Intertidal shellfish use during the Middle and Later Stone Age of South Africa

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ABSTRACT: Middle Stone Age (MSA; 250,000 to 50,000 years ago) and Later Stone Age (LSA; 50,000 years ago to historic times) archaeological sites along the coast of South Africa frequently preserve the remains of marine shellfish, primarily limpets, mussels, and turban shells. These sites are found in two distinct biogeographic regions, the west, Atlantic Ocean coast and the south, Indian Ocean coast, with different marine environments influencing the shellfish species available for human exploitation. We are currently excavating Ysterfontein 1, a Middle Stone Age shell midden on the west coast. Analyses of the mollusks from Ysterfontein 1 and other MSA and LSA assemblages illuminate ancient subsistence practices, environmental changes, and human population densities, and we particularly aim to address issues surrounding the emergence of fully modern humans. The abundance of shells in many sites demonstrates that mollusks were an important source of food for both MSA and LSA people. Throughout the MSA and LSA, the proportions of different shellfish species change through time, suggesting that changing sea levels or ocean conditions may have influenced the available species. However, in many respects MSA and LSA assemblages are different from each other. The MSA samples have a lower diversity of shellfish species than LSA samples; they are poor in granular limpets; and they lack fish and rock lobster, which are common in many coastal LSA assemblages. In general, limpets and turban shells are larger in MSA assemblages than they are in LSA samples. We believe the sum suggests that MSA people foraged less intensively than LSA people, perhaps because they lived at lower population densities.

KEYWORDS: MOLLUSKS, SHELLFISH, LIMPETS, SOUTH AFRICA, MIDDLE STONE AGE, LATER STONE AGE, HUMAN POPULATION DENSITY, MODERN HUMAN ORIGINS

RESUMEN: Los yacimientos costeros del Paleolítico Medio (MSA; 250.000 - 50.000 años) y Tardío (LSA; 50.000 años hasta tiempos históricos) en Sudáfrica frecuentemente incorporan restos de conchas marinas, principalmente lapas, mejillones y bígaros. Estos yacimientos se localizan en dos regiones biogeográficas, la occidental en la costa atlántica y la oriental en la costa meridional del Indico, con distintos ambientes marinos que determinan las especies disponibles para la recolección. Actualmente se excava Ysterfontein 1 un conchero del Paleolítico Medio en la costa occidental que, junto con otros del Paleolítico Tardío atestiguan antiguas prácticas de subsistencia así como cambios ambientales y densidades pretéritas de poblaciones humanas que se confía ayuden a aclarar cuestiones relativas a la aparición de los humanos modernos. La abundancia de conchas apunta a la importancia de los moluscos en las dietas tanto durante la MSA como la LSA. A lo largo de ambos periodos, las frecuencias de las

distintas especies cambiaron sugiriendo que bien los cambiantes niveles del mar como las condiciones oceánicas pueden haber influenciado que especies estaban más disponibles en cada momento. No obstante, desde varias perspectivas, las asociaciones del Paleolítico Medio y Tardío difieren entre sí. Las muestras del Paleolítico Medio exhiben una menor diversidad de especies, son pobres en lapas y carecen de restos de peces y bogavantes, especies comunes en las muestras del Paleolítico Tardío. En general, tanto los bígaros como las lapas son mayores en el Paleolítico Medio que en el Tardío y todo ello nos sugiere que las gentes de la etapa MSA mariscaban de un modo menos intenso de lo que lo hicieron las poblaciones de la etapa posterior, quizás por vivir a más bajas densidades de población.

PALABRAS CLAVE: MOLUSCOS, MARISCO, LAPA, SUDÁFRICA, PALEOLÍTICO MEDIO, PALEOLÍTICO TARDÍO, DENSIDAD DE POBLACIÓN HUMANA, ORIGEN DE LOS HUMANOS MODERNOS

INTRODUCTION

Marine resources have long played a significant role in the diet of people living along the coast of South Africa. Archaeological sites from this area are among the oldest in the world to provide firm evidence for human marine resource exploitation. Numerous remains of shellfish and fur seal bones are preserved in Middle Stone Age (MSA) assemblages dated to between 127 and 50 thousand years ago (kya). After a hiatus in the archaeological record due to increased aridity and lowered sea-levels, faunal assemblages and large shell middens dotting much of today's coast demonstrate that the subsequent Later Stone Age (LSA) people (locally 14 kya to historic times) continued to rely heavily on marine foods. Together, the richness and time depth of the deposits makes the region ideal for archaeomalacological research.

Our research aims to characterize ecological variation during the MSA and to investigate the relationship between technology, subsistence, population size and density, and the environment. Fully modern human cultural behaviors appeared either at the transition from the MSA to the LSA or they evolved piecemeal during the MSA (Henshilwood & Marean, 2003), so understanding variation in MSA ecology, including the exploitation of marine resources, is critical for understanding modern human origins. Following many previous researchers who have made important contributions to understanding prehistoric shellfish exploitation in South Africa and motivated by our excavations at the MSA rockshelter Ysterfontein 1 (Figure 1) (Halkett et al., 2003; Klein et al., 2004), we have three main research objectives based on marine mollusks from MSA and LSA assemblages. First, we are examining changes in species abundance through time to help place the sequences in environmental context and in time. We are trying to understand the relationship between broad changes in species composition and changes in the local environment, which are related to the changes in sea levels associated with the glacial cycles of the Late Pleistocene. Second, we are studying not just the shellfish, but also the entire faunal assemblage, including birds and fish when present, to estimate diet breadth. We would like to further our understanding of the relationship between the environment, tool industries, human population densities and the species included in ancient diets. Finally, we are investigating how the size of the mollusks, primarily limpets but also turban shells, relates to ancient human population density. We propose that smaller mollusks indicate higher predator pressure, which is a result of higher human population densities. To further this research, we are investigating how to best control for environmental influences on shell size.

THE MODERN ENVIRONMENT

The marine and terrestrial environments along the coast of southern Africa are primarily dictated by the Benguela and Agulhas ocean currents (Branch *et al.*, 1981; Branch *et al.*, 1994; Bustamante & Branch, 1996). The Benguela current contains cold water that drifts northward along southern Africa's west coast. A combination of

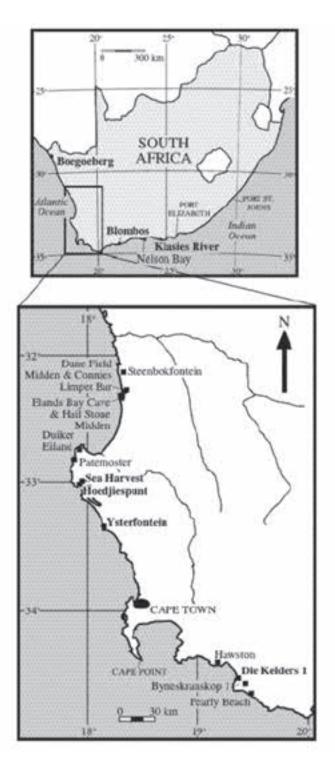


FIGURE 1

Map of South Africa showing the location of the sites discussed in the text. Table 1 provides key references for each site. Sites with MSA occupations are shown in bold.

Blombos Cave	Henshilwood et al. (2001); Henshilwood et al. (2002); D'errico et al. (2005)
Boegoeberg 2	Klein et al. (1999)
Byneskranskop I	Schweitzer & Wilson (1982); Klein & Cruz-Uribe (1983)
Connies Limpet Bar	Buchanan (1988)
Die Kelders I	Tankard & Schweitzer (1976); Schweitzer (1979); Grine et al. (1991); Klein & Cruz-Uribe (2000); Marean et al. (2000)
Duiker Eiland	Robertshaw (1979)
Dune Field Midden	Parkington et al. (1992); Orton (2002); Tonner (2005)
Elands Bay Cave	Klein & Cruz-Uribe (1987); Parkington (1988)
Hail Stone Midden	Buchanan (1988)
Hawston	Avery (1976)
Hoedjiespunt 1 & 3	Berger & Parkington (1995); Stynder et al. (2001)
Klasies River Main	Singer & Wymer (1982); Deacon (1995)
Nelson Bay Cave	Klein (1972); Deacon (1984); Inskeep (1987)
Paternoster 1062	Yates (1998)
Pearly Beach	Avery (1976)
Sea Harvest	Volman (1978)
Steenboksfontein	Jerardino & Yates (1996); Jerardino & Swanepoel (1999)
Ysterfontein I	Halkett et al. (2003); Klein et al. (2004)

TABLE 1
List of MSA and LSA sites discussed in the text, with their key references.

forces generated by the earth's rotation and southeast winds moves the surface water offshore, and deep, cold water upwells near the coast to replace it. This cold water provides little moisture to the adjacent landmass, so the region has long, warm, dry summers. Seasonal changes in the position of the South Atlantic High Pressure Cell create cold fronts that promote short, cool, wet winters. The cold, upwelling water is rich in nutrients, fueling a very productive marine food chain dominated by kelp-forests. Although the rocky shores of this region, extending from Cape Point, South Africa to Walvis Bay, Namibia, contain only about half the number of species as in other coastal regions of South Africa, the biomass along of west coast is significantly higher due to these abundant nutrients (Bustamante & Branch, 1996).

The rocky shores of the west coast are dominated by mollusks and seaweeds, including kelp (Bustamante & Branch, 1996). Today, the most common mollusks are granite limpets (*Cymbula granatina*), granular limpets (*Scutellastra granularis*), Argenville's limpets (*S. argenvillei*), Mediterranean mussels (*Mytilus galloprovincialis*)

and ribbed mussels (Aulacomya ater) (Bustamante & Branch, 1996). Mediterranean mussels were introduced from Europe in the 1970s and have significantly reduced the numbers of native black mussels (Choromytilus meridionalis). Granite, granular, and Argenville's limpets dominate the archaeological record, along with black mussels. Other limpets (S. barbara, S. cochlear, C. miniata, C. compressa, Helcion spp.), topshells (Oxystele sp.), whelks (Burnupena spp., Nucella spp., Argobuccinum pustulosum), and plough shells (Bullia spp.) are found to varying degrees. Ribbed mussels are rare in archaeological assemblages, likely because they live primarily in the subtidal and therefore humans must dive to collect them. White mussels (*Donax serra*) are common in some assemblages. They are sand burrowers, so their frequency may depend on the ratio of nearby sandy to rocky shore. Rock lobsters (Jasus lalandii) are also common in some archaeological samples.

The Agulhas current, one of the most powerful in the world, comes from the subtropical Indian Ocean and runs from northeast to southwest along

the east coast of South Africa, bringing warm water with it (Branch et al., 1981; Branch et al., 1994). The land along the Agulhas current enjoys a higher rainfall than on the west coast, and therefore has a richer terrestrial environment. The coastline from southern Mozambique to about Port St. John's in the Transkei of South Africa, the east coast, is a subtropical zone, with abundant corals, tropical fish, and crabs. Species diversity is high, because Indo-Pacific species also contribute to the local fauna (Bustamante & Branch, 1996). Beginning just south of the Transkei, the continental shelf widens, making the Agulhas current swing away from the south coast, allowing the coastal waters to become slightly cooler and permitting a near-shore counter-current of cooler water (Branch et al., 1981; Branch et al., 1994).

As on the west coast, mollusks and seaweeds are abundant in the rocky intertidals of the south and east coasts, but other common taxa include articulate corallines and barnacles (Bustamante & Branch, 1996). Today, the most common mollusks are brown mussels (Perna perna), goat's eye limpets (C. oculus), long-spined limpets (S. longicosta), pear limpets (S. cochlear), false limpets (Siphonaria spp.), pink-lipped topshells (O. sinensis), and rock oysters (Saccostrea cuccullata) (Bustamante & Branch, 1996). The archaeological record for this region is best known on the south coast from Port Elizabeth westwards. Brown mussels and limpets are the most common taxa in the archaeological assemblages, but turban shells (Turbo sarmaticus) are also quite abundant. Giant limpet (S. tabularis), white mussels, topshells, whelks, chitons (Dinoplax gigas) and abalone (Haliotis spp.) are present in varying frequencies. Black mussels and granite limpets, mollusks typical of the west coast, are commonly found in archaeological assemblages in the western end of the south coast, where eddies from the Bengula current influence water conditions. During the colder periods of the Late Pleistocene, the range of these cold-water adapted species expanded even further east, indicating colder water temperatures during these times.

STUDIES ON THE WEST COAST

Our current research has been motivated by our excavations at the Middle Stone Age rockshelter of Ysterfontein 1 (YFT1) (Halkett *et al.*, 2003;

Klein *et al.*, 2004). YFT1 is on the west coast of South Africa, about 70 km north of Cape Town. Only eight well-documented MSA shell middens are known in South Africa, and YFT1 is the only one to be systematically excavated on the west coast. Many LSA middens provide comparative samples for our research. Although the LSA is older elsewhere in sub-Saharan Africa, these samples extend back only to about 14 kya, because before this time, the coast was mainly displaced too far seawards.

YFT1 is a deeply stratified rockshelter that was exposed in the 1980's when a road leading to a boat harbor was widened. The rockshelter has a diorite platform floor that rises about 7 m above sea level, and the walls and roof are made of calcrete. The deposits are 3.8 m thick and are primarily weakly cemented, highly calcareous, yellowish sands. A calcrete shelf, which may have originated from a roof collapse, divides the fill in two, separating the «Upper» and «Lower» deposits. Five excavation seasons have provided abundant mussel and limpet shells, numerous fragments of ostrich eggshell, and somewhat rarer bones from mammals, birds, tortoises, and snakes. The stone artifacts are classic MSA with denticulate retouch, and there is little variation in typology throughout the sequence, although some variation in raw material is present. Direct human involvement at the site is indicated by hearth structures, including ashy deposits and rubification. Mollusks occur in discrete layers and lenses in the middle and lower parts of the sequence, hearths are also common, indicating intact deposits. Archaeological material, including mollusks, stone artifacts, and mammal bones, is more ephemeral in uppermost deposits. These levels may have originated from human activities occurring on the rear face of dunes that formerly stood between the shelter and the ocean, because by this time the rockshelter would have been filled to the point where it was no longer usable by humans. While containing many large animal bones and stone artifacts, these ephemeral deposits also contain large quantities of dune mole rat bones (Bathyergus suillus) and tiny fish vertebrae, indicating a non-human impact on the deposits from burrowing mole rats and small carnivores or birds adding small fish. Although they are most visible directly below the calcrete shelf, mole rat burrows are visible throughout the sequence. They are marked by a change in soil color and texture, and shells tend to stand on edge in these burrows, while they are sub-horizontal in the intact deposits.

AMS radiocarbon dates on a piece of ostrich eggshell from an initial test excavation provide a minimum age for the deposits (organic component: $33,470 \pm 510$ years B.P. [Beta-169978]; inorganic component: >46,400 years B.P. [Beta-171202]) (Halkett et al., 2003). Because the deposits are older than the effective range of the radiocarbon method, we examined local bathymetry (ocean bottom topography) and global estimations of sea level change during the Late Pleistocene glacial cycles to help place the deposits in time. Ethnographic and archaeological data indicate that people rarely move marine shells more than 10 km from the shore (as summarized in Buchanan, 1988: 88). Bathymetry indicates that if sea level dropped by approximately 40 m, the shoreline would be further than 10 km from YFT1. Examination of hypothesized Late Pleistocene sea levels shows that the shoreline was within 10 km of YFT1 during Marine Isotope Stage (MIS) 3c (ca. 50-57 kya), 5a (ca. 71-88 kya), 5c (ca. 95-105 kya), and 5e (ca. 115 kya) (Miller et al., 2005: fig. S2). Sometimes during MIS 5e (ca. 120-126 kya), the sea was 10 m or more above today's levels, and this very high sea may have produced the rockshelter or flushed it of its previous contents. However, to further determine when the deposits accumulated, we are radiometrically dating the sands in the deposits using Optically Stimulated Luminescence.

Almost 20 taxa of mollusks are present in the YFT1 deposits, and almost all are intertidal species. Using minimum numbers of individuals and shell weight, black mussels and granite, Argenville's and granular limpets overwhelmingly dominate the assemblage, in this order (Klein et al., 2004). These taxa are the most abundant, most visible, and most easily collected intertidal shellfish on the west coast today, and they dominate almost all west coast MSA and LSA samples (Buchanan, 1988; Jerardino, 1997; Halkett, 2003; Parkington, 2003; Klein et al., 2004; Orton et al., 2005). However, the ratio of limpets to black mussels varies through the YFT1 sequence, and also from site to site and time to time (Buchanan et al., 1978; Buchanan et al., 1984; Buchanan, 1988; Parkington, 2003), likely depending on differences or changes in the nature of the nearby rocky coastline and the distance from the site to the collecting area. LSA people tended to carry mussels further from the shore, because mussels have much higher flesh weights relative to shell weight. An increase in mussel abundance may signal either a receding coastline or a change in the geomorphology of the local shoreline. Even small sea level changes could significantly affect the relative numbers of limpets and mussels locally (Jerardino, 1997), and we hypothesize that sea level changes are influencing the variation in relative abundance of limpets and mussels in the YFT1 sequence.

Despite the abundance of mollusks at the site, none of the YFT1 shells show any evidence of human modification, such as use as a scraper or bead. Therefore, we assume that humans brought the overwhelming majority of shells into the site for subsistence purposes. It is possible that kelp gulls (Larus dominicanus) may have introduced some mussels into the archaeological sites, because gulls are known to open both white and black mussels by dropping them from the air onto relatively hard surfaces (Siegfried, 1977; Maclean, 1985; personal observation). However, because only humans are known to transport limpets into sites, we assume that when limpets are common in an assemblage, people are the source of most of the mussels, too.

Local LSA assemblages differ from YFT1 and other west coast MSA assemblages in the overall species present and the shellfish species that dominate the assemblages, reflecting a wider diet breadth during the LSA (Parkington, 2003; Klein et al., 2004). MSA shellfish assemblages are strongly dominated by limpets and black mussels, and other mollusk species appear only in very small quantities. Limpets and black mussels also dominate many LSA assemblages, but other mollusks can be quite frequent, especially white mussels and Burnupena (Buchanan et al., 1978). Among the limpets, MSA assemblages contain relatively more granite and Argenville's limpets than granular limpets, but LSA people collected more granular limpets than MSA people. Granular limpets are smaller than granite and Argenville's limpets, but they are more numerous and occur higher on today's rocky shores (Buchanan, 1988; personal observation). If this were true in the past as well, then granite limpets would have been more visible and accessible to MSA foragers. MSA people must have passed over granular limpets in favor of the larger granite and Argenville's limpets. In addition to their low diversity of mollusks, MSA assemblages totally lack rock lobster chelipeds or claws, which are numerically variable but consistently present in west coast LSA assemblages (Buchanan, 1988; Jerardino et al., 2001; Orton et al., 2005). Finally,

in LSA sites where fish bones are present, fish bones outnumber mammal bones by an order of magnitude, while fish bones are very rare in MSA assemblages. Only LSA sites have produced artifacts that resemble historic fishing implements, such as fish gorges.

MSA and LSA assemblages also differ in the typical size of their mollusks (Parkington, 2003; Steele & Klein, 2005/2006). The maximum lengths of granite limpets from the MSA are significantly larger than those from the LSA (Figure 2). Granular (Figure 3) and Argenville's limpets (Figure 4) show a similar pattern, but not as strongly, possibly reflecting smaller sample sizes. As we describe in more detail elsewhere (Steele & Klein, 2005/2006), we propose that this difference in size is the result of less intense harvesting by MSA people, because they lived at lower population densities than LSA people. Limpets grow slowly and continuously and can be captured with little technology or risk. In many instances, humans tend to take the largest mollusks first, because they are more readily visible or available, provide a higher caloric return rate, or taste better (Bigalke, 1973; Branch, 1975; Hockey & Bosman, 1986; Lasiak, 1991, 1992). Under heavy predation, the consistent capture of the largest mollusks can drive down the median size of the mollusk population (Branch, 1975; Hockey & Bosman, 1986; Hockey et al., 1988; Mannino & Thomas, 2001). However, it is also important to consider environmental influences on mollusk size, because water temperature, water turbidity, mollusk population density, geomorphology, topography, and exposure to wave action all influence mollusk growth rates (Jerardino, 1997; Mannino & Thomas, 2001, 2002; Branch & Odendaal, 2003; Cabral & Da Silva, 2003).

Two lines of evidence suggest that smaller mollusk size during the LSA, compared to the MSA, was caused by higher human predation pressure, not environmental differences (Steele & Klein, 2005/2006). First, our samples are drawn from a range of time periods and geographic settings that represent different temperature regimes, precipitation levels, sea levels, floral and faunal communities, and coastal configurations, as well as probable different seasons of shellfish collection and site functions. By encompassing this variation, it is more likely that the differences in size reflect predation intensity and not environmental factors. Second, our comparisons of granite and granular limpets include modern samples («ten-minute samples») that were collected from previously unexploited rocks near some of the LSA samples (Buchanan *et al.*, 1978; Parkington, 2003). Some of these LSA samples are less that 2,000 years old and, therefore, formed under environmental conditions very similar to modern ones. In almost all cases, the limpets in these «ten-minute samples» are larger than the LSA limpets, further supporting our proposal that high collection pressure during the LSA reduced the size of the archaeological limpets, rather than the environment.

Measurements of the prismatic band breadth of black mussels, which is highly correlated with mussel length (Hall, 1980; Klein & Steele, unpublished data), show that variation in mussel size overlaps during the MSA and LSA (Halkett et al., 2003; Parkington, 2003). Black mussels grow faster and re-colonize more readily than limpets, and unlike limpets they live in both the intertidal and subtidal zones. There is no evidence that people collected mollusks in the subtidal zone, so the mussels that lived in this deeper zone provided a reservoir for rapid replenishment of exploited tidal populations. Therefore, black mussel size may not reflect predation pressure as readily as limpets do, especially when palimpsests must be considered. It may be that human impact on mussels is more detectable when finer samples reflecting shortterm collection events are available (Jerardino, 1997).

In our current research program, we intend to address environmental controls more directly. We hope to investigate the utility of oxygen-isotope analyses, along with other methods that will provide more direct control over key environmental factors. In addition, we can consider limpet shape in conjunction with limpet size, because limpet height may change with exposure and wave intensity, possibly providing information on its environmental context (Claassen, 1998).

THE SOUTH COAST

In general, research into MSA and LSA shell-fish exploitation on the south coast has not been as extensive as on the west coast, and fewer assemblages are available. Klasies River Mouth (Voigt, 1982; Thackeray, 1988; Klein, 2001) and Blombos Cave (Henshilwood *et al.*, 2001) have provided both MSA and LSA samples, and a handful of additional LSA samples are known. Ongoing

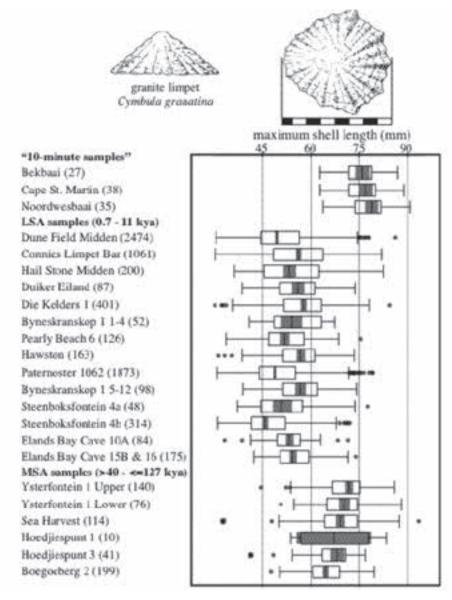


FIGURE 2

Box plots summarizing the maximum length of granite limpets from MSA and LSA sites on the west coast of South Africa. Numbers in parentheses after each site and layer indicate the sample size in each assemblage. The median is represented by the vertical line near the center of each box plot; the open rectangle encloses the middle half of the data (between the 25th and 75th percentiles); the shader cettangle designates the 95% confidence limits of the median; the horizontal line bisecting each plot signifies the range of more or less continuous data; and starbursts and open circles mark outliers. When the 95% confidence limits for two sample medians do not overlap, the medians differ at or below the 0.05 significance level. Box plots were constructed using DataDesk 6.2 (Velleman, 1997).

excavations, such as at Mossel Bay (Marean *et al.*, 2004), should produce additional samples for further comparisons. However, the Transkei has provided opportunities for extensive ecological and

ethnographic research on mollusks and their exploitation (Bigalke, 1973; Branch, 1975; Hockey & Bosman, 1986; Hockey *et al.*, 1988; Lasiak, 1991, 1992).

Mollusk species abundance changes through the long MSA sequence at Blombos Cave, when determined by percentage of total shell weight (Henshilwood *et al.*, 2001). Turban shells are the most common species throughout the sequence, followed by brown mussels and limpets. The youngest layers contain the largest quantities of brown mussels and only modest amounts of limpets, primarily Argenville's and goat's eye limpets. In the oldest level, brown mussels are vir-

tually absent, and Argenville's and goat's eye limpets are relatively more abundant than in the younger levels. Also in the oldest levels, granite limpets are present in significant quantities and black mussels are present in small quantities. This incursion of cold-water-adapted west coast species into the historically warmer south coast indicates that the water temperature was cooler while the oldest deposits at Blombos were accumulating. Black mussels are also found in the Terminal

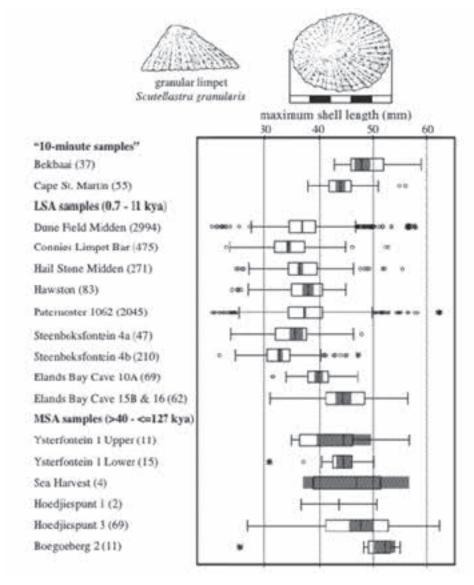


FIGURE 3

Box plots summarizing the maximum length of granular limpets from MSA and LSA sites on the west coast of South Africa. The legend to Figure 2 explains the box plot format.

Pleistocene deposits of Nelson Bay Cave, indicating cooler waters were also present there during the Last Glacial Maximum (Klein, 1972). In the future, we plan to integrate changes in mollusk abundance from the south coast with the data available on the west coast to create an interregional chronology of environmental and technological change.

The south coast assemblages preserve a large number of Cape turban shells, mainly recognizable by their sturdy opercula. Length measurements of opercula from MSA and LSA samples show that MSA Cape turban shells were larger than LSA ones (Figure 5). These results support those obtained for limpets from the west coast sites. Congruent results from multiple taxa living with different habitat preferences thriving under varying environmental regimes further supports the hypothesis that high human predation pressure is influencing the smaller size of LSA limpets rather than environmental factors (Steele & Klein, 2005/2006).

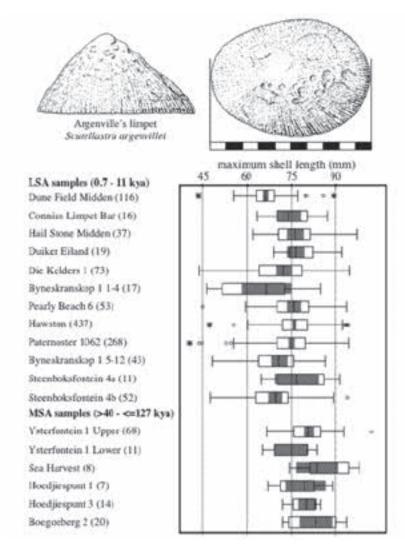


FIGURE 4

Box plots summarizing the maximum length of Argenville's limpets from MSA and LSA sites on the west coast of South Africa. The legend to Figure 2 explains the box plot format.

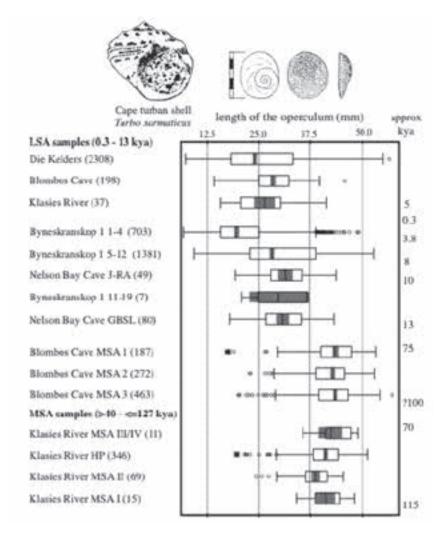


FIGURE 5

Box plots summarizing the maximum length of Cape turban shell opercula from MSA and LSA sites on the south coast of South Africa. The legend to Figure 2 explains the box plot format.

SUMMARY AND CONCLUSIONS

The coast of South Africa provides a rich area for archaeomalacological research. Shellfish remains are abundant and often well preserved, allowing us to use them to address questions relating to human subsistence ecology and paleoenvironments. LSA people had a wider diet breadth than MSA people. They regularly incorporated more shellfish taxa into their diet, including small mollusks and rock lobsters. They also took many more fish and flying birds, such as cormorants

(*Phalacrocorax* sp.). There is no MSA assemblage where fish are common, and African penguins (*Spheniscus demersus*) are abundant only in MSA samples. In addition, limpets are smaller during the LSA, suggesting that LSA people exploited mollusks more heavily than MSA people, possibly because they had a higher population size or density.

Our research into MSA and LSA shellfish exploitation is continuing. We are investigating how to account for the influences of the environment on the composition of the assemblages. This

is particularly relevant for testing the hypothesis that environmental conditions are influencing shell size more than human predation pressure. We are looking into multivariate analyses that will reveal if there is a relationship between shell size, shell shape and proxies for the local environment. Additional samples are important for accomplishing these goals.

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