utilized a grid flight pattern at 40–75 m and 4,024 photos were collected. The resulting models represent a near-absolute representation of the clam gardens, with 1–3 cm spatial resolution and the high density of ground control targets allowed us to validate our high-altitude data products.

Determining wall elevations

We employed structure-from-motion software which uses feature matching geometry between overlapping imagery to create three-dimensional elevation maps (Carrivick et al., 2016). Pix4D photogrammetry software was used to process all drone and survey data. Orthomosaic imagery was created from motion-based images and digital elevation models. The open intertidal environment around Quadra Island is ideal for making elevation models based on RPAS imagery because it is visually complex yet structurally simple. The resulting data showed the clam garden rock walls could be clearly identified in both the high and low-level surveys. The survey ground control targets were used to align the orthomosaics and terrain models. The low-level high-resolution surveys were smaller in area with a higher concentration of ground control targets, resulting in high fidelity to the real world. The high-level surveys were horizontally accurate but had vertical errors in areas of low ground control target density. We augmented the ground control targets by creating virtual control points based on tidal height at the time of the drone image capture survey.

The high-resolution orthophotos and digital surface elevation models created from the RPAS data were analyzed using ArcMap Desktop version 10.8 (ESRI) software. A total of 204 wall lengths delineated by topographic breaks or a change in clam garden form were digitized using air photo and elevation model interpretation and observational field data. RPAS derived elevation models clearly detail the linear topographic wall and clam bed features.

We manually digitized the bottom and top of the wall along each transect to determine their elevations. The bottom of the wall is defined as the base of the incline where the steep rock wall intersects with sediment or bedrock. In some Form two and three walls, we had to truncate the bottom of transect because the wall base was too deep for the model to assess elevation. The top of wall transect points were digitized to the beginning of the clam garden bed sediment, just landward of the rock wall. To characterize the wall elevation along the rock walls, we initially placed sample points perpendicular to the rock walls at 20th percentile lengths. This mostly resulted in four transects per contiguous wall, however additional transects were measured on walls greater than 100 m in length and on walls associated with archaeological sites (e.g., Figure 4). In total, 814 transects were measured.

However, digitizing on the 20th percentile length meant that many more transects were measured per unit length on short walls than long walls; thus, tallying the 20th percentile transects would not give an accurate summary of the lengths of walls at different elevations. Since we aimed to use length of wall and garden bed area as our measures of ancient clam building effort (see below), we interpolated wall elevations between each transect at 5-m intervals. This served not only to eliminate the bias introduced by our sampling effort, but also meant that anomalous wall heights (e.g., a short wall resulting from a fallen rock) would be averaged out over the length of the wall segments. This resulted in 2,887 5-m interpolated wall height measurements. We refer to these measurements as “wall elevation samples”. Enumerating these wall elevation samples gives a proxy measure for wall length of different tidal heights though time. From these data, and in combination with our previous analysis of clam garden spatial data (Lepofsky et al., 2020), we also examine changes in area of clam beds and total length of terrace walls at different tidal heights through time.

To compensate for elevation distortions generated by greater distances to ground control targets, we used local minute resolution chart datum data paired temporally with the RPAS imagery time stamps to correct the transect elevation at every transect. The Canadian Hydrographic Service (CHS) provided chart datum data for Kanish Bay and Waiatt Bay separately. To estimate rock wall heights in Kanish Bay we used the nearest chart datum station of Browns Bay along with the low altitude surveys to validate the high-level models. Validation was performed by extracting chart datum elevations at seven high resolution sites (Figure 1B). 92 validation transects at these seven sites were used by subtracting the difference between top and bottom wall elevations resulting in a mean vertical accuracy of <10 cm between the high and low altitude data.

To estimate rock wall heights in Waiatt Bay, we used a model derivative chart datum for the *Octopus* Islands provided by CHS. One high resolution validation site and 25 transects were used for Waiatt Bay which showed high fidelity within our elevation models but revealed an estimated 65 cm discrepancy between chart datum and the measurements based on the vertical datum used for surveys in Canada (HTv2.0 geoid). This discrepancy,

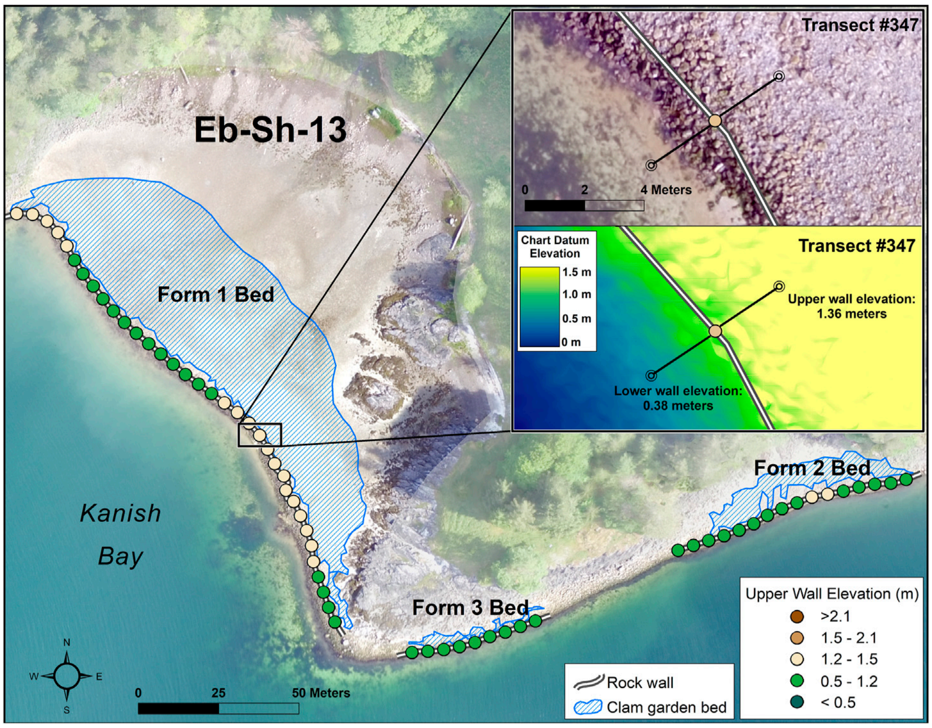

FIGURE 4
Site Eb-Sh-13, showing imagery and elevation model used to create sampling transects.

which is likely due to the differences in tidal regimes, subsidence, and shoreline geography between the two bays, makes comparisons between Kanish and Waiatt walls challenging without further survey data. Because of these unresolvable discrepancies, we report measurements for both bays, but conduct detailed time-elevation analyses only in Kanish Bay.

Assigning ages to wall heights, wall length, and garden area

Our analysis of the historical role of clam gardens in Kanish and Waiatt Bays is based on two fundamental assumptions. First, based on our ecological understanding of clam productivity, we assume that the maximum elevation of the top of walls fronting clam garden terraces will be determined by the tidal height in which butter clams have the greatest growth and survival rates (~1.3 m; Jackley et al., 2016). Littleneck clams have a wider tidal range and flourish higher in the intertidal than butter clams. Thus, butter clam preferred tidal ranges provide an upper limit for the tidal height of a clam garden that would support an abundance of both species of clams. Our second assumption is that to access these tidal zones as local sea level fell through time, people had to reposition or refurbish the clam garden terrace wall. Thus, ordering these wall tidal heights will provide a proxy relative age for clam garden terrace walls.

Based on the ecologically driven assumption that the elevation of the top of the wall fronting the terrace is correlated with sea level and that sea level has dropped through time, we assigned wall and terrace age to wall tidal height. To do so, we ordered all the tops of the wall transects in both bays from tallest to shortest based on height above chart datum. To ensure that the wall height measurements today represent closely the terrace elevation at the time of use, we eliminated from this analysis sections of beaches within 20 m of two or three parallel, multi-tiered walls since older walls may have been deconstructed to build younger walls. We also eliminated walls whose beaches have been dramatically affected by industrial disturbance (fish farming, logging). In both cases, the current wall tidal elevations will be lower than when the terrace was in use and thus, poor age proxies. Removing these beach sections resulted in a total of 2,642 rock wall elevations samples that were analyzed further.

Ordering the top of wall elevations within each bay provides relative ages for the transects. We used top (rather than bottom) wall measurements because 1) they are our most reliable estimates; 2) the top of wall creates a terrace at a specific tidal height that influences clam productivity; and 3) while in many cases the bottom of wall elevations are near to the low-low water line at the time of wall construction, the bottom of walls can also be influenced by the topography of the ocean floor. This is, if there is a steep drop off near the beach (as is the case in many Form two and three clam gardens), the rocks can roll well beyond the lowest tide mark.

We also enumerate the total length of walls and clam garden area at particular tidal heights. These measurements have the potential to provide proxies for the relative amount of shoreline converted to clam gardens. This in turn provides an estimate of the amount of effort put into clam gardening at different times in the past.

As mentioned, the tidal elevations in Kanish Bay have been verified and thus the top of wall measurements are accurate estimates of the "true" tidal elevations. In Waiatt Bay, however, where the tidal elevations were collected using modelled chart datum data and were not verified through survey methods, the distribution of wall heights should be seen as relative measures. That is, the Waiatt Bay tidal heights will be internally consistent as relative temporal indicators but cannot be compared directly to our measurements in Kanish Bay–where we have absolute radiocarbon dates with which we can anchor our temporal sequences.

To assign temporal ranges to the Kanish Bay walls, we used eight radiocarbon dates presented in Smith et al. (2019) from four discrete clam gardens (Supplementary Table S1). Since our previous research was focused on dating older sites (i.e., those higher in the intertidal), our sample of radiocarbon dates is biased towards the beginning of the clam garden sequence. In the current analysis, we consider radiocarbon determinations that we discounted in the 2019 paper. In 2019, we conservatively eliminated the older two or three dates from a single beach even though they were from separate excavation trenches. Our 2019 criteria did not consider that different wall segments could have been initiated at different times, nor did it consider the overlapping error ranges of the radiocarbon dates. Here, we included the dates previously rejected on those grounds. However, we excluded from this analysis the samples from the multi-terraced beaches because using rocks from old walls (higher up in the intertidal) to make new walls would have altered the height of the older walls, thus making the top of wall elevations poor proxies for age.

We used a mix of inferences to determine fuzzy temporal ranges for the height-ordered clam garden wall transects in Kanish Bay. Because cultural choices and various natural taphonomic factors such as auto-compaction of sediment under the wall will affect the tidal height of a wall, and because our radiocarbon determinations have large error ranges, our aim was to assign broad temporal categories to the ordered wall elevations. We start with eight previously collected radiocarbon determinations for garden walls from Smith et al. (2019; Supplementary Table S1). The median calibrated ages of these walls (rounded to the nearest 10 years) provided absolute temporal anchors for the ordered wall elevations between ~3,800–3,170 years ago (N = 6 overlapping calibrated dates) and between 1,690–1,630 years ago (N = 2 overlapping calibrated dates). We note, however, that the radiocarbon ages provide dates for wall initiation, whereas the top of wall inferred ages reflect time of final construction. Thus, the top of terrace wall inferred ages will be some unknown amount of time younger than the below-wall dates.

We created time ranges for the wall elevation samples in several sequential steps. We first created a time range that encompassed the undated walls falling within the tidal heights encompassed by the 3,800–3170-year-old radiocarbon dated walls. Walls with elevations higher than the highest dated wall in this time range were placed into a pre-3800-years time range. Wall elevations lower than the lowest dated wall in this time range were placed in the next time range, with the end of the range defined by the walls with median ages 1,690–1,630 years ago. Finally, we split the remaining elevation-ordered wall samples into two groups by subjectively assigning the lowest elevation walls to the last 300 years. These walls are those that are one-rock high and today sit in the lowest-most intertidal zone (i.e., with the ocean lapping on the rocks during the lowest-low tides). In the field we identified these rock alignments as unfinished walls that had minimal sediments accumulated behind them to create a terrace. We surmise that these alignments were placed since European contact (i.e., post 1780s) and remain unfinished because of a myriad of colonial disruptions to traditional management systems.

By using our previous spatial analyses of clam garden Kanish Bay (Lepofsky et al., 2020), we could also partition total wall length and area of garden into approximate age ranges. These estimates of wall length and area are additional measures of the effort put into clam management in clam gardens. The area measurements in particular are useful proxy measures of the potential food produced from these gardens through time.

Settlement histories

Locations and ages of shell midden sites were collected as part of a study to assess subtle changes in sea level in the mid- and late- Holocene (Crowell 2017). For that study, we primarily dated the basal deposits of sediment cores to determine the relationship between site location and past sea levels. To understand settlement histories, at some sites we also dated upper deposits. We focused our sampling on large sites, although some smaller sites were also dated (Figure 1A). Based on size and presence of terraced house platforms, we surmise that the larger shell midden sites were substantial settlements, possibly occupied year-round. The smaller shell midden sites are more likely "camps", used for more limited activities.

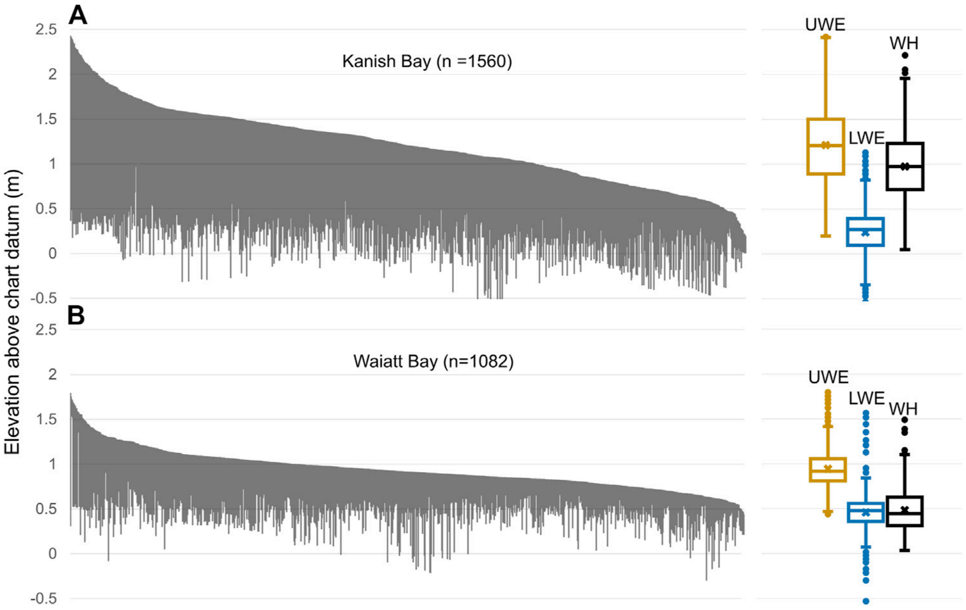

FIGURE 5
Kanish Bay **(A)**, n = 1,560 and Waiatt Bay **(B)**, n = 1,082 wall elevation samples arranged from highest upper wall elevation to lowest above Canadian chart datum (Lower Low Water Large Tide; LLWLT). Each vertical grey line represents an upper and lower elevation of a 5-m length of wall. For the boxplot summaries, UWE = Upper wall elevation, LWE = Lower wall elevation, WH = Wall height. Note the higher median elevations and wall heights in Kanish Bay relative to Waiatt Bay. Thus, while we can compare differences in the overall shape of the plots, we cannot make inferences about change through time between the two bays.

Results

Wall elevations in Kanish and Waiatt Bays

We found the top of wall measurements among our initial transects within beaches were relatively consistent (Supplementary Figure S1). This internal consistency justifies the use of the original transect measurements as the basis for interpolating the RPAS elevation models and sampling wall elevations every 5-m to create the “wall elevation samples”. Internal variation within some gardens may be due to wall refurbishing or natural processes such as compaction of sediments below the walls. Different garden forms tend to have different amounts of variation along the top of wall measurements, with Form three gardens having the least amount of variation (median std dev Form 1: 0.16 m; Form 2: 0.24 m; Form 3: 0.12 m). In general, the tighter range of measurements in Form three gardens is likely due to the shorter digitized length of these features, whereas the longer length of Form two gardens resulted in more variation in measurements. Similarly, Form one gardens tend to be located within expansive, soft sediment beaches that are longer than Form three gardens.

At the scale of Kanish and Waiatt Bays, there is considerable variation in wall elevations (Kanish: min-max = 0.21–2.51 m Waiatt: min-max = 0.13–1.78 above chart datum) which we surmise largely represent different ages of use or localized tectonic influences that may vary between bays (Fedje et al., 2021b; Figure 5; Supplementary Figure S1). Disregarding the difference in tidal heights between the two bays, we note both bays display different distributions in top of wall elevations, especially in the latter two thirds of the sequences. In particular, changes in top of wall elevations in Waiatt Bay are minimal, whereas Kanish Bay elevations decline more dramatically over that same tidal height ranges. The majority of walls in Waiatt Bay are also at lower intertidal heights.

While many of the terrace walls at the end of our sequence were not yet built to the upper optimal tidal height for butter clam growth and survival (~1.3 m above chart datum; Jackley et al., 2016), it is likely that the walls still provided ecological and logistical benefits. Potential benefits include increasing larval clam entrainment, recruitment, and post settlement survivorship. In addition, even walls at lower tidal heights would have increased the tidal window, or length of time, in which clams were accessible for harvesting (Lepofsky and Salomon, Forthcoming).

While all three forms of gardens are found in both bays (Figure 1B), they are distributed in different relative numbers (Figure 6). In Kanish Bay the landscape is dominated by Form

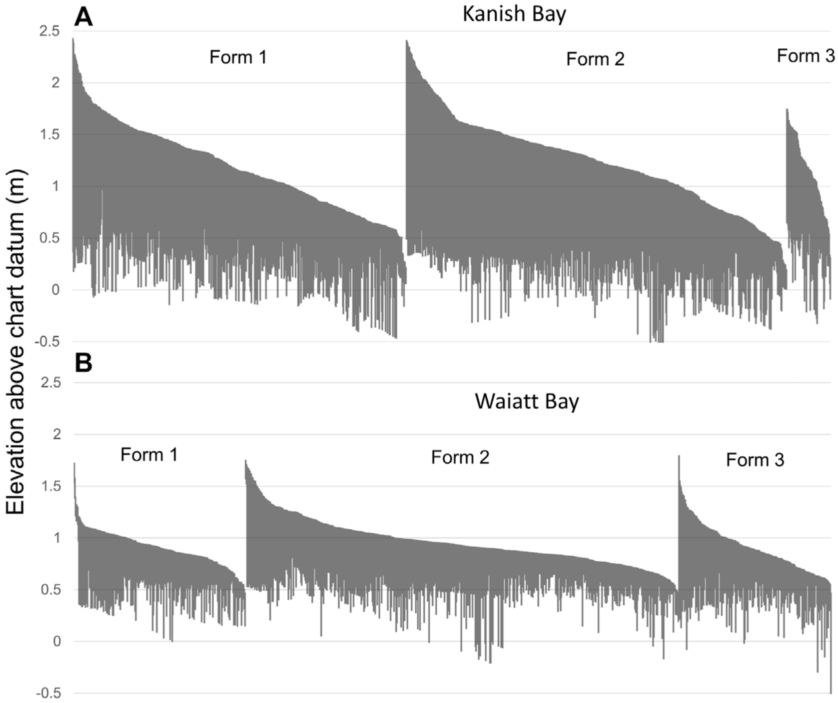

FIGURE 6
Kanish Bay **(A)** and Waiatt Bay **(B)** wall elevation samples of Forms 1, 2, and 3 clam gardens arranged from highest upper wall elevation to lowest above Canadian chart datum (Lower Low Water Large Tide; LLWLT), Each grey vertical line represents an upper and lower elevation of a 5-m length of wall.

one clam gardens (Figure 6A), whereas Form one gardens are relatively rare in Waiatt Bay (Figure 6B). These differences are largely due to underlying geology since there are fewer sandy beaches and more bedrock shelves in Waiatt Bay than Kanish Bay. Our GIS analyses and field observations demonstrate that the Waiatt Bay foreshore is dominated by rocks (81% of foreshore), whereas Kanish Bay foreshore is roughly an equal mix of rocky and soft sediment substrate.

Assigning ages to wall heights, wall lengths, and Garden area in Kanish Bay

Our grouping of the ordered wall elevation samples in Kanish Bay resulted in five approximate time ranges of unequal duration: >3,800 years ago, 3,800–3,170 years ago, 3,170–1,690 years ago, 1,690–300 years ago, and <300 years ago (Figure 7). Each time category encompasses wall elevations within a 50 cm range. Given that our calibrated radiocarbon determinations yielded age ranges of at least 400 years (Supplementary Table S1), and we used the median ages to anchor the sequence, our time ranges should be viewed as having approximate boundaries. Despite this, the robustness of our data set allows us to make inferences about general trends in clam garden wall construction through time.

Only a few wall samples predate the 3,800–3,170 years time range. These wall samples are sitting very high in the intertidal (2.1–2.5 m) in zones well beyond the zone where clams grow today. Possible reasons for the relative paucity of these potentially early gardens are, clam gardening was a relatively new innovation and not yet widely adopted, human population was low enough that this form of mariculture was not needed, and/or other older walls may have been destroyed by various taphonomic processes. Given that this was a time of rapidly dropping sea level, we expect frequent building and refurbishing of walls to adjust for changing tidal elevations. Regardless, if we are correct in our temporal assignments of these high elevation walls, they potentially push the date for the oldest clam garden back at least another few centuries (i.e., pre-3800).

After the initial period of clam garden construction, a substantial number of walled terraces were created in the study area until post-contact times (Figure 7), reflecting the fact that mariculture was widespread and well entrenched in the social-ecological landscape of Kanish Bay. Taking into account the different lengths of time encompassed within the time ranges, more wall elevation samples date to the period 3,170–1,690 cal BP than any other period (average wall elevation samples per 500 years for the three time ranges with begin and

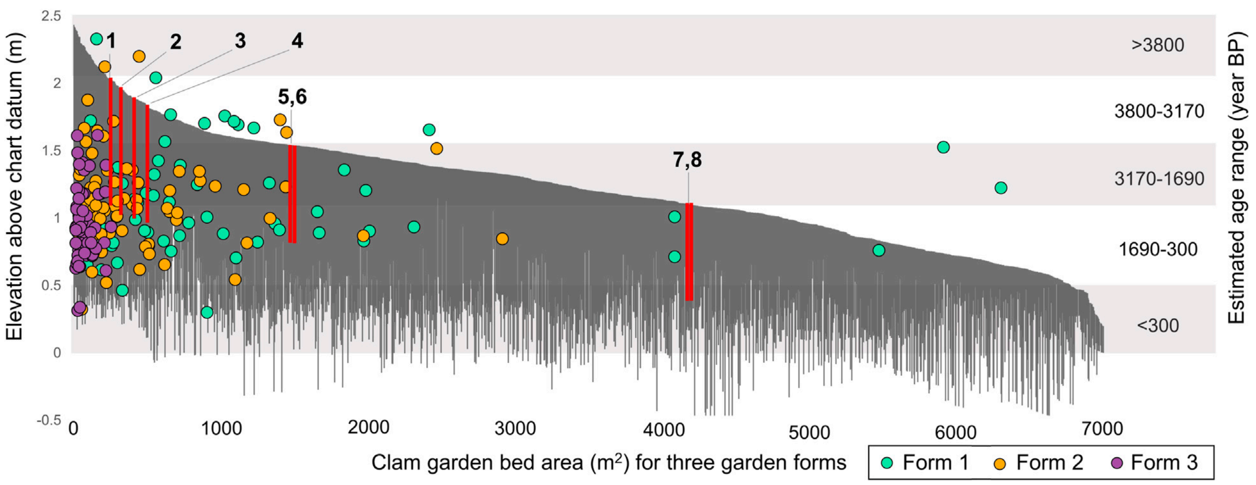

FIGURE 7
Kanish Bay bed area (m^2) of the three form of clam gardens (colored dots) superimposed over the distribution of wall elevation samples (vertical grey lines) arranged from highest to lowest above Canadian chart datum (Lower Low Water Large Tide; LLWLT). Red lines represent radiocarbon dates from clams recovered from under the garden walls (Smith et al., 2019, refer to Supplementary Table S1 for details). Time divisions (grey horizontal bands) based on radiocarbon dates, the local sea level curve (Crowell 2017), and field observations.

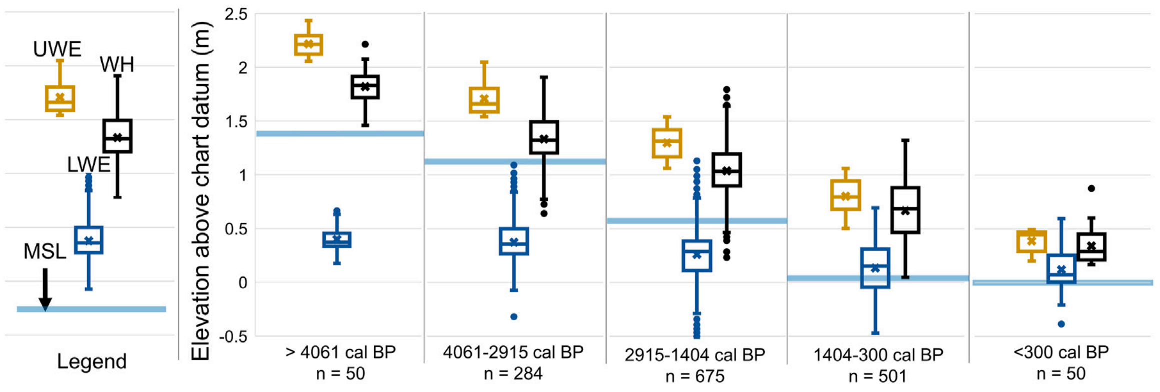

FIGURE 8
Average of top and bottom wall elevations and average wall height in relationship to median sea level per time range showing that clam garden terraces were well within productive clam garden zones. . MSL = Median sea level (horizontal blue lines), UWE = Upper wall elevation, LWE = Lower wall elevation, WH = Wall height.

end dates: 3,800–3,170 = 284; 3,170–1,690 = 675; 1,690–300 = 501). These differences across time reflects greater effort put into wall construction during 3,170–1,690 cal BP than any other time range before and after.

The area's sea level curve (Figure 3A) may in part explain the relatively lower number of wall samples after ~1,690 years ago. There is a somewhat pronounced inflection point in the estimated sea level curve at ~1700 cal BP, where sea level starts to drop more gradually than before this time. A more gradual change in sea level after ~1700 cal BP meant that people would have had to put less effort into maintaining terrace walls at specific tidal elevations. That is, the minute changes in sea level characteristic of this time meant older terraces could have continued to be useful with only minor modifications in wall height. In contrast, the dramatic drops in sea level characteristic of the earlier periods would have made older walls quickly obsolete. For instance, a clam garden built 4,000 years ago would have been much less usable for clam harvesting 1,000 years later since the clam garden terrace would now be situated above the most productive clam habitat (Figure 4). Thus, even though fewer walls were being built on average during the period ~1,690–300 years ago, it is possible that many more of the

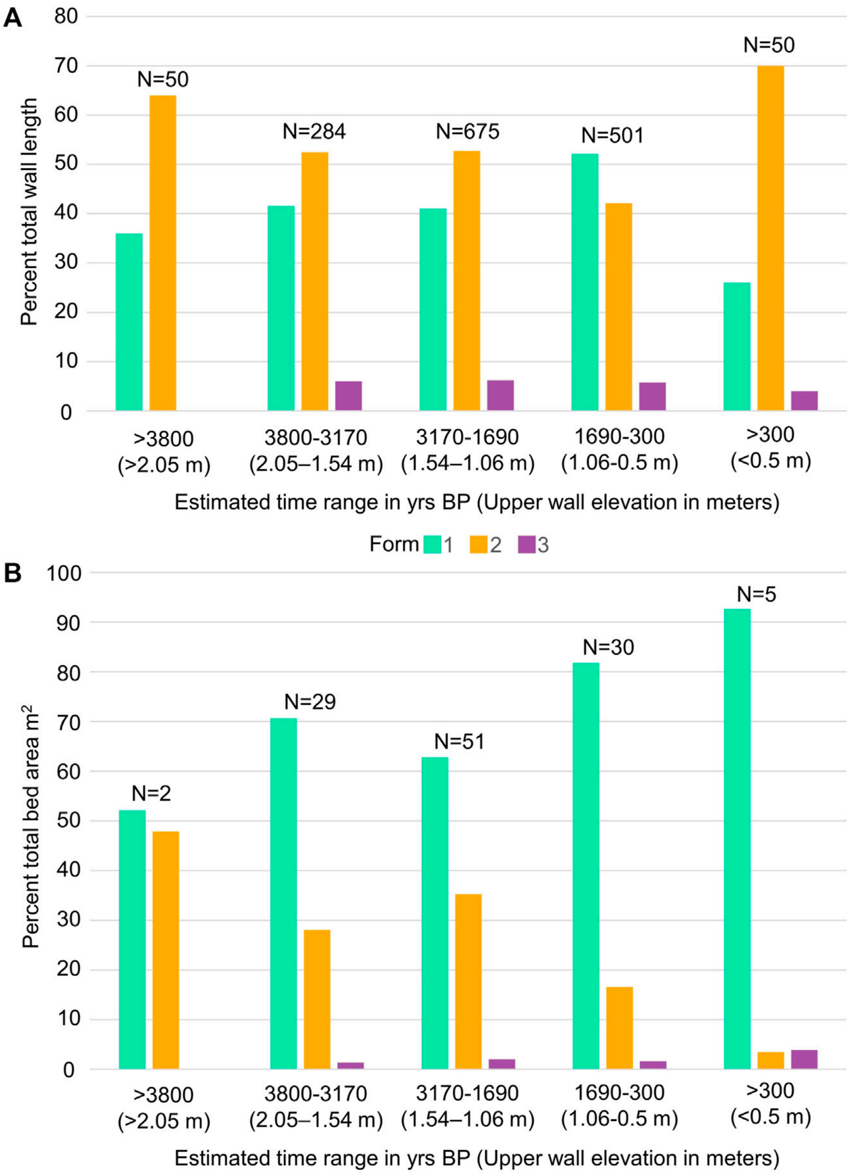

FIGURE 9
(A) Relative percent length and number of wall elevation samples (top of bars) of Forms one, two, and three clam gardens by tidal elevation in Kanish Bay **(B)** Relative percent area and number of clam garden beds (N = 108; Lepofsky et al., 2020) of Forms one, two, and three by tidal elevation in Kanish Bay.

walls on the landscape were in active use than was possible in previous times.

The relationship between median sea level for each time range (Figure 8) and top of wall elevations provides insights into the relative productivity of clam gardens through time. Based on our team's ecological experiments and observations in the study area (Groesbeck et al., 2014) and elsewhere (Jackley et al., 2016), we know that between ~1.0 and 1.6 m above chart datum is the optimal tidal height for both butter clam and littleneck growth and survival in clam gardens. Taking into account the 50 cm error potentially associated with our estimate of ancient sea levels (Figure 3A), our data indicate that clam diggers in each time range had access to highly productive clam garden habitat as well as lower elevation gardens that also accrued other ecological benefits (Lepofsky and Salomon, Forthcoming).

Finally, wall elevation sample measurements from Kanish Bay suggests that through time there is some variation in relative abundance of the linear measurement of the three forms of gardens within time ranges (Figure 9A). When the relative area of the three clam garden forms per time is considered

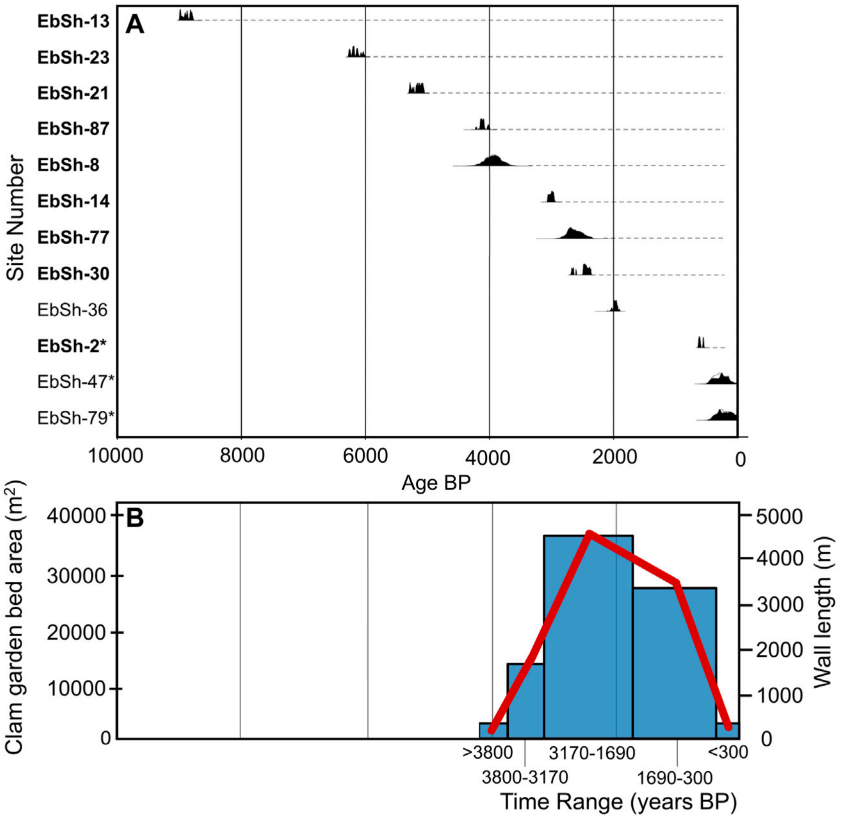

FIGURE 10
(A) Calibrated radiocarbon date ranges from basal deposits in settlements in Kanish and Waiatt Bays. Bolded site numbers are those for which we also have radiocarbon determinations from upper deposits. Based on these radiocarbon dates and stratigraphic profiles, we infer that these sites were occupied more or less continuously into the protohistoric period (dashed lines). We have no upper radiocarbon dates with which to evaluate the other sites, but assume they had similar settlement histories. Small sites are indicated with an asterisk. Dates were calibrated and plotted using OxCal 4.4 (Bronk Ramsey 2009, 2017). **(B)** The total length of terrace walls (red line) and garden area (blue bars) by tidal height in Kanish Bay per time range, showing the relatively greater effort put into cultivating clams in clam gardens 3,170–1,690 cal BP, and the dramatic decline in recent years. The data depicted are summed wall lengths based on previously collected spatial data (Lepofsky et al., 2020), rather than summed sample wall elevations.

(Figure 9B), the clear preference for Form one gardens is evident. In Waiatt Bay, with its rockier foreshore, there are relatively more Form two gardens across tidal elevations, but we are not able to assign time ranges to these data (Supplementary Figure S2).

Settlements histories

Our archaeological surveys indicate that both Kanish and Waiatt Bays were densely settled in the past (Figure 1A). We have radiocarbon dates from 12 settlements in the two bays, including nine sites that we judge to be substantial, permanent settlements, and three smaller sites that likely served as special purpose or short-term camps (Figure 10A; Supplementary Table S2). Our spatial coverage of sites is uneven, with a large portions of settlements in both bays remaining undated (Figure 1).

By dating the basal deposits of sites, we know that the larger sites were initiated at various times in the past, but no new, large sites were built after ~2000 cal BP. The radiocarbon determinations from the eight larger settlements for which we have upper radiocarbon dates indicate that once a settlement was established, it continued to be occupied into the early post-contact period. The three small sites in our sequence date to the last 500 years and probably into the historic period. The period beginning about 300 years ago and into the early contact period was a time of dramatic social change in the northern Coast Salish region. Central among these changes was the forced displacement and dramatic depopulation from European diseases (Harris 1994) in the post-contact era.

The placement and age of the larger settlements and their pattern of internal growth reflect the high density of occupation in the study area. Based on the current sample of radiocarbon dates and our field observations in both Kanish and Waiatt Bays, the earliest settlements were often established in prime locations that were gently sloped, not especially constrained by surrounding topography, were associated with a watercourse, and in Kanish

Bay are associated with existing clam beaches that could be enhanced (i.e., Form one). The more recent sites (<~3,000 cal BP) seem to be located in spots that are steeper and more spatially constrained, sometimes without an associated watercourse. Our limited dataset suggests that through time the larger sites expanded laterally, whereas the more spatially constrained, younger sites expanded by building terraces upslope behind the existing settlement. These internal expansion patterns, combined with the fact that new large settlements were not being established after 2000 years ago (Figure 10A) speak to the fact the landscape was densely settled with limited options for expansion. It also reflects peoples' long-term connections to specific places as well as well-developed and highly local governance and management systems.

Discussion

Radiocarbon dates of settlement sites and the inferred temporal distribution of clam gardens suggest there was an increase in the establishment of large human settlements in Kanish Bay (and likely Waiatt Bay) ~4,000 years ago coinciding with the initiation of clam gardens (>3,800 years ago). From ~3,000–2000, more settlements were constructed, corresponding to our approximate temporal range of 3,170–1,690 years ago when there is an uptick in clam garden bed area and length of garden walls (Figure 10B). The increased economic and social needs of the expanding human population, combined with the dramatic changes in sea level resulting in most previous walls no longer being usable, meant that the period from ~3,170–1,690 witnessed considerable clam garden construction and use.

Taking into account the uncertainties associated with our time ranges, the decline in new walls and in garden bed area ~1,690 years ago likely corresponds to a time when large settlements cease to be initiated and settlements instead expand internally (Figure 10). Since the slowed rate of decline in sea level meant that previously constructed walls could have been used for longer periods with only minor adjustments in tidal height, there may have been less of a need to construct new clam gardens. However, the relative decline in clam garden construction and the apparent cessation in the establishment of new, large settlements, suggests that the communities of northern Quadra Island may have reached some kind of social-ecological carrying capacity. New gardens continued to be constructed and tended to meet the needs of the already dense human population and eventually, clam gardens were built on all the foreshore that could be converted into a terraced garden. After 300 years ago, low population numbers and the partially built, low garden walls reflect a fragmentation in a millennium-old, social-ecological system—in which clam cultivation played a central role.

The relatively greater total wall length in Kanish Bay dating to ~3,170–1,690 is especially pronounced when we consider that our sample of clam garden walls may be biased to some degree towards younger rock walls (i.e., after 1,690 years ago). In part, this is simply because older walls would have been subject to relatively more storms over the millennia that may have disturbed the top of walls. In addition, and perhaps more importantly, we suspect that on some beaches people would have refurbished older rock walls terraces seaward as dropping sea levels changed the location of the most productive clam habitat. We especially expect this to have occurred adjacent to the oldest settlements, where an obsolete terrace wall sitting too high in the intertidal would have interfered with canoe and pedestrian access to the settlement. In beaches associated with settlements, we imagine that people continuously knocked down the height of the rock walls and then added the rocks seaward to move the clam garden terrace downslope. In both bays, this process of constant wall refurbishing is reflected by the fact that older walls are taller than younger ones (i.e., as rocks were added to the wall base, the overall height of the wall from base to top increased; Figure 5).

While we have empirical evidence for ongoing refurbishing of individual walls, we have only limited evidence to support the idea that old walls upslope were often dismantled for younger ones built downslope. Our field surveys did reveal that in some beaches with no associated settlement, there are multiple clam garden walls at different tidal elevations–indicating that obsolete terraces were left standing as newer ones were constructed downslope. However, in one of the oldest and most expansive settlements in the study area (EbSh-13, Supplementary Table S1), our admittedly limited excavations in the clam garden wall and associated terrace did not reveal older landward walls. Rather, both trenches produced overlapping dates, suggesting a narrow window of time in which the wall was constructed or reconstructed. Similarly, our multiple excavations into other clam garden terraces have not revealed prior walls. Thus, we cannot evaluate the extent to which our sample of garden walls is biased towards younger gardens.

Parsing out the temporal relationship among the three clam garden forms built on different substrates has the potential to provide additional insights into the social and ecological underpinnings of clam gardening through time. We hypothesize, based on our understanding of the local topography and observations of clam productivity, that the three forms differed in terms of effort invested in construction and maintenance (input) relative to clam productivity (output). In particular, we suggest that Form one gardens were the most productive overall, followed by Form two gardens. While the latter gardens are often quite small (and thus required considerable labour per unit area to create), they tend to be highly productive. Based on our observations, Form three gardens—which are narrow terraces along the boulder slopes—would have required the most on-going effort to keep clear of fallen rocks and maintain productivity. A reasonable hypothesis is that through time, as populations and food needs increased, people needed to put more labour into food production; this would mean that Form three gardens should be added later in temporal sequences than the other two clam garden forms. The relatively greater area of Form one gardens through time suggests a preference for these potentially lower-cost gardens. While the relatively rockier foreshore in Waiatt Bay precluded extensive construction of Form one gardens as in Kanish Bay, the preference for Form two gardens over Form three gardens in Waiatt Bay also conforms to our predictions. Going forward, the relationship between labour input and food output in these three forms needs to be evaluated empirically with field surveys and experiments.

For at least 3,800 years—almost 200 generations—the Indigenous Peoples of northern Quadra Island tended clams in clam gardens to create resilient, accessible, and productive food systems. These food systems not only nourished people, but were foundations of social systems that cemented connections across generations as well as relations with other groups through trade. These relations were sustained by on-going decisions about where and how to build gardens so that they provided the greatest ecological and social benefit. While the details of these decisions are no longer known, the very presence and abundance of garden walls in different locations and at different tidal heights, reflect some of these now forgotten conversations.

In many ways, our exploration of clam gardens in Kanish and Waiatt Bays highlights the complex and intertwined social and ecological underpinnings of ancient food systems, including management of the relationships between people and clams. Understanding the long-term context of these ancestral management systems is foundational to assertions by contemporary Indigenous Peoples of their rights to manage their own food systems (e.g., Joseph and Turner 2020; Dick et al., 2022). Bringing together diverse kinds of knowledge systems is a powerful and respectful way to understand these age-old social-ecological systems and to bring this knowledge forward (Sigona et al., 2021).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

DL, KH, NS, TC, and AS conceived of the paper. KH, DL, NS, and TC conducted the fieldwork. KH conducted the GIS analysis; KH, DL, NS, TC, and AS analyzed the other data. DL, KH, NS, TC, and AS wrote the paper.

Acknowledgments

We respectfully acknowledge the Northern Coast Salish and Laich-Kwil-Tach Nations in whose traditional lands and waters this research took place. We are grateful to the many members of the Clam Garden Network (www.clamgarden.com) for sharing their excitement and knowledge about traditional mariculture practices. Louie Wilson, Christine Roberts, Will Hall, and Will McInnes provided invaluable help in the field and during the analysis of the data. Many thanks to Eric Peterson and Christina Munck of Tula Foundation for their on-going logistical, financial, and intellectual support of clam garden research. Thank you also to Marlene Jeffries at the Canadian Hydrographic Service for providing valuable tide station data.

Conflict of interest

Author TC is employed by Davis MacIntyre and Associates.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.988111/full#supplementary-material

SUPPLEMENTARY FIGURE S1
Variation in 20th percentile wall transects of tidal heights within discrete clam gardens in Kanish Bay after disturbed walls have been removed from the dataset.

SUPPLEMENTARY FIGURE S2
Relative percent and number of wall elevation samples of Forms one, two, and three clam gardens by tidal elevation in Waiatt Bay.

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TYPE Original Research
PUBLISHED 07 November 2022
DOI 10.3389/feart.2022.1001370

OPEN ACCESS

EDITED BY
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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 23 July 2022
ACCEPTED 07 October 2022
PUBLISHED 07 November 2022

CITATION
Wurz S, Pickering R and Mentzer SM (2022), U-Th dating, taphonomy, and taxonomy of shell middens at Klasies River main site indicate stable and systematic coastal exploitation by MIS 5c-d.
Front. Earth Sci. 10:1001370.
doi: 10.3389/feart.2022.1001370

U-Th dating, taphonomy, and taxonomy of shell middens at Klasies River main site indicate stable and systematic coastal exploitation by MIS 5c-d

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The archaeological record, particularly of shellfish, from the Klasies River main site (KRM) is important in understanding the fluctuating nature of coastal occupational patterns and changing coastal ecologies. In this paper, we provide new uranium–thorium (U-Th) dates for one of the earlier phases of coastal exploitation at KRM, and the microstratigraphic analyses generate novel information about the taphonomy of shell-bearing deposits from the Later Stone Age (LSA) to the MSA I period that, in turn, provide a broader context for middening at the site. A wide range of syndepositional taphonomic processes related to human activities and post-depositional effects include burning, fragmentation and compaction, chemical alteration, and cementation. Despite such issues influencing recovery, shellfish data are informative and are presented from three layers of the Witness Baulk: Shell Midden One (SMONE), Black Occupational Soils (BOS), and Silty Black Soils (SBLS). These coarse shell midden deposits exhibit visible decalcification coupled with cementation with secondary carbonate formation in association with conditions of high moisture and soft sedimentation deformation of the underlying sediments of SBLS. This stratigraphy section is chronologically anchored for the first time using U-Th dating of speleothems associated with a hiatus after the deposition of BOS. The three ages, 110,060 ± 1,100, 109,800 ± 970, and 106,000 ± 2,100 years, place the BOS layer as the base of the SASL sub-member at over 110 ka, making the underlying middens from the LBS member even older. The zooarchaeological analyses of the three layers indicate coastal ecological changes from more sheltered conditions prior to the hiatus, with the exploitation of alikreukel and brown mussels predominating. Before 110 ka, in BOS and SBLS, more exposed coastal conditions occurred, and the diversity of exploited shellfish increased. SMONE and BOS are associated with MSA II/Mossel Bay lower lithic technology and SBLS with MSA I technology, indicating asynchronous coastal ecological and technological changes. The MIS 5c-d evidence for early coastal occupation at KRM provides details on the period during which coastal occupation became stable and systematic on the

South African coast and puts the KRM amongst the handful of sites with shell-bearing deposits, occurring prior to 110 ka in South Africa.

KEYWORDS

Klasies River, shell midden analysis, micromorphology analysis, U-Th ages, coastal exploitation

1 Introduction

Coastal archaeological sites with shell middens that reflect regular, intentional, and systematic exploitation of coastal resources such as shellfish, fish, birds, and other terrestrial resources through hunting, gathering, and scavenging provide evidence for coastal adaptation in various degrees (Jerardino, 2016a; Will et al., 2016, 2019). Shell middens are inferred when occupational debris is shell supported, and the shell thus dominates the matrix as shell middens would have formed quickly with deposition rates of shell exceeding that of sediments (Marean, 2014). Some researchers prefer the term "shell matrix sites," which include shell middens, shell mounds, and shell-bearing deposits, all composed of at least 50% shells (Andersen, 2000; Villagran, 2019). Within the Cape region of South Africa (Figure 1), most of the shell middens relate to the later Middle Stone Age (MSA) dating back to 100,00 years ago (ka) (Klein and Bird, 2016; Will et al., 2016, 2019) and the Later Stone Age (LSA), with rich Holocene data from the West Coast. The Holocene data document the complexity and variability of coastal occupational patterns and present an ideal opportunity for theoretical developments (Jerardino, 2016a). Although studies on MSA coastal adaptation from the Cape feature prominently in the research landscape, especially in relation to modern human origins, only a few MSA shell middens occur before 100 ka (Tribolo et al., 2022). The exploitation of marine resources at early MSA coastal sites has been linked to socio-biological evolutionary advances for *Homo sapiens*. It has, for example, been theorized that the fatty acids from shellfish provided significant nutritional benefits to early modern human populations on the coast (Parkington et al., 2010; Kyriacou et al., 2016) and that the Cape coastal sites demonstrate the first instance, 110 ka, of the exploitation of dense predictable resources (Marean, 2016).

A key aspect of research into the relationship between early modern humans and their adaptation to coastal living and the level to which their lifestyles depended on these marine resources has been the identification of the earliest incidences of coastal resource exploitation. At Pinnacle Point Cave 13B (PP 13B), optically stimulated luminescence (OSL) ages of ca. 164 ka indicate the earliest evidence for shellfish collection on the South African coast and globally (Jacobs, 2010; Jerardino and Marean, 2010; Marean, 2010, 2016). It has been suggested that coastal occupation occurred between 130 and 115 ka on the Cape West Coast (Will et al., 2013; Kyriacou et al., 2015), and this is supported by recent chronologies. Ysterfontein 1 (YFT 1) (Figure 1) shell-bearing deposits (Klein et al., 2004; Avery et al., 2008) have been dated to between 119.9 and 113.1 ka using ^{230}Th/U burial dating on ostrich eggshells (Niespolo et al., 2021a). At Hoedjies Punt 1 (HDP 1), situated close to YFT 1, OSL dating yielded ages of between ~130 and 100 ka (Tribolo et al., 2022) for layers with shellfish (Kyriacou et al., 2015). It seems that a strong signal for organized and systematic exploitation of coastal resources emerged only from around 100 ka in the southern Cape, at sites such as Blombos Cave (BBC), Klasies River main site (KRM) (Henshilwood et al., 2001; Will et al., 2016, 2019; Brenner et al., 2022), and Pinnacle Point 13B (Jerardino and Marean 2010). However, earlier systematic coastal foraging may have taken place, but the evidence has been largely eroded away (Fisher et al., 2010; Marean et al., 2010).

A key and long-studied site with shell middens is KRM (Figure 1). This site provides an ideal opportunity to investigate *Homo sapiens* coastal exploitation on the southern Cape coast as it was made home by many generations of hunter-fisher-gatherers, from early MIS 5 into MIS 3, and again in the LSA (Singer and Wymer, 1982; Deacon, 1995; Wurz et al., 2018). The lowermost MSA I and MSA II/Mossel Bay layers at KRM are broadly dated to between 80 and ca 115 ka, with very few dates that can be directly associated with the deposits themselves. Moreover, interest is growing in detailed microscopic studies on formation processes and taphonomy in middening (Oertle et al., 2022), a perspective that is key to understanding coastal exploitation. The aim of this paper is thus threefold: to report new dates for a section of the earliest MSA II/Mossel Bay shell-bearing deposits, to provide new information on the taphonomy of the middens and other shell-bearing deposits through the sequence by means of micromorphological analysis, and to report on the analysis of the shellfish from the most recently excavated middens from KRM.

KRM is currently situated within the Greater Cape Floristic Region within the Fynbos biome (Allsopp et al., 2014) and, presently, the vegetation is characterized by a mixture of thicket, forest, grass, and fynbos (van Wijk et al., 2017). The nearby Tsitsikamma mountain's southern slopes receive an average of 875–1,375 mm rainfall per year, and at Storms River, 25 km west from KRM, 810 mm is received (van Wijk et al., 2017). KRM falls within the year-round rainfall zone (YRZ) close to its eastern boundary (Chase & Meadows 2007). In the YRZ, precipitation is determined by the South Atlantic Anticyclone system, which frequently leads to stratiform

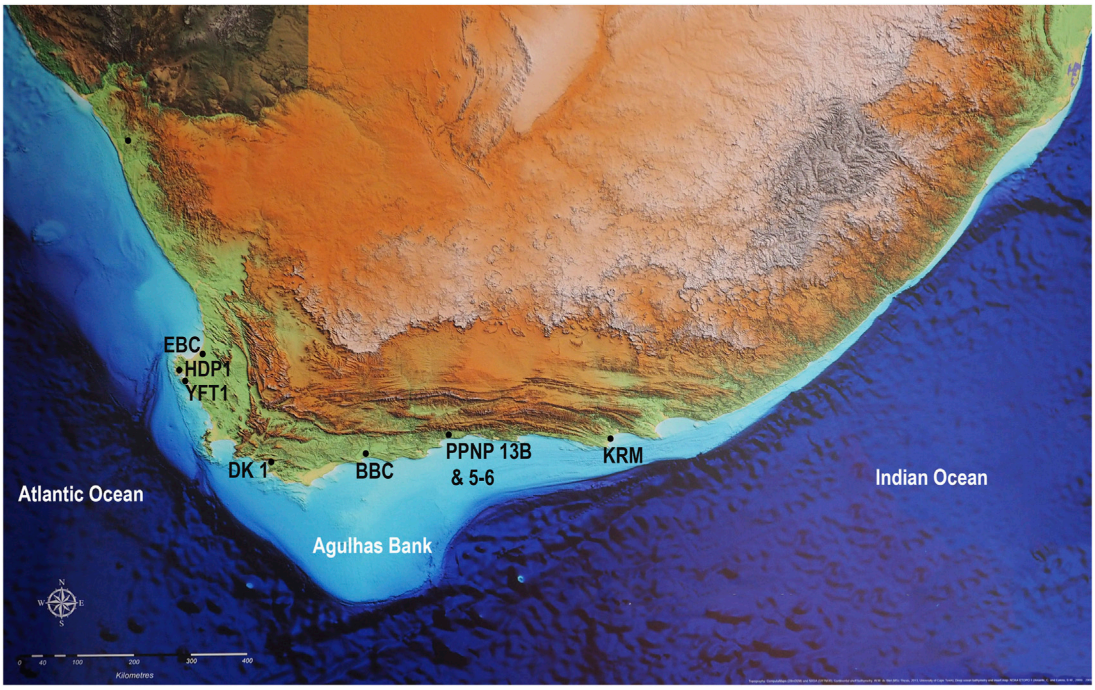


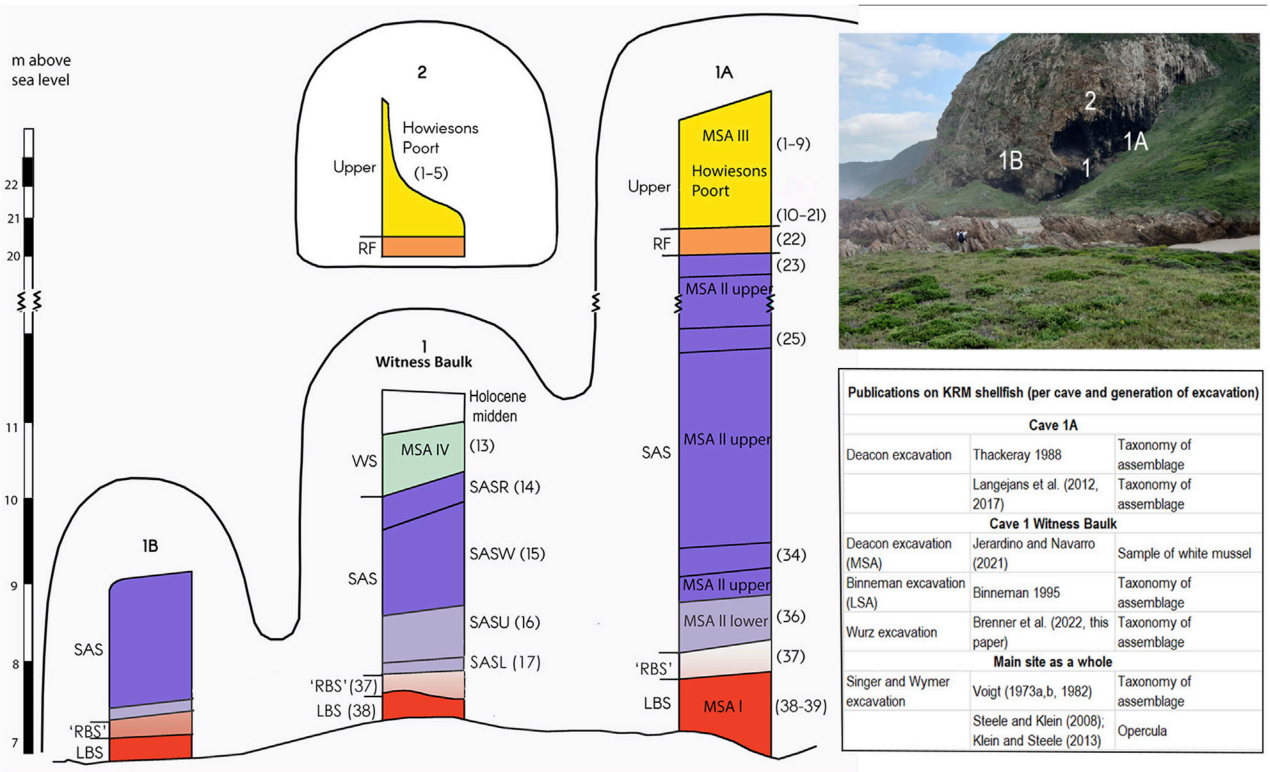
FIGURE 1
Map with sites with shell midden deposits discussed in the text: Elands Bay Cave (EBC), Hoedjies Punt 1 (HDP1), Ysterfontein 1 (YFT1), Die Kelders (DK1), Blombos Cave (BBC), Pinnacle Point sites 13B and 5–6 (PP 13B & 5-6), and Klasies River Main site (KRM).

rainfall in the winter months and tropical temperate troughs that form convective rain, mostly in summer (Engelbrecht et al., 2015; Braun et al., 2017).

The narrowness of the Palaeo-Agulhas Plain and the steep topography of the coastline along the south east coast (de Wet and Compton 2021) (Figure 1) suggest that the shore was in close proximity to KRM during many time periods of relatively lower sea levels during the Late Pleistocene (Van Andel 1989; Langejans et al., 2017). KRM is thus a suitable location to investigate coastal adaptation because it was frequently near the coast. The presence of MSA shell middens at KRM has been known for a long time (Voigt, 1973a, b; Singer and Wymer, 1982; Thackeray, 1988; Klein et al., 2004); however, the current dating framework for especially the earlier deposits provides an overlapping array of age determinations (Niespolo et al., 2021b; Morrissey et al., 2022). Furthermore, many middens are impacted by post-depositional processes that result in poor recovery of the identifiable shell during excavation.

The KRM site consists of a group of two caves formed in quartzite, Cave 1 and Cave 1C, one large recess, Cave 2, and two cliff-face rock-shelters, 1A and 1B (termed "caves" hereafter), which collectively preserve around 21 m of MSA and LSA deposits. KRM was excavated in three cycles, in the 1960s (Singer and Wymer, 1982), in the period between 1984 and 1995 (Deacon, 1995), and most recently, since 2015 (Wurz et al., 2018). Singer and Wymer recognized several large-scale layers occurring across the different areas of the main site. These were incorporated in Deacon's more detailed lithostratigraphic system that consists of members (Figure 2), comprising many small-scale excavation units (Morrissey et al., 2022). The earliest layers occur in Cave 1 and Cave 1B, and occupational debris might have built up continuously in the Caves, but the possible connection was lost due to erosion (Morrissey et al., 2022).

Singer and Wymer excavated large areas of Cave 1 but left a Witness Baulk. The LBS, SAS Lower, and SAS Upper sub-members in Cave 1 contain *in situ* deposits, and the SAS Wedge (SASW) and SAS Rubble (SASR) sub-members relate to *ex situ* material that accumulated when primary occupation took place against the cliff face of Cave 1A. A 1.5 X 1.5 area at the southern end of the Witness Baulk was excavated by Deacon and subsequently by Wurz. The LBS and parts of the SAS member in cave 1/1A also occur in Square AA43, where Cave 1A and Cave 1 intersect, but the stratigraphic relationship between this area and the Witness Baulk is uncertain (Morrissey et al., 2022). The topmost deposits of the Upper member occur only in Caves 1A and 2. The members relate to various cultural stages, with the LBS member containing MSA I lithic artifacts, the SAS associated with the MSA II or the Mossel Bay technocomplex, and the Upper member with the Howiesons Poort (HP) and post-Howiesons Poort (also known as the MSA III) cultural stages



Publications on KRM shellfish (per cave and generation of excavation)		
Cave 1A		
Deacon excavation	Thackeray 1988	Taxonomy of assemblage
	Langejans et al. (2012, 2017)	Taxonomy of assemblage
Cave 1 Witness Baulk		
Deacon excavation (MSA)	Jerardino and Navarro (2021)	Sample of white mussel
Binneman excavation (LSA)	Binneman 1995	Taxonomy of assemblage
Wurz excavation	Brenner et al. (2022, this paper)	Taxonomy of assemblage
Main site as a whole		
Singer and Wymer excavation	Voigt (1973a,b, 1982)	Taxonomy of assemblage
	Steele and Klein (2008); Klein and Steele (2013)	Opercula

FIGURE 2
KRM schematic plan of the main site with the Singer and Wymer layers and Deacon members, a photograph of the main site, and the publications on shellfish relating to the various caves and generations of excavation.

(Singer and Wymer 1982; Deacon and Geleijnse 1988; Wurz 2002).

The deposits of the Witness Baulk in Cave 1 from MIS 5c-d [93-115 ka, see Wadley (2015) for the boundaries of the MIS stages] are the focus of this contribution, although shell middens from various parts of the site are described from a micromorphological perspective to elucidate the taphonomy and provide the broader context. The SAS member in Cave 1 is associated with MIS 5a-d. For the SASR sub-member at the top of the Witness Baulk, U-series dating of stalagmites, not connected to the deposits, yielded ages of between ca. 85–100 ka (Vogel et al., 2021). The underlying SASW sub-member is associated with an OSL age of ca. 70 ka (Feathers, 2002), and the SASU sub-member with ages of 89 ka [amino acid racemization (AAR) age, Bada and Deems (1975)] and 68 ka [OSL age using multi- and single aliquot techniques, Feathers (2002)]. A uranium–thorium (U-Th) date of ca. 126 ka on flowstone from the base of SASU in the Witness Baulk provides a maximum age for this part of the sequence. An age older than 100 ka has been suggested for the base of SASU (Wurz et al., 2018), as the SASR, Singer and Wymer's Layer 14, relates to U-series ages of 85–100 ka as mentioned above.

The age estimates that relate most closely to the SASL sub-member are from a tooth from Singer & Wymer's layer 17 (Figure 2) dated using ESR (Grün et al., 1990). Late uptake results are 93.5 ± 10.4 ka and 88.3 ± 7.8 ka for sub-samples of this tooth, whereas later combined *in situ* U-series and ESR dating of the same tooth gave an age estimate of 101 ± 12 ka (Eggins et al., 2005). The SASL sub-member is thus older than 100 ka. As Brenner et al. (2022) mentioned, dating has been undertaken for stalagmite material from an excavated unit of the SASL called BOS Three. In this study, U-Th dating of *in situ* speleothem material from this layer is reported in detail, which narrows down the age range of this layer and the SASL sub-member.

Coastal occupation involves exploiting a range of marine-related resources, but shellfish is highlighted in this study. Over the years of research at KRM, the various excavation projects reported on shellfish data (see Figure 2 for publications on shellfish for the various caves and excavation cycles at the main site). Voigt (1973) and Voigt (1982) first published on the shellfish of the layers from the whole site excavated by Singer and Wymer (1982) at a time when molluscan fauna was frequently neglected by archaeologists. The sample available was heavily selected (Voigt, 1982). However, it provided some indication of the changing shellfish species through the sequence, especially in relation to the relative quantities of the dominant species, brown mussel (*Perna perna*) and alikreukel (*Turbo sarmaticus*). Deacon's excavation followed more modern methods and retained all the shellfish and fragments thereof; thus, the shellfish material from Cave 1A and square AA43 from Cave 1/1A (See Figure 2) provide valuable insights into subsistence and paleoenvironmental trends from MIS 3–MIS 5 (Thackeray, 1988; Langejans et al., 2012, 2017; Dusseldorp and Langejans, 2013, 2015). The shellfish from Cave 1 Witness Baulk (SASR–SASU sub-members) comprises a large MIS 5 sample and is currently under study. Jerardino and Navarro (2021) analyzed some of the white mussels (*Donax serra*) from this sample. The shellfish recorded at KRM include species such as top shells (*Oxystele sinensis*), alikreukel (*Turbo sarmaticus*), and whelk (*Burnupena limbosa*) that reflect the Algoa marine province with its warm waters (Langejans et al., 2012). Throughout the sequence high ranked mollusc species such as alikreukel and brown mussel from the mid-intertidal zone were targeted (Voigt, 1982; Thackeray, 1988; Langejans et al., 2012), but there are changes in the collected species through time that indicate changing coastal environments fluctuating between relatively rocky and sandy coastal habitats (Langejans et al., 2017).

2 Shell middens, dating, and geoarchaeology

2.1 Dating of middens

The LSA midden at the top of the Cave 1 sequence has been previously dated using radiocarbon on shell and charcoal (Singer and Wymer, 1982; Binneman, 1995; Nami et al., 2016) and paleomagnetism (Nami et al., 2016). At KRM, the calibrated ages obtained for the LSA II on charcoal (2,795 ± 85 cal yr. BP) (Singer and Wymer, 1982) agree with those obtained on the shell (2,655 ± 30 cal yr. BP) (Nami et al., 2016). However, in other contexts, radiocarbon dating of shell middens can be complicated by variations in the marine reservoir effects over time and also secondary disposal activities of humans (Deo et al., 2004). Other approaches to directly date marine shells, such as U-Th measurements, remain experimental and can be plagued by low reliability (Sherwood et al., 1994). However, a breakthrough development of the U-Th technique applied to ostrich eggshell fragments, which are also discarded in middens and are less susceptible to post-depositional alteration (Niespolo et al., 2021a), is rapidly changing this picture. Dating techniques that target geogenic lenses or layers within the middens, such as OSL or paleomagnetism, have likewise also proven successful in some South African contexts, including KRM (Nami et al., 2016). However, intercomparisons of ages on other LSA middens suggest that OSL can be complicated by human disturbance (Bateman et al., 2008). Another approach tested in South African contexts is AAR, which Bateman et al. (2008) reported as potentially applicable in settings where materials were deeply buried.

U-Th dating of geogenic and pedogenic carbonates is a reliable approach to directly date their formation (Hellstrom and Pickering, 2015). The most important consideration in archaeological contexts is how the datable carbonate layer relates to the archaeological strata of interest. When U-Th dating is applied to secondary carbonates in open-air settings, these may have formed below the ground surface some time after the deposition of the midden material. Shell middens can develop post-depositional horizonation over time, but weathering does not always follow a typical pedogenic surface-downward trajectory (Stein, 2008). Sub-surface secondary carbonates in shell middens have been observed by Aldeais and Bicho (2016), Duarte et al. (2019), and Stein et al. (2011). However, to our knowledge, these types of materials have never been directly dated. In caves, secondary carbonates can form as flowstones and speleothems from water dripping directly onto an exposed ground surface. In these contexts, the ages obtained provide information about the timing of hiatuses in the use of the middens. U-Th dating of speleothem carbonate in shell middens is not a common approach, possibly because worldwide, a vast majority of shell middens are located in open-air settings rather than caves. However, cave middens are common in certain regions, such as Southern Africa and Scotland for marine middens and the Maghreb and Vietnam for land snail middens (Gutiérrez-Zugasti et al., 2011; Taylor et al., 2011; McAdams et al., 2022). In KRM and other sites, such as those in the PP complex, speleothems form in the quartzite caves due to the presence of an overlying lithified calcareous dune complex, which saturates the percolating water in carbonate (Bar-Matthews et al., 2010).

2.2 Geoarchaeology of middens

Geoarchaeological analysis of shell middens dates back to the pioneering work of Stein (1982, 1992, 2008). Following some of the earliest applications of micromorphology to shell middens by Goldberg and Byrd (1999). The analyses that emphasize and interpret the microstratigraphy of shell middens became more widespread with the experimental, ethnoarchaeological, and archaeological work of Villagran and colleagues (Villagran et al., 2011a; Villagran et al., 2011b; Villagran, 2014; Villagran, 2019; Villagran et al., 2021). Microstratigraphic analyses of large shell middens in South America and Europe typically reveal complicated sequences of deposition related to actual middening behaviors (e.g., dumping of food wastes); *in situ* features such as cooking hearths, trampling, and phases of weathering; and geogenic deposition (Aldeias and Bicho, 2016; Duarte et al., 2019; Ward et al., 2019). Previous micromorphological analyses of shell-midden deposits in the KRM Witness Baulk reveal a similar mixed use of space in Cave 1 during the MSA I, with two intact hearths containing evidence for multiple firing episodes—at least one associated with the cooking of tubers—on top of layers of anthropogenic debris that included both fragments of shell and bone (Larbey et al., 2019).

Studies that employ micromorphology as a tool for studying shell midden taphonomy frequently emphasize either the impacts of human activities, such as burning and trampling (Villagran et al., 2011a; Villagran, 2014), or shoreline processes, such as marine transgressions (Ward et al., 2019; Hale et al., 2021). Villagran and Poch (2014) documented the effects of the removal of the organic component of shell and freeze-thaw processes under cold, open-air conditions. In another open-air setting, Aldeias and Bicho (2016) and Duarte et al. (2019) document the dissolution of shells near the surface and in localized areas in association with organic matrix and secondary carbonate formation as pendants on shell and cementation at depth. In caves and rock-shelters, a wider range of taphonomic processes might be expected. Linstädter and Kehl (2012) reported high variability in the preservation of shells in the Ifri Oudadane coastal rock-shelter, some of which related to human activities such as trampling and burning; however, post-depositional processes such as gypsum precipitation and the presence of soluble salts were also reported. A recent study of land snail middens in two Vietnamese caves documented some unique diagenetic processes, such as phosphatic alteration of bones in the midden, formation of secondary phosphate minerals and carbonate cement, and alteration of the shell to secondary carbonate (McAdams et al., 2022).

In South African caves and rock-shelters, similar processes have been observed impacting shell-rich deposits. At Die Kelders, for example, Goldberg (2000) documented spatially constrained dissolution of carbonates that impacted a layer that, elsewhere within the cave, was rich in both marine molluscs and land snails. In intermediate zones, he observed shell fragments undergoing decalcification and attributed the dissolution to water saturation of the sediment just above the bedrock floor of the cave. This model is similar to the basal weathering by groundwater proposed for an open-air midden by Stein (2008). Decalcification was also observed in certain layers of PP 5–6 (Karkanas et al., 2015), and in the Waterfall Bluff rock-shelter, shell dissolution was especially pronounced under the dripline (Oertle et al., 2022).

Another process observed in cave middens is the phosphatization of calcareous materials and bone. Goldberg (2000) and McAdams et al. (2022) attributed phosphatization to the possible presence of guano in the studied caves, an interpretation consistent with other studies of diagenesis in archaeological caves inhabited by bats and birds (Karkanas et al., 2000). At Elands Bay Cave—a site known for its LSA shell midden—secondary phosphatization significantly impacted the preservation of the MSA deposits such that bones and shells were completely dissolved (Miller et al., 2016). The diagenesis there is attributed to water that entered the back of the shelter after first passing through a series of rock ledges on which birds and rock hyrax lived.

Although shell dissolution and secondary phosphatization may be enhanced in middens deposited in caves and rock-shelters, comparative micromorphological analyses of MSA age open-air middens in South Africa are exceptionally limited. One thesis conducted on the open-air site of Hoedjies Punt found the presence of phosphatic grains that may have an anthropogenic origin related to the accumulation of organic material in a mixed occupation horizon (Göden 2014). A similar anthropogenic source for secondary phosphates in Brazilian open-air shell mounds was proposed by Corrêa et al. (2013) and Villagran (2019).

At KRM, diagenetic processes impacting shells and other carbonates have been previously documented in Caves 1 and 2. Deacon (1995) reported on the differential preservation of the shell of the brown mussel, which he attributed to the major differences in the nature of the LBS middens relative to the LSA middens in Cave 1. Butzer (1982) noted that shells in Wymer's layer 37 and base 17 were partially decalcified. Deacon and Geleijnse (1988) also described load structures and soft sediment deformation in this part of the sequence (Figure 3). In Cave 2, Deacon and Geleijnse (1988) and Feathers (2002) described the significant post-depositional dissolution of carbonates that impacted the Upper Member deposits. Deacon and Geleijnse (1988) noted the preservation and cementation of "substantial shell lenses" in the western portion of the chamber, where speleothems are also present. However, in the eastern part of the chamber, they attributed volume loss to shell dissolution, which—along with bone—was sparse and fragmented in the area excavated by Wymer. Feathers (2002) applied OSL to quartz grains from the cutting in the eastern part of the chamber and found that this sample had the highest concentration of radioisotopes out of all samples collected from the site. He modeled the effects of rapid and slow dissolution of shells on the dose rates and age outcomes and found that the results favored a rapid (early) dissolution scenario.

Based on the published field observations, post-depositional processes, including compaction, soft-sediment deformation, and dissolution, have impacted the preservation of shell middens or shell-bearing deposits in different site areas (Table 1).

3 Materials and methods

3.1 Micromorphology and microanalysis

Several micromorphology blocks were collected from shell middens and shell-rich layers at KRM to observe variability in taphonomic processes (Table 1). In 2013 and 2015, blocks were carved from exposed profiles from the Deacon and Wymer excavations. The blocks were stabilized in the field with plaster and then transported to the University of Tübingen,

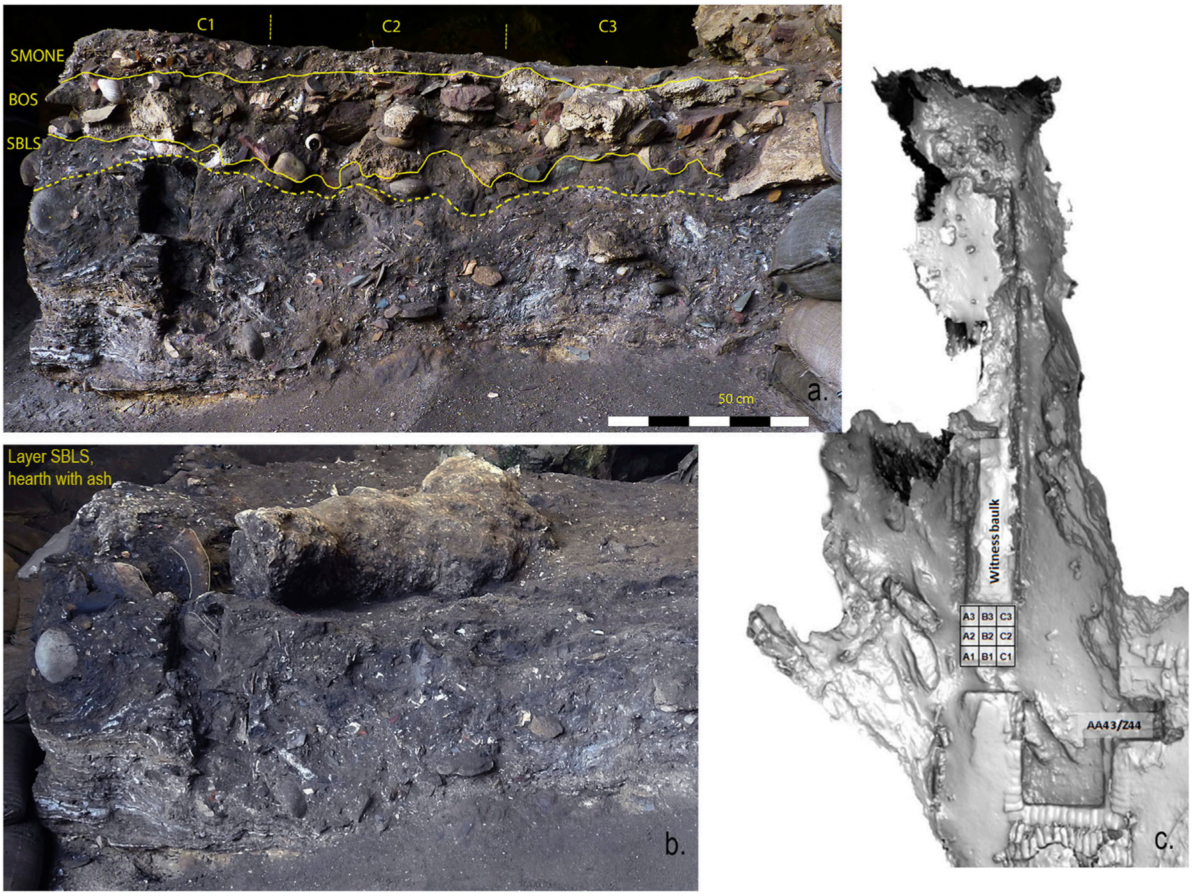


FIGURE 3
(A) East face Witness Baulk, showing the layers excavated with locations of two of the micromorphology blocks; the upper contains the very base of the SBLS. **(B)** Layer SBLS exposed, showing the fallen stalactite and bluebuck horncore that indicate the direction of the impact. **(C)** Plan of Cave 1 with Witness Baulk and excavation grid. Note that the stratigraphy presented by Wurz et al. (2018) has been revised slightly to distinguish the SBLS from the underlying deposits.

where the blocks were dried and then indurated with a mixture of polyester resin and styrene catalyzed with MEKP. After curing, the blocks were sliced, and areas were selected from the cut faces for thin-section production. In some cases, thin sections were ground thicker than the standard thickness of 30 μm due to the observed loss of the softer shell relative to the harder materials such as secondary carbonate and quartz during the grinding process. Following thin section production, the samples were scanned with a Bruker M4 Tornado micro-X-ray-fluorescence analyzer (μXRF) to yield major and trace element distribution maps. The maps were produced using dual detectors with a pixel spacing of 60 microns, a spot size of ~25 microns, a rhodium tube voltage of 50 kV, and a current of 600 micro-amps.

The thin sections were studied under plane- and cross-polarized light (PPL and XPL) using a petrographic microscope. Descriptive terminology followed Stoops (2003), and observations specific to shells in thin sections followed Canti (2017) and Villagran et al. (2011b), whereas fabric analysis of shell-supported sediment followed Aldeias and Bicho (2016). Mineralogical identifications were made using optical properties, in some cases supplemented with a combination of elemental mapping and micro-Fourier transform infrared (μFTIR) spectroscopic measurements. The μFTIR measurements were made with a Cary 610 (Agilent Technologies) FTIR microscope in reflectance mode or with a germanium attenuated total reflectance accessory to yield reflectance or absorbance spectra (respectively) that were compared to an in-house digital reference library for identification purposes.

3.2 Dating

During the 2017 excavation season, several *in situ* speleothem features were encountered. These features included small stalagmites, carbonated masses, and flowstone. Lithic

TABLE 1 List of micromorphology blocks referenced in this study and their contexts, with the presence of taphonomic processes that impacted the shell.

Sample number	Site area	Stratigraphic context	Cultural context, archaeological feature	Clast-supported lenses? >50%	Heat alteration	Dissolution	Calcite cement	Phosphatization
KRM-13-01	Cave 1/ Cave 1A	SAS4 SHC, SAS4 SHB, SAS4 SH	MSA I, shell midden	×		×	×	Present, but not impacting shell
KRM-13-08	Cave 1	LBS	MSA I, shell midden, and hearths	×	×	×		Present, but not impacting shell
KRM-13-07	Cave 1	LBS	MSA I, shell midden, and hearths	×	×	×		Present, but not impacting shell
KRM-13-06	Cave 1	LBS	MSA I, shell midden, and hearths	×	×	×		Present, but not impacting shell
KRM-13-05	Cave 1	LBS, contact with SBLS	MSA I, shell midden, and hearths		×			×
KRM-15-112	Cave 1/1A	YS1B, YS1, SCB1; equivalent to SASL	MSA II, distal shell midden					
KRM-13-02	Cave 1/ Cave 1A	SAS1S, SCB2; equivalent to SBLS	MSA II			×	×	Present, but not impacting shell
KRM-13-13	Cave 1A	Upper member: CPx5, YSx3, CPx4	HP, trash midden with shell		×			
KRM-15-103	Cave 2	Upper member	HP, shell midden	×	v. Rare		×	×
KRM-15-107	Cave 2	Upper member	HP, lateral equivalent to KRM-13–103 but impacted by diagenesis			×		×
KRM-13-25	Cave 1		LSA, shell midden	×	×			

TABLE 2 U-series results.

R	Mass (g)	U Conc ± 2SE (ppb)	230Th/ 238ThA ±95% ext	234U/ 238UA ± 95% ext	232Th/238UA± 2SE	230Th/ 232Thi ± 2sd	230Th/ 232ThA	Age ± 2SE (years)	[^{234}U/^{238}U]i corr ± 2SE
5384 (KRM1, WB, A2, BOS)	0.037	655 ± 49	0.9038 ± 0.0035	1.3642± 0.0034	0.006287 ± 0.000045	1.50 ± 1.50	143.8	**110,060 ± 1,100**	1.4970 ± 0.0042
6478 (KRM1, WB, C3, BOS)	0.018	440 ± 33	0.8068 ± 0.0042	1.2498 ± 0.0034	0.014507 ± 0.000081	1.50 ± 1.50	55.6	**106,000 ± 2,100**	1.3369 ± 0.0045
6819 (KRM1 WB, B1, BOS)	0.032	519 ± 39	0.9275 ± 0.0037	1.4001 ± 0.0035	0.004511 ± 0.000035	1.50 ± 1.50	205.6	**109,800 ± 970**	1.5455 ± 0.0042

The final U-Th ages are marked in bold for emphasis.

artifacts and bone recovered from this layer also exhibited encrustations of secondary carbonate. Three of the speleothems from BOS were documented and removed for U-Th dating, one each from excavation rows A, B, and C. These samples were assigned lab numbers 5384, 6819, and 6478. Sample 5384 from square A2 is a carbonated mass. Sample 6819 from square B1 is a small stalagmite with flowstone extending off its edges, yielding an appearance of a fried egg. Sample 6478 from square C3 is a small stalagmite of approximately 10 cm in height (Table 2).

These three speleothem samples were visually inspected and carefully cut along a vertical axis using a diamond-tipped geological saw. The flat sections were lightly polished, and the cleanest, densest carbonate layers were visually selected for

U-Th dating. A hand-held hobby drill and dentist birr was used to drill out around 1 g of powder from each chosen layer. These samples were deliberately selected to date the oldest layer of speleothem formation to provide an age estimate for the beginning of the hiatus in sedimentation. Around 300 mg of each sample was weighed out into an ultra-clean Teflon vial, spiked a mixed ^{229}Th-^{233}U spike, calibrated against a standard HU-1 uranite solution in secular equilibrium, dissolved, and run through a standard ion-exchange chromatography set of protocols to isolate and concentrate the Th and U isotopes (Hellstrom, 2003). U and Th isotopic concentrations and ratios were then measured simultaneously using a Nu Instrument Plasma multicollector inductively coupled plasma mass spectrometer (MC-ICP-MS), again following standard measurement protocols (Hellstrom, 2003, 2006). A correction assuming an initial ^{230}Th/^{232}Th of 1.50 ± 1.50 was applied to all final ages to account for a detrital phase (Hellstrom, 2006).

3.3 Excavation of the SASL sub-member in the Witness Baulk and field observations

Shellfish evidence relating to coastal adaptation for three layers from the Wurz excavations of Square C1 of the Witness Baulk, Shell Midden One (SMONE), Black Occupational Soils (BOS), and Silty Black Soils (SBLS) are discussed (Figure 3). The three layers are equally well presented in square C1 (50 × 50 cm), in contrast with the rest of the Witness Baulk, where deposits from the layers occur unevenly. All tufa, speleothem material, fauna, stone, and other artifacts >20 mm were piece-plotted, and these items were not included in the calculation of the deposit volume (Table 1). The excavated deposits were first dry-sieved through 5 and 2 mm meshes. Subsequently, the coarse and fine fractions were wet sieved through very fine domestic sieves (0.5 mm), resulting in the retention of very small shell fragments, microfauna, and lithic chipping debris. The archaeological material occurs as palimpsests, and the winnowing of soils led to it being tightly stacked, often precluding the precise determination of the angle of the finds. Lithics and microfauna are plentiful, and the large mammal fauna is well preserved but frequently fragile. The marine shell is less well preserved, although it was possible to excavate a few complete shells. Land snails that occur in significant numbers (Brenner et al., 2022) are much better preserved. The lithics from SMONE–BOS relate to the MSA II lower or Mossel Bay technocomplex (Wurz, 2002; Brenner & Wurz, 2019; Wurz, 2021; Brenner et al., 2022), and a prepared core or Levallois technology was followed to produce points and some blade end products. Formal tools, when present, are mostly notched artifacts. The SBLS layer has MSA I affinities (Brenner et al., 2022), in which blade technology becomes more prominent (Wurz, 2002).

The Wurz excavation follows the Deacon stratigraphic system, and SMONE and BOS are from the SASL sub-member. Layer SMONE is equivalent to Singer and Wymer's layer 17a and BOS to layer 17b (Singer and Wymer 1982; Wurz et al., 2018). The matrix of SMONE consists of relatively loose soils and rubble with disintegrated tufa blocks, patches of leached ash and charcoal, and no *in situ* combustion features. Layer SMONE was up to 15 cm thick in square C1 but much thinner in the other squares.

The sediments from BOS, discussed in more detail in this study as it relates to the dating samples, are darker and more clayey than those of SMONE. Although the matrix is generally similar to that of SMONE with no preserved combustion features, significantly more speleothem and tufa material are present in BOS than in SMONE, and some of the lithics and anthropogenically altered fauna are covered in flowstone. A large stalactite, more than 1 m in length, fell into the BOS deposits and came to rest on SBLS, deforming them in the process. The angle of a horn core (Figure 3) captures the extent and direction of the impact. Singer and Wymer (1982) mentioned numerous blocks of soft calcite from Layer 17 excavated from other cave areas. This accords with the findings from the BOS layer, and tufa or phytokarren/photokarren may be calcite deposits that formed by biophysical/biochemical activity and dripping water (Viles, 1984; Vanara and Maire, 2006).

Due to its thickness, around 35 cm in total, BOS was excavated in arbitrary spits determined by the year of excavation (BOS One, BOS Two, and BOS Three), which assisted in investigating the site formation processes. In the top part of the layer, BOS One and BOS Two, the highest number of carnivore tooth-marked bovid specimens occurred, and more bones with transverse, stepped, and right-angled fracture angles show that depositional bone breakage took place (Lap 2020). This contrasts with the taphonomic faunal signals in the lower part of the BOS layer (Bos Three). It is thus very likely that there was an occupational hiatus after the formation of the BOS soils contributed to these taphonomic signals. Secondary carbonate precipitation, including speleothem formation, occured during the occupational hiatus, after the formation of the BOS layers, and this was associated with increased amounts of dripwater that also led to loosening the base of the stalactite that fell into the deposits. Butzer (1982: 37) commented that there was "active stalagmite accumulation, leading to cementation" and local calcrete "lenticles" in layer 17, the equivalent of BOS. He observed evidence for the abundance of water during the formation of this layer and suggested that this indicates a substantially wetter climate during this period (Butzer, 1982: 39). An analysis of ostracods in the sediment indicated freshwater to slightly saline conditions (Faul, 2021).

Layer SBLS consists of very dark silty sand with patches of clay comprising part of the matrix. In contrast to SMONE and BOS, this layer contains intact combustion features with ash layers preserved. SBLS is currently under excavation, but the shellfish reported on here is from around 5 cm thickness of deposit in square C1. This layer is attributed to another member that will be further discussed in the future.

3.4 Shellfish analysis

The methods employed to analyze the shellfish from these layers are discussed in detail by Brenner et al. (2022). The shellfish data reported complement those by Brenner et al. (2022), but this sample is slightly larger. Although the BOS layers have been discussed separately by Brenner et al. (2022), they are combined in this study. The layers were initially separated to interrogate site formation processes. However, as the deposit volume in BOS One and BOS Two is low, faunal exploitation patterns are best discussed for all the layers combined. Incidentals (non-food species) are not included in the taxonomic discussion here. The minimum number of individuals (MNI) and the weight values were calculated, and the maximum diameter of *Turbo sarmaticus* (alikreukel) opercula was measured using a digital caliper. Most of the shells were highly fragmented and decomposed, and there were no complete specimens of limpets and brown mussels available to measure. *Patella* sp. include fragments of limpets such as *Scutellastra longicosta*, *Scutellastra argenvillei*, and *Cymbula oculus*, which could not confidently individually be identified to species level because of their fragmentary state.

4 Results

4.1 Micromorphology and microanalysis

The 11 samples described in this study provide a range of shell middens (or middens containing shell) and shell-rich layers of various cultural contexts and from different areas of the main site. Some observations of the site-scale formation processes help contextualize the samples. Six of the blocks were collected from the Witness Baulk area of Cave 1, which is located well inside the chamber where the deposits are protected from open-air processes such as rainfall, overland flow, and winnowing by the wind. This area is, however, impacted by aeolian deposition and internal cave processes such as roof collapse events, dripping water, speleothem formation, and localized ponding. Whether this area could have been impacted by seawater inundation during storm surges is unknown, but this process has been proposed by Butzer (1982). Three of the blocks were collected from the area where the cliff-face overhang that forms Cave 1A meets the dripline of Cave 1. In this area, the deposits are also protected from rainfall. One block was collected from Cave 1A. Deposits in this area are somewhat protected from rainfall, depending on the wind direction. However, they are exposed to overland flow, colluvial processes, and deposition of biogenic wastes by birds of prey that roost along the cliff face. Finally, two blocks were collected from the interior of Cave 2, which was protected from rainfall but was differentially impacted by diagenesis and either the formation of speleothems or dissolution of carbonates as a result of dripwater of variable acidity entering the cave's eastern and western sides. The diagenesis in Cave 2 has been previously described by Deacon and Geleijnse (1988) and Feathers (2002), and its impacts on the preservation of shell are described in this study at the microscale.

4.1.1 Cave 1 Witness Baulk: MSA I and MSA II/ Mossel Bay lower

The four blocks from the MSA I deposits of Cave 1 Witness Baulk (LBS member) contain abundant shell fragments visible in the thin section, particularly in the lowest two blocks. During sampling, the shells were exceptionally fragile and soft and could be easily cut through with a knife. The shells are roughly horizontally oriented and distributed in discrete layers interbedded with layers of charred material overlain by wood ashes, layers of mixed debris that include fragments of bone, and thin lenses of sand. Many of the shells are fragmented in place (Figures 4A,B) with a displacement of originally curved portions onto a roughly horizontal plane, an indicator that significant compression has occurred. Observations of the shell fragments at high magnification revealed that many are internally porous due to decalcification (Figures 4C,D). In some cases, porosity is greater in the fibrous layer relative to the nacreous layer, whereas the opposite is true in others. When present in association with ashes and charred plant material, the shells are darker gray in color under PPL, and some exhibit delamination or exfoliation planes (Figure 5). Other shells in ash layers are visibly recrystallized. μFTIR analyses reported previously by Larbey et al. (2019) showed that one layer of shell fragments associated with a hearth in these samples was impacted by heating above 400°C, the temperature at which biogenic aragonite converts to calcite (Yosioka and Kitano, 1985). The observations of delamination and recrystallization show that heating may have also impacted the structural integrity of the shell.

Although some secondary minerals are present, these are limited to small hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$) nodules, thin phosphatic crusts, and zones of alteration of wood ashes. In places, ashes are replaced by hydroxyapatite in close proximity to shell fragments that are unaffected. Minor amounts of gypsum ($CaSO_4{\cdot}2H_2O$) are also present in the LBS deposits (Figures 4K,L), and there are a few examples of gypsum crystals formed within exfoliation planes in the shell. In addition, halite (NaCl) crystals form on the cut surfaces of the micromorphology blocks within weeks of slicing, which indicates that halite crystals are likely present in the samples. However, information about their spatial distribution has been lost due to dissolution during thin section production. The presence of gypsum and halite and the

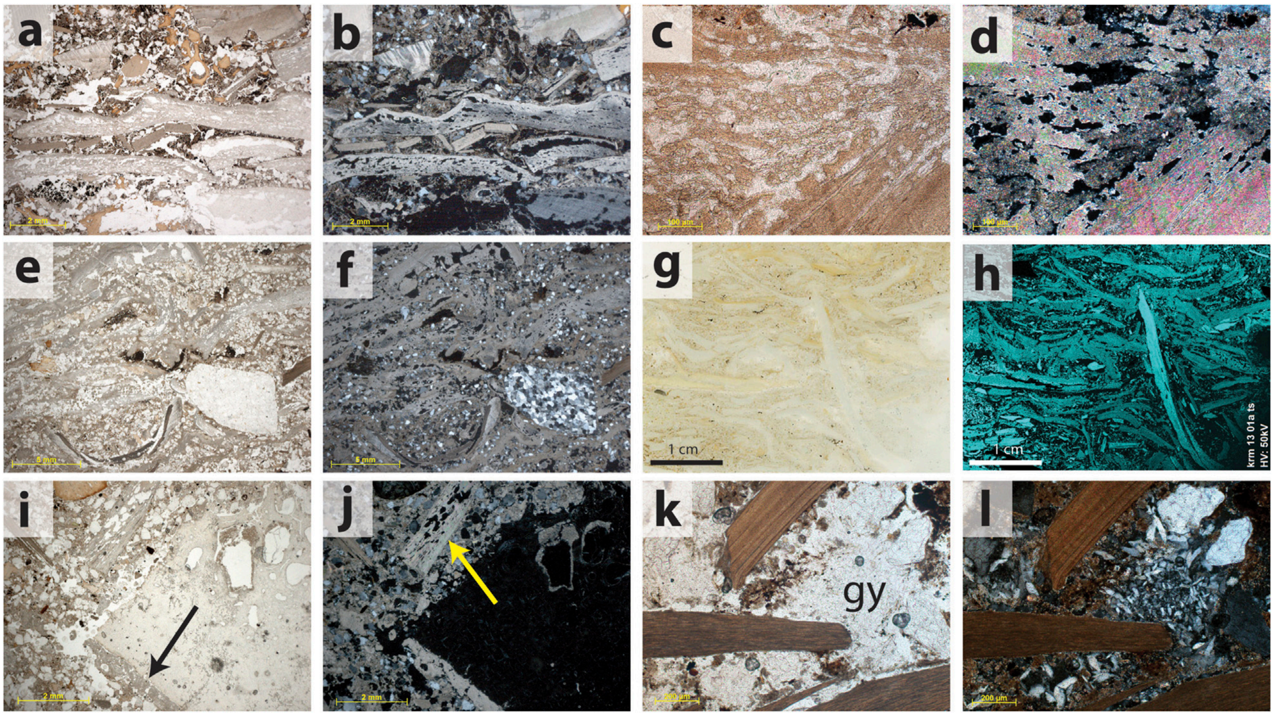


FIGURE 4
The dominant taphonomic processes impacting shell in the MSA deposits of Cave 1. **(A)** This sample from the Witness Baulk contains at least 8 discrete shells, illustrating a range of internal porosity due to decalcification, as well as fragmentation and deformation in place. PPL. **(B)** Same view as **(A)**, XPL. **(C)** High magnification detail of a shell composed of aragonite that has internal porosity due to decalcification. PPL. **(D)** Same view as **(C)** XPL. **(E)** Sample from the MSA I deposits located at the point of connection between Cave 1 and Cave 1a (KRM-13-01). Although difficult to see due to the calcareous matrix, over 50% of the image is composed of horizontally oriented shell. PPL. **(F)** Same view as **(E)**, XPL. **(G)** Incident light scan of a thin section from sample KRM-13-01. **(H)** An elemental distribution map of calcium produced from the same area as **(G)**. Here, the shells and their abundance are easier to see compared to the photomicrographs, and the shells composed of aragonite exhibit a lower Ca abundance relative to the shells composed of calcite. One particular shell composed of calcite is oriented vertically, and the shells composed of aragonite are deformed over its pointed edge. **(I)** A fragment of bone from sample KRM-13-02 exhibits a pendant of secondary calcite (arrow). PPL. **(J)** Same view as **(I)**, XPL. The arrow indicates a porous shell fragment. **(K)** Three relatively well-preserved shell fragments from the base of the Witness Baulk have a nodule of secondary gypsum (gy) in between them. PPL. **(L)** Same view as **(K)**, XPL.

association between gypsum and shell could indicate that secondary precipitation of gypsum and other soluble salts contributed to some of the fragmentation we see today.

At the top of the sequence, in the SASL sub-member, corresponding to the contact with the SBLS, soft-sediment deformation under conditions of high moisture, perhaps related to the stalactite that fell into the overlying deposits, has impacted the hearths and the layers containing shell. Ash layers at the contact with the SBLS show optical evidence of phosphatization with yellow color in PPL and isotropic zones in XPL, with μFTIR analysis showing a more extensive presence of the mineral hydroxyapatite. The layers were deformed after phosphatization, suggesting a period of weathering, exposure to phosphatic materials such as guano under conditions of high moisture, and then deformation related to rockfall coincident with the SBLS. Phosphatization rims are observed on speleothem fragments, and some bones are internally recrystallized to an unknown mineral. One fragment of the operculum is observed to also have phosphatized edges, whereas the remainder of the shells in this portion of the sequence have a stronger brown color in PPL and exhibit less internal porosity compared to samples lower down. The shell fragments in this sample comprise less than 50% of the area and are therefore not abundant enough to qualify this portion of the deposit as a midden.

4.1.2 Cave 1/1A interface: MSA I and MSA II/ Mossel Bay lower

Of the three blocks at the interface between Cave 1 and Cave 1A, the lowest, which is associated with MSA I cultural materials from the LBS member, contains shells that are fragile and soft. The upper two blocks contain much larger shells that are well-preserved and can only be cut through with the help of a hammer and chisel. These two blocks are from the same member and are the approximate lateral equivalent to the shell midden layers analyzed and dated in this study. However, due to the removal of sediment during previous excavations, there are issues with

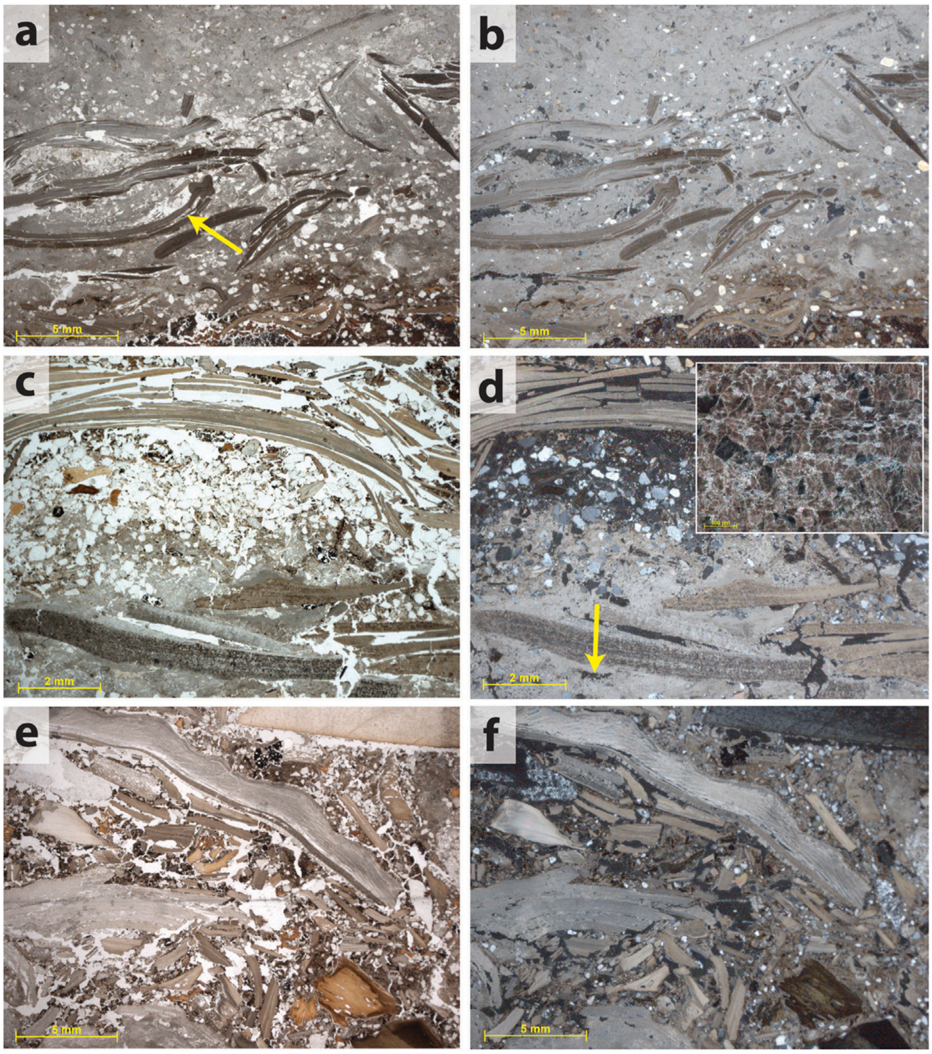


FIGURE 5
Impacts of human activities on the preservation of shell. **(A)** Burned shells in a hearth, sample KRM-13-07 from the LBS of Cave 1. According to the results of the μFTIR analyses, all of the shells in this hearth are now composed of calcite due to heating [see also Larbey et al. (2019)]. Burned shells are also darker in PPL, ranging from medium to dark grey in color. Here, some shells exhibit delamination. The arrow indicates a fissure void formed within a bivalve shell from delamination between the inner nacreous and outer prismatic layers that extends to the hinge plate. PPL. **(B)** Same view as **(A)**, XPL. The fine matrix surrounding the shells is ash, while a small portion of the basal charred layer of the hearth is visible in the lower left corner. **(C)** The lower part of the image shows shells embedded in the ash layer of a hearth located several cm below the previous images. The shells are both heated and recrystallized. A similar change in orientation of calcite crystals has been reported in heated shell by Villagran et al. (2011b). The upper part of the image shows shells that are fragmented in place due to compression, possibly related to trampling (c.f. Villagran et al., 2011a). μFTIR analyses indicate that all of the recrystallized shells within the hearth are composed of calcite, while the upper fragmented shell is composed of aragonite. PPL. **(D)** Same view as **(C)**, XPL. Arrow indicates a small zone of phosphatized ashes, confirmed as hydroxyapatite with μFTIR. The inset image shows the recrystallization of one of the shell fragments at high magnification, also XPL. **(E)** This image from KRM-13-06a (also in the LBS) shows the impact of fragmentation due to trampling followed by local reworking of shell with other wastes, including fragments of bone, ash and charcoal. μFTIR analyses indicate that the bone fragments visible in this image were burned at a range of intensities. PPL. **(F)** Same view as **(E)**, XPL.

correlating the layers directly. Sedimentary differences possibly reflect lateral facies changes or variations in nature and the degree of post-depositional color change.

Unlike the nearby deposits in the corresponding area of the Witness Baulk, the deposits in the lowest block are clast-supported by shell fragments (Figures 4E–H) with a fine matrix composed of wood ashes and sand cemented in place by secondary carbonate. *In situ* layers of charred plant material and ashes are not present. Nevertheless, charcoal and partially recrystallized ashes are present in the poorly sorted sedimentary matrix, suggesting that these materials were redeposited from a location where both shells and hearths were present. Large fragments of lithic debitage are also present. The sampled midden deposit can be divided into two main shell-rich units with geogenic sediment in between. In addition, thin lenses of geogenic and biogenic material, including sand-sized hydroxyapatite nodules that are typical of bird guano, are present within the two main units, suggesting that the thicker shell-supported units accumulated intermittently with pulses of non-anthropogenic sediment. Many of the shells appear deformed, and many have internal porosity. μFTIR analyses indicate that these shells are composed of aragonite.

The two blocks laterally equivalent to the SASL contain much larger shells mixed with coarse fragments of other materials, including charcoal, bones, tufa, and quartzite clasts. The coarse nature of these units is consistent with the SASL layers in the Witness Baulk. Like the lower sample from the same area, the deposits are variably cemented with secondary calcite, which forms pendants on some bone fragments (Figures 4I,J) and infills bone pores. Shell fragments in these samples are generally well-preserved, but some show increased internal porosity suggestive of decalcification.

4.1.3 Cave 1 Witness Baulk: LSA

One block from the LSA shell midden from the Witness Baulk in Cave 1 provides a contrast to the MSA I and earliest MSA II deposits. This sample contained so many large shells that it was carved with a hammer and chisel. Like the earlier deposits, this midden contains layers of shell, as well as other layers containing mixed debris such as bone fragments (consistent in appearance with fish, see Villagran et al., 2017) and lenses of sand. Relative to the MSA I deposits, the intact shell layers have large amounts of void space, with much of the original morphology and curvature of the shell fragments preserved. This sample, with its large voids, exemplifies the compression and volume loss that must be accounted for in the earlier MSA deposits, which have the effect of making those middens thinner in appearance.

4.1.4 Caves 1A and 2: Howiesons Poort

The one sample from Cave 1A comes from the base of the Upper Member with Howiesons Poort artifacts in a midden context where shells are present but do not form the dominant component of the midden. In the field, the feature is dark gray. In the thin section, the feature contains four discrete microstratigraphic units that contain different proportions of materials, including fragments of shell, bone, burned bone, fat-derived char, wood ash, charcoal, charred seeds, quartzite clasts, fragments of tufa, and sand. The units also vary in porosity. The uppermost unit is composed of abundant wood ashes, which are locally recrystallized and cemented by secondary carbonate. The other unit boundaries show no evidence of decalcification or lenses of geogenic sediments that would suggest periods of stasis between depositional events.

The interpretation of this sequence is that of a midden that contained dumped materials from primary features, such as hearths, mixed with other types of food-related debris. Although shell fragments are present, this feature is not considered to be a shell midden. Decalcification is present only at the very top of the feature, and, in general, this midden is well-preserved.

In Cave 2, at a slightly higher stratigraphic position compared to the sample from the Upper Member in Cave 1A, the sample from the western side contained large visible shells in the field, which required a hammer and chisel to cut into for block removal. Visible flowstones were also present nearby. The sample from the eastern side of the chamber contained no visible shell, and the deposits were dark brown, greasy, soft, and easy to cut, with visible bands of sediment grading laterally from white to yellow, including what appeared in the field to be a phosphatic mineral crust or phosphatized flowstone.

The sample from the western side of the cave is illustrated in Figures 6A–F and contains two thick (~2–3 cm) packages of sediment that are composed almost entirely of shell fragments (>50%), as well as one thinner layer that contains large fragments of shell mixed with other sediments. The lowest package of the shell is capped by a thin layer of secondary phosphate that, in places, is pseudomorphic after plant ashes. A thin layer of charcoal beneath suggests that the shell deposit was originally capped by an *in situ* hearth that subsequently became phosphatized. μFTIR analyses indicate that the mineral replacing the original wood ashes is hydroxyapatite. The middle layer of the shell also contains evidence of secondary phosphatization, this time with direct replacement of the aragonite of the shell by hydroxyapatite. The very top of the sample is ashy sediment cemented by micrite, which is capped by a thin concentration of shell fragments that are embedded in the carbonate and exhibit thin calcite spar pendants. Overall, this sequence represents at least three main phases of shell deposition punctuated by the use of the same area for the construction of hearths and stasis during which weathering occurred. Despite being located in a zone of shell and bone preservation, the micromorphological analyses indicate that some degree of post-depositional diagenesis occurred here.

In contrast, the sample from the eastern side of the Cave 2 chamber contains no shell (with one exception illustrated in Figures 6H–J) or bone fragments, and the sand component is non-calcareous. Instead, the light-colored bands visible in the field contain the mineral leucophosphite $(KFe_2(PO_4)_2(OH) \cdot$

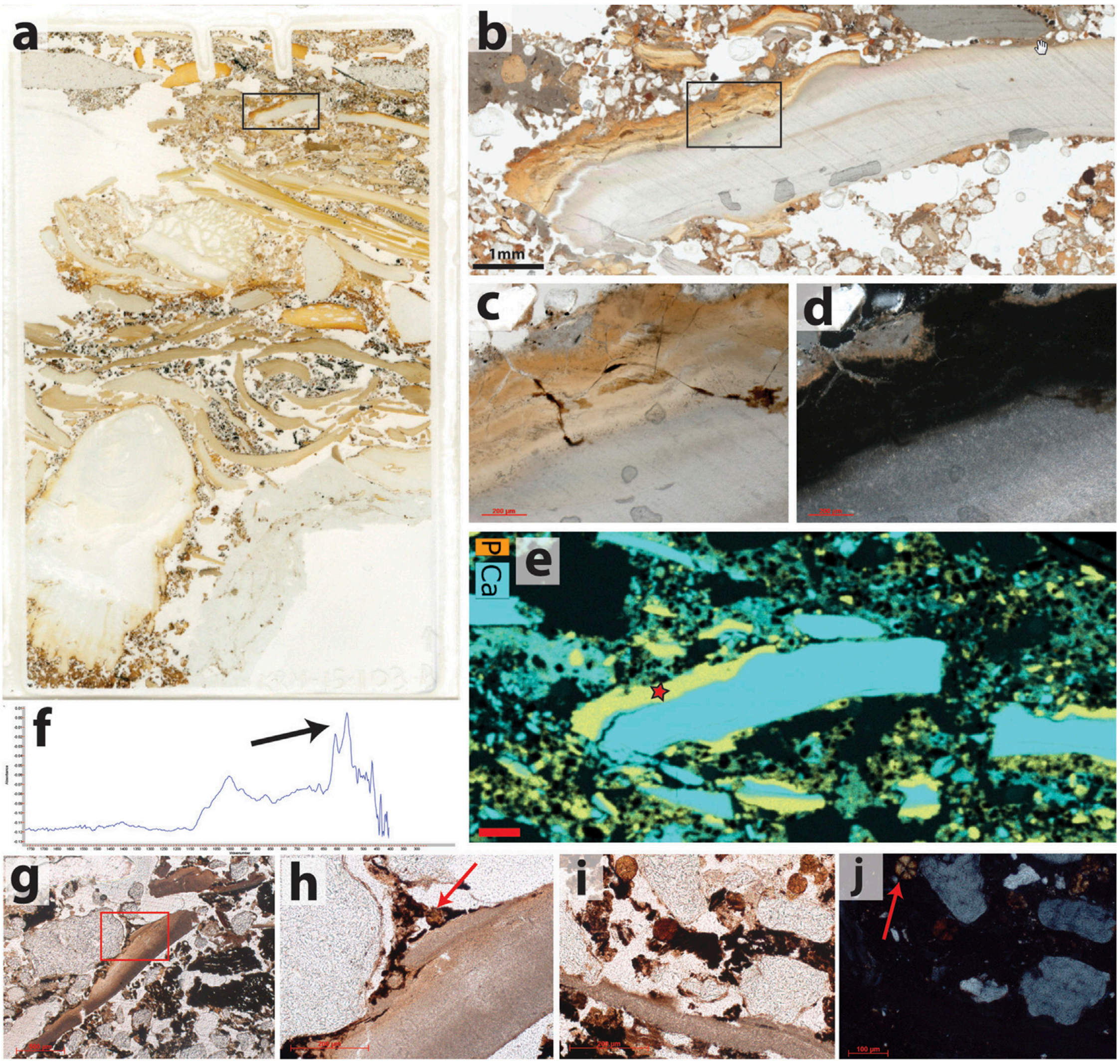


FIGURE 6
Phosphate-induced diagenesis of shell in Cave 2. **(A)** Flatbed incident light scan of a thin section from the preserved HP shell midden in Cave 2. Two distinct layers of shell are visible here, approximately 2 cm in thickness each. The lower shell layer is well-preserved and is composed of > 50% shell. The upper shell layer is more compressed, and has been impacted by post-depositional phosphatization. The box indicates the location of the photograph in **(B)**. **(B)** Detail of an altered shell fragment. PPL. The box indicates the location of the photographs in **(C,D)**. **(C)** Under PPL, the alteration zone is yellow. **(D)** Under XPL, the alteration zone is isotropic. **(E)** Distribution map of the elements Ca and P. The alteration zone contains both elements. The location of the µFTIR measurement in **(F)** is indicated by the star. The scale bar is 1 mm. **(F)** µFTIR spectrum collected directly off the thin section using a germanium ATR objective. The arrow indicates the position of the doublet at 605 and 565 cm^{-1} that is characteristic of hydroxyapatite. **(G)** The only shell present in the sample from the eastern side of the chamber is broken into multiple fragments, but retains its color in PPL. The matrix is rich in micro-charcoal. **(H)** Detail of the area indicated by the red box in **(G)**. The original fabric of the shell is preserved. The red arrow indicates a leucophosphite crystal aggregate. PPL. **(I)** One of the shell fragments located just to the right of the image in **(G)**, with five leucophosphite crystal aggregates above it. PPL. **(J)** Same view as **(I)**, XPL. The shell fragment is completely isotropic, but due to the presence of silica rather than hydroxyapatite. The radial crystal habit of the leucophosphite is visible here, with the well-developed extinction cross in one aggregate indicated with the arrow.

$2H_2O$) in a matrix of amorphous silica. The leucophosphite has a radial crystal habit (Figure 6J), and pseudomorphs of original calcareous materials, such as ashes or shells, are not present; however, the dark matrix is rich in finely comminuted charcoal, which suggests that hearths may have been present. According to Karkanas et al. (2000), the combination of leucophosphite and amorphous silica is one possible diagenetic outcome of the exposure of wood ashes to phosphatic solutions, such as those derived from weathered bat or bird guano. The observations support the previous interpretations

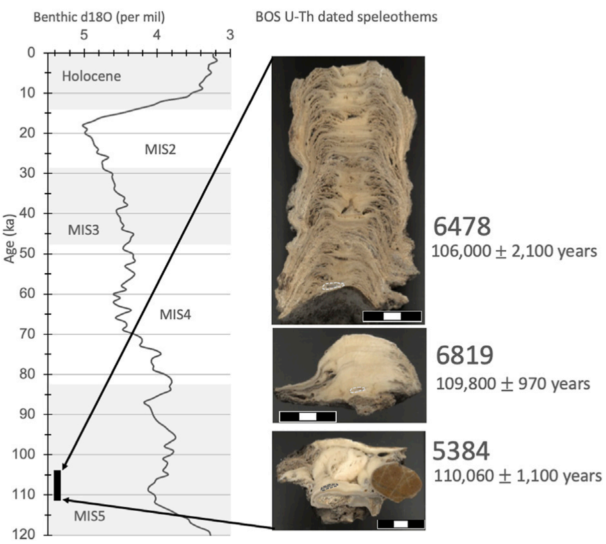


FIGURE 7
BOS U-Th dated speleothems 6478, 6819, and 5384, plotted in age order and compared to the LR04 benthic stack, on which MIS stages 5–2 are marked with gray bars. Layers drilled for U-Th dating are marked with dashed freeforms, and the scale bar is 3 cm.

of extreme post-depositional diagenesis and carbonate dissolution in this cave area. The diagenesis is so advanced that it is impossible to determine whether shell middens were located here. Relative to the sample from the western side of Cave 2, the sample from the eastern side has significantly lower porosity, which is one aspect of the deposits that Feathers (2002) considered when assessing the potential impacts of diagenesis on the OSL dating.

One possible microscopic shell was observed in the sample from the western portion of Cave 2. The shell, which had an original length of a maximum of 5 mm, is fragmented in place into more than ten individual pieces. It retains its typical gray color in PPL, but under XPL, it is isotropic. Elemental mapping reveals a depletion in Ca and an enrichment in Si, which suggests that this shell may be partially replaced by secondary silica. The µFTIR spectrum is also consistent with the presence of opal. The shell is located in a layer of charred plant material directly beneath a concentration of leucophosphite. Although suggestive of another diagenetic process that impacted the heated shell at the site, this single observation would suggest that it is not a widespread phenomenon. Overall, the micromorphological analyses show a wide range of taphonomic processes that impacted the preservation of the middens.

4.2 Dating

The results of the U-Th dating, including all the isotopic concentrations and ratios, are presented in Table 2. U concentrations for all three dated speleothem samples are 655–440 ppb (ng/g), which is not untypical for carbonates in archaeological settings (Hellstrom and Pickering, 2015). The similarity in U concentration hints at the same source of U for all three samples, as do the similar $^{234}U/^{238}U$ activity ratios. The $^{230}Th/^{232}Th$ ratios are all well below 30, but a detrital thorium correction was still applied, and the corrected ages are reported in this study. Sample 5384 is the oldest, with an age of 110,060 ± 1,100 years, which is within the error of sample 6478, dating to 109,800 ± 970 years. This is unsurprising as these two carbonate pieces are from the same archaeological horizon, BOS Three. Sample 6478 is the youngest, with an age of 106,000 ± 2,100 years, and is at least 2,000 years younger than the other two carbonates (Table 2).

All three speleothems consist of layers of dense white calcite with clear breaks, marked by very thin (under 1 mm) dark brown to gray layers (Figure 7). The dated layers in all three cases are from the base of the speleothem and therefore date as close to the onset of speleothem formation as possible. This means there was a time conducive to speleothem formation at KRM starting at 110,060 ± 1,100 years, lasting for around 4,000 years until 106,000 ± 2,100 years ago. The oldest sample, 5384, is best described as a carbonated mass and marks the beginning of an increase in dripwater to this part of the cave, which points to a shift to wetter external conditions. Within a thousand years, the increase in dripwater was sufficient to sustain the growth of a small stalagmite, sample 6819. By 106,000 ± 2,100 years, drip rates are fast enough to produce sample 6478, which, given its open textures, appears to have grown fast. There are several areas along the central growth axis of 6478 where some dissolution of the previous layer is evident, suggesting a very fast drip rate. Further dating is needed to constrain the length of time represented by 6478. However, taken together, these U-Th ages provide a maximum age for the hiatus after the formation of the BOS layer at around 106 ka and a minimum age of around 110 ka for Layer SBLS and the underlying layers.

4.3 Shellfish density and taxonomy in the Witness Baulk layers SMONE-BOS

The shellfish density in SMONE is the highest, at 90.3 kg/m^3, followed by SBLS at 43.3 kg/m^3, with BOS at a little lower density of 37 kg/m^3 (Table 3). The shellfish exploitation from SMONE is characterized by mainly two species in terms of MNI: alikreukel (47.5%) and brown mussel (41.4%). When the weight of marine shellfish is considered in SMONE, alikreukel still dominates, but abalone (*Haliotis midae*) is almost as numerous as the brown mussel. In BOS, brown mussel becomes the best-represented taxon in MNI (34.1%) and weight (23%). Alikreukel is still well represented in MNI (23.1%) and weight (32.8%), but whelks contribute almost as much in MNI (19.2%). Limpets (*C. oculus*)

TABLE 3 Shellfish MNI and weight; shellfish density and opercula size (median); and layers SMONE, BOS, and SBLS. The ecoprofile for the top > 85% taxa is indicated through light gray shading (sheltered conditions) and dark gray shading (exposed wave interaction conditions). The taxa are ordered according to rank in terms of handling costs (Langejans et al. 2012).

Layer Shellfish density Opercula size median	SMONE 90.3 kg/m^3 35.7 mm (n = 47)				BOS 37 kg/m^3 38 mm (n = 31)				SBLS 43.3 kg/m^3 29.3 mm (n = 3)				Total			
	MNI	% MNI	g	%g	MNI	% MNI	g	%g	MNI	% MNI	g	%g	MNI	% MNI	g	%g
Dinoplax gigas (giant chiton)	0	0	0	0	4	1.7	11.4	0.8	2	4	12.7	3.5	6	1.3	24.1	0.6
Turbo sarmaticus (alikreukel, Cape turban)	94	47.5	1,036	52.1	53	23.1	447.4	32.8	6	12	48.5	13.3	153	32.1	1,531.9	41.2
Cymbula oculus (limpet)	1	0.5	11.8	0.6	4	1.7	110.1	8.1	3	6	19.7	5.4	8	1.7	141.6	3.8
Diloma sinensis (top shell)	1	0.5	9.3	0.5	44	19.2	142.1	10.4	3	6	33.7	9.2	48	10.1	185.1	5.0
Donax serra (white mussel)	1	0.5	5.6	0.3	2	0.9	3.7	0.3	1	2	11.1	3.0	4	0.8	20.4	0.5
Perna (brown mussel)	82	41.4	453.8	22.8	78	34.1	475.1	34.9	18	36	115.4	31.6	178	37.3	1,044.3	28.1
Haliotis midae (abalone)	4	2.0	369.2	18.6	2	0.9	11.6	0.9	0	0	0	0	6	1.3	380.8	10.3
Scutellastra argenvillei (limpet)	2	1.0	39.3	2.0	2	0.9	23.3	1.7	0	0	0	0	4	0.8	62.6	1.7
Burnupena limbosa (whelk)	10	5.1	11.1	0.6	29	12.7	77.1	5.7	11	22	34	9.3	50	10.5	122.2	3.3
Scutellastra longicosta (limpet)	1	0.5	0.3	0.0	2	0.9	8.2	0.6	1	2	1.2	0.3	4	0.8	9.7	0.3
Patella sp.	1	0.5	49.8	2.5	4	1.7	47.3	3.5	4	8	88.7	24.3	9	1.9	185.8	5
Other*	1	0.5	1.1	0.1	5	2.2	4.9	0.4	1	2	0.6	0.2	7	1.5	6.6	0.2
Total	198	100	1987.3	100	229	100	1,362.2	100	50	100	365.6	100	477	100	3,715.1	100

*"Other" comprises *Turritella carinifera, Aulacomya atra, S. barbara*, and *bulli sp.*

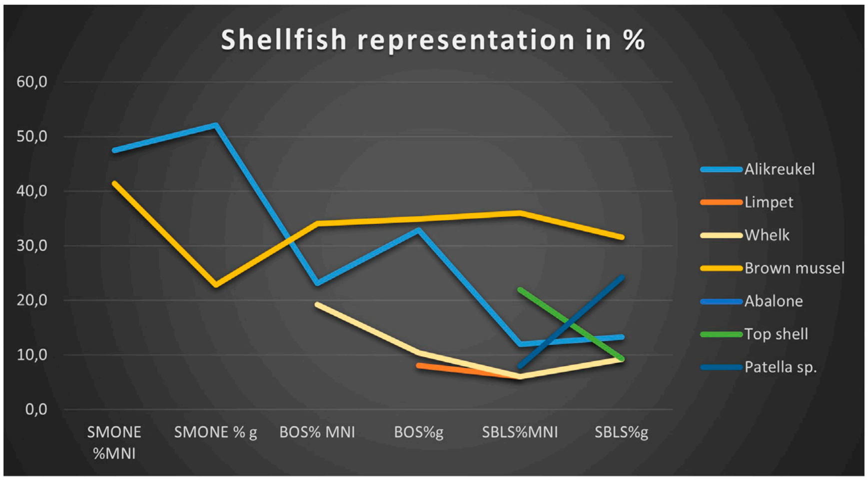


FIGURE 8
Shellfish representation SMONE-SBLS (top 85%–91%) (see Table 3 for percentages).

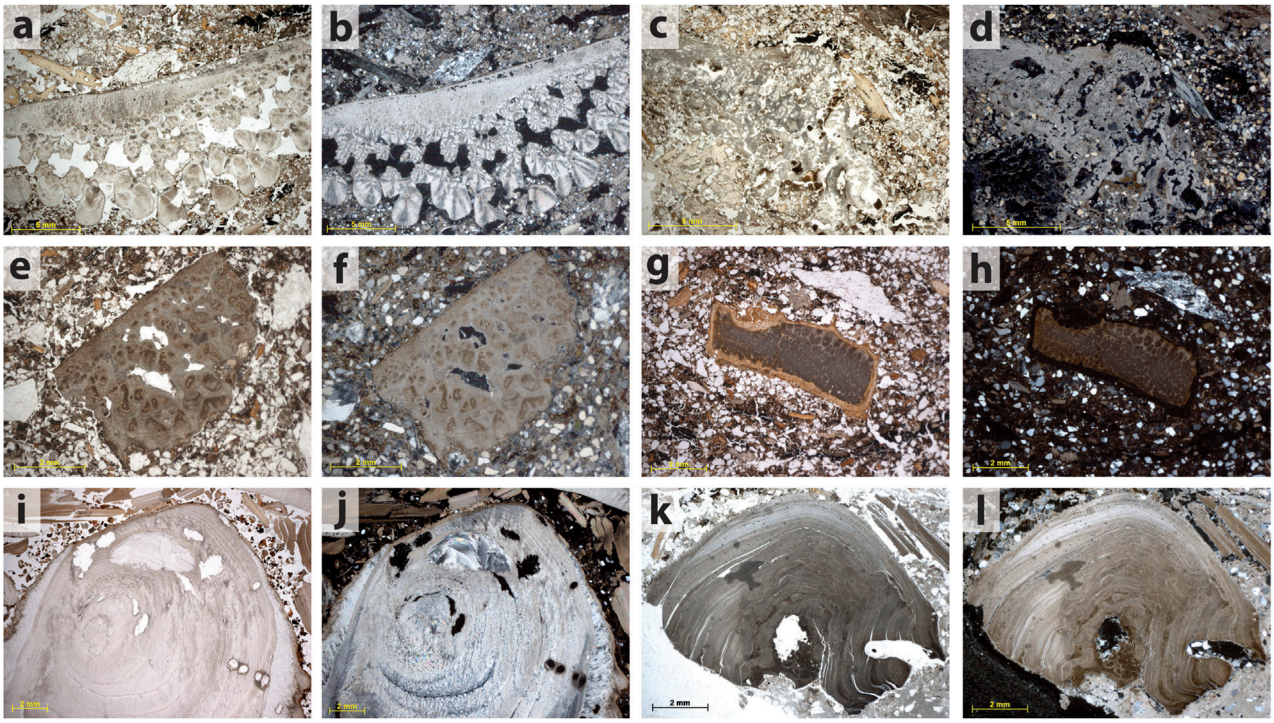


FIGURE 9
Differential preservation of opercula. **(A)** A well-preserved operculum from sample KRM-15-112, collected from the lateral equivalent of the SBLS. The inner part is oriented downwards. Porosity here is original. PPL. **(B)** Same view as **(A)**, XPL. The birefringence of the carbonate, and original crystallite orientation fabric indicates that the shell has not been chemically altered. μFTIR analyses indicate that all parts are composed of aragonite. Inner part oriented downwards. **(C)** A partially dissolved, recrystallized and compressed operculum from sample KRM-13-08, collected within the LBS. PPL. **(D)** Same view as **(E)**, XPL. The porosity here is secondary, and nearly all of the original crystallite orientation fabric is lost, but the composition is aragonite. **(E)** An altered operculum from sample KRM-13-05, collected from the contact between the SBLS and the LBS. The color in PPL indicates possible heating, and the composition is calcite. Inner part oriented downwards. PPL. **(F)** Same view as **(C)**, XPL. The matrix contains quartz and carbonate sand, as well as ashes. **(G)** A different altered operculum, also from sample KRM-13-05, just below the contact between the SBLS and the LBS. The outer edge of the fragment has been replaced by secondary hydroxyapatite, confirmed with μFTIR. PPL. **(H)** Same view as **(G)**, XPL. The matrix contains little carbonate and is enriched in microcharcoal and organic material. **(I)** A well-preserved operculum from sample KRM-15-103. This operculum—located in the eastern side of Cave 2—is composed of aragonite. The orientation of the cut is perpendicular to that of the previous images. PPL. **(J)** Same view as **(I)**, XPL. **(K)** A burnt operculum from sample KRM-13-07. The orientation of the cut is similar to that of **(I)** and **(J)**. PPL. **(L)** Same view as **(K)**, XPL. The matrix is ash.

and top shells (*B. limbosa*) also occur in relatively high percentages, contributing to the top 85% of species in this layer (Figure 8).

In SBLS, the brown mussel remains the best-represented species and occurs in similar proportions to those of BOS (36% MNI, 31.6% in weight). However, this layer stands out in the higher diversity of shellfish that make up the top 85% in this layer (Table 3; Figure 8). In terms of MNI, top shells almost comprise a quarter of the composition, with alikreukel, limpets, whelks, and *Patella* sp. occurring in similar proportions. The weight representation better indicates that *Patella* species have been an important part of the diet, representing 24.3% of the total weight. Figure 8 shows the increased importance of alikreukel over brown mussels in the youngest layer, SMONE, the switch to brown mussels as the most represented species in BOS and SBLS, and the increasing diversity of shellfish representation in the older layer, SBLS.

5 Discussion

5.1 Taphonomy of shell middens at KRM

The presence and positioning of shell middens in caves and rock-shelters can expose the archaeological materials to negative taphonomic processes, such as secondary phosphatization and complete dissolution. However, they can provide contexts favorable to rapid burial and protection of archaeological materials, and depending on the sedimentation rate, either cemented deposits or speleothems for dating.

At KRM, various taphonomic processes were observed impacting the shells and shell middens. Some of the processes documented here at the microscale and, to a lesser extent, during excavation include the syndepositional effects of anthropogenic activities. Micromorphological analyses of the LBS middens in the Witness Baulk and nearby profiles revealed a range of anthropogenic activities. Construction of hearths on top of shell layers and possible discard of shell directly into the fires resulted in burning, which caused a color change, thermal fracture, change in mineral composition, and recrystallization. In addition, some *in situ* fragmentation and compression of the shell may be attributed to trampling. Finally, the thicker, poorly sorted, clast-supported deposit at the intersection between Cave 1 and Cave 1A shows that the shell and other materials were removed from their original place of processing and redeposited by humans.

Other taphonomic processes resulted in shell dissolution and degradation. In many samples from Cave 1, partial dissolution caused an increase in internal porosity visible only at the microscale. Dissolution is a common process in shell middens worldwide (Aldeias and Bicho, 2016; Duarte et al., 2019). In open-air sites, dissolution can be initiated by localized acidic conditions within the mounds that result from the decomposition of organic material coupled with a terrestrial moisture source (Stein 2008). This mode of dissolution may have impacted the upper surface of the LBS deposits, as well as the SMONE, BOS, and SLBS layers studied here. At greater depth, dissolution also occurred within alkaline sediments rich in ash, which suggests that the process at KRM might be more complicated than in open-air sites.

Dissolution may have preferentially impacted shells composed of aragonite, particularly the thinner shells of the brown mussel (Deacon 1995). However, Figure 9 illustrates differences in the preservation of opercula (an anatomical portion that is absent in brown mussels) in all of the different areas of the site, with one operculum from the LBS exhibiting a similar degree of decalcification as the brown mussel shells (Figures 9C,D). The partially dissolved shells were then more susceptible to compression and soft sediment deformation. These effects lead to a transformation from a highly porous clast-supported shell deposit to a "dominant interconnected shell" deposit (Aldeais and Bicho, 2016), wherein shells are fragmented in place, with loss of the original void space resulting from the internal chambers and concavity of the shells. Partial shell dissolution is a process that can be observed in hand samples and during excavation.

In Caves 1 and 2, phosphatization impacted calcareous materials, including shells. This process occurred at the top of the LBS deposits in the center of Cave 1. In Cave 2, lateral variation in dripwater composition resulted in one area where shells are relatively well-preserved but locally phosphatized with the replacement of the original aragonite by hydroxyapatite. However, in the other areas, shells have been completely dissolved, yielding a decalcified deposit containing the secondary mineral leucophosphite.

Finally, the precipitation of additional secondary minerals may have contributed to the fragmentation of the already fragile shell. Delamination, or fracture along the growth layers, appears to be common in certain species and can be caused by heating (Villagran et al., 2011a) and precipitation of secondary salts, a process that impacts the lowest deposits of the Witness Baulk. Other secondary precipitates include secondary carbonate, which forms pendants and encrustations on the shell and bone at the connection point between Cave 1 and Cave 1A, as well as in the eastern area of Cave 2. In the Witness Baulk, a hiatus in sedimentation, coupled with precipitation of secondary carbonate from dripping water, resulted in the formation of crusts and stalagmites, which were directly dated here.

Overall, the shell analyses presented here from the SASL and underlying SBLS layer also show that despite some issues of preservation that have impacted both shells and other calcareous materials such as ashes, valuable information about fluctuations in species abundance can still be obtained when the deposits are excavated carefully. Nevertheless, the preservation issues have impacted the perception of the scale and, therefore, the potential for the interpretation of the action of shellfish collecting, consumption, and discard at the site. Marean (2014), for example, noted the poor visibility of deposits or layers that would technically qualify as shell-supported middens based on field observations of profiles. The taphonomic processes documented here help us to understand why shellfish remains are not necessarily obvious in profile and why the differential recovery has hindered the publication of high species counts, which, for example, are used to evaluate the lower intensity of MSA shellfish collection relative to the LSA (Will et al., 2019). Marean (2014) suggested different strategies for documenting shell density in different layers. In Figure 10, we use the micromorphology samples to illustrate the abundance of shell relative to other components in four middens from the site, three of which contain layers with greater than 50% abundance. One of the most striking differences is between the middens of the LBS (Figures 10B,C) and those of the Holocene (Figure 10A), wherein it is very clear that much volume has been lost in the LBS deposits due to the reduction of void space, compaction of the shell, fragmentation of the shell, and deformation coupled with decalcification. Other metrics for documenting density include counts and weights of shells, as well as piece plotting, which are addressed in the excavation data presented here and by Brenner et al. (2022).

5.2 Significance of middening and dumping

Deacon (1995: 126) noted that one of the most significant aspects of one of the MSA II shell middens in Cave 1A is that it is evidence for "patterned disposal of food refuse in localised heaps." He emphasized this point as equally important as the systematic use of coastal resources. Middening, in the form of sweeping and dumping of hearths, is a well-established behavior

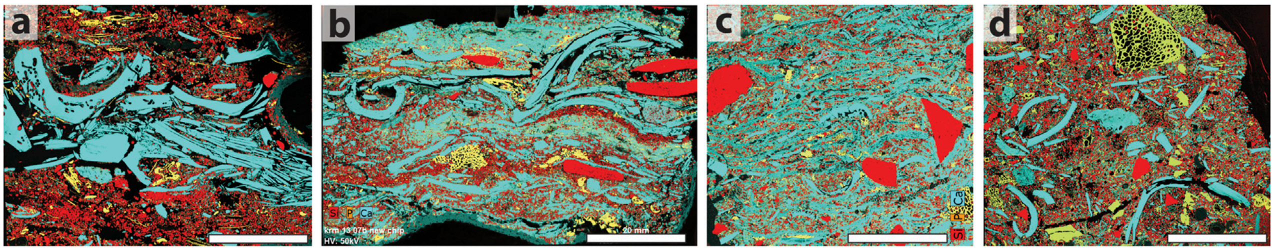


FIGURE 10
Fabric analysis of middens using compositional maps showing the distribution of the elements Ca, P and Si. In these images, shell, ash and secondary carbonate are blue; sand and quartzite are red, and bones are yellow. All images are the same scale; the scale bar is 2 mm. **(A)** LSA midden in Cave 1 (sample KRM-13-25) showing a discrete layer composed only of shell debris in between two layers rich in quartz sand with inclusions of bone. Several of the larger shells contain tubular pores that form as a result of invertebrate boring. Shell fragments are roughly horizontally aligned. **(B)** MSA I midden in the LBS deposits of Cave 1 (sample KRM-13-07) showing multiple discrete layers containing more than 50% shell interbedded with lenses of sand, mixed debris layers containing quartzite, shell, sand and bone, and layers of ash. Shell, quartzite and bone fragments are roughly horizontally aligned. Many of the shells are fragmented in place. **(C)** MSA I midden in the LBS deposits where the Cave 1 and Cave 1a deposits connect (sample KRM-13-01) showing no discrete layers. Shells are roughly horizontally aligned and embedded in secondary carbonate and ashes, yet still comprise greater than 50% of the deposit. In this sample, there are as many as eight shells per cm of thickness, which indicates significant post-depositional compression. Quartz sand is mixed throughout and the large fragments of quartzite debitage have random orientations. Under the microscope, fragments of charcoal and recrystallized ashes are also randomly mixed. This type of midden is interpreted as a reworked version of **(B)**. **(D)** HP midden in Cave 1a (sample KRM-13-13) that is rich in shell (<50%), but is not classified as a shell midden. Here all materials including the shell fragments have random orientations, suggesting that these materials were scooped up from their original place of deposition and dumped here.

in other MSA sites (Goldberg et al., 2009) that has been interpreted as evidence of intensification of site occupation, and in caves, the organization of activities within a more limited space. Herein, we see middening occurred in the same location as habitation, beginning in the MSA I and continuing through the HP (Figures 5, 6), evidenced by interbedded layers of discarded shell, *in situ* hearths, and locally reworked and trampled materials. Additionally, we see discrete areas used as dumps (Figures 4E–H and Figure 9D). Finally, the microstratigraphic observations and excavations reveal evidence for frequent hiatuses in anthropogenic sedimentation, which can be interpreted as periods of site abandonment that, in the case of the SASL layers discussed here, coincided with a phase of dripping that resulted in the formation of stalagmites observable in all the areas of Cave 1.

5.3 The paleoclimate and environment during MIS 5c-d

Altogether, the speleothem U-Th ages presented here provide a time window from 110,060 ± 1,100 to 106,000 ± 2,100 years ago, during which cave conditions were conducive to speleothem growth. Drip rates into the cave increased, and the influx of sediments into the cave decreased, as sedimentation and speleothem formation are mutually exclusive for the most part (Pickering et al., 2007). The oldest sample, 5384, is a carbonated mass, suggesting that, at 110,060 ± 1,100 years ago, we saw the onset of increased dripwater flow, but this may not have been enough to sustain the growth of even small stalagmites. We only saw these around 1,000 years later. This period of increased drip flow is then sustained for the next 4,000 years, as evidenced by the age of 6478 at 106,000 ± 2,100.

The conditions during speleothem formation at KRM between ca. 110 and 106 ka relate to a period when increased moisture was available. The Tswaing crater lake pollen record indicates a wet phase between 111 and 103 ka (Partridge et al., 1997; Kristen et al., 2007). The data from the marine mud core, CD154 10-06P, that track the Agulhas Current near-surface temperature and salinity (Simon et al., 2015, 2020; Cawthra et al., 2021) correspond closely to those from the Tswaing crater lake. An explanation for this wet phase, suggested by Simon et al. (2015), is the role of the 19-23 ka orbital precession cycle, driving stronger summer insolation and, in turn, increased precipitation over eastern South Africa. This may be supported by other evidence from the Vankersvelsvlei coastal wetland pollen record, which also suggests an increase in summer rain during this period and that this allowed the development of a more extensive forest in the area (Quick et al., 2016). Analyses of spores, pollen, and micro-charcoal from the IODP Site U1479 deep-sea sediments, which capture the regional signal for the southern and western Cape GCFR (Dupont et al., 2022), further support that the presence of Podocarpaceae (occurring in Knysna type forests) increases substantially after the Last Interglacial maximum at 125 ka. This collection of local and more distant records is consistent with the presence of the small stalagmites in BOS, which by their presence alone suggest an increase in local effective precipitation.

Serial $\delta^{18}O$ measurements of the alikreukel opercula from AA43 in Cave 1/1A show that sea surface temperatures were not depressed during this period and that the mean temperature was 13.2°C (Loftus et al., 2019). Alikreukel were collected mainly in summer (Loftus et al., 2019). It remains to be explained why the average alikreukel opercula size is smaller in all of the MSA II layers than in the rest of the MSA as indicated in the Singer and Wymer sample (Steele and Klein, 2008; Klein and Bird, 2016), the Deacon sample (Thackeray, 1988), and the opercula from SMONE-SBLS. The smaller size may relate to lesser food availability in relatively warmer waters (Sealy and Galimberti, 2011; Langejans et al., 2017) or, as suggested for the Holocene, to increased human predation (Klein et al., 2004). An increased estuarine component in the environment, as reflected by the fish in the Mossel Bay lower, may also be one of the factors involved in the decreased opercula size (Langejans et al., 2017: 72). The relatively smaller size is not only related to alikreukel opercula, as a sample of white mussels from the earlier MSA II/Mossel Bay phase at KRM is also smaller than those from after 90 ka (Jerardino and Navarro 2021). This same trend has been observed at PP 13 B aggregate LRS and a contemporaneous assemblage from Herolds Bay Cave, but larger samples are necessary to fully test this.

The fauna from KRM indicates that more closed environments, in which trees and shrubs dominated, prevailed during the formation of the MSA II/Mossel Bay phase (SAS member) as a whole. Relatively more browsers and mixed feeders occur, and lower ungulate diversity values may indicate increased forest elements in the environment (Reynard and Wurz, 2020). For the MSA II lower specifically, small mammals (size 1) are the most prevalent large mammal fauna (LMF) and, with seals occurring second most frequently, demonstrate that the coast remained close to KRM during this phase.

5.4 Coastal exploitation prior to 100 ka on the South African coast

The most abundant species targeted in the MIS 5c-e layers at KRM, PP 13B, HDP 1, and YFT 1, such as mussels, alikreukel, and limpets, are highly ranked as they provide relatively high amounts of meat yield in relation to handling cost (Langejans et al., 2012). This focus on a relatively narrow range of species exploited by these populations is similar to that observed for modern coastal foragers from SA and Australia (Kyriacou et al., 2015).

For the deposits older than 100 ka from KRM discussed here, there are differences in the shellfish density, proportional changes in the shellfish taxonomy indicating changing coastal ecologies, and shifts in the lithic technology. SMONE has the highest shellfish density and is dominated by alikreukel, which with abalone, comprise 70% of the taxa. This points to the availability of rock pools with sandy substrates sheltered from wave action. This coastal ecology is similar to that of the Deacon sample for the MSA II/Mossel Bay lower from Cave 1A (Langejans et al., 2017). The shell midden from SMONE is associated with lithics from all stages of the reduction system, and many tools have edge damage (Brenner et al., 2022). Layer SMONE reflects coastal foraging similar to the Blombos Cave M3 phase (ca 97–82 ka) and MIS 5c PP 13B (ca 91–101 ka) in terms of the narrow range of taxa exploited, mainly alikreukel at the former and white mussels, brown mussels, and alikreukel at the latter (Jerardino and Marean, 2010; Langejans et al., 2012; Brenner et al., 2022). Similar shellfish densities do not occur at all southern Cape sites during this period—the shellfish density in SMONE and BBC M3 is similar, but noticeably lower densities occur in PP 13B MIS 5c layers. Furthermore, BBC M3 and PP 13B MIS 5c assemblages have a much lower proportion of artifacts per liter of sediment than SMONE, but the assemblage composition and technology are broadly comparable. The lithic density and characteristics coupled to the shellfish density suggest that KRM was used as a residential site during the formation of SMONE (Brenner et al., 2022) and that perhaps BBC and PP were less frequently visited during this period.

For the older than 110 ka BOS layer, the shellfish density is less than half that of SMONE, and a change in the coastal ecology toward more rocky exposed conditions is indicated by an increase in brown mussels, a concomitant decrease in alikreukel, and a greater variety of taxa (Figure 8). The higher artifact density in this layer and fewer edge-damaged pieces relative to SMONE may show that residential occupation may have been less intensive during this phase. In the pre-110 ka SBLS layer, similar shellfish densities occur as in BOS, but the diversity of taxa is higher. As in BOS, a rocky exposed coast is reflected, but to a larger extent. The shellfish density in BOS and SBLS needs to be interpreted against the significant taphonomic impact of dripwater and calcification, leading to the alteration and dissolution of the shellfish. The artifact density is much higher in SBLS than in SMONE and BOS, and miniaturization of the lithics occurs. The lithic technology is now more similar to the MSA I/Klasies River industry at KRM (Wurz, 2002). As the technology in SBLS differs and intact features such as hearths are well preserved, this layer likely belongs to a different member. The coastal ecology and lithic technology of SMONE are similar to those of the Mossel Bay lower phase in the Deacon sample. In contrast, BOS and SBLS correspond more to the coastal ecology for the MSA I phase in the Deacon sample (Langejans et al., 2017). The lithic technology of BOS, however, is similar to the MSA II/Mossel Bay lower and that of SBLS to the MSA I; indicating that coastal ecological changes did not occur synchronously with lithic technological approaches. Interestingly, the Tip Cross Sectional Area (TCSA) values for the points from SBLS are midway between the values for dart and javelin tip ranges, and the TCSA values for points in SMONE and BOS and MSA II, in general, are in the range for thrusting spears (Lombard, 2021). This may indicate a change in prey availability and capture methods in SBLS. Smaller lithics and prevalence of bovid 1 processed elements may be linked to the trapping and snaring of smaller fauna that might have made an appearance during MIS 5, as suggested by Dusseldorp and Langejans (2015). The large mammal fauna from layers SMONE to SBLS signals intense occupation and resource extraction in this phase. The abundant small fauna, especially size 1 bovids, have been burnt and have cutmarks. Furthermore, elements considered low-ranking, such as pelves and phalanges, show significantly more processing marks than other elements, perhaps indicating environmental stress (Reynard, 2022b).

The BOS-SBLS layers are broadly contemporaneous with PP 13B MIS 5d-e assemblages (Brenner et al., 2022) and with YFT 1 and HDP 1 on the west coast. The shellfish densities for PP 13B MIS d-e are very low, especially for the earliest evidence of shellfish exploitation at 164 ka (0.2 kg/m^3). A changing coastal environment is also reflected during MIS 5c-e at PP 13B. Brown mussels are completely dominant in MIS 5e, and white mussels become much more prevalent in MIS 5d. The lithic artifacts at PP 13B also occur in low densities from MIS 5d-e, with especially the MIS 5e assemblage showing infrequent retouch and edge damage (Thompson et al., 2010; Brenner et al., 2022). This may point to sporadic visits to the coast during this time period at PP 13B.

At HDP 1, episodic visits to the Atlantic west coast are also indicated during MIS 5d-e by the shellfish and lithic evidence. Granite limpets (*Cymbula granatina*) and black mussels (*Choromytilus meridionalis*) are dominant, and for stone tools, complete reduction sequences for local raw materials and importation of higher quality raw material tools are evident (Will et al., 2013). The consistency in the foraging and lithic behavior is interpreted as an indication of systematic coastal adaptation in MIS 5e (Will et al., 2013; Kyriacou et al., 2015). These authors consider that the fast deposition rate that might be implied by the dates may indicate LSA intensity of shellfish exploitation (Niespolo et al., 2021a, b, Klein et al., 2004). At YFT 1, limpets and black mussels are the most numerous taxa (Klein et al., 2004; Avery et al., 2008) in the ca. 120–113 ka layers (Niespolo et al., 2021a). The lithic technology is very similar to that of HDP1 (Wurz, 2012; Will et al., 2013). Although coastal exploitation was not as intensive as in the LSA (Klein et al., 2004; Avery et al., 2008), stable adaptation to the coast with systematic foraging of shellfish occurred (Tribolo et al., 2022).

For the period between 100 and ca.130 ka, systematic exploitation of coastal resources occurred on the south and west coast of South Africa, but seemingly at various levels of intensity. Layer SMONE at KRM, older than 100 ka, showed the highest degree of residential occupation for the sites discussed in this study, whereas the other two layers, BOS and SBLS, and the PP 13B MIS 5c assemblage indicated somewhat lesser degrees of residential occupation. The visits to PP13B during MIS 5d-e, HDP1 and YFT 1 during MIS 5c-e show sporadic low-intensity occupation.However, these suppositions based on shellfish densities need to be interpreted with care and do not necessarily relate to occupation intensity and shellfish exploitation patterns (Jerardino, 2016a, b). Herein, we have shown that the taphonomic alteration of shell midden deposits is an important factor that needs to be considered when discussing shellfish densities. Furthermore, occupational intensity is reflected by various measures (Gravel-Miguel et al., 2022; Reynard, 2022), and the inferences made here need to be interpreted within this wider context.

KRM presents an extended sequence covering more than 70 ka, and most publications on the site discuss broad changes for the whole period on the basis of time-averaged data (Langejans et al., 2012, 2017; Reynard and Wurz 2020; Reynard, 2022b for recent examples of this). This is an important approach, but further progress in understanding landscape-wide changes and correlations is more likely when more specific information can be compared that involves limited time averaging (Braun et al., 2021). This is especially relevant for exploring pre-100 ka coastal adaptation. For KRM, it has been shown that fluctuations in shellfish exploitation patterns, coastal ecology, and lithic technology occur within a temporal window between just before 106 ka and after 110 ka. Capturing these changes would have been lost if the data were combined in a larger grouping, as is customary when time-averaged data are presented to investigate palaeo-environmental trends.

Although some models regard coastal environments as primary in the development of innovations and symbolic behaviors (Marean, 2014; Will et al., 2016), innovations occur in other regions across the globe within this time period as well, sporadically at first, with a stronger signal that emerges at around 100 ka (Wadley, 2021). In South Africa, for example, crystals were collected at Ga-Mohana in the Kalahari basin at 105 ka (Wilkins et al., 2021), and on the Cape coast at Pinnacle Point, seashells may have been collected as beauty objects (Jerardino and Marean, 2010). Ochre-related innovations from the Cape coastal region occur at this time, for example, the possible heating of ochre at Pinnacle Point (Watts, 2010) and abalone shells with remnants of a compound ochre liquid from BBC (Henshilwood et al., 2011). It is the establishment of such innovations on a sub-continental scale and interaction between populations, coastal and inland, that is relevant to understanding cumulative cultural evolution and the human niche (Kissel and Fuentes, 2018; Meneganzin and Currie, 2022). The layers discussed in this paper are older than 100 ka and contain limited evidence of ochre and other artifacts conventionally interpreted as symbolic and innovative.

6 Conclusion

One of the goals of this paper was to contextualize middening at KRM throughout the sequence to provide a more detailed framework for understanding coastal exploitation. Shell middens occur throughout the sequence at KRM in various stages of preservation. A wide range of post-depositional taphonomic processes, such as secondary carbonate formation, compaction, soft-sediment deformation, and shell dissolution, impacted the preservation of shell-bearing deposits at KRM. The LSA middens contain well-preserved intact shells within highly porous layers, and the Howiesons Poort layers show variable post-depositional processes, with some samples, especially from the western area of Cave 2, showing abundant intact shell fragments. The MSA II/Mossel Bay lower shell middens are from a coarse context and cemented with secondary carbonate, and the internal porosity of some samples may be indicative of decalcification. The microstratigraphic sample from the SBLS contact in the Witness Baulk demonstrates conditions of high moisture and soft sediment deformation. The older MSA I shell middens from the base of the Witness Baulk contain more intact evidence for shell middens and secondary processes such as dumping. The microstratigraphic analysis underscores that shellfish density and visibility must be interpreted with care when inferring the degree of shellfish exploitation, as post-depositional processes significantly impact the preservation and chemical conditions of the shell.

A more precise temporal framework for the base of the MSA II shell-bearing deposits at KRM is provided. The MIS 5c-d MSA II deposits at KRM are, for the first time, precisely integrated into a window of time before 110 ka and after 106 ka based on U-Th dates on stalagmites. The dating relates to a hiatus after forming BOS, during which secondary carbonate formed on an exposed surface. The BOS layer, older than 110 ka, represents the base of the SASL sub-member, and SBLS likely falls within another member. The coastal environment in layer SMONE, younger than 106 ka, contained sheltered areas within a rocky coast. However, in BOS and especially in SBLS, dating to after 110 ka, the degree of shelteredness decreased. BOS and SBLS probably relate to a period with more rocky exposed shores. The lithic technology changed only in layer SBLS underlying BOS and is similar to the MSA I. The dated early Mossel Bay shell middens discussed in this study are broadly contemporaneous with those from YFT 1, HDP 1, and some of the PP 13B shell-bearing deposits and provide further evidence for the time period during which systematic coastal exploitation became more established on the South African coast.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors without undue reservation.

Author contributions

SW is the principal investigator of the Klasies River main site, generated the data, co-analyzed the shellfish sample, conceptualized the article, and co-wrote the paper. RP undertook the U-Th dating and co-wrote the paper. SMM conducted the micromorphological and geoarchaeological analysis and co-wrote the paper.

Funding

SW was funded by a National Research Foundation African Origins Platform grant (AOP no. 98826) and a DST-NRF Centre of Excellence in Palaeosciences Operational Support Grant (COEOP2020-20). Funding received by Robyn Pickering is from the NRF African Origins Platform (AOP150924142990) and DST-NRF Centre of Excellence in Palaeosciences Operational Support Grant (COE2018-10OP). Funding for instrumentation used in the analysis of the micromorphology samples was provided by a Deutsche Forschungsgemeinschaft grant to C. Miller (MI 1748/1-1). We are indebted to the Baden-Württemberg Stiftung for the financial support for the micromorphology component of this research project by the Elite programme for Postdocs (grant to SM).

Acknowledgments

We would like to thank the topic editor, Manuel Will, and the two reviewers, Erich Fisher and Ingrid Ward. U-Th dating was undertaken at the University of Melbourne, thanks to John Hellstrom, Helen Green, and Petra Bajo. The authors thank Kokeli Ryano for assisting with data on the shellfish and Silje Bentsen for aiding greatly in the sampling of the deposits. The authors thank Chris Miller for collecting two of the micromorphology blocks and Panos Kritikakis for the preparation of thin sections.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 18 November 2022
DOI 10.3389/feart.2022.974582

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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 21 June 2022
ACCEPTED 20 October 2022
PUBLISHED 18 November 2022

CITATION
Reynard JP (2022), Human occupational intensity and palaeoecology at Klasies River from MIS 5–3: Preliminary taphonomic analyses of faunal remains from the Deacon and Wurz excavations.
Front. Earth Sci. 10:974582.
doi: 10.3389/feart.2022.974582

Human occupational intensity and palaeoecology at Klasies River from MIS 5–3: Preliminary taphonomic analyses of faunal remains from the Deacon and Wurz excavations

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Klasies River is a key site in understanding the behaviour of coastal foragers in the southern Cape of South Africa. Faunal remains from Klasies River, recovered from an almost 70,000 year sequence over the Late Pleistocene, are a valuable dataset in investigating subsistence and occupational dynamics, yet few taphonomic studies have been conducted on the fauna from Klasies River. Here, the first taphonomic analyses of faunal remains from the Deacon and Wurz excavation is presented. The aim of this paper is to link occupational patterns during the Late Pleistocene at Klasies River with coastal ecology using taxonomic data from previous studies, and recently analysed taphonomic data. Taphonomic analyses of samples from the MSA II Lower, the Howiesons Poort and the MSA III periods were used to examine occupational intensity based on proportions of anthropogenic and zoogenic bone surface modification, trampling marks, transverse fractures and faunal density. Declining foraging efficiency or subsistence intensification was also investigated using indicators for expanded diet breadth (e.g., small fauna exploitation and increases in juveniles), more intensive marrow extraction and evidence for greater foraging distances. Herbivore functional types and dietary preferences were examined using taxonomic data and these show three main ecological phases at Klasies River: the MSA I; the upper and lower MSA II; and the HP and MSA III phases. Taphonomic data show increased occupational intensity in the MSA II Lower, with subsistence intensification also more evident here than other layers. Trampling data suggests that occupational intensity was greater in the earlier Howiesons Poort than later phase with little evidence of declining foraging efficiency then. The data indicate that, while humans contributed significantly to the MSA III assemblage, carnivores were the main accumulators here suggesting lower occupational intensity in this phase. The results of this study shows a possible link between increased occupational intensity and declining foraging efficiency at Klasies River but larger taphonomic samples are needed to explore this relationship further.

KEYWORDS

Middle Stone Age, zooarchaeology, taphonomy, occupational intensity, Southern Cape, South Africa, Late Pleistocene, Coastal palaeoenvironments

1 Introduction

Examining how humans have systematically exploited coastal environments is an important means of understanding human behaviour during the Late Pleistocene (Parkington, 2001, 2003; Stringer, 2000; Joordens et al., 2009; Marean, 2010; Kyriacou et al., 2014; Jerardino, 2016a; Klein and Bird, 2016; Will et al., 2016, 2019; Niespolo et al., 2021). Given their rich resources and productive environments, coastal regions have probably always been desirable destinations for human settlements. Current population densities of coastal and near-coastal regions, for example, are significantly higher than that of other regions (Small and Nicholls, 2003). Their proximity to the shore is probably an important reason why coastal rockshelters are crucial repositories of Stone Age archaeology. Prehistoric human settlements at coastal locations were generally more intensely occupied when shorelines were closer (Wilkins et al., 2017; Reynard, 2022) suggesting that marine resource were key to settlement strategies (Loftus et al., 2019; Jerardino, 2021). Coastal habitats contain highly nutritious food resources. Shellfish and fish are high in vitamin B12, omega-3 fatty acids and iron (Öhrvik et al., 2012; Kyriacou et al., 2014) with seals providing valuable fats. Shellfish would have likely been the first coastal resource to be systematically exploited with evidence of its exploitation documented at c. 164,000 years ago (ka) at Pinnacle Point in the southern Cape of South Africa (Marean et al., 2007). Yet, while the focus is often on marine fauna, terrestrial mammals are vital food resources in coastal adaptation strategies (Marean et al., 2014). The southern Cape is a good example of how the coastal landscape and these various food resources were utilised by Middle Stone Age (MSA) people.

It has been suggested that the Cape Floristic Region (CFR) of the southern Cape—particularly its food resources—played an important role in human evolution in the later Pleistocene (Jerardino and Marean, 2010; Parkington, 2010; Marean, 2010, Faith, 2011; Marean et al., 2014; but see Brink 2016 and Wurz et al., 2018 on the important role of the interior of southern Africa). Besides highly nutritious marine resources along the coast, the CFR is rich in geophytes, which both modern and ancient people have exploited as a reliable source of high-quality carbohydrates (Marean, 2010; De Vynck J. C. et al., 2016a; Botha et al., 2019). The topography of the southern Cape is important in human development through the MSA. The region sits at the edge of the Agulhas Bank, a broad, shallow continental shelf off the coast of southern Africa. During glacial periods, marine regressions exposed a vast landmass referred to as either the Southern Coastal Plain (Compton, 2011) or the Palaeo-Agulhas Plain (Marean et al., 2020). This exposed landscape may have been up to c. 73,000 km^2 during extreme glacial periods (Fisher et al., 2010; Marean et al., 2014) and would have had a significant impact on regional ecology. Marine regression would have opened up herbivore migratory routes and habitats (Marean et al., 2014). Productive floral environments and large terrestrial herbivores such as wildebeest (*Connochaetes gnou*), hartebeest (*Alcelaphus buselaphus*) and buffalo (*Syncerus* spp.) (Cowling et al., 2020; Reynard, 2021) demonstrate the diversity of food resources in this region, especially during marine regressions (Helm et al., 2020; Venter et al., 2020).

The southern Cape is also considered a critical region in our understanding of technological innovation and cognitive complexity (Deacon, 1989; Henshilwood et al., 2002, 2004; Marean et al., 2007, 2014; Wadley, 2015; Way et al., 2022; but see Wilkins et al., 2021 on innovation in the interior). Heat-treatment in the manufacture of lithic tools may be evident at the c. 164 ka layers at Pinnacle Point (Brown et al., 2009) and the ability to produce 'paint' from ochre is apparent in the 100 ka layers at Blombos Cave (Henshilwood et al., 2011). The recovery of shell-beads and engraved ochre from Blombos Cave suggests symbolically-mediated behaviour before 70 ka (Henshilwood et al., 2002, 2004). The Howiesons Poort (HP) techno-complex is especially significant in that it is associated with engraved ostrich eggshell, microlithics, complex hafting and increased social connectivity (Texier et al., 2010; Henshilwood et al., 2014; Way et al., 2022). The backed lithic artefacts of the HP suggest significant advancements in hunting strategies with the possible presence of bow-hunting by Marine Isotope Stage (MIS) 4 (Wurz and Lombard, 2007; Lombard and Phillipson, 2010).

Demographic pressure and its role in innovation is an important focus of current research (Mackay et al., 2014; Sealy, 2016; Archer, 2021; Wadley, 2021; Reynard, 2022). Many researchers suggest strong links between population expansions and the transmissibility of technological and cultural innovation (Ash and Gallup, 2007; Powell et al., 2009; Mackay et al., 2014). As populations expand, the argument goes, the chances of a novel idea or tool spreading to neighbouring populations increases (Henrich, 2004; Powell et al., 2009; Richerson et al., 2009). An important question is whether coastal environments had significant effects on demographic dynamics in the southern Cape. Changes in occupational intensity at coastal sites could be a useful means of inferring demographic trends, which may help us understand larger-scale settlement dynamics. In this regard, local-scale data from sites with long chronological sequence are especially valuable. Klasies River Main site (KRM) is an important site in documenting human behaviour in the MSA with a near-continuous Late Pleistocene sequence encompassing almost 70,000 years. The faunal remains from the site have had a significant impact on our understanding of bone taphonomy and hominin subsistence behaviour (Binford, 1984; Blumenschine, 1986; Marean and Kim, 1998; Pickering et al., 2003). An abundance of fauna was recovered from the original Singer and Wymer (1982) excavations and analysed in a seminal paper by Klein (1976). However, the significance of its implications for subsistence has been contentious (Binford, 1984; Thackeray, 1990; Bartram and Marean, 1999; Klein et al., 1999; Outram, 2000), with some suggesting that the sampling methods used to recover the fauna had biased any meaningful interpretations of the assemblage (Turner, 1989; Bartram and Marean, 1999; Marean et al., 2004. See discussion in Van Pletzen-Vos et al., 2019). Excavations by H.J. Deacon in the 1980s and 1990s used more modern methods where all faunal material was retained. His excavations sampled sections from the Singer and Wymer cuttings in a finer resolution incorporating natural stratigraphy (Deacon and Geleijnse, 1988). Beginning in 2014, excavations by Wurz and colleagues (2018) followed on from the protocols of the Deacon excavations. These excavation are still ongoing. It is from these two excavations that the analyses in this paper are based.

To explore coastal occupational intensity at a site like KRM, it is useful to examine both the taphonomic data and the environment of the site. Faunal remains offer a good opportunity to investigate both. Combining taxonomic and taphonomic analyses is useful in unpacking human subsistence behaviour (e.g., Faith J. T. 2013a), especially at sites with extensive chronological sequences such as KRM. Taphonomic analyses are particularly critical in understanding subsistence patterns, site formation and occupational intensity (Lyman, 1987, 2010; Reynard, 2022). Only two taphonomic studies (incorporating bone surface modification assessments) were undertaken on the faunal material from KRM (Binford, 1984; Milo, 1998). Both these studies, however, were conducted on the contentiously excavated Singer and Wymer material. Here, I present taphonomic analyses on fauna from the Deacon and Wurz excavations. Although preliminary, this is the first taphonomic study of either of these collections. The aim of this paper is to use these taphonomic data to investigate occupational intensity and to explore its relationship with the environment at KRM from c. 110 ka to c. 55 ka. This will be done by integrating previous palaeoecological analyses of the Deacon fauna with the recent taphonomic analyses of the Deacon and Wurz excavations.

2 Theoretical framework

In this study, zooarchaeological data are used to assess occupational intensity. Here, occupational intensity is defined as the size of the groups that occupied a site, the frequency of visits, and the duration of stay at a site (Munro, 2004; Haaland et al., 2021). It has been shown that various taphonomic indicators are a valuable means of investigating occupational intensity (Reynard and Henshilwood, 2018; Reynard, 2022). In addition to occupational intensity, declining foraging efficiency or subsistence intensification is also investigated. Occupational intensity can be linked to the over-exploitation of resources, with dietary diversification an important indicator of subsistence intensification (Stiner and Kuhn, 2006; Lupo et al., 2013). Here, I treat intensification and occupational intensity as two separate criteria. However, it is assumed that evidence of intensification at the site could inform on more intensive human occupations, and it is expected that there would be close links between more intensively occupied layers and intensification (*sensu* Boserup, 1965). The focus of this paper is not subsistence behaviour (future studies will focus on subsistence strategies through the sequence), rather, the taphonomic data presented here is used to document and explore shifts in occupational patterns and to assess whether these relate to environmental conditions.

2.1 Occupational intensity

The main objective of this study is to use taphonomic data to infer occupational intensity at KRM, and to compare these to taxonomic data as a proxy for the environment of the region. In assessing occupational intensity at KRM, the following criteria are used:

2.1.1 Bone surface modification

While measuring increased occupations at a site is complex (Haaland et al., 2021), taphonomic data may be a good proxy (Reynard, 2022). The relative proportions of anthropogenic *versus* zoogenic bone surface modifications (BSM) is often used to infer whether humans or carnivores were the dominant bone collector (e.g., Brain, 1981; Blumenschine, 1988), and these may be a useful means of assessing how frequently or intensively a site was occupied. Higher frequencies of tooth-marked bone may therefore reflect more intense carnivore activity, signifying lower human occupations in those periods (Thompson et al., 2017). It then follows that anthropogenic marks may be useful measures of higher occupations. In comparing taphonomic to micro-morphological and geoarchaeological data, Reynard (2022) showed that higher frequencies of anthropogenic marks such as percussion and cut marks correlate well with increased occupations along the southern Cape coast. This is not to suggest that higher occupational intensity is intrinsically linked to more intensive butchery events at a site, but rather that it is likely that increased site-use activity would result in a greater probability of faunal remains being modified or damaged by people. Other taphonomic modifications such as burnt bone and trampling marks are also useful indicators of occupation since these are closely linked to anthropogenic activities in rockshelters (Marean, 2010; Reynard and Henshilwood, 2018).

2.1.2 Transverse bone fracture patterns

Higher frequencies of transverse fractures may be a useful indicator of more intensive occupations at archaeological sites. It has been shown that higher frequencies of transverse fractures in MSA assemblages along the southern Cape coast correlate well with more intense occupations (Reynard, 2022). It is likely that the relationship between transverse breakage and occupational intensity may be the result of the accumulated weight of occupants within enclosed rockshelters. However, geomorphic and site formation processes such as rock falls may also account for higher frequencies of transverse fractures. An increase in transverse breaks has been linked to sediment compaction (Villa and Mahieu, 1991).

2.1.3 Faunal density

Artefact, lithic and bone density is often used to inform on occupational intensity (e.g., Shiffer, 1987; Mitchell, 1993; Marean 2010; Reynard et al., 2016). However, volumetric density may be affected by sediment accumulation rates (Jerardino, 1995; Jerardino, 2016b) and faunal density may also be influences by carnivore activity at a site. That said, faunal density may be a useful proxy for greater occupational intensity in southern Cape MSA sites (Reynard, 2022).

2.2 Subsistence intensification

Another objective of this study is to investigate evidence for intensification at KRM. Subsistence intensification can be defined as the extraction of increased energy from food resources at the expense of foraging efficiency (Munro 2009: 141). The diet breadth model predicts that low-ranked prey are added to the diet as the abundance of high-ranked prey declines (MacArthur and Pianka, 1966; Dusseldorp, 2012). Various constraints and costs aside, prey is usually ranked according to body size, with body size a proxy for caloric value. Intensification—or declining foraging efficiency—is associated with a broadening of diet breadth and more intensive—and costly—carcass processing. Initially, intensification entailed increases in economic productivity linked to population expansions (Boserup, 1965) and was later used to explain declining foraging efficiency at the onset of domestication (Flannery, 1969). Intensification has been widely used to contextualise MSA subsistence strategies and has been linked to occupational intensity and demographic pressure (Stiner et al., 1999; Munro, 2009; Steele and Klein, 2009; Clark, 2011; Dusseldorp, 2012; Dusseldorp and Langejans, 2013; Reynard and Henshilwood, 2017). Yet environmental-induced stress may be an equally significant factor in intensification (Winterhalder and Smith, 2000; Clark, 2011; Morgan, 2015). It is important to reiterate that, here, intensification is not assumed to be intrinsically linked to greater occupational intensity, but rather the objective is to examine whether any relationship between them exists. I follow Reynard and Henshilwood (2017) and use the following three indicators of intensification:

2.2.1 Exploitation of low-ranked prey

Under the diet breadth model, increases in lower-ranked, smaller prey would indicate declining foraging efficiency given the higher search and handling costs of hunting small fauna (Dusseldorp, 2012). Small fauna associated with the southern Cape region during the MSA includes hyrax (*Procavia capensis*), Cape dune molerats (*Bathyergus suillus*), size 1 bovids and shellfish. Juveniles would be considered lower ranked prey because they have less meat and fat than adults so increase in juveniles may also reflect a broadening diet breadth (Munro, 2004; Clark, 2011). Fat is a particularly important criterion in prey selection (Brink, 1997) and with juveniles particularly lacking fat, they were unlikely to have been targeted by hunters. Thus, while seasonality of foraging expeditions may affect juvenile abundance, Speth and Clark (2006, p. 15) argue that, given their low-rank as a source of lipids, seasonal fluctuations in the abundance of juveniles should have little effect on prey choices.

2.2.2 Intensive marrow extraction

Marrow extraction from high-utility long bones is common at Stone Age sites. During periods of resource stress, it is assumed that more marrow and meat-scarce (low-utility) elements would be exploited (Binford, 1978; Morin, 2007). It is expected that elements with little marrow such as phalanges, pelves and mandibles would more likely be processed with more evidence of percussion marks on them. Because carpal and tarsal bones are mostly dense cancellous bone with virtually no marrow fat (Marean 1991), these were excluded.

2.2.3 Variation in transport distances

Under the central place forager prey choice model, it is expected that foraging is more likely to have occurred closer to base-camp, and that increases in foraging distances implies a decline in hunting efficiency (Cannon, 2003). The patch choice model also predicts that foragers exploit productive regions (or 'patches')—usually close to home—and only move to another area once the productivity of the patch has dropped below a specific threshold (Winterhalder, 2001). Intensification may be evident when foraging distances increase (Faith, 2007; Clark, 2011). Ethnographic studies suggest that foragers are more likely to transport high meat-yielding post-cranial bones than skulls back to base-camp (O'Connell et al., 1988; Monahan, 1998). Statistical models by Schoville and Otárola-Castillo (2014) show that skull abundance is a particularly good proxy for transport distances, with skulls for large ungulates decreasing significantly as distances to kill-sites increase.

3 Site background

Klasies River Main site (KRM) is on the Tsitsikamma coast in the southern Cape, and consists of two caves, 1 and 2, and two

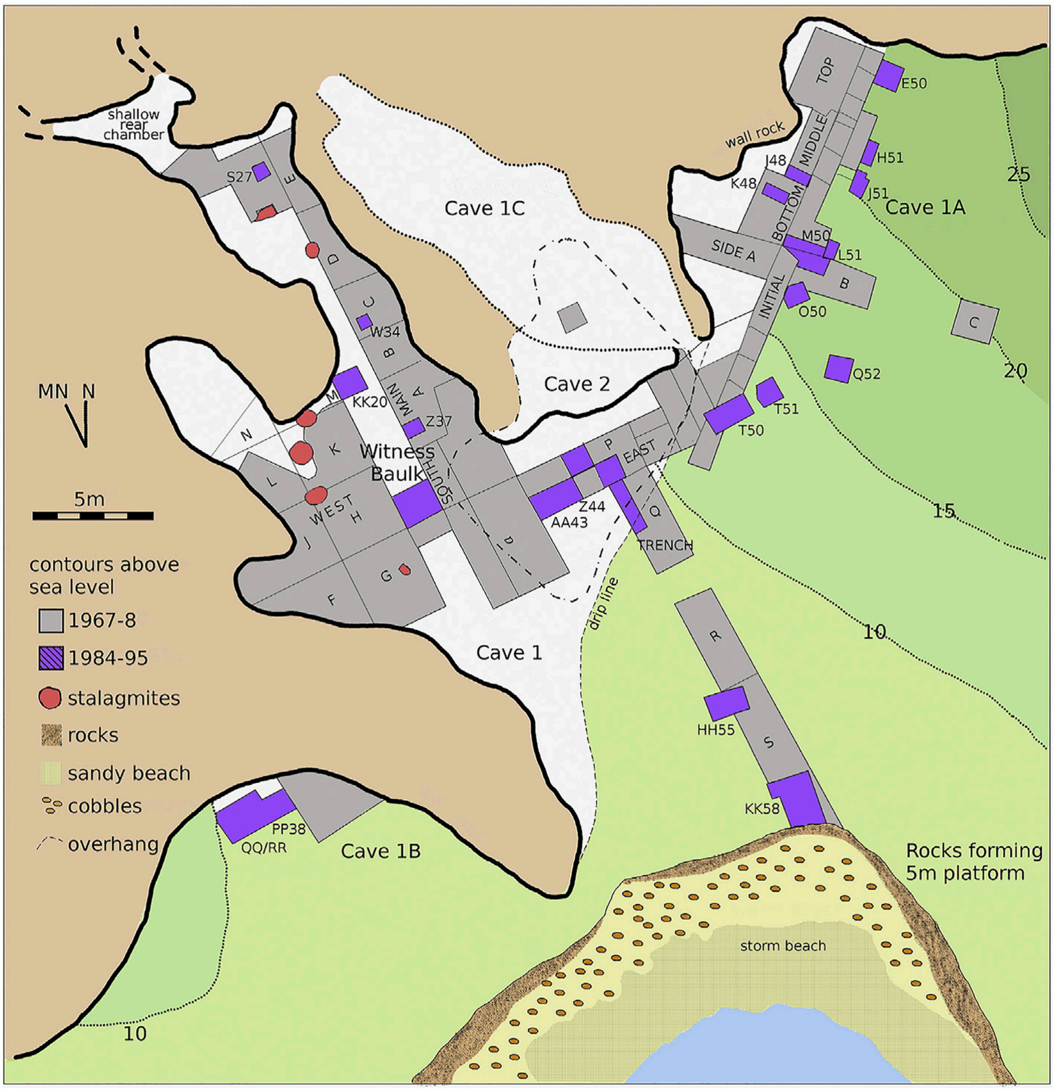

FIGURE 1
Site map of Klasies River main site.

shallow overhangs, caves 1A and 1B. Together, these contain more than 21 m of deposits (Wurz et al., 2018). The faunal remains examined in this paper were recovered from caves 1 and 1A (Figure 1). The lowermost deposits in the Witness Baulk in cave 1, and squares AA43–Z44—the overlap of cave 1 and 1A—are associated with MSA I artefacts (also termed MSA 2a) (Volman, 1984) and Klasies River (Wurz, 2002) techno-complexes) and dated to MIS 5e (Wurz, 2002). Layers overlying the MSA I deposits are associated with MSA II artefacts (MSA 2b (Volman, 1984) or Mossel Bay (Wurz, 2002)) and are dated to c. 101 ka at the base and c. 77 ka at the top (Vogel, 2001). The MSA II deposits are divided into MSA II Upper and Lower (Wurz, 2002). U-Th dates from the base of MSA II Lower indicates it formed prior to MIS 5c (c. 100 ka) (Wurz et al., 2018). Recently, U-Th dating of flowstone on tufa that fell into layer HHH in the MSA II Lower deposits obtained an age of 126.0 ± 1.5 ka (Wurz et al., 2018). MSA I deposits lie almost a metre below this layer, likely representing several thousand years of occupations (cf. Deacon and Geleijnse, 1988). This suggests that the MSA I is probably significantly earlier than previously described, and may date to early MIS 5e or the MIS 5e/MIS 6 transition. The approximately 2 m thick HP and 1 m thick MSA III (post-HP) layers occur in the overlying Upper member of cave 1A. The HP currently dates to c. 65 ka and the MSA III to c. 57ka (Wurz, 2002; Grine et al., 2017). A more detailed discussion of the site chronology is in Morrissey et al., (2022).

TABLE 1 Herbivore functional groups at Klasies River based on Hempson et al. (2015).

Herbivore functional type	Taxa
Small non-social browsers (SNB)	Steenbok/grysbok
	Klipspringer
	Bushbuck
	Grey rhebok
Medium-sized social mixed diets (MSM)	Springbok
	Eland
Large social water dependent browsers (LWB)	Kudu
Large-medium social water dependent grazers (LWG)	Impala
	Hartebeest
	Wildebeest
	Bontebok/Blesbok
	Roan
	Sable
	Bluebuck (?)
	lechwe
	Waterbuck
	Southern reedbuck
	Mountain reedbuck
	Buffalo
Large water dependent non-ruminants (LWN)	Rhino
	Zebra
	Hippo
	Warthog
	Bushpig

4 Materials and methods

Two key sources of data are used in this study. The first is taxonomic data from Van Pletzen's analysis of the Deacon excavations (Van Pletzen, 2000; Van Pletzen-Vos et al., 2019). The second is taphonomic data from a sample of fauna analysed from the Deacon and Wurz excavations.

4.1 Taxonomic data

The faunal remains used to infer palaeoenvironments are from samples excavated by Hilary Deacon and colleagues between 1984 and 1995. Taxa were identified by Brink and Van Pletzen-Vos using the South African National Museums comparative faunal collections in Bloemfontein (Van Pletzen-Vos et al., 2019). Only mammals the size of, or larger than, the Cape dune molerat were analysed. The number of identified specimens (NISP) was used to quantify specimens following Klein and Cruz-Uribe (1984). Bovidae (bovids) not assigned to a Linnaean Family were categorised to size classes originally based on Klein (1976), but here are referred to using Brain's (1974) nomenclature. Ungulate dietary preferences (i.e., grazers, browsers and mixed-feeders) and taxonomic diversity data are taken from Reynard and Wurz (2020). All *Raphicerus* species were identified as Cape grysbok (*Raphicerus melanotis*) (Table 3; Klein, 1976; Van Pletzen-Vos et al., 2019) but to account for the possibility of the inclusion of some steenbok (*R. campestris*) in the assemblage, I use *Raphicerus* when referring to the Cape grysbok. Large mammal herbivores—defined here as bovid size class (Bov) 1 and larger—were assigned herbivore functional types and categorised into five groups based on Hempson et al. (2015) (Table 1). These herbivore groups encompass habitat characteristics of species which are closely linked to environmental conditions and regional ecology (Hempson et al., 2015).

4.2 Taphonomic data

Taphonomic data are from faunal samples from the Deacon and Wurz excavations. While the taxonomic data cover the entire Late Pleistocene sequence of KRM, taphonomic data are from samples from three periods at KRM: the MSA II Lower, the HP and the MSA III. The faunal remains taphonomically analysed from the MSA II Lower are from the lower Witness Baulk layers of cave 1 from the Wurz excavations (Table 2). The HP taphonomic samples are from the E50 and J51 units and MSA III sample is also from the E50 unit from the Deacon excavations of cave 1A.

In the taphonomic sample, indeterminate mammal specimens that could only be identified to element (e.g., cranial, rib and vertebral remains) were assigned to 'small', 'medium' or 'large' indeterminate mammal size classes. Small mammal is comparable to size 1 bovids, medium mammals to size 2 and 3 bovids, and large mammals to size 4 and 5 bovids. Specimens referred to as 'identified small mammals' are non-ruminant size 1 animals such as hyrax, Cape dune molerat and lagomorphs that could be identified to species.

All taxonomically identified specimens, piece-plotted specimens and specimens >2 cm were taphonomically analysed. Types of surface modification element, skeletal portion, side, and state of epiphyseal fusion were recorded for all specimens. Bone surface modifications (BSM) including cut, percussion and carnivore tooth marks, gastric acid etching, gnaw marks, weathering and rootlet etching were recorded following standard criteria (Behrensmeyer, 1978; Blumenschine and Selvaggio, 1988; Fisher, 1995; Blumenschine et al., 1996) using a Nikon binocular light microscope (10–4×0 magnification) under oblique, unidirectional lighting. Burning was reported for carbonised (mostly black) and calcined (mostly grey or white) specimens (Stiner et al., 1995). Trampling marks include lines and pits defined by Reynard (2014) on un-burnt specimens (Reynard and Henshilwood, 2018). The complete

TABLE 2 Stratigraphy of the taphonomically analysed faunal sample at Klasies River.

Cave	Techno-complex	Layers	Units	Dates	References
Cave 1A	MSA III	CP2, BSS1, BSS2, CP3, BSS3, CP4	E50	c. 57 ka	Wurz, (2002)
Cave 1A	Howiesons Poort	CP5, YS4, CP6, CP9	E50	c. 60 ka	Wurz, (2002)
		CPx4, YSx5	J51	c. 70 ka	Wurz, (2002)
Cave 1	MSA II Lower	SMONE, BOS, SBLS	WB	c. 108 ka	Wurz et al. (2022)

sample reported here includes all specimens identified to element, specimens >2 cm and unidentified long bone fragments (Reynard et al., 2014). A sub-set taphonomic sample was restricted to long bone mid-shafts following Thompson et al. (2017). These were used to assess whether humans or carnivores were the dominant accumulator of the assemblage by noting the proportion of percussion marks (PM) to tooth marks (TM) calculated as PM/(PM+TM) following Thompson et al. 2017. Values more than 50% suggest anthropogenically accumulated assemblages.

Transverse fracture analyses were based on fracture outlines for long bone mid-shafts (Villa and Mahieu, 1991). Because of small samples, all size classes were combined to assess fracture patterns. The circumference of long bone shafts was also noted under the assumption that more compete long bone shafts (i.e., those with more than half the circumference retained) are more indicative of carnivore activity (Bunn, 1983; Villa and Mahieu, 1991; Marean et al., 1992). More ‘splintered’ fragments was assumed to reflect human processing. Faunal density was measured using previously recorded excavation volumetric data from Thackeray (1988) and NISP data from Van Pletzen (2000). Density based on weight used MSA III and HP data from Pearson (2021) and MSA II Lower data from Lap (2020). Because small fauna may have also been collected by carnivores and raptors, only taxa with taphonomic evidence of human accumulation are considered when examining small mammal exploitation. The abundance of percussion marks on phalanges, pelves and mandibles were used to assess more intensive marrow extraction.

The proportion of skull *versus* long bone remains was used to investigate transport decisions. Only high-survival elements (i.e., high-density elements comprising the skull and long bones) are included in this study to limit the influence of bone density-mediated attrition (cf. Faith and Thompson, 2018). Here, skull remains include the crania, mandible and horn cores. Long bones include the forelimb (humerus and radius), the hindlimb (femur and tibia) and the distal limbs (metacarpal, metatarsal and metapodium). By using high survival elements, there was no need to ‘normalise’ the NISP of these elements. Because skull bones and long bones are paired (cf. Clark, 2013), raw NISP values can be used (the exception is metapodia, which was divided by two).

Taphonomic data between and within layers were grouped using Principal Component Analyses (PCA; PAST® free software; Hammer et al., 2001). A PCA incorporating anthropogenic and zoogenic BSM on small, medium and large mammal size classes was used to assess the impact of human and carnivore activity in the MSA II Lower, the HP and the MSA III. Data in PCA were rescaled to percentages. Hereafter, faunal remains from the Singer and Wymer excavations are referred to as the S-W sample, those from the Deacon excavations as the D sample and the Wurz excavations as the W sample. The faunal remains taphonomically analysed from both the D and W samples are referred to as the taphonomic sample.

5 Results

5.1 Taxonomic data

Previous analyses of the D sample show that a broad range of taxa was recovered from KRM (Table 3). Identified small mammals are generally the most abundant (40.1% of identified species; NISP=612), followed by seals (30.1%; NISP=460), which are also the most common taxa in the S-W sample. As a percentage of identified taxa, seal remains are particularly common in the upper MSA II (39% of species in this period; NISP=110) and HP layers (57%; NISP=62), dropping significantly from the HP to the MSA III (χ^2=80.747; df=1; $p<$ 0.001). *Raphicerus* (6.6% of all identified species; NISP=101), eland (5.2%; NISP=80) and African buffalo (2.8%; NISP=43) are the most common bovids. Both the MSA III and MSA II Lower yield substantial numbers of identified small mammal remains. *Raphicerus* is a common fynbos species and relatively prevalent throughout the sequence. To compare the ratio of fynbos to grasslands at KRM, the proportion of *Raphicerus* (from the total number of identified species in each phase) was compared to the proportion of grazers throughout the KRM sequence. There is a significant inverse relationship between the frequencies of *Raphicerus* and grazers (r_s = -0.9; p= 0.0374).

The various herbivore categories show that the MSA I was significantly different to the other periods. In terms of ungulate dietary preferences, grazers are proportionally higher in the MSA I (68.2%; NISP=15) than in any other phase (Figure 2A). There is a significant decrease in grazer proportions from the MSA I to the MSA II Lower (Table 4). While grazers are proportionally quite prevalent in the MSA III (60%; NISP=24) and HP (50%; NISP=12), there is no significant difference in grazer abundance between the

TABLE 3 Number of identified specimens (NISP) in cave 1 and 1A at Klasies River. Data from Reynard and Wurz (2020). Taxonomic names based on Skinner and Chimimba (2005).

		Techno-complex	**MSA III**	**HP**	**MSA II U**	**MSA II L**	**MSA I**	
		Cave	**1A**	**1A**	**1 & 1A**	**1/1A AA43/Z44**	**1/1A AA43/Z44**	**Total**
Order	Taxa	Common name						
Primate	*Papio ursinus*	Baboon				2		2
	Primate: indet.	Primate				1		1
Rodentia	*Bathyergus suillus*	Cape dune mole rat	2	1	1	5		9
	Hystrix africaeaustralis	Porcupine			2			2
Lagomorpha	*Lepus* sp. (? *capensis*)	Hare			1	3		4
	Leporidae	Hare	2					2
Hyracoidea	*Procavia capensis*	Hyrax	121	18	87	340	29	595
Carnivora	*Aonyx capensis*	African clawless otter	1			2		3
	Hyaena brunnea	Brown hyena				4		4
	Arctocephalus sp.	Seal	21	62	110	254	13	460
	Carnivore: indet.	Carnivores	17	3	18	14	2	54
Tubulidentata	*Orycteropus afer*	Aardvark	4		6	22		32
Whippomorpha	*Cetacea* sp.	Whale/dolphin sp.				1	1	2
	Hippopotamus amphibius	Hippopotamus				8	5	13
Perissodactyla	*Equus* sp.	Zebra	1	1	1	5	2	10
Suiformes	*Suid* sp.	Bushpig/Warthog		2	2	1	1	6
Ruminantia	*Tragelaphus oryx*	Eland	2	2	14	61	1	80
	cf. Tragelaphini	Tragelaphine				2		2
	Tragelaphus strepsiceros	Greater kudu	1	2	1	18	1	23
	Tragelaphus scriptus	Bushbuck			2	21		23
	Syncerus antiquus	Long-horned buffalo	9	3		6	2	20
	*Syncerus africanus**	African buffalo	6	2	8	25	2	43
	Sylvicapra grimmia	Common duiker				6	1	7
	Kobus sp.	Waterbuck/lechwe	1					1
	cf. *Redunca* sp.	Reedbuck				6		6
	Redunca arundinum	Southern reedbuck	1		2			3
	Hippotragus sp.	Roan/sable/bluebuck	1		2	4		7
	Hippotragus leucophaeus	Bluebuck	2		1	19	1	23
	Damaliscus pygargus	Bontebok/blesbok	2		1			3
	Alcelaphus/Connochaetes	Hartebeest/wildebeest	1	5	6	11	3	26
	Megalotragus cf. *priscus*	Giant hartebeest		1				1
	Philantomba monticola	Blue duiker			1			1
	Raphicerus melanotis	Cape grysbok	10	6	22	62	1	101
	Pelea capreolus	Grey rhebok	2	1		4	3	10
	Antidorcas sp.	Springbok	1	1				2
	Indet. Bovidae Size class 4	Bovid 4	47	61	77	248	34	467
	Size class 3	Bovid 3	97	81	91	366	73	708
	Size class 2	Bovid 2	56	66	131	284	48	585
	Size class 1	Bovid 1	187	100	350	422	26	1,085
Mammal: Indeterminate					189	469	24	682
Total			595	418	1,178	2,852	282	5,325

*Due to the racists nature of the original species name (*Syncerus caffer*), we use this name following Dusseldorp and Reynard (2022).

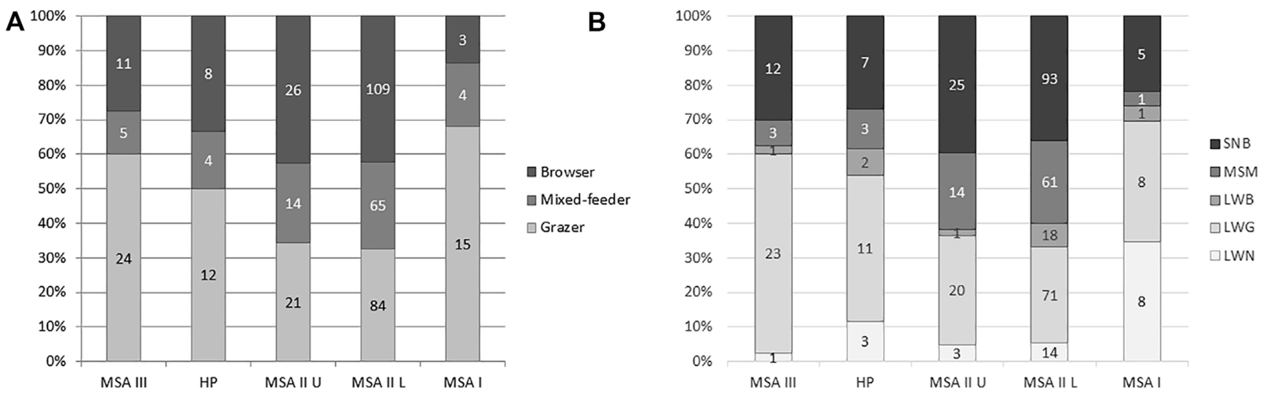

FIGURE 2
(A) Ungulate dietary preference proportions at Klasies River. **(B)** Herbivore functional type proportions based on Hempson et al. (2015). SNB = small non-social browser, MSM = medium-sized social mixed-diets, LWB = large water dependent browsers, LWG = large-medium water dependent grazers, LWN = large water dependent non-ruminants. Number of specimens in columns.

TABLE 4 Chi-squared tests of significance for ungulate categories at Klasies River. 'Mixed-browsers' are mixed-and intermediate feeders and browsers. Herbivore functional types based on Hempson et al. (2015).

Phases	Grazers vs. mixed-browsers			Herbivore functional types		
	χ^2 value	*p*-value	Significance	χ^2 value	*p*-value	Significance
MSA I & MSA II L	11.256	0.0008	Yes	10.482	0.005	Yes
MSA II L & MSA II U	0.078	0.78	No	0.267	0.875	No
MSA II U & HP	1.759	0.185	No	4.184	0.124	No
HP & MSA III	0.61	0.435	No	0.337	0.845	No

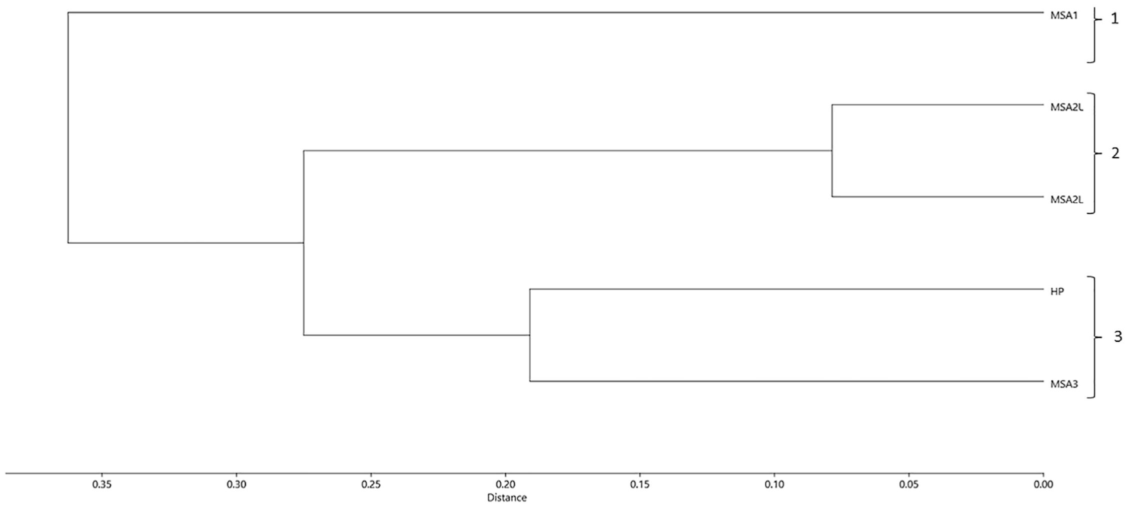

FIGURE 3
Cluster analysis of herbivore functional types based on Hempson et al. (2015) at Klasies River.

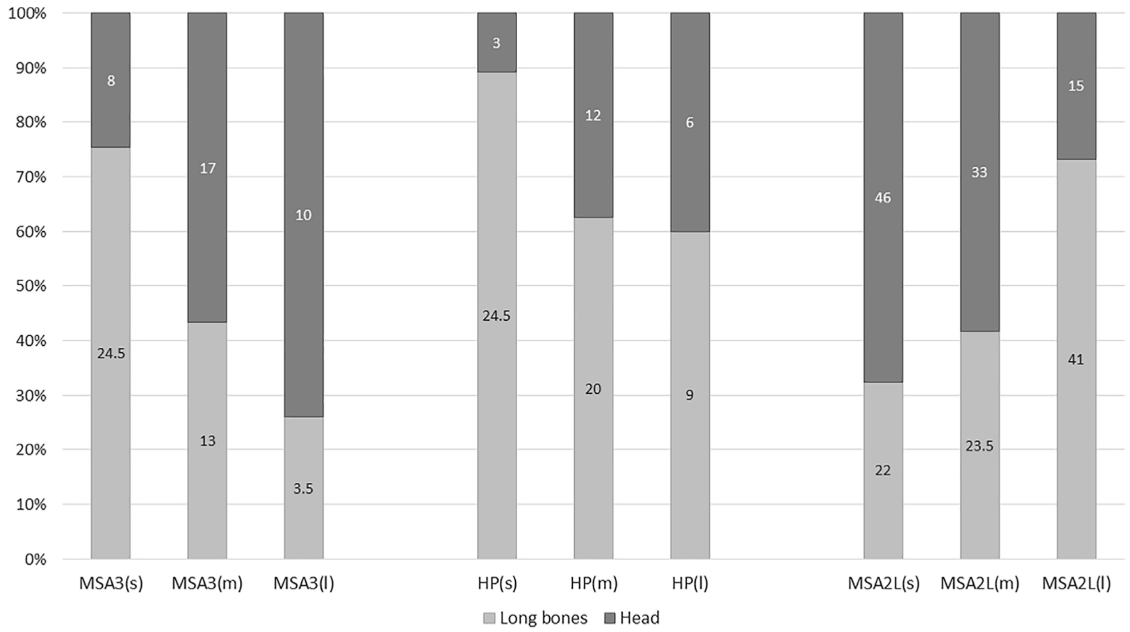

FIGURE 4
Head *versus* long bone distribution patterns for small (s), medium (m) and large mammals (l) at Klasies River. Number of specimens in columns.

HP and MSA III (Table 4). Grazers are not significantly different to mixed-browsers between these layers (χ^2= 0.610; df=1; p=0.435). Herbivore types are generally not significantly different through the sequence (Figure 2B). Again, the exception here is the MSA I layer where a chi-squared test shows a significant difference between this layer and the lower MSA II (Table 4). A hierarchical cluster analysis using the UPGMA algorithm in the PAST4 package (Hammer et al., 2001) indicates three groupings for herbivore functional types (Figure 3). Group 1 encompasses the MSA I, the upper and lower MSA II layers encompass group 2 and group 3 includes the HP and MSA III.

TABLE 5 The proportion of percussion (PM) *versus* tooth marks (TM) at Klasies River based on Thompson et al. 2017. Values above 50% indicate anthropogenically accumulated assemblages.

Sample	PM	TM	PM/(PM + TM)	Transverse fractures
MSA II Lower				
Small	21	24	46.7%	56 (19.3%)
Medium	38	23	62.5%	
Large	33	35	48.8%	
Total	92	82	53.3%	
HP				
Small	9	11	45.5%	26 (13.1%)
Medium	18	10	65.1%	
Large	27	10	73.3%	
Total	54	31	65.4%	
MSA III				
Small	6	73	7.7%	14 (7.9%)
Medium	40	37	51.7%	
Large	33	33	50.0%	
Total	79	143	34.3%	

5.2 Skull vs. long bone distribution

Skull and long bone profiles were constructed using the taphonomy sample with only patterns from the lower MSA II, the HP and MSA III presented. Skull abundance patterns in the MSA II Lower layers are notably different to the MSA III and HP (Figure 4). Here, skulls are more prevalent as animal size decreases and are significantly less common among large compared to medium mammals (χ^2=14.076; df=1; p=0.0002). Skulls are less common in the HP (Figure 4) but more common in larger mammals. In the MSA III sample, skulls are substantially more common in larger mammals. In both the HP and MSA III, skulls become more prevalent as animal size increases.

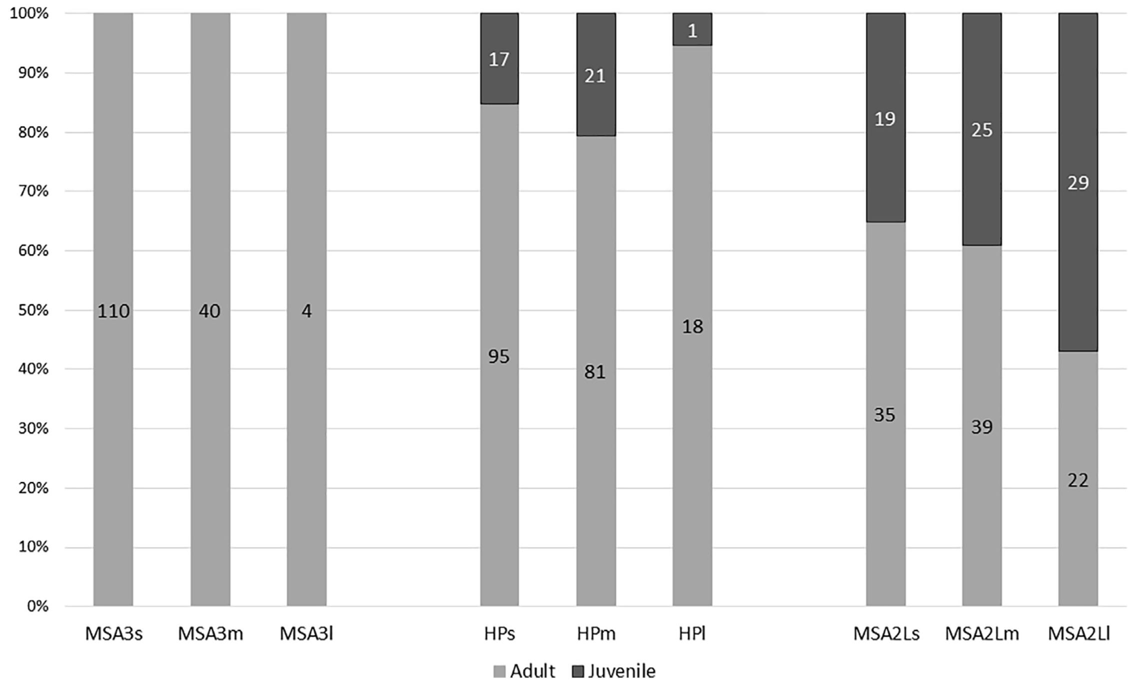

FIGURE 5
Mortality profiles for small (s), medium (m) and large mammals (l) at Klasies River. Number of specimens in columns.

5.3 Mortality profiles

The majority of assessable specimens have fused ends and could be considered adult (79.9%; *n*=444) with 20.1% (*n*=112) displaying unfused or recently-fused ends and considered juvenile (Figure 5). No juveniles were recovered from the MSA III, while 16.7% (*n*=39) of the HP sample are juvenile and 83.3% (*n*=194) are adult. The MSA II Lower sample contains significantly more juvenile specimens than the HP (χ^2=34.114; df=1; p<0.0001) with 43.2% (*n*=73) classed as juvenile and 56.8% (*n*=96) considered adult. There is no significant difference in adults and juveniles in the MSA II Lower between small *versus* medium mammals (χ^2=0.188; df=1; p=0.664) but a weakly significant difference between medium *versus* large mammals (χ^2=3.611; df=1; p=0.057).

5.4 Taphonomy

Proportions of percussion *versus* tooth marks show that values for medium and large mammals were generally over 50% and likely anthropogenically accumulated (Table 5). The exception is large mammals in MSA II Lower (48.8%). Small mammals all suggest carnivore contributions since none are over 50%. The small mammal values from the MSA III is especially low (7.7%) indicating very little human contribution. Transverse fractures are relatively low with the highest values from the MSA II Lower layers (19.3%; *n*=56) and the lowest from MSA III (7.9%; *n*=14) (Table 5). Faunal density is significantly higher in MSA II Lower (789 NISP/m^3; 159.1 kg/m^3) compared to the MSA III (366 NISP/m^3; 9.54 kg/m^3) and HP (402 NISP/m^3; 9.56 kg/m^3) phases (Table 6). Trampling modification is more common in the HP phase (17.8%; *n*=411) and the least common in MSA III (4.4%; *n*=47) (Table 7). Tooth marks are the most prevalent BSMs in all phases at KRM (14.8%; *n*=778) with percussion marks also common (10.8%; n=569).

5.4.1 MSA I and MSA II Upper

No taphonomic analyses were conducted on remains in these layers but a study by Ezmeiro, 2022 on the faunal remains from the MSA I layers in cave 1B shows that burning was relatively common (13%; *n*= 2,520). No percussion marks were reported, and cut marks (0.3%; *n*=65) and tooth marks (0.02%; *n*=5) were rare.

5.4.2 MSA II Lower

Tooth marks are the most prevalent BSM in the MSA II Lower (15.1%; *n*=299) although percussion marks (11.5%; *n*=228) are also common (Table 7). Cut marks (8.3%; *n*=165) are significantly more common here than in the HP

TABLE 6 Faunal and lithic density at Klasies River. Excavated volume of deposit from Thackeray (1988). Numbers of identified specimens (NISP) of fauna from Van Pletzen (2000). Faunal density data for weight (kg) based on data from Lap (2020) and Pearson (2021). Lithic density for MSA III and HP from Wurz (2000) using Thackeray's (1988) excavated volumes. Lithic density for MSA II Lower from Brenner et al. (2022).

Layers	Excavated volume (m^3)	Fauna NISP	Faunal density ($NISP/m^3$)	Faunal density (kg/m^3)	Lithic density (N/m^3)
MSA III	1.626	595	366	9.54	3070.7
HP	0.928	373	402	9.56	11002.2
MSA II U	1.513	303	200	----	----
MSA II L	0.445	376	845	159.1	84888.6
MSA I	0.254	205	807	----	----

TABLE 7 Bone surface modification at Klasies River. Percentages in brackets. PM = percussion marks. CM = cut marks. TM = tooth marks. GM = gnaw marks. AE = acid etching. Burn = burnt bone. Tramp = trampling marks. %ShC = percentage of circumferentially complete long bone shafts.

Layers	N	PM	CM	TM	GM	AE	Burn	Tramp
MSA III	1,070	124 (11.6)	53 (5.0)	334 (31.2)	4 (0.4)	149 (13.9)	101 (9.4)	47 (4.4)
HP	2,305	251 (10.9)	58 (2.5)	152 (6.6)	11 (0.5)	118 (5.1)	720 (31.2)	411 (17.8)
MSA II L	1982	228 (11.5)	165 (8.3)	299 (15.1)	16 (0.8)	45 (2.2)	76 (3.8)	211 (10.6)
Total	5,274	569 (10.8)	266 (5.0)	778 (14.8)	31 (0.6)	310 (5.9)	897 (17.0)	669 (12.7)

Long bone mid-shaft subset

Layers	Size class	N	CM	PM	TM	GM	AE	%ShC
MSA III	Small	33	3 (9.1)	2 (6.1)	24 (72.7)	0	3 (9.1)	29.0
	Medium	38	5 (13.2)	15 (39.5)	14 (36.8)	0	4 (10.5)	5.3
	Large	18	3 (16.7)	6 (33.3)	6 (33.3)	1 (5.6)	1 (5.6)	0
	Total	89	11 (12.4)	23 (25.8)	44 (49.4)	1 (1.1)	8 (9.0)	---
HP	Small	56	2 (3.6)	5 (8.9)	6 (10.7)	1 (1.8)	7 (12.5)	9.1
	Medium	227	6 (2.6)	41 (18.1)	22 (9.7)	1 (0.4)	32 (14.1)	0
	Large	83	2 (2.4)	22 (26.5)	8 (9.6)	1 (1.2)	4 (4.8)	1.2
	Total	366	10 (2.7)	68 (18.6)	36 (9.8)	3 (0.8)	43 (11.7)	---
MSA II L	Small	33	4 (12.1)	7 (21.2)	8 (24.2)	0	2 (6.1)	40.0
	Medium	53	10 (18.9)	20 (37.7)	12 (22.6)	0	0	9.8
	Large	63	18 (28.6)	21 (33.3)	22 (34.9)	0	1 (1.6)	13.2
	Total	149	32 (21.5)	48 (32.2)	42 (28.2)	0	3 (2.0)	---

(χ^2=72.916; df=1; p<0.0001). Despite the high frequency of tooth marks, acid etched bones (2.2%; n=45) are significantly less common in this phase compared to the HP (χ^2=23.647; df=1; p<0.0001). Data from the long bone mid-shaft subset show that frequencies of tooth marks (35%; n=22) are almost on par with percussion marks (33%; n=21) in large mammals (Table 7). Cut marks (29%; n=18) are also common on large mammals and percussion marks are especially prevalent in medium mammals (38%; n=20). While tooth marks are common in all size classes (28.2%; n=42), percussion marks are slightly more prevalent (32.2%; n=48) (Table 5). Long bone shaft are less splintered in this phase, with 13% of large (n=7) and 40% of small mammal specimens (n=12) retaining a near-complete circumferences (Table 7).

5.4.3 Howiesons Poort

In the HP, burning is the most dominant BSM (31.2%; n=720) and substantially higher here than in the other periods (Table 7). Percussion marks are also prevalent (10.9%; n=251). Tooth marks (6.6%; n=152) are significantly less common in this phases compared to the MSA II Lower (χ^2=81.627; df=1; p<0.0001). Cut marks are not especially common (2.5%; n=58) but still within the norm for Stone Age assemblages (cf. Bunn, 1991). Trampling marks are significantly more prevalent in this phase compared to the MSA II Lower

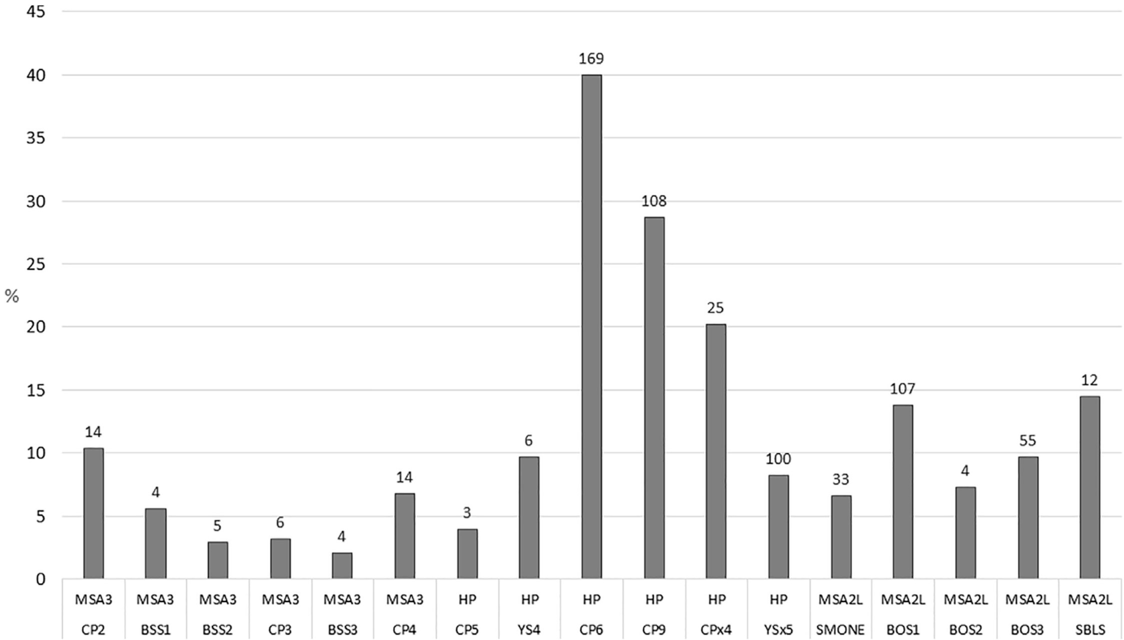

FIGURE 6
Frequencies of trampled bone in the MSA III, Howiesons Poort (HP) and MSA II Lower (L) phases per layer at Klasies River. Number of specimens above columns.

(χ^2=44.352; df=1; p<0.0001). A breakdown of trampling marks per layer shows that trampling is significantly more prevalent in the early HP (layers CP6, CP9 and CPx4) than the later HP (CP5 and YS4) (Figure 6). The long bone subset shows that about 10% of small (n=6), medium (n=22) and large mammal (n=8) specimens display tooth marks (Table 7). Percussion marks are more prevalent on large (27%; n=22) rather than small mammal (9%; n=5) long bones, with relatively low cut mark frequencies for all size classes. Very few long bones retain near-complete circumferences with only one large mammal (1.2%) and no medium sized specimens.

5.4.4 MSA III

Evidence of carnivore activity such as tooth marks are especially prevalent in this phase (31.2%; n=334) and substantially higher than in other layers (Tables 5, 7). The frequency of gastric acid etching (13.9%; n=149) is also significantly higher here than in the HP (χ^2=77.783; df=1; p<0.0001). A fair number of bones display percussion (11.6%; n=124) and cut marks (5%; n=53), and burning (9.4%; n=101). Regarding the long bone sunset, most small mammal bones display tooth marks (73%; n=24) with few percussion marks (6%; n=2). Compared to other size classes, more small mammals long bone retain near-complete circumferences (29%; n=9) (Table 7). Medium (40%; n=15) and large mammals (33%; n=6) generally have relatively high frequencies of percussion marks, with similar frequencies of tooth marks on medium (37%; n=14) and large mammals (33%; n=6). Only two long bones of medium mammals (5.3%) and no large mammal have relatively completed circumferences (Table 7).

To examine occupational patterns using anthropogenic (cut and percussion marks) and zoogenic (tooth marks and acid etching) BSM, a PCA was conducted incorporating small, medium and large mammals from the three periods under analysis (Figure 7). Components 1 and 2 explain 63% and 31% of the variance of the PCA, respectively. Positive values on component 1 and 2 for medium and large mammals from MSA III, and large mammals from MSA II Lower group these classes in the first quadrant. HP mammal classes are tightly bunched in the third quadrant with small mammals from MSA III isolated with significantly higher values on component 1.

5.4.5 Small mammal and low-ranked element exploitation

Small mammals are more common in the MSA II Lower and MSA III but, as can be expected, few small mammals display anthropogenic marks (Table 8). Over 40% of size 1 mammals in the MSA II Lower layers are burnt (n=85), with percussion marks (10%; n=21) and anthropogenic marks (17.1%; n=36) relatively common in this phase. Anthropogenic marks are significantly more common on size 1 mammals in the MSA II Lower than in the HP layers (17.1%; n=36; χ^2=5.214; df=1; p=0.022). Regarding identified small fauna, nine specimens (24.3%) in the MSA II Lower show evidence of burning with a cut mark visible of one hyrax specimen (2.7%). Half of the porcupine specimens (50%; n=5) and three rodent specimens (30%) are burnt. Percussion marks do not occur on any of these remains with no evidence of anthropogenic modification on Cape dune mole rate and hare

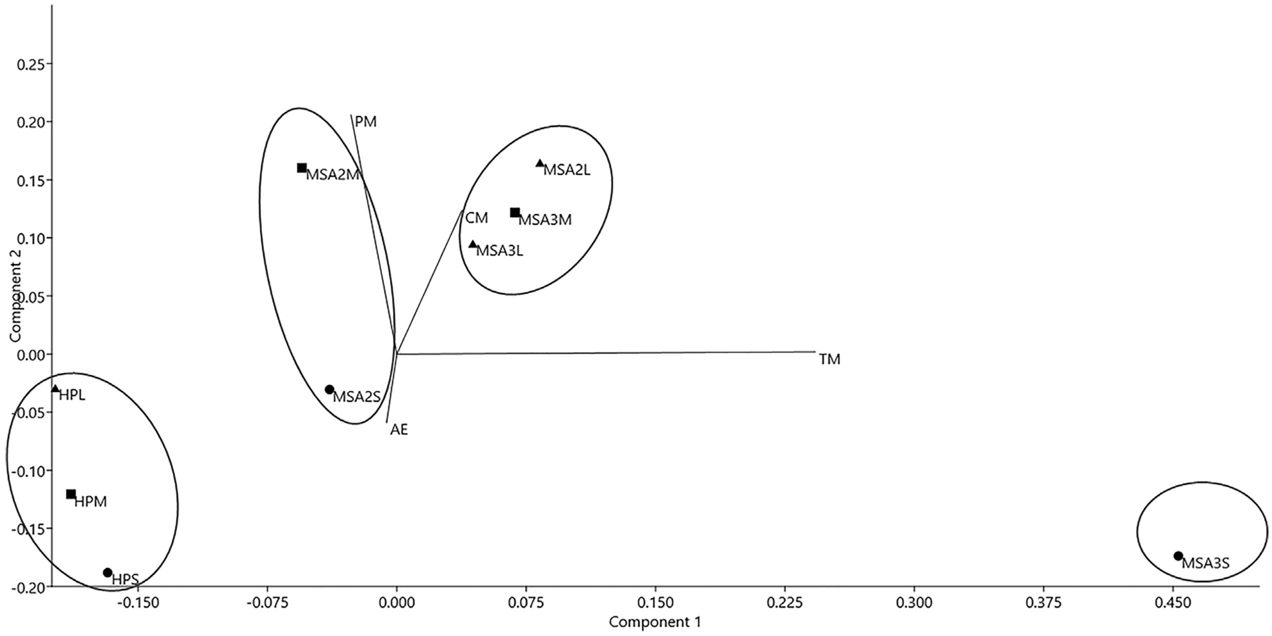

FIGURE 7
Principal component analysis of anthropogenic and zoogenic bone surface modification for small (s), medium (m) and large (l) mammal size class at Klasies River. Triangles are large mammals, squares are medium-sized mammals, and circles are small mammals. PM = percussion marks. CM = cut marks. TM = tooth marks. AE = acid etching.

specimens. Low utility element processing frequencies are highest in this phase (10.2%; *n*=6) although not significantly higher than those from the HP (χ^2 =2.003; df=2; *p*=0.157) (Table 8).

In the HP, 13% (*n*=15) of size 1 mammals are burnt with 8% (*n*=9) displaying anthropogenic marks (Table 8). Only three identified small mammals were noted in the sample with one burnt and one displaying cut marks. For all size classes in the HP, only two specimens display percussion marks (4%) on low utility specimens. In the MSA III, 19% (*n*=20) of size 1 mammals display burning modification. For identified small mammals (all of these identified as hyrax), 22.6% (*n*=7) are burnt. Few of these specimens show cut or percussion marks (8.5%; *n*=9) with only two cut marks (6.5%) and one percussion mark (3.2%) recorded (Table 8). Across all size classes in MSA III, there is no significant difference between anthropogenic marks on low utility bones (8%; *n*=5) and high utility bones (20%; *n*=11) (χ^2 =3.261; df=1; *p*=0.071).

6 Discussion

6.1 Terrestrial ecology

Generally, the region surrounding KRM had a fairly stable environment over the Late Pleistocene (Klein, 1976; Reynard and Wurz, 2020). However, the data presented here show evidence of environmental changes that may have had significant effects on regional ecology. Dietary categories and functional herbivore groups suggest three relatively distinct habitat clusters through the KRM sequence (Figure 3).

The first phase (group 1) corresponds to the MSA I with faunal data indicating a particularly significant difference between the MSA I and MSA II environments. Ungulate diversity indices are significantly higher in the MSA I compared to other phases with significantly more grazers here compared to the MSA II (Reynard and Wurz, 2020). Micromammal data also suggest that the MSA I was associated with a mosaic of grassland, fynbos and forested environs. Grassland-indicator species such as Soricidae and xeric four striped grass rats are relatively more common in the MSA I than MSA II Lower implying an MSA I environment dryer than the MSA II Lower (Nel et al., 2018). Analyses of lithic data also indicate that MSA I lithic end-products are generally significantly different to those in the preceding MSA II lower layers (Wurz et al., 2003).

The second ecological phase (group 2) comprises the MSA II layers. This is the largest recovered sample at KRM encompassing a palimpsest of deposits likely corresponding to MIS 5d-b. Here, browsers are the most common taxa suggesting a more closed environment (Figure 2B) corresponding to browse-dominated environs at the c. 100 ka layers at other MSA sites

TABLE 8 Anthropogenic marks on small mammal remains and low utility elements. Burn = burnt bone, PM = percussion marks, CM = cut marks, Anthro = anthropogenic marks (cut and/or percussion marks per specimen). 'Small mammals' are all specimens identified to size 1 and smaller. 'Small mammal ID' are identified small mammals such as hyrax, Cape dune mole rat and porcupine. Low utility elements = phalanges, innominate and mandibles.

Small mammals

Layers	N	Burn	PM	CM	Anthro
MSA III	106	20 (18.9)	5 (4.7)	5 (4.7)	5 (4.7)
HP	114	15 (13.2)	6 (5.3)	4 (3.5)	9 (7.9)
MSA II Lower	211	85 (40.3)	21 (10.0)	20 (9.5)	36 (17.1)

Small mammal ID

Layers	N	Burn	PM	CM	Anthro
MSA III	31	7 (22.6)	1 (3.2)	2 (6.5)	3 (9.7)
HP	3	1 (33.3)	0	1 (33.3)	1 (33.3)
MSA II Lower	37	9 (24.3)	0	1 (2.7)	1 (2.7)

Low utility elements (all size classes)

Layers	N	PM
MSA III	60	5 (8.3)
HP	57	2 (3.5)
MSA II L	59	6 (10.2)

such as Blombos and Ysterfontein (Avery et al., 2008; Badenhorst et al., 2016; Niespolo et al., 2021). Ungulate diversity indices, such as species richness and Fisher's alpha, are lowest in this phase (Reynard and Wurz, 2020). This may be linked to the MSA II being dominated by browse, with a wetter environment than currently and a mean annual precipitation above 750 mm/year (Cowling et al., 2020). The southern African vlei rat (*Otomys irroratus*), a species often occurring in Afromontane forests, also increases significantly from MSA I to MSA II (Nel et al., 2018). Wetter, more closed environs are often associated with lower herbivore biomass (Olff et al., 2002; Faith J. T., 2013b), which could explain the lower ungulate diversity. Lithic data also indicate that the MSA II layers are closely aligned, and both these phases show more connection with each other than the MSA I (Wurz et al., 2003).

The third phase (group 3) encompasses the HP and MSA III in the upper layers. The HP and MSA III are usually associated with MIS 4 and 3, respectively (Reynard and Wurz, 2020). MIS 4 is a glacial period while the MIS 3 is variable interstadial phase linked to cooler periods with warmer oscillations (EPICA Community Members, 2004). The increase in grazer abundance in the HP from the browser dominated MSA II layers reflects a noticeable shift in terrestrial environment, likely linked to the advent of MIS 4. Other sites dated to MIS 4 such as Klipdrift Shelter and Die Kelders also show a significant increase in grazing herbivores (Klein and Cruz-Uribe, 2000; Reynard et al., 2016). The prevalence of long-horned ('giant') buffalo is indicative of the persistence of open, grassland-dominated environments in the MSA III. Klein (1976) also noted the presence of black wildebeest in this layer—some of the few examples of this species in the southern Cape at this time, which aligns with a more open environment. This is supported by the dominance of grass-indicator micromammals such as golden moles (*Amblysomus hottentotus*) (Nel et al., 2018).

6.2 Coastal ecology

Changes in the coastal environment may be linked to fluctuating shorelines off KRM. The continued presence of marine taxa such as shellfish and seal throughout the KRM sequence indicates that the site remained relatively close to the shoreline through much of the Late Pleistocene. However, the effects of glacial/interglacial-induced marine regressions combined with local offshore bathymetry meant that the site may have been over 30 km away from the coast during intense glacial periods (Dor, 2017). KRM would have been part of the eastern edge of the Palaeo-Agulhas Plain during glacial phases. This vast coastal plain would have encompassed diverse habitats with a narrow band of the shoreline dominated by fynbos vegetation, and more grasslands further inland (Marean et al., 2020). The significantly inverse correlation between the proportions of *Raphicerus* and grazers suggests a dominance of fynbos-indicator species when shorelines were close, with grassland-indicator species more prevalent during regression phases (Compton, 2011; Cowling et al., 2020). Reynard and Wurz (2020) have previously argued that, given new U-Th dates of tufa in the MSA II Lower deposits, the basal layers of MSA I may well date to the transition between MIS 5e and 6. Large herbivore data from multiple analyses of cave 1, 1A and 1B show a significant abundance of grazers in this period, concordant with MIS 6 sites such Pinnacle Point 30 (Klein, 1976; Rector and Reed, 2010; Van Pletzen-Vos et al., 2019; Ezmeiro, 2022). However, molluscan data indicate that this phase was likely deposited during an interglacial period (Langejans et al., 2017; Loftus et al., 2017). Furthermore, the D sample from MSA I is quite small so it is important not to overestimate statistically significant trends in this phase. Refined dates from these layers are therefore critical to establish the provenance of these chronologies.

Shellfish data are a particularly useful means of inferring coastal environments such as shore topography and sea surface temperatures (SST) (Kilburn and Rippey, 1982). KRM is located within the Algoa Marine Province, a marine biogeographical zone influenced by the relatively warm Agulhas current flowing south from the Indian Ocean (Kilburn and Tankard, 1975; Sink et al., 2005). Brown mussels (*Perna perna*) are the most prevalent species at the site (Thackeray, 1988). Virtually all the large shellfish specimens identified in the MSA I layers require a rocky shore environment, and are indicative of relatively warm SSTs (Langejans et al., 2017). This would be consistent with a closer shoreline and interglacial period associated with MIS 5e. Although slightly cooler than the MSA I, SSTs may not have varied significantly throughout MSA II (Loftus et al., 2017). Using Thackeray's (1988) data, Loftus et al. (2017) argue that the relative stability of SST during MIS 5 at KRM suggests that these layers were generally deposited during interstadial periods (but see Brenner et al., 2022; Wurz et al., 2022). This may be associated with a short-lived sea-level stillstand at c.108 ka that is possibly linked to extensive dune deposition at c. 110 ka (Cawthra et al., 2018). More recent data from Brenner et al. (2022) show that, while *Perna perna* still dominate (%MNI= 39), alikreukel (*Turbo sarmaticus*) become almost equally common in the MSA II Lower (%MNI=29). Wurz et al. (2022) also indicate that opercula and the sizes of alikreukel are noticeably smaller in the MSA II Lower layers. Taken together, this could suggests a change in coastal ecology or foraging strategies in this phase. Shellfish density appears to drop significantly from the MSA II layers to the HP, suggesting a relatively distant shoreline from the site during MIS 4. Interestingly, species linked to warm waters are slightly more common in this period than in the preceding MSA II deposits—seemingly inconsistent with expected cooler, glacial MIS 4 conditions (Langejans et al., 2012, 2017). Compared to other layers, more shellfish from the MSA III prefer a sandy/muddy environment and indicator species suggest cooler SST (Langejans et al., 2017). This conforms to extensive marine regressions at this time.

Unlike shellfish, seal remains are a more complex proxy for shoreline distance since their occurrence along the coast would be linked to seal ecology, taphonomy and human transport decisions (Marean, 1986; Dusseldorp and Langejans, 2013). Most of the recovered seal remains are from the earliest HP layers, which may have been closer to the coast than the later periods (Klein, 1976; Reynard and Wurz, 2020). The abundance of seal remains in the HP are in stark contrast to the lack of shellfish in most HP layers. Seals also make up between 34% and 10% of identified remains from the various phases in the S-W sample (Marean, 1986). In the S-W sample, seal mortality profiles show a mixture of juvenile and adults suggesting that young seals were not necessary targeted at this time (Klein and Cruz-Uribe, 1996). However, in the taphonomic sample, almost 40% of the remains in the HP (36.8%; *n*= 16) and three out of the five specimens measurable in the MSA II Lower are juveniles (60%), with no juveniles identified in MSA III deposits from. This does imply that seasonality may have been a factor in coastal visits at KRM but research on seal seasonality is still ongoing (Richardson et al., in prep.).

The prevalence of species such as reedbuck, otter, *Kobus* spp. and hippo shows that wetlands would have been a prominent aspect of the Late Pleistocene habitat near KRM. Studies of the shoreline bathymetry shows undersea terraces and a prominent palaeo dune cordon off the coast of KRM (Van Andel, 1989; De Wet and Compton, 2021). This would have likely resulted in lagoons beyond the mouth of the Klasies River when sea levels regressed (Singer and Wymer, 1982; Van Andel, 1989). Wetland-linked species are proportionally the most common in the MSA I phase which suggest the presence of lagoons, vleis or floodplains at that time. Wetland-linked species are also common in the MSA III. The HP and MSA III also yield more sandy-beach and lagoon molluscan species (Langejans et al., 2017) which suggest that wetlands and/or lagoons played in important role in the ecology of the region then. The data suggest that wetland formations were more prevalent when shorelines receded (which again pose interesting questions about the nature of the glacial/interglacial positioning of the MSA I phase). One scenario is that the undersea terraces and dune cordon off the coast of KRM would have functioned as natural breakwater barriers aiding the formation of lagoons and attracting wetland-linked fauna apparent in these layers.

6.3 Taphonomy and occupational intensity

The taphonomic analyses reveal some interesting occupational trends. Tooth marks on bone are substantial throughout the sequence, showing that carnivore activity was always common at the site and that KRM was never continuously occupied by people. It is possible that the pervasiveness of carnivore activity, in especially the MSA III and MSA II Lower, may have obscured anthropogenic marks in these layers, but the fact that anthropogenic marks are higher in these layers suggests otherwise. Human/carnivore accumulation patterns indicate that human accumulation was more prevalent in the MSA II and HP, with carnivore ravaging a dominant feature of the MSA III (Table 5). Faunal density, anthropogenic BSM and transverse fracture patterns indicate higher occupational intensity during the MSA II Lower (although density values may have been affected by sediment compaction and depositional rates (Jerardino, 2016b)). The HP appears to be the phase least affected by carnivore activity suggesting more intensified human occupations in the HP layers analysed (Table 5). Other taphonomic proxies for occupational intensity such as trampling marks and burning (Reynard 2022) are relatively common in the MSA II Lower and exceptionally abundant in the HP (Table 7; Figure 6). By the MSA III, these marks become less common. Generally then, the HP—and particularly the MSA II Lower—show evidence for the most intensely occupied phases.

Interestingly, BSM associated with butchery are not as prevalent in the HP compared to other layers. Burnt bone is abundant in the HP and while burning often damages the cortical surfaces of bone making it problematic to identify BSM, cut marks (1.5%; *n*=19) and percussion marks (4.8%; *n*=60) are even *less* common in the unburnt sample. The lack of butchery marks may signify a change in subsistence behaviour then which will be discussed later. It must be noted that studies of modern Central African foragers show that butchery marks are not associated with intensification (Lupo et al., 2013), so cut mark data may be problematic in this regard. The MSA III displays a different taphonomic signature to the other layers. Small fauna are very prevalent in this layer but over 70% display tooth marks. Given the abundance of carnivore marks and gastric-etched bone, the MSA III was likely a low occupational phase. The site was probably often used as a carnivore or raptor den.

Although occupational intensity appears high in the MSA II Lower, there is also good evidence for significant carnivore contributions to this assemblage. This is the only period where large mammal human/carnivore proportions are below 50% (Table 5). The shaft circumference of large mammals are also significantly more complete in the MSA II (Table 7). This could mean that large carnivores were using the site as a den at this time; however, acid-etched bone is not common in this phase (Table 7). Micro-morphological analyses also show that occupational hiatuses occurred in this phase (Wurz et al., 2022), which may be apparent as periods of carnivore activity. It is likely then that, during these hiatuses in the MSA II, carnivores may have ravaged the remains of large herbivores. Binford (1984) interpreted the prevalence of tooth marks at KRM as evidence that scavenging was the dominant subsistence strategy. Yet carnivore ravaging of discarded bone is a common form of bone attrition at MSA sites (Marean et al., 1992). A more detailed discussion of subsistence behaviour in the MSA II is outside the scope of this paper and will be addressed in a forthcoming study (Reynard et al., in prep.). Suffice to say that the disparate patterns of large herbivore skeletal patterns between the MSA II and upper layers may indicate differential subsistence patterns between the earlier and later KRM sequence.

6.4 Is it intensification yet?

Evidence for subsistence intensification at KRM reveals some interesting patterns. Outside of the MSA III (where most small mammals were likely accumulated by carnivores or raptors), identified small mammals are not particularly common. Indeed, in the HP they are rare, making up less than 5% of the assemblage. The MSA II Lower yields a moderate amount of hyrax and small mammals, but relatively few of these species show evidence of human processing. Size 1 bovid processing is significantly higher in the MSA II Lower compared to the MSA III and HP (Table 8). Small bovids are not especially common in the MSA II Lower (Table 3) so higher frequencies of processed bone are probably not a by-product of larger sample sizes. Therefore this does suggest that, to a certain extent, people focused more on size 1 bovids in this phase.

Other evidence of intensification also occurs in the MSA II Lower. Juveniles are significantly more common here and low-ranked elements such as phalanges and pelves are significantly more likely to have been processed. The lack of large mammal crania suggests increasing transport distances or extensive foraging ranges during the MSA II Lower. In fact, while human-processed small fauna and low-utility element frequencies are low throughout the sequence, they appear to pulse in the MSA II Lower. High shellfish densities and the occurrence of fish and bird remains also suggest an expanded diet breadth for Klasies people then (Von den Driesch, 2004; Van Niekerk, 2011; Reynard et al., in prep.). Wurz et al. (2022) reports smaller sizes of *Turbo sarmaticus* opercula from the MSA II Lower layers which is often used as evidence for more intensive shellfish harvesting as large species become more depleted (Steele and Klein, 2009). Furthermore, micro-morphological data show intensive shell middening in the MSA II (Wurz, et al., 2022) indicating more intensified site-use activities at this time. Overall, the taphonomic and faunal data show more evidence of intensified resource extraction in the MSA II Lower than in other layers.

An important question is whether these data signify decline foraging efficiency or changing environmental conditions. While shellfish exploitation was clearly a significant subsistence strategy during the MSA II, by far the dominant species were *Turbo* and *Perna*, both high-ranked mollusc that could be accessed relatively easily (Langejans et al., 2012). If over-exploitation was a factor then we would expect more lower-ranked shellfish dominating the molluscan assemblage. However, *Perna* is a relatively low-ranked species and only rises in rank because it was mass collected and mass processed (Langejans et al., 2012). The abundance of both *Turbo* and *Perna* over lower-ranked species may be because these species are more likely to be transported over greater distances than other shellfish (Dusseldorp and Langejans, 2013).

Likewise, given its ubiquity in the region, we should see more evidence of the exploitation of small fauna such hyrax in the sample. However, any evidence of human processing on small fauna would be rare (Armstrong, 2016) since tools are not needed to process these taxa (Henshilwood, 1997). In any case, the sample from which hyrax were taphonomically analysed is significantly smaller than the larger D sample, so it is possible further analyses of larger samples could reveal more evidence of small fauna exploitation. Interestingly, while ungulate diversity is generally low, overall taxonomic diversity is quite high in the MSA II Lower with richness (NTAXA) and the richness index (NTAXA/logNISP) especially high (Reynard and Wurz, 2020). This suggests that as encounter rates with large herbivores decreased, the focus may have shifted to small game and non-ungulates. Dusseldorp and Langejans (2015) propose that small nocturnal animals began to be targeted in MIS 5 in the southern Cape, which, they argue, could be indicative of trapping and snaring at this time. Blue duiker (*Philantomba monticola*) are extraordinarily abundant in the c. 71 and c. 77 ka layers at Sibudu Cave—accounting for over 40% of the faunal assemblage in some layers—which suggests that remote capture may have been used in their procurement in the MIS 5 period there (Clark, 2019). This may explain the abundance of size 1 bovid processing in the MSA II Lower, with technology playing an important role in prey selection. Size 1 bovids are also generally associated with bushier habitats so the combined impact of environmental conditions and technology may have had a significant effect on prey selection.

If this indeed represents intensification, the question remains as to whether demographic pressure during MIS 5 may have contributed to this possible decline in foraging efficiency during MSA II. Bayesian skyline plots by Rito et al. (2019), p. 3 show no significant shifts in population expansions in southern Africa until between c. 20 and 15 ka. The demographic shift during the terminal Pleistocene may be linked to more evidence of intensification in the LSA compared to the MSA (Klein and Cruz-Uribe, 1996; Klein, 2000; Steele and Klein, 2009). The systematic, more intense resource extraction apparent in the Holocene may differ from the patterns seen during the MSA II at KRM because intensification in the LSA may have been associated with large-scale, regional demographic expansion. For example, the significantly smaller shellfish and tortoise sizes in the LSA compared to the MSA layers at sites that transcend both periods such as KRM, Blombos Cave and Die Kelders has been argued to suggest more intensive harvesting by LSA people (Henshilwood et al., 2001; Steele and Klein, 2009). In contrast, evidence of intensification during MSA II Lower may be linked to either environmental-induced stress, small-scale local demographic changes, or a combination of both. Generally, the relatively small sample sizes makes it challenging to unpack these taphonomic patterns. More taphonomic analyses of comparative samples, particularly from the MSA Upper and the MSA I, are needed to explore these issues further.

6.5 Why no intensification in the Howiesons Poort?

Trampling and burning data suggests that occupations may have been relatively intense in the HP at KRM, yet there is little indication of intensification here. While small bovids may have been targeted in the MSA II, this does not appear to be the case in the HP. Small mammals and size 1 bovids seemed to be a focus of prey selection at other HP sites such as Sibudu, Klipdrift Shelter and Die Kelders (Klein and Cruz-Uribe, 2000; Clark, 2017; Reynard and Henshilwood, 2017). Yet, in the HP at KRM, small mammals are relatively rare, and size 1 bovids are not particularly common. This is all the more surprising since there is good evidence that bow hunting occurred in the HP at KRM (Bradfield et al., 2020). The cognitive capacity associated with bow hunting (knowledge of remote capture), and the technology (elastic twine and high-tensile string), are closely linked to trapping and snaring, so it is reasonable to assume that people at that time would have had the know-how and ability to construct snares (Wadley, 2010). It may be that foraging strategies may not have been affected by resource depression here, with little need for a broadening of diet breadth. The low frequencies of anthropogenic marks during the HP may, in fact, reflect this decrease in hunting pressure which may be linked to changing settlement patterns at this time. Other studies have shown some evidence of increased social connectivity during the HP (Douze et al., 2018; Way et al., 2022) possibly linked to demographic expansion (Reynard et al., 2016; Rito et al., 2019; Archer, 2021), so the lack of evidence of intensification may suggest that declining foraging efficiency in the HP and occupational intensity are not necessary linked.

It is also possible that the relatively scant evidence of faunal processing during the HP may be linked to increased plant consumption. The Cape south coast is rich in geophytes and plants with underground storage organs, which would have been a key source of carbohydrates (De Vynck J. C. et al., 2016b). Micro-morphological analyses show that carbohydrate-rich plants were cooked at KRM at c. 120 ka and again in the HP (Larbey et al., 2019). Deacon (1993, p. 89) argued that the numerous small, circular hearths at KRM may contain burnt plant residues, and suggested that people in the Late Pleistocene may have 'farmed' geophytes by burning fields. It is possible that this type of strategy may have been more effective in grassier periods such as during the HP.

6.6 Lithic data

Non-faunal data such as lithics may also highlight occupational and mobility trends at KRM. Lithic density has been used to indicate increased occupational intensity (Shiffer, 1987; Deacon, 1984; Brenner et al., 2022), and the abundance of 'non-local' raw material is sometimes used to infer greater foraging ranges (e.g., Singer and Wymer, 1982). Barton and Riel-Salvatore (Barton et al., 1999; Riel-Salvatore and Barton, 2004; Barton and Riel-Salvatore, 2014) have proposed that higher frequencies of retouched lithics may signify more resource stress since retouch would conserve limited lithic resources by extending the life of a stone tool (Riel-Salvatore and Barton, 2004). Correlations between retouch and lithic density, they argue, may be associated with residential or logistical mobility (Barton and Riel-Salvatore, 2014).

Lithic data generally show similar patterns to the faunal data. Both lithic and faunal density is highest in the MSA II Lower (Table 6). Retouch is relatively rare at KRM with only 0.9% (*n*=22) of pieces retouched in the MSA II Lower. This is comparable to Blombos Cave and Pinnacle Point 13B where the overall percentages of retouch there are generally between 0.2 and 2% (Henshilwood et al., 2001; Thompson and Marean, 2008; Reynard and Henshilwood, 2018). Frequencies of retouch in the HP at KRM (2.6%; *n*=61) are similar to those at other HP deposits such as Klipdrift Shelter (Henshilwood et al., 2014).

Informal retouch is generally slightly higher in the MSA II layers, with 13% (*n*=311) of pieces in the MSA II Lower notched, compared to 0.5% (*n*=11) and 0.9% (*n*=7) in the HP and MSA III, respectively. The relative abundance of notched lithics in the MSA II Lower suggests that tools were often re-used and may imply more lithic scarcity at this time. Non-local raw material (i.e., silcrete) is significantly more common in the HP compared to other periods at KRM (Wurz, 2000). However, silcrete was likely sourced from nearby beach cobbles and local bedrock which were probably relatively close to the site during marine regressions (Van Andel, 1989; Minichillo, 2006), so its prevalence may be linked to the manufacture of microlithic and backed tools in general (Will and Mackay, 2017). Overall, the lithic data support other research (e.g., Douze et al., 2018; Way et al., 2022) suggesting more extensive foraging ranges during the HP.

6.7 Ecology, taphonomy and occupations

Occupational intensity may be linked to the regional environment. Size 1 bovids such as *Raphicerus* are ubiquitous in fynbos habitats and a key reason these bovid were targeted in the MSA II Lower may relate the predominance of fynbos vegetation then. However, small bovids were not only selected. As with all phases at KRM—and most MSA fauna (e.g., Thompson, 2010; Reynard and Henshilwood, 2019)—evidence of anthropogenic processing is more common on larger herbivores and, being high-ranked, these were preferentially targeted. Nevertheless, it again highlights the complexity of disentangling demographic and environmental factors in assessing resource intensification. This is not to say that hunting pressure was not a factor in increased small bovid exploitation here. Other data also show an increase in extraction of food resources at this time, and there is good evidence of higher occupations during the MSA II Lower.

The upper members (the HP and MSA III) display quite different occupational histories. The HP shows some conflicting occupational signals. On the one hand, the lack of anthropogenically-marked bone, the relatively low faunal densities and little-to-no evidence of over-hunting does not correspond with intense occupations. On the other hand, the high frequencies of burnt and trampled bone, and the relatively low incidence of tooth marks suggest that human activities were relatively intense in the HP. Other evidence such as the abundance of hearths (likely linked to high frequencies of burnt bone), high artefact densities and the sheer scale of HP anthropogenic deposits also imply more intense occupations (Wurz, 1997; Deacon and Wurz, 2005). Yet, the HP sequence has an extensive age range (Feathers, 2002; Jacobs and Roberts, 2017) consist of alternating dark, highly carbonised layers—representing higher occupational intensity—and light, sandy geogenic strata, probably reflecting less intense occupations (Singer and Wymer, 1982; Deacon and Geleijnse, 1988). The HP taphonomy sample reflects a time-averaged palimpsest and, in all likelihood, includes intensively occupied periods interspersed with occupational hiatuses (Achieng, 2019).

There is good evidence the MSA III was a less intense occupational phase. Besides the taphonomic data presented here, Singer and Wymer (1982, p. 21) observed that Layers 1 to 9—corresponding to MSA III—consists of mostly ‘sandy scree’, with ‘laminated ash’ occurring in the lower layers with some carbonised partings occurring throughout. This suggests that the MSA III was probably more intensely occupied in the earlier periods indicating gradually decreasing occupational intensity from the HP through the MSA III. It must also be noted that data from these phases are combined palimpsests made up of multiple, often thin, layers very likely representing variable occupational events. Evidence of increased occupational intensity in any phase is a time-averaging of numerous occupations over thousands of years, and does not necessary correspond to larger populations or increased demographic density. It may relate to more frequent occupational events or changes in mobility patterns (Fisher et al., 2010; Haaland et al., 2021). Furthermore, given that cave 1 and 1A had dissimilar taphonomic histories (Wurz et al., 2022), it can also be expected that site formation processes played a significant role in these deposits. Variations in depositional rates, formation events and water and aeolian processes may have affected the more exposed deposits in cave 1A (MSA III and HP), and the more sheltered assemblage in cave 1 (MSA II) differently (Morrissey et al., 2022). Given its importance and the fact that these issues exceed the scope of this paper, site formation processes will be addressed in a forthcoming study.

Although the HP and MSA III reflect different taphonomic signatures, they appear to share similar habitats (Figures 2, 3). Both periods seem to be marked by major marine regressions. In fact, the differences in skeletal part profiles between these layers and the MSA II may be linked to transport decisions resulting from shifting shorelines. Furthermore, more intensive occupations are often linked to a site’s proximity to the coast (Gravel-Miguel et al., 2022; Reynard, 2022), which may be the case at KRM. More intense occupations are evident in the early HP, for example, when the coast was likely closer, while the later HP shows more evidence of occupational hiatuses. This may explain the conflicting taphonomic signals for occupations in this phase since the palimpsests of deposits would reflect evidence of both more and less intense occupations. By all accounts, the shoreline during the MSA III phase was never close, hence its association with less intense occupations.

Occupational intensity could have been impacted by changing environmental conditions and available resources. The eastern regions of the southern Cape near KRM probably would not have been as affected by marine regressions as the more central regions near Blombos (Van Andel, 1989; Cawthra et al., 2020). Nevertheless, shifting land availability resulting from stadial/interstadial fluctuations would have had a destabilising effect on occupations at KRM as population densities change and the ecology of the area is disrupted (Marean et al., 2020). Even if the most significant effects of the Palaeo-Algulhas Plain contractions were further to the west, this would have still had a substantial impact on human landscape use and herbivore communities further east near KRM (Compton, 2011; Reynard and Wurz, 2020). Another factor could be changing precipitation. Processional forcing of rainfall regimes may be an important driver of environmental change in the south-eastern Cape (Partridge et al., 1997; Dupont et al., 2022) and this may have affected subsistence strategies and resource availability. The smaller shellfish and shifting species abundance reported by Wurz et al. (2022) may not reflect periods of anthropogenic intensification, but may rather point to environmental instability at this time. Any declining foraging efficiency during the MSA II Lower phase may be linked to environmentally-induced resource stress. In contrast, marine transgressions and more land availability during the MSA III and HP may correspond to lower population densities, with less evidence of intensification or increases in diet breadth. This is not to suggest that foraging groups were isolated and restricted within the southern coastal plain, rather that fluctuating shorelines, disrupted herbivore migrations and/or changing rainfall regimes together with an expected focus of occupations at the coast, may explain lower occupational intensity during the later HP and MSA III at KRM.

7 Conclusion

In this paper, taxonomic and taphonomic data were used to explore trends in occupational intensity during the Late Pleistocene at KRM. This study is an example of how zooarchaeological analyses incorporating taphonomic data can be used to examine the links between settlement patterns and the environment at long-sequence sites. Ungulate dietary preference and functional herbivore groups suggest three relatively distinct habitat clusters through the KRM sequence: the MSA I, the MSA II, and the HP and MSA III. Marine resources remain important at KRM throughout the sequence but shellfish contribution appears to diminish from the MSA II to the HP, probably linked to marine regressions. The MSA I shows a significantly different ecological pattern to the other layers. This may be linked to glacial/interglacial changes but it could also be a result of the small sample of specimens in the Deacon sample.

This is the first study to report on taphonomic data from the Deacon assemblage, and from the HP and MSA III periods at KRM. Various taphonomic indicators was used to explore occupational intensity and subsistence intensification in the MSA II Lower, the HP and the MSA III at KRM. Similar to the environmental data, the taphonomy suggest different taphonomic histories between the MSA II, and the HP and MSA III. While humans were the dominant bone accumulator in most layers, carnivore activity was common in all phases indicating that human occupations were never continuous and suggesting abundant occupational hiatuses in the sequence. This is especially evident in the MSA III where most small mammals were likely accumulated by non-humans. Faunal density, increased frequencies of transverse fractures and BSM data indicate that the MSA II Lower was the most intensely occupied period, with trampling marks and burning also suggesting intensive occupations in the early HP. This appears to be supported by other, non-faunal data such as lithic density and micro-morphological analyses (Wurz et al., 2022). Density, bone fracture pattern and BSM data show less intense occupations in the MSA III.

Subsistence intensification is more apparent in the MSA II Lower. There is more evidence of the exploitation of low-ranked fauna in this period. For example, size 1 mammals are significantly more processed in this phase than in any other, and mortality data indicate significantly more juveniles here than the other layers. Low-ranked elements such as phalanges, pelves and mandibles show more evidence of marrow extraction here as well. Large mammal cranial remains are significantly rarer in this phase, suggesting more extensive foraging ranges at this time. It is important to note that intensification in the Late Pleistocene was probably not as systematic and extensive as later periods of intensification in the LSA. Declining foraging efficiency in the MSA II Lower may be linked to changing environmental conditions and/or fluctuating available land. That said, the fact that intensive occupations and declining foraging efficiency are both prevalent in the MSA II Lower suggests that these two phenomena may be linked.

Lower occupational intensity during the later HP and MSA III appears to be associated with marine regressions during MIS 4 and 3. The data presented here and other studies (e.g., Villa et al., 2010; Pearson, 2021; Wurz et al., 2022) show that the transition from the HP to MSA III was not as abrupt as the combined data may suggest with a more gradual drop in occupational events through time, possibly as coastlines regressed. While changing depositional rates and other site formation processes linked to environmental change may have contributed to this, it is fair to assume that shifting occupational intensities can be associated with fluctuating population densities as shorelines migrate. This is supported by other research that indicates that occupations in coastal regions are more intense as shorelines become closer (e.g., Reynard, 2022; Gravel-Miguel et al., 2022). In the southern Cape, there may be a particularly close relationship between occupational intensity and marine regressions, and it is reasonable to suggest that contracting landscapes could have resulted in increased population densities during glacial periods. In contrast, marine transgression may have led to an increase in available land, lower population densities and less resource stress.

This study shows that, while occupational intensity may be associated with declining foraging efficiency in the MSA II Lower, this is not necessarily the case in all periods at KRM, or at different sites. The early HP at KRM, for example, although displaying good evidence of increased occupational intensity shows no indication of intensification. However, more data is needed to explore these factors. It is important to note that these are relative, site-specific datasets, and the evidence presented here of declining foraging efficiency in the MSA II is only in relation to the MSA III and HP at KRM. This study only reports on preliminary taphonomic analyses. Larger samples need to be taphonomically analysed and the MSA I in particular should be further studied.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors on request, without undue reservation.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

Funding

JR is funded by a South African Department of Science and Technology (DST) National Research Foundation (NRF), Thuthuka grant (grant # 129689). Any opinion, finding, conclusion or recommendation expressed in this article is that of the author, and the NRF does not accept any liability in this regard.

Acknowledgments

I thank Sarah Wurz, Amy Lap, Alexandra Pearson and Pam Achieng for permission to use their data. I am grateful to Manuel Will for inviting me to contribute to the Living on the Edge volume. I also thank the anonymous reviewers whose insightful comments improved this paper significantly.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer GLD declared a past collaboration with the author to the handling editor.

Publisher's note

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frontiers | Frontiers in Earth Science

TYPE Original Research
PUBLISHED 10 March 2023
DOI 10.3389/feart.2023.1064197

Indigenous stewardship of coastal resources in native California

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SPECIALTY SECTION
This article was submitted to Quaternary Science, Geomorphology and Paleoenvironment,
a section of the journal
Frontiers in Earth Science

RECEIVED 07 October 2022
ACCEPTED 27 February 2023
PUBLISHED 10 March 2023

CITATION
Sanchez GM, Grone M and Apodaca A (2023), Indigenous stewardship of coastal resources in native California.
Front. Earth Sci. 11:1064197.
doi: 10.3389/feart.2023.1064197

Indigenous people have profoundly influenced terrestrial and marine ecosystems by modifying coastal habitats to increase the productivity of target species and altering local biotas through their harvesting practices. In some cases, these actions led to local resource depression, while in other instances, Indigenous people engaged with terrestrial and marine resources in sustainable ways, increasing the resilience of ecosystems. In this paper, we interrogate human-environmental relationships that span the last ~7,000 years of Indigenous engagement with coastal resources on the central California coast. Through a historical ecological framework, we assess how Indigenous peoples interacted with terrestrial and marine ecosystems differently across space and through time. In the Middle Holocene, the region's archaeology is typified by mobile populations using diverse terrestrial and marine resources. By the Late Holocene, Indigenous peoples intensified their economies towards a limited number of marine and terrestrial species. During this time, Indigenous people initiated sustained fire management practices that created habitat mosaics still reflected in the contemporary landscape. In the Late Holocene, people also developed resource harvesting strategies for California mussels and forage fishes geared towards long-term productivity.

KEYWORDS

Indigenous archaeology, historical ecology, eco-archaeology, zooarchaeology, paleoethnobotany, selective harvesting, habitat modification

1 Introduction

Indigenous people in California have maintained long-term relationships with terrestrial and marine resources that have persisted since time immemorial. Coastal landscapes and marine resources feature prominently in Native Californian cultural lifeways, serving dietary, symbolic, and ritual purposes (Luby and Gruber, 1999; Gamble, 2017; Lightfoot et al., 2017). Archaeological evidence from the California coast provides a record of ~12,000 years of human relationships with fauna, flora, algae, and a variety of abiotic resources (Jones and Hildebrandt, 1990; Jones, 1991; Erlandson, 2007; Hildebrandt et al., 2009; Tushingham, 2009; Jones and Perry, 2012; Erlandson et al., 2015; Gill, 2015; Tushingham et al., 2016; Ainis et al., 2019; Gill et al., 2021; Lightfoot et al., 2021; Rick et al., 2022). Given the time depth of Indigenous peoples' engagement with coastal resources, the cultural diversity of Native California, and differences in the socio-political organization, researchers encounter significant variation in human-environmental relationships with coastal resources across space and through time. These differences also reflect the diversity of ecosystems and habitats that Indigenous peoples encountered and altered across the state. Indigenous connections to coastal landscapes persisted during three successive waves of European

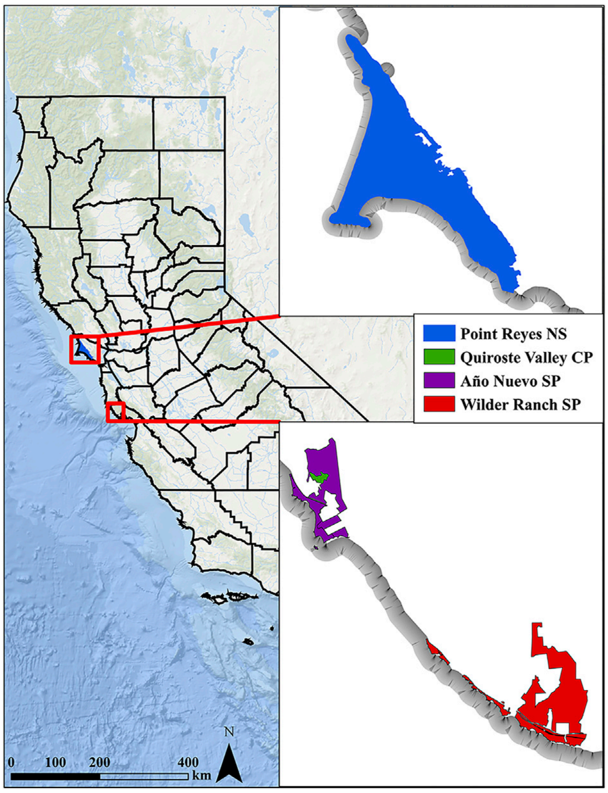

FIGURE 1
Overview of the central California coast with study areas discussed. Specific locations of the archaeological sites have been omitted to protect these sensitive cultural resources.

and Euro-American colonialism and continue in the present (Schneider, 2015; Schneider and Panich, 2019; Sigona et al., 2021).

Native Californian groups ranged from highly mobile populations to sedentary communities with inherited status and complex social organization (Lightfoot, 1993; Ames, 1994; Arnold, 1996; Rick et al., 2005; Lightfoot and Parrish, 2009; Arnold et al., 2016). Archaeological sites along the California coast also include complex mounded landscapes, such as those found on the Channel Islands and the San Francisco Bay Area (Lightfoot and Luby, 2012; Gamble, 2017). These archaeological sites provide evidence for a range of human-environmental interactions that suggest instances of local resource depression, while in others, evidence suggests that Indigenous people engaged with terrestrial and marine resources in sustainable ways, possibly increasing the resilience of coastal ecosystems (Broughton, 1994; Whitaker, 2009; Cuthrell et al., 2012; Cuthrell, 2013a; Broughton et al., 2015; Sanchez et al., 2018; Grone, 2020).

In this paper, we interrogate human-coastal relationships that span the last ~7,000 years of Indigenous engagement with coastal resources on the central California coast, from Point Reyes National Seashore to Monterey Bay, through a historical ecological framework to assess how Indigenous peoples interacted with terrestrial and marine resources differently across space and time (Figure 1). In the Middle Holocene, the region's archaeology is typified by mobile populations using diverse terrestrial and marine resources. Our findings suggest that by the Late Holocene, Indigenous peoples intensified their economies towards a limited number of marine and terrestrial species (See Bettinger et al., 2015 for this perspective broadly in California). By the Late Holocene, people developed resource harvesting strategies for California mussels and forage fishes geared towards long-term productivity through size-selective harvesting practices (Sanchez et al., 2018; Grone, 2020; Sanchez, 2020). In addition, during this time period, Native Californian tribes used fire to alter the successional stages of vegetation communities, with particular evidence of enhancement of coastal prairies (Lightfoot et al., 2021; Lightfoot et al., 2013; Cuthrell, 2013a). There is increasing evidence that Indigenous burning practices created habitat mosaics still reflected in the contemporary landscape (Kelly et al., 2020; Lake and Christianson, 2020; Lightfoot et al., 2021). However, Indigenous engagement with particular resources may have contributed to population declines and local extirpation in other instances. These examples highlight the complexity of human-environmental relationships across space and through time in Native California.

Along the Pacific Coast of North America, variation in human-environmental relationships have been documented in the archaeological record, both regionally and diachronically. This variation has contributed to ongoing debates regarding Indigenous engagement with coastal ecosystems. On a broad scale, these differences suggest various outcomes of Indigenous relationships with coastal resources, including, but not limited to, stewardship, management, epiphenomenal non-conservation, unsustainable harvesting, overharvesting or the tragedy of the commons, resource depression, and local extirpation and variation in topography, environment, among others (Broughton, 1999; Cannon and Burchell, 2009; Cuthrell, 2013a; Augustine and Dearden, 2014; Groesbeck et al., 2014; Jones and Codding, 2019; Grone, 2020; Sanchez, 2020; Lightfoot et al., 2021). Below we outline the theoretical and methodological implications that have contributed to these debates and offer possibilities for future strategies to contribute to this area of research.

1.1 California archaeology, evolutionary ecology, and human behavioral ecology

The field of California archaeology, especially the archaeology of ancient and pre-contact populations, is heavily influenced by evolutionary ecology (EE), human behavioral ecology (HBE), and the application of a diversity of optimization models linking human behaviors to expected material outcomes (Basgall, 1987; Beaton, 1991; Broughton, 1994; O'Connell, 1995; Wohlgemuth, 1996; Hildebrandt et al., 2009; Tushingham and Bettinger, 2013; Bettinger, 2015; Bettinger et al., 2015; Codding and Bird, 2015). Archaeologists working through these theoretical frameworks have significantly contributed to our understanding of California archaeology.

Drawing from evolutionary biology, behavior in EE is considered adaptive when it tracks environmental variability in ways that enhance an individual's inclusive fitness—or the propensity to survive and reproduce (Bird and O'Connell, 2006). In archaeology, EE and HBE are often associated with optimal foraging theory (OFT) and OFT models (Smith et al., 1983; Cronk, 1991; Winterhalder and Smith, 2000; Bird and O'Connell, 2006). These models attempt to predict behaviors in a range of hunter-gatherer societies. According to the theoretical assumptions of these models, maximizing behavior occurs under certain conditions because of Darwinian selection for strategies that maximize individual fitness (Smith et al., 1983).

As Douglas Bird and O'Connell (2006) note, the models are never tested. Instead, situation-specific assumptions or hypotheses are formulated to be tested against predictions. As Lee Cronk (1991) highlights, one advantage of working with simple models is that it is easy to see when people's behavior does not fit the theory or its expectations. These instances have received significant attention in archaeology as examples of social and symbolic behavior, such as feasting, that cannot be explained as serving solely dietary requirements (Hildebrandt et al., 2009). As Bruce Winterhalder and Smith (2000) note, EE models and predictions seek to capture essential features of an adaptive problem and neglect "ancillary variables" of concern in the more particularistic tradition of anthropology (see Gremillion et al., 2014).

Given the theoretical underpinnings and assumptions inherent in EE and HBE, researchers applying these models often consider immediate gains (i.e., immediate return economies) rather than long-term perspectives (i.e., delayed return economies) when considering human-environmental relationships, although exceptions exist (see Bettinger, 2006; Codding and Bird, 2015; Winterhalder and Kennett, 2009; Woodburn, 1980). Recent discussions of delayed return economies have focused almost exclusively on the transition from hunting-gathering economies to agriculture. While archaeologists applying HBE to agricultural societies offer some possibilities for economies and human agency that would provide long-term (i.e., agriculture) rather than immediate-return (i.e., foraging) decision-making, the same possibilities have not generally been extended to hunting, gathering, and fishing societies like those found in California.

In those instances where Indigenous cultivation of wild foods in California has been documented, the catalyst to these relationships may be "thought to result from intensified subsistence economies required by population pressure or a decline in the abundances of high-ranked prey taxa" (Whitaker, 2008, see also Anderson and Wohlgemuth, 2012 regarding the development of protoagriculture in California). Indigenous stewardship and/or management would suggest that Indigenous peoples engage with resources with long-term harvesting regimes rather than to meet immediate or short-term goals. These actions likely do not result from population pressure or resource depression alone. From a cursory review of the California archaeological literature, when possible sustainable human-environmental relationships are identified, these cases are often explained as epiphenomenal non-conservation, epiphenomenal conservation, epiphenomenal sustainable hunting, incipient aquaculture, pseudo-aquaculture, pseudo-cultivation, among others (Whitaker, 2008; Jones and Codding, 2019). Although archaeologists applying EE and HBE theories in California have represented a prominent approach in evaluating the diachronic interactions Native people had with ecosystems, there are other notable ecological and economic approaches outlined below.

1.2 Common-pool resources and the tragedy of the commons

As outlined by ecologist Garrett Hardin (1968), the tragedy of the commons is a theoretical perspective that suggests the inevitable outcome of shared common-pool resources, increasing human population, and individual maximization assumptions culminate in the eventual overexploitation of resources. The application of the tragedy of the commons in California archaeology has often occurred by proponents of EE and HBE, likely given the shared emphasis on rational and parsimonious behavior, individual maximization assumptions, and the primacy of population (Jones and Hildebrandt, 1995; Porcasi et al., 2000; Jones and Codding, 2019).

As economist Elinor Ostrom (2008) outlines, common-pool resources occur on such a scale that it is difficult, but not impossible, to define recognized users and exclude other users altogether. According to Ostrom (1990, 2008), common-pool resources can be managed by a diversity of institutions such as governments, privately, and by communities, or comanaged among these institutions. However, open-access or common-pool resources accessible for entry or harvest by anyone are likely to be overharvested and potentially destroyed (Ostrom, 2008).

Jones and Codding (2019) highlight that resource locales for California Indians were common-pool resources or finite, and when an individual extracts from this pool, this inevitably takes resources from another individual. For Jones and Codding (2019), this situation of the commons allows three trends to emerge from the archaeological record. The first is evidence of harvesting having a negligible or limited impact on the wild resource base and no clear indication of resource depression. The second is resources mediated by cultural, ceremonial, and practical reasoning about how and when to harvest (Butler, 1993; Butler and O'Connor, 2004; Thornton et al., 2015; Royle et al., 2018). The third example of common-pool harvesting trends is extinction and local extirpation (Morejohn, 1976; Jones et al., 2021; 2008; Grayson, 2008; Rick et al., 2012).

1.3 Indigenous archaeology, eco-archaeology, and Indigenous stewardship

In California archaeology, there has been a growing interest in Indigenous archaeology, collaborative archaeology, community-based participatory research, and community-engaged research protocols working in collaboration with Native Californian Tribes (Gonzalez et al., 2006; Lightfoot, 2008; Gonzalez, 2016; Sanchez et al., 2021). One outcome of the development and growth of Indigenous and collaborative archaeology in California is the advancement of eco-archaeological approaches.

Lightfoot et al. (2021) define eco-archaeology as a research approach that integrates multiple ecological and archaeological datasets to construct robust perspectives about human-environmental interactions. In contrast to the perspectives outlined in the sections above, Indigenous and collaborative archaeologists working through an eco-archaeological framework often conduct their research following the tenets of historical ecology. Historical ecology is an interdisciplinary field that traces

TABLE 1 Expectations and archaeological correlates of human-environmental relationships in Evolutionary Ecology, the Tragedy of the Commons, Historical Ecology, and Indigenous Stewardship.

Framework	Expectations	Archaeological correlates
Evolutionary Ecology/Human Behavioral Ecology/Optimal Foraging Theory (OFT) Models	• Models human foraging in terms of prey abundance, energy gained per item, and energy and time expended	• Changing relative abundances of taxa
	• High-return (high-caloric) resources will be selected for over lower return or low-ranked items	• Changes in the age/sex of fauna represented
	• High-ranked resources generally correlate with body size	• Shift in high-ranked to low-ranked taxa
		• Reduction in size of high value prey species through time
Tragedy of the Commons	• Shared common-pool resources, increasing human population, and individual maximization assumptions culminate in the eventual overexploitation of resources	• Evidence of overexploitation of resources
		• Shift in high-ranked to low-ranked taxa
		• Changes in the size of taxa such as shellfish
		• Reduction in vertebrate species size or relative abundance of plants and animals
Historical Ecology	• Societies impact environments in distinctive ways	
	• Human nature is indifferent to species diversity	
	• Human activity does not necessarily lead to environmental degradation or increasing biodiversity	
Indigenous Stewardship	• Resources can be sustainably stewarded through habitat enhancement and selective harvesting practices	• Evidence of habitat enhancement *via* ecosystem engineering (i.e., fire management practices)
	• Size selective harvesting practice geared towards maintaining demographic stability	• Shifts in the relative abundance of taxa
		• Alterations to the size or age of targeted species
		• Size classes of prey species represented in the archaeological record reflective of limited impact to population demography of targeted species
		• Evidence of economic intensification of specific taxa

the relationship between our species and the planet through multiple temporal and spatial scales—these relationships and human agency manifest in the landscape (Crumley, 1994; Balée, 1998; Balée, 2006; Crumley, 2007).

Historical ecology is uniquely positioned to interrogate Indigenous stewardship, given that its postulates do not assume that human activity inevitably increases nor degrades species abundance and diversity but instead posits that these issues must be interrogated using multiple independent datasets from a diversity of scientific approaches (Balée, 1998). Building from Fowler and Lepofsky's (2011) conceptualization of traditional resource and environmental management, we follow Lightfoot et al. (2021) in defining Indigenous stewardship "as the application of traditional ecological knowledge to maintain or enhance the abundance, diversity and/or availability of natural resources or ecosystems." Therefore, Indigenous stewardship is more closely reminiscent of discussions regarding resource management, but we use the term stewardship to reflect local Indigenous perspectives of these practices.

Building from the nuanced perspective of the spectrum of Native Californian engagement with diverse resources, we synthesize the current literature on Indigenous resource stewardship. Below we outline the theoretical and archaeological evidence for Indigenous stewardship of coastal prairies through fire management strategies and size-selective harvesting techniques applied to Pacific herring (*Clupea pallasii*) and California mussels (*Mytilus californianus*) spanning the last ~1,300 years.

1.4 Archaeological expectations

Based on the human behavioral ecology literature, if Native people were acting optimally to maximize net gains in their subsistence practices, we could expect that people would be focusing on the highest net return gain for their efforts (Table 1). These decisions might involve the prioritization of high-ranked plant and animal resources such as storable seed and other plant foods and large-bodied animals with the highest return rates. We recognize that scholars conducting research through this framework have also identified social factors in resource use such as prestige hunting (McGuire and Hildebrandt, 2005).

Expectations from the tragedy of the commons literature evaluate the relationship between shared common pool resources, population growth, and individual maximization assumptions. While models recognize that social structures may limit some harvesting of resources, especially those considered private, the tragedy of the commons literature does suggest that those resources that are common pool will inevitably become overexploited. Archaeological correlates for these models tend to suggest patterns of overexploitation of resources and economic intensification often similar to human behavioral ecology explanations of changing or widening diet breath (Broughton, 1997; Porcasi et al., 2000).

Indigenous stewardship and traditional resource and environmental management literature suggest human practices to maintain or enhance the abundance, diversity and/or availability of natural resources or ecosystems can be recognized archaeologically through material correlates. These approaches have emphasized four aspects of Indigenous peoples that would contribute to these practices such as harvesting methods, enhancement strategies, tenure systems, and worldviews and social relations (Anderson, 2005; Lepofsky and Caldwell, 2013). We could expect Indigenous stewardship practices to result in evidence of habitat enhancement such as fire management strategies, size-selective harvesting practices of plants and animals, shift in the relative abundance of taxa as economic intensification occurs with stewarded resources, and changes in the age and/or size of targeted species. For example, if Native people were stewarding or managing a resource, such as Pacific herring, we could expect to see the limited take of the largest adult-sized individuals and juveniles to allow the fish population to reproduce and mature. However, if Native American fishing practices were selecting the largest sized fishes within the fishery, which would be correlated with the oldest fishes, we could expect to see a reduction in the size of fishes through time, consistent with other archaeological fisheries studies (Broughton, 1997; Broughton et al., 2015). This idea has also been discussed in the context of plant resources as well, such as selective harevesting of large cormlets, and the return or replanting of small cormlets to maintain the abundances of geophytes (Anderson, 2005).

2 Methods

Along the central California coast, four primary research areas have been testing grounds for Indigenous stewardship practices that have informed our current understanding of the time depth and development of these practices. From north to south, these include Point Reyes National Seashore, Año Nuevo State Park, Quiroste Valley Cultural Preserve, and Wilder Ranch State Park (Figure 1). The research has been completed collaboratively with several Native Californian tribes, including the Amah Mutsun Tribal Band at Año Nuevo State Park, Quiroste Valley Cultural Preserve, and Wilder Ranch State Park. In addition, research was conducted with the Federated Indians of Graton Rancheria at Point Reyes National Seashore. These projects span nearly 2 decades of research with, for, and by Native Californian tribal communities with research goals and priorities towards supporting Indigenous leadership in the world of natural resource conservation and cultural revitalization.

2.1 Amah Mutsun Tribal Band

Most of the data presented in this paper are derived from collaborative research with the Amah Mutsun Tribal Band, the California Department of Parks and Recreation, the University of California, Berkeley, and several other institutions. The Amah Mutsun Tribal Band became engaged in archaeological research in 2007. Working with Professor Kent Lightfoot and Dr. Rob Cuthrell, University of California, Berkeley and the California Department of Parks and Recreation, the Amah Mutsun Tribal Band initiated an eco-archaeological study of Indigenous fire use at Quiroste Valley in Año Nuevo State Park (Cuthrell, 2013a; Gifford-Gonzalez et al., 2013; Hylkema and Cuthrell, 2013; Lightfoot et al., 2013; Lightfoot et al., 2021). Later research was conducted at Wilder Ranch State Park during the summers of 2016-17 (Sanchez, 2019; Grone, 2020; Lightfoot et al., 2021).

The foundation of the research protocols in working with the Amah Mutsun Tribal Band was an agreement that all research would work to minimize adverse impacts on the archaeological site(s) studied. Tribal members were included in all field research to build capacity within the tribe, so their members could gain training and increase their ability to advocate for their own archaeological resources in the future (see Sigona et al., 2021 regarding how the tribes' experience with archaeologists has evolved into applied management programs). The research team agreed to integrate low-impact field methodologies, such as geophysics, to identify discrete deposits which might contain high-densities of cultural materials and artifacts related to Indigenous foodways and other activities of particular interest to the tribe (Cuthrell, 2013a; Lightfoot and Lopez, 2013; Grone, 2020; Lightfoot et al., 2021; Sanchez et al., 2021).

2.2 Archaeological field methodologies

Through the two primary field projects with the Amah Mutsun Tribal Band, diverse research and sampling strategies have been developed, modified, and refined. The initial field project developed in 2007 at the Quiroste Valley Cultural Preserve centered around CA-SMA-113, otherwise known as Quiroste Village. The Quiroste termed the coastal village *Mitine* (Hylkema and Cuthrell, 2013) (Figure 2). The field research at *Mitine* from 2007-09 was guided by geophysical survey techniques, including gradient magnetometer survey, soil resistivity, and ground penetrating radar (Cuthrell, 2013a). Based on the findings of these surveys, 22 1 m^2 excavation units were excavated at 10 cm arbitrary levels unless cultural or natural stratigraphy was encountered. In addition, five to 10-L samples were collected for flotation. Further in-depth discussion of field methodologies and sampling can be found in Cuthrell (2013).

During the 2016-17 field research, the research team focused on a series of archaeological sites south of *Mitine* along the Santa Cruz coastline. Four archaeological sites were excavated during these field seasons, including CA-SCR-7, CA-SCR-10, CA-SCR-14, and CA-SCR-15 (Figure 2). While each site had site-specific sampling strategies, the field methodologies followed similar protocols as those applied at *Mitine*. However, by the 2016 field season, the sampling strategies had changed. Specifically, the quantity and size of excavation units had been reduced. Therefore, in later iterations of field research, excavations utilized 1 m^2 and 0.5 m^2 units but a reduced number of units per site. See Grone (2020) and Sanchez (2019) for further information.

The collaborative research team studied multiple independent lines of evidence supporting this research throughout the years.

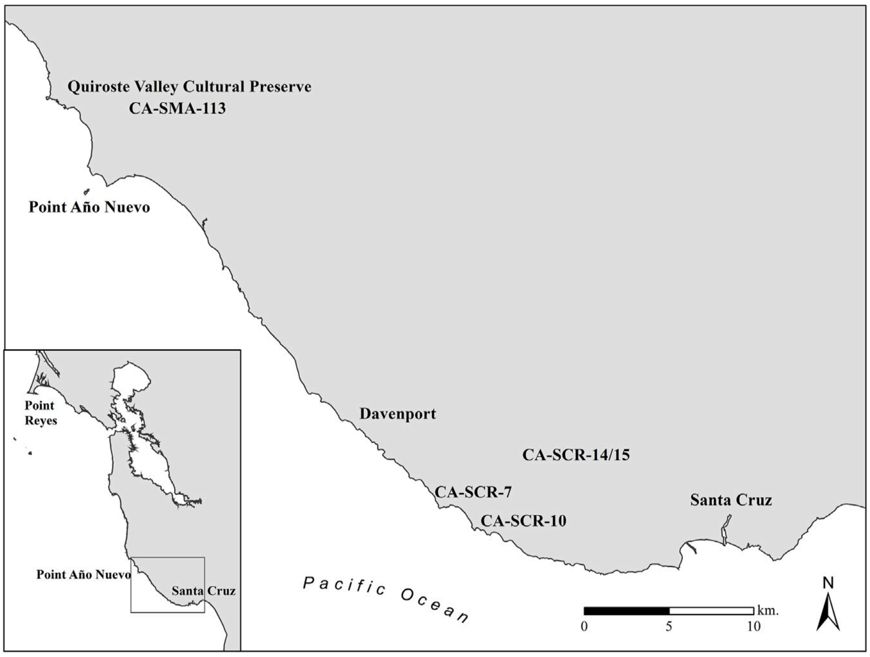

FIGURE 2
The Quiroste Valley and Santa Cruz Coast Study Areas from the 2007–09 and 2016–17 field seasons. Specific locations of the archaeological sites have been omitted to protect these sensitive cultural resources.

These data include fire ecology modeling, analysis of historical photos for the reconstruction of vegetation histories, ethnohistorical and ethnographic documents, paleoethnobotanical data including phytoliths, zooarchaeological remains, the study of sediment cores for palynological and charcoal accumulation rates, dendrochronology, and fire scar histories to reconstruct fire return intervals, and ancient DNA analyses of plant and animal remains. For in-depth details of sampling strategies, excavation techniques, and sample processing, please refer to the following sources (Cuthrell, 2013a; Lightfoot and Lopez, 2013; Sanchez, 2019; Grone, 2020).

2.3 The Federated Indians of Graton Rancheria

During the summer of 2015, fieldwork was conducted at Point Reyes National Seashore as part of a collaborative eco-archaeological project involving the University of California, Berkeley, the National Park Service, and the Federated Indians of Graton Rancheria with participation by Sacred Sites Committee Members (Figure 3). The project was designed to assess the temporal and material record of sites threatened by sea level rise and coastal erosion, as well as to contribute to ongoing landscape and seascape management research (Sanchez, 2019). As part of this project, crew members surveyed, recorded, and tested nine archaeological sites from Point Reyes National Seashore, sampling from all major habitats within the park (i.e., bay, open coast, inland localities, and reef sites). The nine sites were selected from a sample of 88 documented archaeological sites.

All Point Reyes National Seashore sites were surveyed using low-impact and minimally invasive field methodologies following Lightfoot (2008). These include surface survey applying the “dog-leash” method (Binford, 1964), catch and release surface survey sampling (Gonzalez, 2016), subsurface geophysical survey, auger sampling (10 cm diameter auger sampled in 20 cm arbitrary levels), and one opportunistic column sample (50 cm × 50 cm) at CA-MRN-224. For in depth details of sampling strategies, excavation techniques, and sample processing please refer to Sanchez et al. (2018), Sanchez (2019), Grone (2020), Sanchez (2020).

3 Results

3.1 Santa Cruz and San Mateo coast: Middle Holocene trends in plant and animal use

Of the four study areas only Wilder Ranch includes evidence of Middle Holocene occupations at CA-SCR-7. CA-SCR-7 is an imposing shell mound that lies adjacent to Laguna Creek and extends along the coastal bluff and uplifted marine terrace. The site is a remnant of a large dune complex with intermingled cultural deposits. Radiocarbon dates from CA-SCR-7 suggest an occupation from 6,740-6,660 cal BP (CA-SCR-7 Component A in Figure 4, see below) to 4,240-4,090 cal BP (CA-SCR-7 Component B in Figure 4, see below) (Sanchez, 2019; Grone, 2020; Lightfoot et al., 2021). Paleoethnobotanical data from CA-SCR-7 and other coastal and inland sites from the study are is summarized by Cuthrell (in review). Cuthrell (in review) analyzed paleoethnobotanical

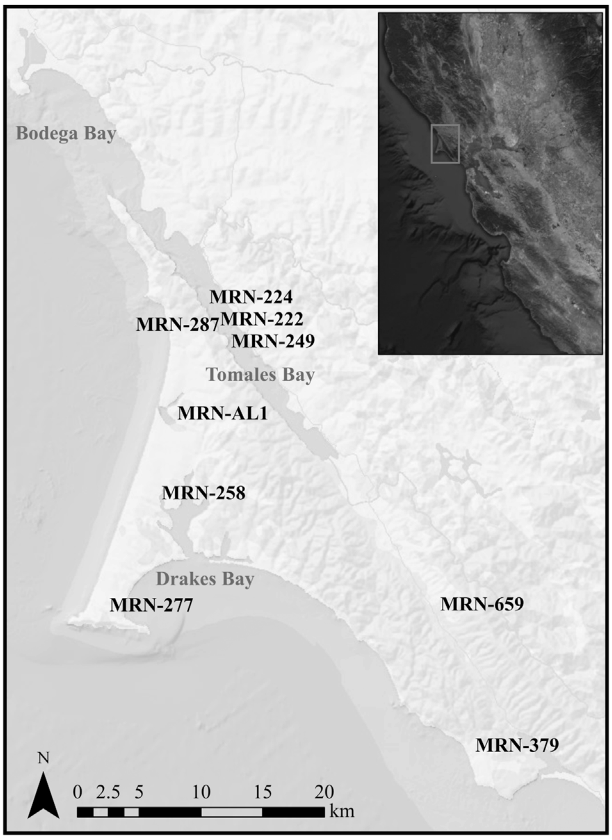

FIGURE 3
The Point Reyes National Seashore Study Areas from the 2015 field season. Specific locations of the archaeological sites have been omitted to protect these sensitive cultural resources.

remains, anthracological samples, and phytoliths from the Año Nuevo, Quiroste Valley, and Wilder Ranch study areas.

Phytolith content from CA-SCR-7 suggest relatively weak evidence for long-term grasslands near the site, especially when compared to Late Holocene occupations across the study areas. As Cuthrell (in review) notes, these results are unsurprising, as CA-SCR-7 and the surrounding area was once an active dune field that would be expected to support more ephemeral grasslands than locations with stable soils. According to Cuthrell (in review) at CA-SCR-7 driftwood represents the main source of wood fuel. The primary wood fuel recovered and identified was redwood (*Sequoia sempervirens*) and alder (*Alnus* sp.). Cuthrell (in review) suggests it is unlikely that redwood or alder could have grown in proximity to the site (active sand dune habitat), even in the mid-Holocene and likely represent the use of driftwood for fuel.

Following trends for coastal sites in the Año Nuevo and Wilder Ranch study areas, especially when compared to inland locales, CA-SCR-7 is marked by relatively low densities of edible plant remains, such as nuts and edible seeds (Figure 4). These trends are generally consistent across the Middle and Late Holocene coastal bluff sites, where evidence of plant processing is minimal when compared to inland sites, see discussion below. However, CA-SCR-7 Component A contained a relatively high percentage of edible nut remains, at 20.3%, while CA-SCR-7 Component B had 36.4% edible nut remains (quantified by count). Other coastal sites displayed edible nut percentages from 4.6%–13.9%, and inland sites had values ranging from 3.8%–21.1%. Chi-square comparisons of edible nut count vs. other identified macrobotanical specimen count between CA-SCR-7 Component B and all other coastal sites/components returned statistically significant differences in all cases ($p < 0.05$) (Cuthrell, in review). In sum, the archaeobotanical analysis of 176 flotation samples indicates a shift to focusing on inland sites to process plant foods, while coastal sites indicate a primary emphasis on marine resource use.

At CA-SCR-7, the primary zooarchaeological data recovered is related to ancient vertebrate and invertebrate fisheries. While mammal and bird remains have been recovered, their abundances are best representative of the presence and absence of species rather than relative abundance, given the small-scale and fine-grained excavations strategies that improve the recovery of minute remains (Grayson, 1984). In terms of vertebrate fisheries at SCR-7, the >2 mm samples are principally surfperches (Embiotocidae), which comprise ~28% of the assemblage. Surfperches include pile perch (*Damalichthys vacca*), shiner perch (*Cymatogaster aggregata*), and barred, calico, or redtail surfperch (*Amphistichus* sp.). Greenlings comprise 21% of the assemblage by relative abundance and include lingcod (*Ophiodon elongatus*), kelp, rock, or masked greenling (*Hexagrammos* sp.). Skates (Rajidae) make up 15% of the assemblage. Rockfishes (*Sebastes* sp.) make up another 10%. Together surfperches, greenlings, rockfishes, and skates make up 74% of the assemblage, with 18 genera making up the remaining 26%. The density of fish remains recovered and identified within the assemblage to at least the taxon Actinopterygii is 3.5 NISP/l. The Shannon Index for the assemblage, calculated at the genera level, is 2.4, suggesting more significant heterogeneity, with evenness or equitability measured at 0.85, signifying an assemblage closer to equal distribution. Analysis of this fishery suggests Indigenous peoples had a broad-based economy with a diversity of genera (n = 25) targeted. These trends of highly mobile populations with broad-based economies typify the region's archaeology during the Middle Holocene (Hylkema, 2002), (Hylkema, 1991).

3.2 Santa Cruz and San Mateo coast: Humans and coastal prairies

Research by Cuthrell (2013a, 2013b) interrogates Indigenous fire management strategies with particular emphasis on the Quiroste Valley. Later research by Cuthrell and others focus on the Santa Cruz coast sites south of *Mitine* in the Wilder Ranch study area (Lightfoot et al., 2021). The collaborative research team has studied multiple independent lines of evidence supporting this research. These data included fire ecology modeling, analysis of historical photos to reconstruct vegetation histories, ethnohistorical and ethnographic documents, paleoethnobotanical data including macro and micro remains, zooarchaeological samples, the study of sediment cores for palynological and charcoal accumulation rates, dendrochronology and fire scar histories to reconstruct fire return intervals, and ancient DNA analyses of plant remains (Cuthrell, 2013a; Cuthrell, 2013b; Cowart and Byrne, 2013; Evett and Cuthrell, 2013; Fine et al., 2013;

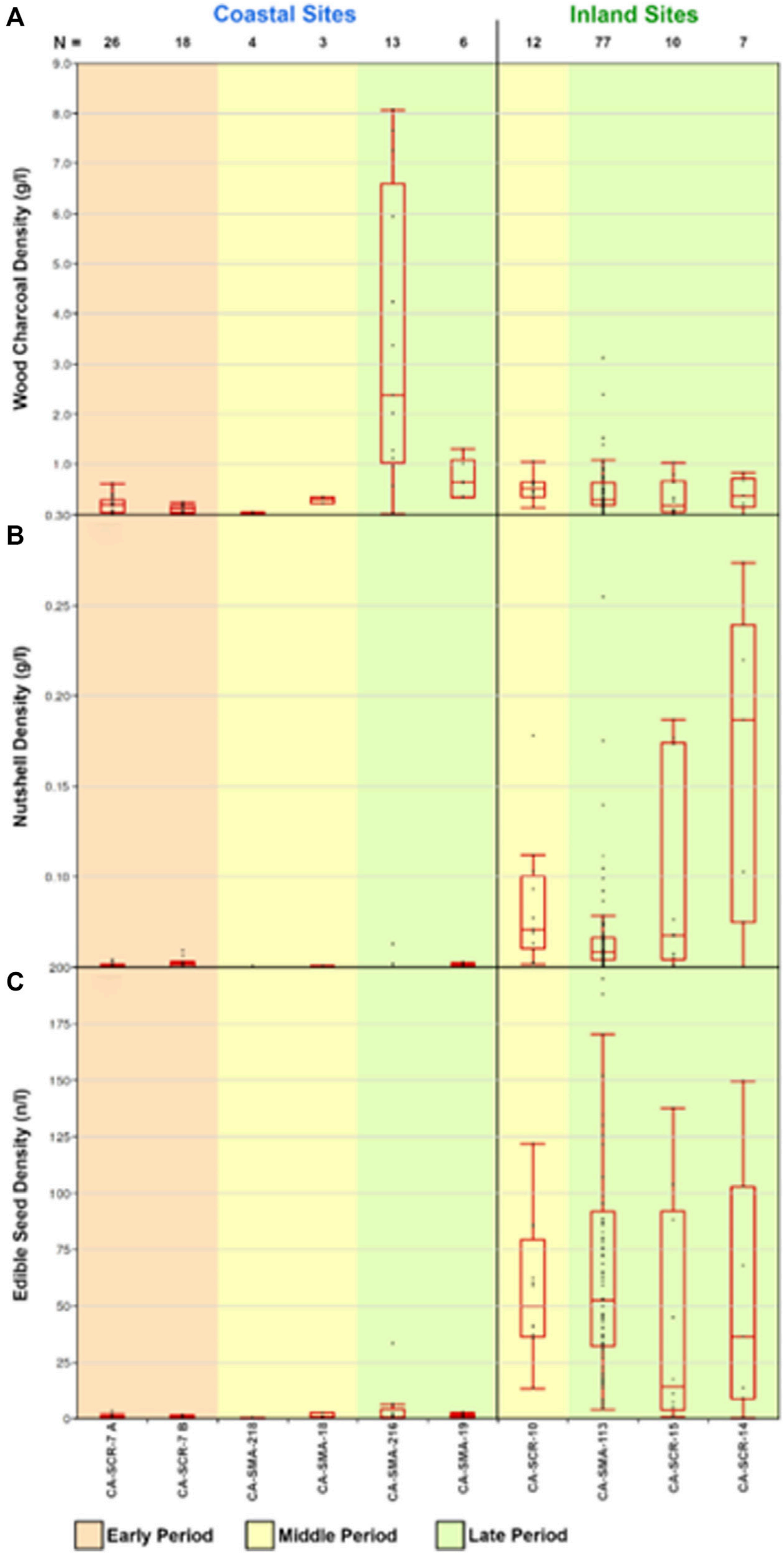

FIGURE 4
Box plot inter-site comparison of: **(A)** wood charcoal density (g/L); **(B)** edible nutshell density (g/L); and **(C)** edible seed density (n/l). Each data point represents a flotation sample (Cuthrell, in review).

TABLE 2 Point Reyes National Seashore sites, calibrated radiocarbon dates, clupeid NISP, Pacific herring NISP, and mean Pacific herring SL.

Site	(95.4% CI)	Clupeid NISP	Pacific herring NISP	Mean P. herring SL
CA-MRN-287	810–110 cal BCE	13	1	---
CA-MRN-277	100 cal BCE to cal CE 780	22	1	---
CA-MRN-224 (Auger)	cal CE 760–1800	3165	195	177 mm
CA-MRN-222	cal CE 1030–1800	2011	114	178 mm
CA-MRN-224 (Column)	cal CE 1260–1800	817	58	177 mm
CA-MRN-AL1	cal CE 1300–1640	554	24	175 mm
CA-MRN-258	cal CE 1310–1430	173	8	---
CA-MRN-659	cal CE 1400–1800	89	3	---
CA-MRN-379	cal CE 1430–1630	0	0	---
CA-MRN-249	cal CE 1450–1800	587	62	176 mm
Total		7431	466	

Gifford-Gonzalez et al., 2013; Hylkema and Cuthrell, 2013; Lightfoot et al., 2013; Lightfoot and Lopez, 2013; Lopez, 2013; Striplen, 2014). The Research by Cuthrell (2013a, 2013b) is particularly relevant as it directly interrogates the issue of natural and anthropogenic fire regimes and fire return intervals, setting important expectations for vegetation communities with and without disturbance. Below we synthesize data from Cuthrell (2013a, 2013b) that highlight key points from the broader research program.

In his seminal research interrogating Indigenous fire use in the Late Holocene, Dr. Rob Cuthrell (2013) combined fire ecology models, historical records, and archaeobotanical methods to investigate anthropogenic fires to understand how burning practices may have structured local biotic communities. Cuthrell (2013) set observable baseline expectations regarding vegetation and forest successional stages in natural fire conditions based partly on lightning strike densities along the central California coast.

Based on the low incidence of lightning fires within the Quiroste Valley and evidence of historical vegetation change, he suggests anthropogenic burning would have been required to maintain the availability and abundance of plant food resources that are reflected in the archaeological record. Macrobotanical and anthracological evidence suggests the assemblages are compatible with models of anthropogenic burning through the abundance of fire-adapted plant communities in the past, which are rare today in the modern population structure. The archaeological research at CA-SMA-113 also indicates that during the Late Holocene (ca. cal AD 1,000–1,300), site inhabitants relied heavily on grassland seed foods and nut species that are culturally or ecologically fire-associated. The findings from this project suggest that the ancestors of the Amah Mutsun Tribal Band conducted cultural burning from at least cal AD 1000 to the time of Spanish colonization (Cuthrell, 2013b; Lightfoot et al., 2013; Lightfoot and Lopez, 2013).

Comparing trends in plant use across coastal and inland sites from the Middle to Late Holocene, Cuthrell (in review) identified significant differences in the paleoethnobotanical assemblages across space and time. For example, Cuthrell (in review) found that the densities of edible nuts differed between coastal and inland sites, with all coastal sites containing median edible nut density <0.8 mg/L (<0.6 n/l) and all inland sites displaying median edible nut density >8.2 mg/L (>2.0 n/l). In addition, Cuthrell (in review) observed higher densities of edible seeds were consistently observed among inland sites in comparison to coastal sites. Median edible seed density at inland sites ranged from 14.1-52.5 n/l, but only 0.3–1.4 n/l at coastal sites (Figure 4). Among inland sites, the edible seed assemblages of the three sites in Santa Cruz County were dominated by seeds of grasses, which comprised 66.0%–87.5% of edible seeds and 39.6%–71.8% of identified macrobotanical specimens. This archaeobotanical study by Cuthrell (in review) also provides detailed discussion on grass silica phytolith abundances over time, which also support interpretations of active stewardship of coastal prairie ecostyems during the Late Holocene through the use of fire within the study area. While marine resource management is the focus of our paper, we elect to highlight coastal archaeobotanical research as an example of Indigenous coastal stewardship because we believe it provides evidence that supports the discussion of Indigenous stewardship as a broader phenomena.

3.3 Point Reyes National Seashore: Pacific herring fishery

The Pacific herring remains reported in this study were previously reported by Sanchez (2020) and Sanchez et al. (2018). In total, the Point Reyes faunal assemblage resulted in the identification of 9071 fish specimens from the >2 mm mesh size class. At least 33 species were represented within 19 families. Clupeids represent the bulk of the assemblage, accounting for 8005 of the total NISP or ~88% (Table 2). See Sanchez (2020) and Sanchez et al. (2018) for further information. Using modern clupeid atlas and axis elements from Pacific herring specimens of known standard length (SL), Sanchez (2020) created linear regression models that show statistically significant ($p < 0.05$)

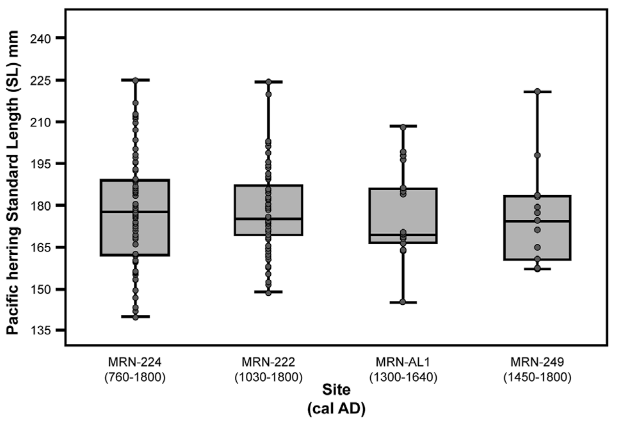

FIGURE 5
Box and whisker plot of Point Reyes Pacific herring standard length based on the atlas and axis vertebral width measurements. Archaeological data presented chronologically with radiocarbon date ranges from Sanchez (2020).

and significant (R^2 values) relationships between SL and maximum vertebral centrum dimensions (Sanchez, 2020).

Applying these formulae to ancient Pacific herring from Point Reyes National Seashore from sites CA-MRN-224, CA-MRN-222, CA-MRN-249, CA-MRN-AL1, the linear regression analyses based on archaeological atlases suggest that the mean size of Pacific herring sampled in the study ranged from ~174 to ~178 mm SL. The size of the Pacific herring based on the axis measurements suggests that the mean size of Pacific herring at the four sites ranged from ~173 to ~185 mm SL. Sanchez (2020) compared the mean SL estimates calculated from the atlas to those of the axis. He conducted a *t*-test in the statistical program PAST comparing the mean SL estimates from atlases and axes (Hammer et al., 2001). The results of the *t*-test revealed no statistical difference between the two samples ($t = 0.48$, $p = 0.64$, critical t value = 2.4). Based on the results of the *t*-test, Sanchez (2020) merged the Pacific herring atlas and axis data. These data illustrate that Coast Miwok peoples were consistently harvesting similar size classes of Pacific herring with insignificant variation at the sampled sites (Figure 5; Table 2). These findings suggest that Pacific herring with a mean SL of 175-178 mm were harvested by Coast Miwok ancestors from cal CE 760 to ~1800. These data demonstrate that the Point Reyes Pacific herring fishery was in place by at least cal CE 760, if not earlier, and that the Coast Miwok Pacific herring fishery persisted until the contact era.

3.4 Santa Cruz and San Mateo coast: California mussel fishery

The California mussel remains reported in this study were previously reported by Grone (2020). In the study, Grone (2020) analyzes data from three sites in Santa Cruz and San Mateo Counties with dates ranging from 4750 cal BCE to cal CE 1920 (Table 3). Taxa from all sites display a heavy reliance on marine resources in the Middle Holocene through to the Late Holocene, evidenced by a broad range of species that span the entirety of the intertidal zone.

Research on mussel assemblages has resulted in the development of multiple regression formulae to broaden the interpretive value of fragmented California mussel remains beyond relative abundance, providing methods for measuring mussel umbones to reconstruct individual size (Campbell and Braje, 2015; Singh and McKechnie, 2015). While there is some debate about the application and interpretation of these formulae (Campbell, 2015; Singh et al., 2015), they appear to be an effective way to estimate mussel size from archaeological materials and make the most out of fragmented shellfish assemblages. These formulae used in Campbell and Braje (2015) were developed by using modern comparative specimens collected in Southern California. Due to the observed biogeographical morphological variation of California mussels north and south of Point Conception (Glassow and Wilcoxon, 1988), Grone (2020) developed an experimental morphometric formula from n = 151 modern specimens collected from Pescadero State Beach by Dr. Rob Cuthrell. After measuring the same elements used by Campbell and Braje (2015) and Singh and McKechnie (2015), Grone (2020) used umbo thickness in his study as it tends to be the most well preserved in archaeological specimens. Therefore, Grone (2020) created linear regression models that show statistically significant ($p < 0.05$) and significant (R^2 values) relationships between California mussel length and umbo thickness.

3.5 Comparison of harvesting patterns

To assess mussel harvesting practices, Grone (2020) applied morphometric data analyses and stable isotope isotope analyses (Apodaca et al., in review)[1] to model mussel harvesting profiles through time. While these data provide a robust perspective regarding California mussel harvesting trends by people that lived in the Quiroste and Cotoni polity areas, a complete review of the study is beyond the scope of this paper. Therefore, Grone (2020) applied the morphometric formulae to n = 2901 umbones from SCR-7, SCR-14, and SMA-216 (spanning 4785 cal BCE to cal CE 1920). The results are outlined below.

As displayed in (Figure 6; Table 4), the average size of mussels is significantly greater at CA-SCR-7 than at CA-SCR-14 or CA-SMA-216. This trend suggests that the mean size of mussels decreased in size over time from Middle Holocene to Late Holocene times, consistent with expectations of resource depression. However, while there is a smaller average size in the two Late Holocene sites compared to the Middle Holocene sites alone, the average size of California mussels increases slightly during the Late Holocene (Figures 7, 8; Tables 5, 6). These data suggest that people may have employed harvesting methods that maintained the stability of the mussel populations over several centuries in Late Holocene times. In addition, there is a greater density of umbones per sample in the two

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[1] Apodaca, A. J., Brown, J. F., and Grone, M. A. (in review). "Seasonality of Mussel harvesting at three Holocene sites on the Santa Cruz coast: Insights from isotopic variation in marine mollusks," in *The study of indigenous landscape and seascape stewardship on the central California coast: The findings of a collaborative ecosrchaeological investigation*. Editors K. G. Lightfoot, M. A. Grone, and G. M. Sanchez (Berkeley, CA: Contributions of the University of California Archaeological Research Facility).

TABLE 3 Shellfish data from the Año Nuevo and Wilder Ranch study areas outlining most abundant shellfish taxa by weight.

Sites	Site type	(95.4% CI)	Most abundant	Second most abundant	Third most abundant
CA-SCR-7	Coastal Midden	4785–2200 cal BCE	*Mytilus californianus* (70.4%)	*Balanus spp.* (28.7%)	*Pollicipes polymerus* (0.9%)
CA-SMA-216	Coastal Midden	cal CE 1300–1640	*Mytilus californianus (40.9%)*	*Tegula funebralis (37.4%)*	Chitons (8.3%)
CA-SCR-14	Upland Village	cal CE 1160–1920	*Mytilus californianus* (93.2%)	*Balanus* spp. (2.9%)	*Pollicipes polymerus* (1%)

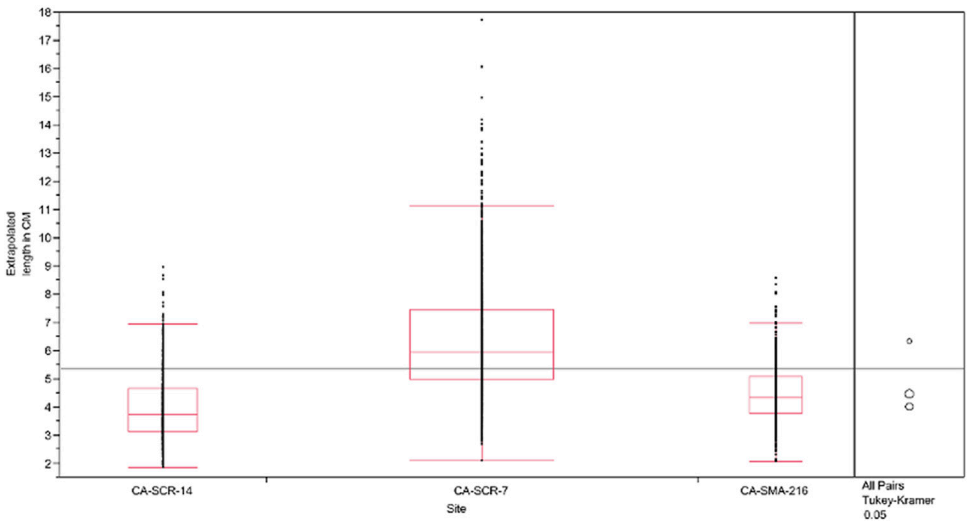

FIGURE 6
Comparison of California mussel umbone data from sites.

TABLE 4 Estimated average sizes of mussels from the Año Nuevo and Wilder Ranch sites.

Site	Age	n=	Average size (cm)	Std. Deviation
CA-SCR-7	4785–2200 cal BCE	1,409	8.0	2.9 cm
CA-SMA-216	cal CE 1300–1640	796	5.0	1.9 cm
CA-SCR-14	cal CE 1160–1920	696	4.7	1.8 cm

Late Holocene sites, suggesting mass harvesting events of greater numbers of individual mussels than at CA-SCR-7.

These harvesting profiles may indicate a stripping method of harvesting, as Whitaker (2008) described, which could account for both the reduced size and greater number of individuals per context. The standard deviation of mussel size is also less for CA-SMA-216 and CA-SCR-14, consistent with expectations of a stripping method of harvest. At CA-SCR-7, there is a higher standard deviation of mussel size, which may indicate plucking larger mussels as well as stripping entire beds.

The isotopic seasonality research by Apodaca et al. (in review)[1] suggests a proportionally greater likelihood that mussel harvesting occurred along a broader seasonal window for the coastal midden sites (CA-SCR-7 and CA-SMA-216). This differs from the readings obtained from isotope samples from the Late Holocene inland village site CA-SCR-14, where the shellfish recovered appear to have been harvested during a much tighter seasonal window consistent with winter months. The studied sites show that mussel harvesting patterns have a stronger relationship with site type and spatial proximity to shoreline rather than as a function of chronological time. The mussel assemblage at the inland site reflected a winter harvesting trend, while the coastal site assemblages suggested a broader harvesting window throughout the year. The interpretations regarding harvesting trends at the three sites should be considered tentative, considering the limited sample size.

4 Discussion

As outlined in this review, Indigenous people have profoundly influenced marine and terrestrial ecosystems by modifying coastal habitats to increase the productivity of target species and shape local biotas through their stewardship and harvesting practices. While these practices span a spectrum of effects and scales on ecosystems, there has been growing evidence that Native Californian communities may have relied on these practices interacting with specific resources, landscapes, and ecosystems with long-term rather

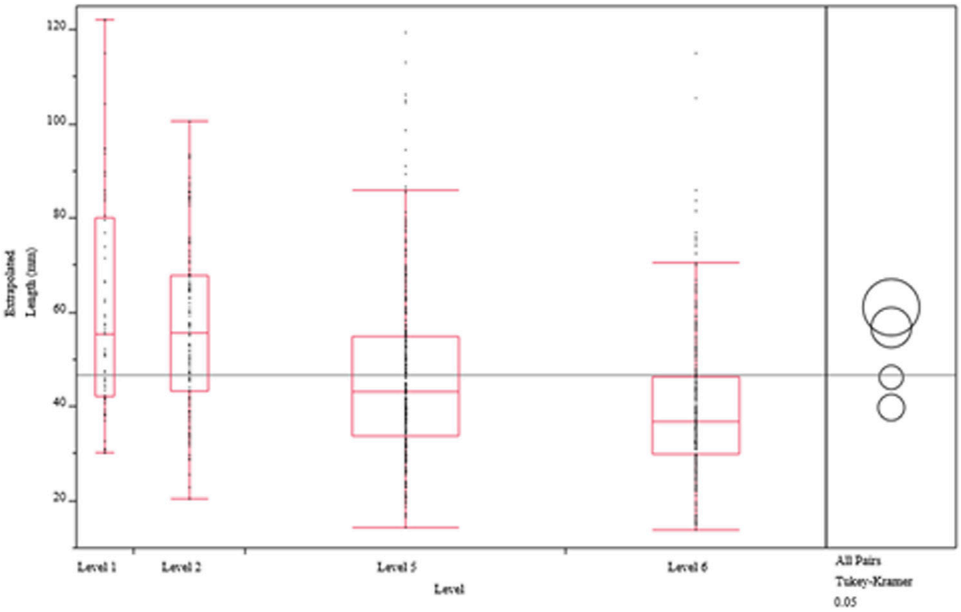

FIGURE 7
Mussel umbone data from CA-SCR-14. Data from Excavation Unit 2 and separated by excavation level. AMS Range 1160 CE- 1920 CE. N = 696.

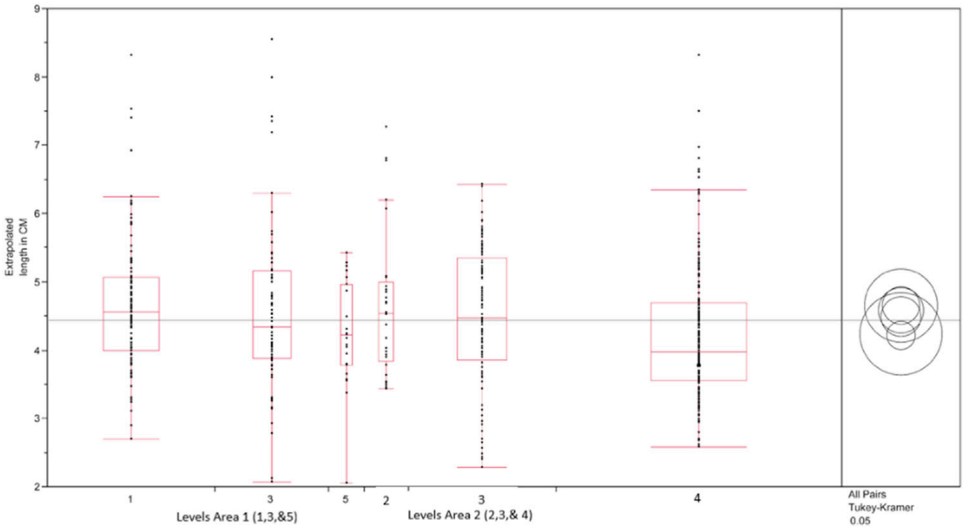

FIGURE 8
Mussel umbone data from CA-SMA-216. Data from Area 1 and 2. AMS Range 1300 CE-1640 CE. N = 796.

than short-term subsistence goals, especially by the Late Holocene. However, while some scholars conducting archaeological research on small-scale societies have recognized these practices, others have tended to overlook the likelihood of long-term perspectives in human-environmental relationships, such as traditional resource and environmental management, traditional ecological knowledge, and Indigenous stewardship practices. For example, Jones and Codding (2019) recognize that evidence supports the conclusion that the Quiroste used fire to meet intermediate goals. However, they suggest that the practice within the Quiroste case study does not meet the *scale* necessary to make the resources fit within the modern concept of the commons, meaning birds, fish, marine and terrestrial mammals that are accessible to "hundreds of unrelated, autonomous communities" (Jones and Codding, 2019).

Although the scale of the cultural practice of controlled burning along the central California coast (Cuthrell, 2013b; Lightfoot et al., 2021) does not meet the criteria of common pool resources available across a large scale, it does provide an example of Indigenous

TABLE 5 Average size of mussel from Excavation Unit 2 at CA-SCR-14.

Level	Age	n=	Average size (cm)	Std. Dev. (cm)
1	NA	55	5.9	2.4
2	1695-1725 CE (0.27); 1815-1840 CE (0.20); 1870-1920 CE (0.49)	113	5.7	1.8
5	1270-1410 CE	321	4.6	1.8
6	1160-1210 CE	262	4.0	1.5

TABLE 6 Average size of mussel from Area 1 and 2 at CA-SMA-216.

Area/Level	Age	n=	Average size (cm)	Std. Dev. (cm)
1/1	NA	186	5.0	1.5
1/3	1300 CE-1420 CE	105	5.2	1.8
1/5	NA	27	4.8	1.1
2/2	NA	37	4.7	2.1
23	1460 CE-1640 CE	129	4.9	1.8
2/4	NA	312	4.5	1.4

engagement with resources that suggest human-environmental relationships do not inevitably result in the tragedy of the commons or overexploitation. Instead, the case of controlled burning provides an excellent example of Indigenous stewardship, habitat modification, and niche construction. Therefore, these data provide a possibility of understanding Indigenous practices beyond individual maximization assumptions. Furthermore, through the long-term perspective from the Middle to Late Holocene of the sites studied, trends emerge that diverge from expectations from the maximization literature. For example, Middle Holocene populations in the Wilder Ranch study area appear to have been highly mobile and their economies focused on a broad swath of resources, yet few fit the model of high-ranked taxa based on the invertebrate and vertebrate fisheries (Sanchez, 2019; Grone, 2020). However, by the Late Holocene we find evidence in Point Reyes National Seashore, the Quiroste Valley, and Wilder Ranch, that Indigenous economies intensified towards a limited number of species. These findings also conflict with expectations from EE and HBE that suggest shifts in economic focus towards low-ranked taxa represent a widening diet-breadth that is often driven by resource depression and overexploitation, while we suggest this represents a narrowing diet-breadth that emphasized culturally important ecosystems, habitats, and species (Broughton, 1997).

In this review, we have provided an example of probable long-term intentionality of Indigenous engagement with fisheries, a resource that commonly fits the conceptualization of common pool resources (Ostrom, 1990; Ostrom, 2008). In the case of Pacific herring, they represent a fishery that occurs on a large scale, spanning the coast of North America from Alaska to Baja California (Fisheries, 2022). Pacific herring live in depths from the surface to around ~396 m. In California, Pacific herring spawn from October through April in large estuaries like Tomales Bay and San Francisco Bay (California Department of Fish and Wildlife, 2022) (Figure 3). Therefore, Pacific herring fits the criteria of common pool resources as previously described. They occur across a large scale through various habitats, from nearshore environments to offshore depths. During the spawning season, which spans several months, herring are available through mass capture fishing techniques, such as seines and gill nets, feeding humans and a diversity of organisms, serving as an umbrella and keystone species (Sanchez et al., 2018; Sanchez, 2020).

Coast Miwok fishing practices at Point Reyes National Seashore appear to have persisted from cal CE 760 to ~1800, based on the archaeological samples recovered from the 2015 excavations. However, the mean SL of Pacific herring from four archaeological sites does not vary significantly, with sites CA-MRN-224 (177 SL mm), CA-MRN- 222 (178 SL mm), CA-MRN-249 (176 SL mm), and CA-MRN-AL1 (175 SL mm) having nearly identical mean values (Figure 5; Table 2). Therefore, it does not appear that there is a reduction in the size of the Pacific herring caught within Point Reyes through time, based on the mean SL. These data suggest that Coast Miwok people may have been catching and retaining a narrower size range of Pacific herring based on the mean, which could relate to gear selectivity or release of unwanted size classes.

Since fishing nets represent a technology created based on net mesh gauges, these data suggest long-term cultural practices (i.e., traditional ecological knowledge, traditional resource and environmental management, and Indigenous stewardship) and knowledge related to fish net production and herring fishing techniques. As further evidence of this long-term perspective, we must consider that the Pacific herring fishery at these four sites are not contemporaneous. CA-MRN-224 provides the initial radiocarbon dates available for intensive Pacific herring fishing within Point Reyes dating to cal CE 760. CA-MRN-222 is inhabited after CA-MRN-224–300 years later at cal CE 1030. CA-MRN-AL1 follows CA-MRN-222 after another ~300 years dating to cal CE 1300. Lastly, CA-MRN-249 dates ~150 years following the earliest dates available for CA-MRN-AL1, dating to cal CE 1450. Thus, these sites offer an excellent opportunity to trace human-fish relationships diachronically and to identify long-term continuity or declines in the size of Pacific herring through time.

Lastly, in the case of California mussels, their spatial scale is confined, as harvesting practices, much like the case of coastal prairies, are restricted to specific habitats, such as nearshore environments, to ~24 m in depth. However, the harvesting techniques and seasons vary significantly in contrast to coastal grasslands. Researchers have devoted much time to developing methods for assessing the archaeological signatures of different harvesting strategies and the seasonality of harvest of California mussels (Basgall, 1987; Jones and Richman, 1995; Bettinger et al., 1997; Whitaker, 2008; Cuthrell, 2013b; Grone, 2020). Two primary methods of harvesting have been proposed and modeled: plucking individual mussels or stripping entire beds. According to a study by Bettinger et al. (1997), plucking is always a superior method of harvesting based on energy expenditure return rates. However, it has been demonstrated (Bouey and Basgall, 1991) that return rates for California mussel beds are higher when mussels beds have been periodically disturbed by human predation, similar to some plants that become more productive when subject to disturbances, such as fires. Fortunately, these different harvesting strategies result in differences in shellfish assemblages. In the case of the plucking method, we expect to see a decrease in shell size through time with non-seasonally specific harvesting practices. However, in the case of the stripping method, we could expect to see the presence of a wide range of size classes with small to medium average sizes and a seasonally specific range of harvest of mussel beds.

In the case of California mussels studied by Grone (2020), there is a decrease in the size of mussels from the Middle Holocene at CA-SCR-7, with an average size of ~8 cm. By the Late Holocene at CA-SMA-216 and CA-SCR-14, California mussels range from 5.0 cm to 4.7 cm, respectively. While these data could be interpreted as an indication of resource depression based on size differences alone, Grone (2020) suggests that these assemblages represent differences in harvesting strategies at these three sites rather than indicative of resource depression or overexploitation. The stripping method as a harvesting strategy targeting medium sized mussels has been proposed to ensure continued and consistent mussel harvests, as the harvest of larger mussels could impact the larger brooding stock of mussel populations responsible for proliferation of a larger number of gamete, while the harvest of smaller mussels which have yet to reach reproductive viability could similarly disrupt mussel population. There, the harvest of medium size mussels *via* a repetitive stripping method of harvest may be indicative of Indigenous stewardship practices (Whitaker, 2008; Grone, 2020).

5 Conclusion

Indigenous people have profoundly influenced marine and terrestrial ecosystems by modifying coastal habitats to increase the productivity of target species and shaping changes in local biotas through their harvesting practices. In some cases, these actions have led to local resource depression, while in other instances, it appears Indigenous people engaged with marine resources in sustainable ways, increasing the resilience of coastal ecosystems. However, some scholars believe that there is still little evidence that California Indians employed sophisticated stewardship practices as a way to increase the carrying capacities of circumscribed territorial resources [See Jones and Codding, (2019) regarding discussion of Anderson (2005); Lightfoot and Parrish (2009)].

Eco-archaeological research of Indigenous stewardship is still an emerging field in California archaeology, and programs are learning how to best evaluate stewardship practices in the archaeological record (Sanchez, 2019; Grone, 2020; Lightfoot et al., 2021; Sigona et al., 2021; Reeder-Myers et al., 2022). Nevertheless, the approach contributes to alternative ways of thinking about the long-term foodways and stewardship practices of California Indians and how these communities augmented vegetation from the individual (organism) to the landscape (ecosystem) scale during the Late Holocene. Lightfoot et al. (2013) and Lepofsky and Lertzman (2008) indicate the empirical challenges with analyzing archaeological signatures of cultural burning and other Native management strategies in the archaeological record alone. We emphasize that, when possible, eco-archaeological research should maximize its relevance for supporting Tribal cultural and ecological revitalization goals. Today, coastal habitats that are essential for Indigenous cultures are becoming increasingly impacted. One of the reasons is the exclusion of people from their traditional homelands and their connection to cultural burning and other Indigenous stewardship practices, such as resource harvesting, representing long-term rather than solely short-term goals.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

GS, MG, and AA contributed to the conception of the study. GS wrote the first draft of the manuscript. GS, MG, and AA all wrote sections of the manuscript. All authors contributed to the manuscript revisions, read, and approved the submitted version.

Acknowledgments

We want to thank the Amah Mutsun Tribal Band, the Native Stewardship Corps, and the Federated Indians of Graton Rancheria for the privilege of conducting these studies and making this research a reality. We also greatly appreciate the support of Kent Lightfoot, Roberta Jewett, Rob Cuthrell, and Mark Hylkema.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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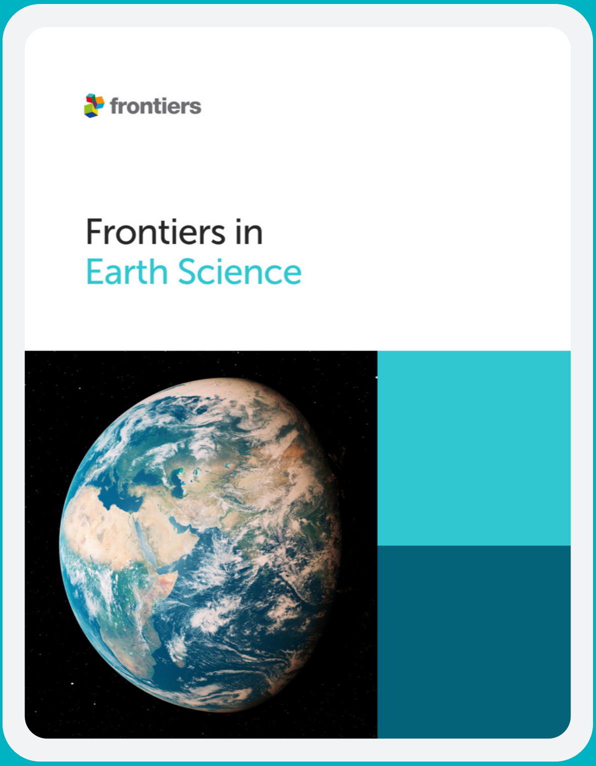

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