

Archaeological shellfish size and later human evolution in Africa

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Approximately 50 ka, one or more subgroups of modern humans expanded from Africa to populate the rest of the world. Significant behavioral change accompanied this expansion, and archaeologists commonly seek its roots in the African Middle Stone Age (MSA; ~200 to ~50 ka). Easily recognizable art objects and “jewelry” become common only in sites that postdate the MSA in Africa and Eurasia, but some MSA sites contain possible precursors, especially including abstractly incised fragments of ocher and perforated shells interpreted as beads. These proposed art objects have convinced most specialists that MSA people were behaviorally (cognitively) modern, and many argue that population growth explains the appearance of art in the MSA and its post-MSA florescence. The average size of rocky intertidal gastropod species in MSA and later coastal middens allows a test of this idea, because smaller size implies more intense collection, and more intense collection is most readily attributed to growth in the number of human collectors. Here we demonstrate that economically important Cape turban shells and limpets from MSA layers along the south and west coasts of South Africa are consistently and significantly larger than turban shells and limpets in succeeding Later Stone Age (LSA) layers that formed under equivalent environmental conditions. We conclude that whatever cognitive capacity precocious MSA artifacts imply, it was not associated with human population growth. MSA populations remained consistently small by LSA standards, and a substantial increase in population size is obvious only near the MSA/LSA transition, when it is dramatically reflected in the Out-of-Africa expansion.

modern human origins | prehistoric coastal foraging | stone age population size | Still Bay | Howieson's Poort

Fossils and genes show that modern humans evolved in Africa and expanded from there to Eurasia beginning 60–50 ka. Most archaeologists attribute the expansion to behavioral change, which they trace to the African Middle Stone Age (MSA) between approximately 200 and 50 ka. Evidence for change comes primarily from two South African MSA variants—the Still Bay and the succeeding Howieson's Poort—and it especially comprises abstractly incised fragments of ocher, perforated shells interpreted as beads, and other proposed symbolic objects or jewelry. These are seen as precursors to the more abundant, more finely made art objects that appear in African Later Stone Age (LSA) and contemporaneous European Upper Paleolithic sites after 50 ka. The precise dating of the Still Bay and Howieson's Poort variants is debated (1, 2), but the Still Bay antedates the Howieson's Poort, and together they probably fall mainly in the interval between 85 and 65 ka.

The artifacts that define Still Bay assemblages are well-made bifacial leaf-shaped points, and Still Bay layers at Blombos Cave have provided most of the incised ocher fragments and perforated shells that are thought to signal the appearance of symbolism in the MSA (3). The artifacts that distinguish subsequent Howieson's Poort assemblages are steeply retouched (backed or truncated) flakes and blades that resemble small, thin segments of an orange. Except for incised fragments of ostrich eggshell

from Diepkloof Rock Shelter (4), proposed art objects are rare in Howieson's Poort layers, but the segments themselves are sometimes considered an index of modern cognition (5).

Today, specialists commonly propose that population growth explains both the initial flickering of modern behavior in the Still Bay and Howieson's Poort and its full florescence after 50 ka (6, 7). Our purpose here is to examine this proposition through an analysis of average mollusc size in coastal South African middens. We argue that average size in oft-exploited rocky intertidal species mostly reflects the number of human collectors, and if this is accepted, we infer that by LSA standards, MSA human populations were consistently small. Comparably small populations characterized all MSA variants, including the Still Bay and Howieson's Poort. Population growth is thus unlikely to explain artifactual (behavioral) innovation within the MSA, and alternative explanations must be explored.

Antiquity of Human Shellfishing

Pinnacle Point Cave 13B, South Africa (8) and Bajondillo Cave, Spain (9) show that human shellfishing began at least 160–150 ka, during the MSA in Africa and the coeval Middle Paleolithic (also known as Mousterian) of Europe. Neither site has provided human fossils, but where human remains occur with similar artifacts elsewhere in Africa and Europe, the Africans were anatomically derived toward modern humans, whereas the Europeans were Neanderthals (10). Ancient shellfishing in two such geographically and morphologically distinct groups could represent behavioral convergence, or it could have been inherited from the last ancestor they shared between 700 and 400 ka (11).

In both Africa and Eurasia, stratified coastal occupation sites that demonstrably antedate 150–160 ka remain unknown. However, ethnographic observations like those initiated by Bigalke along the Transkei coast of South Africa (12) and those undertaken by the Birds and colleagues in the Meriam Islands, Australia (13) show that shellfishing requires little or no special knowledge, technology, or bodily risk, so long as it is restricted to intervals of low tide that can be observed from the shore. Shellfishing by numerous nonhuman species (14, 15), including coastal baboons (*Papio* spp.) in Africa (16), coastal macaques (*Macaca fascicularis*) in Thailand (17), and kelp gulls (*Larus dominicanus*) in South Africa and elsewhere (18), underscore this conclusion. In sum, the nutritional value and easy accessibility of shellfish imply that when coastal occupation sites older than 160–150 ka are found, they will likely reveal yet earlier shellfishing, perhaps from the time that people first occupied sea coasts.

So far, South African coastal caves dating primarily to the Last Interglacial [marine isotope stage (MIS) 5], between roughly 130 and 71 ka, have provided the most extensive evidence for ancient

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shellfish collection. The shells at each site tend to be as densely packed as they are in the much later prehistoric middens that dot the coasts of every inhabited continent, and they thus imply a broadly comparable, if much older interest in shellfishing. Among the ancient South African sites, the best known are Klasies River (19, 20) and Blombos Cave (21) on the south (Indian Ocean) coast, and Ysterfontein 1 (22), Hoedjies Punt (ref. 23, pp. 99–100), Sea Harvest (24), and Boegoeberg 2 (25) on the west (Atlantic) coast. Fig. 1 locates these sites and others we mention below. The dating in each case depends mainly on optically stimulated luminescence (OSL) [especially by Jacobs et al. (26)] or on artificial similarities to other sites dated by OSL (27). The sites all contain MSA artifact assemblages, including ones assigned to the Still Bay variant at Blombos Cave and to the Howieson's Poort variant at Klasies River. Deeply stratified MSA sequences at Diepkloof Rock Shelter (28) and Sibudu Cave (29) confirm that the Still Bay variant antedates the Howieson's Poort variant, and they show that both variants were preceded, succeeded, and perhaps partly contemporaneous with other less distinctive variants that are represented at Klasies River, Blombos, and the other sites.

South African Coasts and Their Intertidal Shellfish

At present, the south and west coasts of South Africa differ conspicuously in their intertidal environments, reflecting the contrasting influence of the warm Agulhas Current, which flows westward along the south coast, and of the cold Benguela current, which flows northward along the west coast (30). The intertidal contrast is particularly obvious in the most numerous, most visible, and most readily collectible molluscs, all of which attach to intertidal rocks. On the south coast, these are the brown mussel (*Perna perna*), Venus ear and perlemoen abalones (*Haliotis spadicea* and *Haliotis midae*), Argenville's limpet (*Scutellastra argenvillei*), long-spined limpet (*Scutellastra longicosta*), goat's eye limpet (*Cymbula oculus*), and Cape turban shell (*Turbo sarmaticus*). On the west coast, they are the black mussel (*Choromytilus meridionalis*), granite limpet (*Cymbula granatina*), granular limpet (*Scutellastra granularis*), and Argenville's limpet. South and west coast molluscan species mixed to some extent on intertidal rocks between Cape Agulhas and Melkbosstrand, and eddies of warm water spun off from the Agulhas current sometimes allowed south coast species to establish small colonies as far north as Sea Harvest and

Hoedjiespunt (Saldanha Bay). However, LSA middens show that outside the region of mixture, the fundamental geographic contrast in rocky intertidal species persisted throughout the Present Interglacial (MIS 1), from 11.5 ka to the present.

The intertidal communities may have differed less during the Last Glaciation (MIS 4–2), between roughly 71 and 11.5 ka, when the southern ocean was generally cooler. Cooler water, perhaps associated with increased near-shore upwelling, explains why black mussels, which were historically restricted to west coast rocks, abound in south coast middens that formed between 12 and 10 ka at Nelson Bay Cave (31) and Matjes River Shelter (32). Black mussels and granite limpets, another west coast endemic, occur occasionally in the MIS 5 MSA middens at Klasies River and Blombos Cave, but they are always far outnumbered by brown mussels, Cape turban shells, goat's eye limpets, long-spined limpets, abalones, and other species that dominated south coast intertidal rocks historically and that dominate all south coast middens postdating 10 ka. The sum implies that the historic difference in rocky intertidal molluscan communities that marked LSA sites dating to MIS 1 also characterized MSA middens dating to MIS 5.

On both the west and south coasts, different molluscs favor different depths within the rocky intertidal zone, and their relative abundance thus depends on the flatness or steepness of the zone and on other factors, such as the degree of exposure to waves. In general, mussels, which are filter feeders, prefer more exposed settings where moving water renews their food supply, whereas limpets, which mostly graze on algae attached to rocks, prefer more protected settings from which they are less likely to be dislodged. On each coast, fluctuations in sea level and coastal configuration probably explain variation in the overall abundance of rocky intertidal species and in their relative proportions from layer to layer within deeply stratified stone age sites, including MSA sites like Klasies River (33), Blombos Cave (21), and Ysterfontein 1 (22), and LSA sites like Nelson Bay Cave (31), Byneskranskop Cave 1 (34), and Elands Bay Cave (ref. 23, pp. 63–81). Shifts in collector behavior may sometimes also have played a role.

Shellfish Size and Human Collection Intensity

Water temperature, salinity, turbidity, nutrient availability, species population density, and overall community composition all affect intertidal molluscan growth rates and may thus contribute to geographic or temporal variation in average size within a molluscan species (35). However, we will probably never have information on the factors that could have affected growth rates near prehistoric sites, and temporal and spatial averaging within the MSA and LSA limits the likelihood that such factors underlie the size differences we report between MSA and LSA gastropods. Moreover, recent observations suggest that it is the intensity of human predation that most commonly produces substantial differences in mean size, particularly in attractive, highly visible, rocky intertidal gastropods like those that MSA and LSA people targeted on both South African coasts. On the South African south coast, for example, goat's eye limpets (36) and perlemoen abalone and Cape turban shells (37) in similar intertidal settings are all much larger where they are protected from human collection. On the west coast, granite and granular limpets on currently unexploited rocks average much larger than in any known archaeological site, including recent LSA middens that probably formed under the same environmental conditions (38). Variation in the intensity of human predation pressure is particularly likely to impact average size in slow-growing species like limpets, abalones, and turban shells, in which undisturbed individuals can take a decade or more to achieve maximum possible adult size. Human collection pressure is less likely to substantially reduce average size in intertidal mussels, because they grow much more rapidly than limpets and because substantial subtidal populations often provide a source for rapid intertidal recolonization.

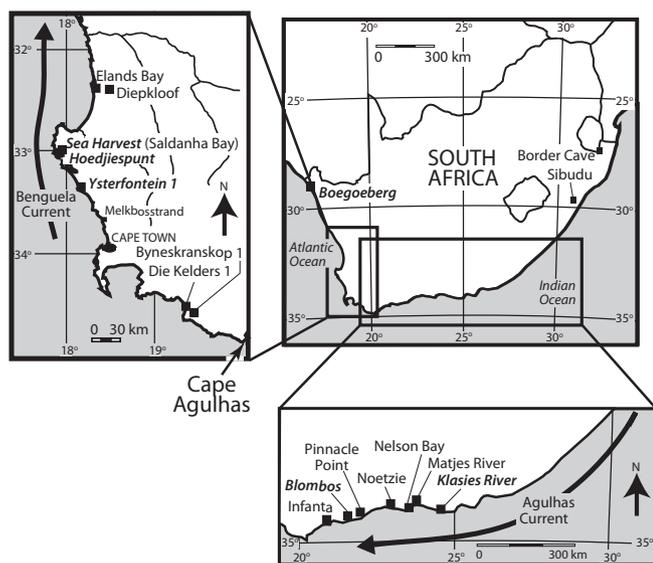


Fig. 1. Map showing the locations of the sites mentioned in the text. Italics and boldface mark the MSA sites that provided our measured gastropod samples.

Human predation is probably also less likely to reduce average size in molluscs that inhabit sandy intertidal beaches, because the largest individuals tend to occur low on the shore where they are relatively inaccessible (39). On both South African coasts, stone age people sometimes collected a sandy beach mollusc, the white mussel (*Donax serra*) (40). Overall, however, the species is too rare in stone age middens for a meaningful analysis of intersite size variation, and we therefore do not consider it here.

With historic observations in mind, archaeologists now frequently conclude that changing human collection pressure underlies size variation in the molluscs that dominate deeply stratified sequences (41), and they often attribute changing collection pressure to changing human population density. For example, growth in collector numbers almost surely explains a conspicuous decline in mollusc size after the initial human colonization of New Ireland, Papua New Guinea, approximately 33 ka (42). It also probably explains size declines in key mollusc species after initial human occupation of islands in the Santa Barbara Channel, southern California, 10 ka or more, not only because the declines followed on local human population growth but also because they occurred independently of demonstrated past variation in overall marine productivity and sea surface temperatures (43, 44). A further particularly notable case is Moloka'i, Hawaiian Islands, where size decline in a common limpet species after initial Polynesian colonization at roughly 1200 AD was reversed when European contact beginning 450 y later led to massive human depopulation (45).

We have shown previously that on average, MSA granite limpets, granular limpets, and Argenville's limpets on the South African west coast were significantly larger than their LSA counterparts (22). The MSA and LSA sites formed under broadly similar

interglacial conditions over thousands of years, or in the case of the MSA sites, perhaps over tens of thousands of years. In addition, in previous work (22), we found that the angulate tortoise (*Chersina angulata*)—a readily collectable resource that is abundant in many west coast MSA and LSA sites but that inhabits a totally different, terrestrial ecosystem—also tends to be larger in MSA sites. From the sum, we concluded that smaller LSA limpet size implied more intense LSA collection, and we suggested that more intense collection was probably a function of larger, denser LSA populations. Further in support of this conclusion, compared with west coast MSA middens, local LSA middens are richer in species other than the basic mussels and limpets, and they are significantly richer in granular vs. granite limpets (46). The granular limpet and the other species that occur more frequently in LSA middens tend to be relatively small, and LSA people collecting more intensively would have been less likely to overlook them.

South Coast Sites and Their Measured Shell Samples

In previous reports, we emphasized west coast MSA and LSA limpets and briefly explored south coast Cape turban shells (47, 48). Here, we introduce measurements on goat's eye limpets and Argenville's limpets from south coast MSA and LSA sites, and we greatly expand the sample of accompanying MSA and LSA turban shells. We show that all three species exhibit the same pattern as on the west coast—MSA representatives tend to be significantly larger than their local LSA counterparts. The main south coast MSA sites are Klasies River and Blombos Cave, referenced previously. Relevant LSA sites are more common, and they are often well dated by radiocarbon. Some important LSA sites, especially Die Kelders Cave 1 (49) and Byneskranskop Cave 1 (34), occur in the region west of Cape Agulhas where south and west coast rocky intertidal communities mix, and they contain species from both communities. In such sites, the west and south coast gastropods that we highlight tend to be as small as representatives of the same species in LSA sites outside the region of mixture, but we have excluded the "mixed" sites to avoid the possible influence of a mixed intertidal community on species size. For present purposes then, we consider only samples from east of Cape Agulhas—from Nelson Bay Cave, which spans MIS 1 from 12 to 11 ka to the historic present (50, 51), Noetzie Midden (Knynsa), which formed mostly between approximately 5 and 2 ka (52), Cape Infanta middens 3, 16, and 18, which formed between 4.5 and 3.5 ka, and the LSA deposits at Blombos Cave and Klasies River, which mainly postdate 3 ka.

Nelson Bay is particularly important, because together with Matjes River Shelter and Byneskranskop 1, it shows that the south coast was continuously inhabited throughout MIS 1, including the interval between 8 and 5–4 ka, when the interior and west coast of South Africa were mainly too dry to support archaeologically visible populations (53). Various paleoenvironmental indicators summarized in ref. 54 imply that the southern coastal region also became moister after approximately 5 ka, and the rocky intertidal gastropods from Nelson Bay, supplemented by those from Noetzie, the Cape Infanta middens, and the LSA deposits at Blombos Cave and Klasies River, allow a further check on the notion that larger human populations, promoted in this case by increased moisture, reduced average gastropod size.

With respect to south coast species that could be important to our analysis, we excluded long-spined limpets, abalones, and brown mussels for varying reasons. The problem with the long-spined limpet is that the spiny projections for which the species is named are most pronounced in young individuals, and they tend to retreat with age. Older individuals can thus have shorter shells, and in the archaeological samples we have examined, individuals that were surely older according to shell bulk were often shorter than individuals that were surely younger according to the same criterion. The problem with abalones and brown mussels is extreme

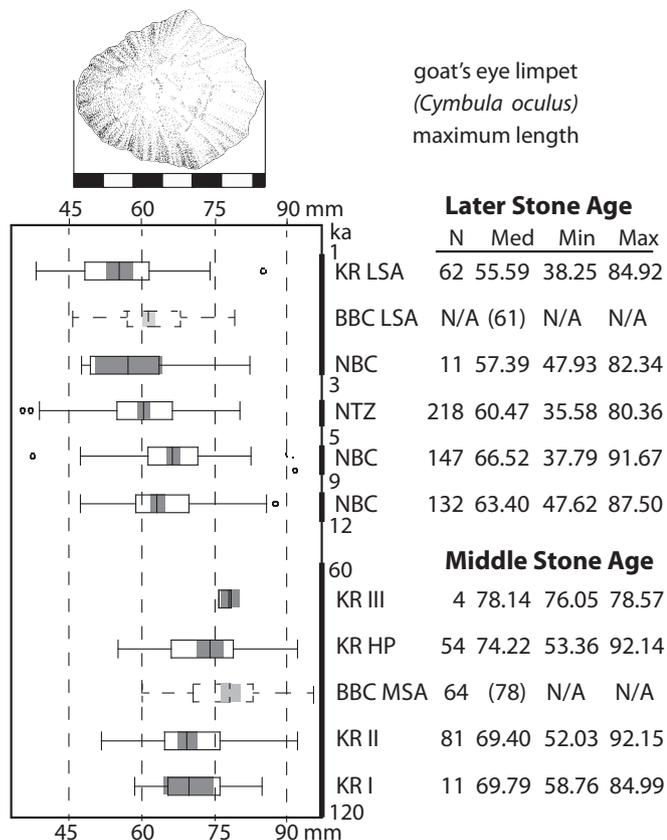


Fig. 2. Variation in the maximum length of goat's eye limpets (*C. oculus*), arranged roughly from oldest (bottom) to youngest (top).

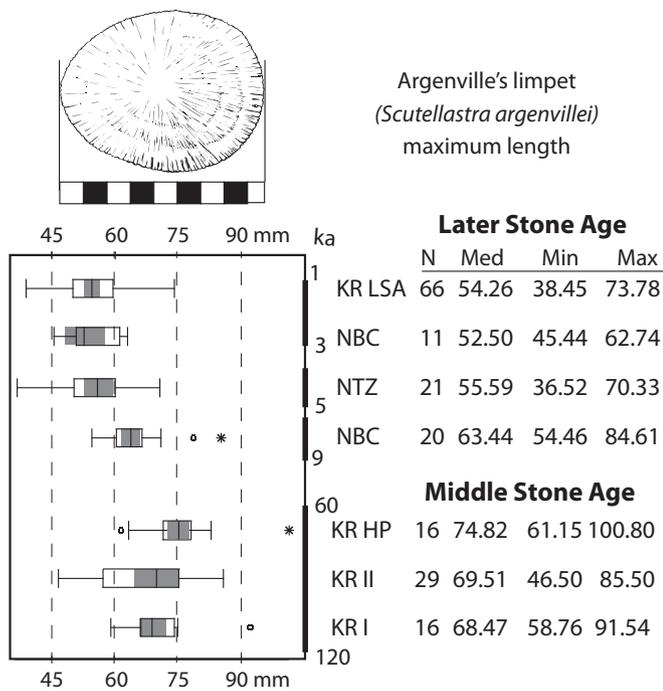


Fig. 3. Variation in the maximum length of Argenville's limpets (*S. argenvillei*), arranged roughly from oldest (bottom) to youngest (top).

fragmentation, combined with the absence of a readily measurable dimension on fragments. Black mussels in west coast sites tend to be equally fragmented, but the anterior margin of each valve exhibits an easily measurable prismatic band whose breadth reflects overall size (55). Our measurements suggest that average black mussel size varied significantly within both the MSA and the LSA (22) but not between them. We attribute the lack of an MSA/LSA difference to the rapid growth and substantial subtidal backup populations that distinguish mussels from limpets. Subjectively, and for the same reasons, we think that brown mussel size might not differ significantly between the MSA and LSA, but if possible, this needs to be verified directly, because studies of mussels elsewhere have sometimes identified long-term size changes that probably reflect more intensive human predation (43).

Results of Shellfish Measurements

Like most other shellfish analysts, to compare shellfish size among samples, we have focused on the largest readily definable dimension on a shell, which for simplicity's sake, we call "length." This dimension is a function of age, and if we could, we would use age itself, because this would control for the possibility of environmentally determined changes in growth rates (41). Unfortunately, for the species that concern us, direct estimation of individual age is not possible.

Because shellfish length is a function of age, it cannot be normally distributed, and we have therefore used the median to describe its average, and boxplots, produced by DataDesk 6.3 (56), to compare the medians among samples. In the boxplot for each sample, as presented in Figs. 2–4, the vertical line near the center marks the median, the open rectangle around the median encloses the middle half of the data (between the 25th and 75th percentiles), the shaded rectangle indicates the 95% confidence limits for the median, and the line bisecting the rectangles signifies the range of more or less continuous data. Asterisks and open circles designate outliers (values that are especially far from the median). In conventional statistical terms, when the 95% confidence limits for two medians do not overlap, the medians differ significantly, that

is, for reasons other than chance. The median-based boxplots allow statistical comparisons even between samples of greatly different size.

Figs. 2–4 summarize our measurements for south coast goat's eye limpet, Argenville's limpet, and Cape turban shell, respectively. To designate the different samples the figures abbreviate Blombos Cave as BBC, Cape Infanta as CI, Klasies River as KR, Nelson Bay Cave as NBC, and Noetzie as NTZ. To produce numerically meaningful boxplots, we have sometimes amalgamated the samples from stratigraphically adjacent cultural units. The column just to the right of the boxplots presents known or inferred ages for each sample. The LSA samples represent successive, artifactually defined LSA variants that have been directly dated by radiocarbon at each site. The dates conform to ages obtained elsewhere for the same artifactual variants (27). The MSA samples are less firmly dated, but they can be arranged according to stratigraphically successive artifactual units. For Klasies River, the recognized units are the MSA I, MSA II, HP (for Howieson's Poort), and MSA III. For Blombos, they are the MSA 1, MSA 2, and MSA 3. The Roman and Arabic numerals designate non-equivalent units at Klasies River and Blombos, and the Blombos MSA 1 is a widely publicized Still Bay occupation that is not represented at Klasies River.

For Blombos Cave, we could not calculate medians for the goat's eye limpets, because we lack individual measurements. However, published means for the Blombos turban shell opercula (21) closely approximate our medians, and such close correspondence between median and mean is common in our experience, probably because stone age collectors mostly neglected individuals at the bottom end of the size (age) spectrum. To create boxplots for the Blombos goat's eye limpets then, we substituted the published means for the medians, and we assumed that the distribution around each median would closely resemble the distributions

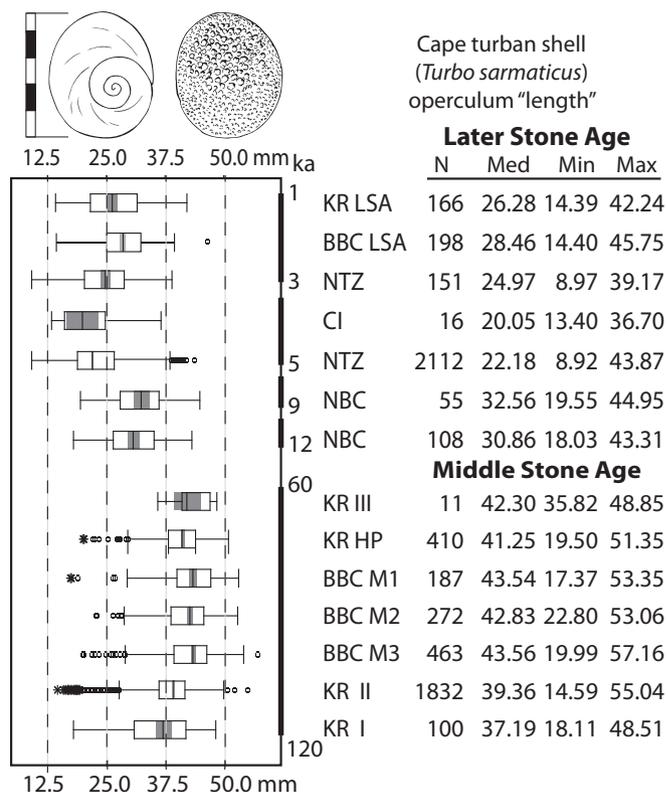


Fig. 4. Variation in the maximum length of the operculum of Cape turban shells (*T. sarmaticus*), arranged roughly from oldest (bottom) to youngest (top).

in other gastropod samples for which we have individual measurements. We dimmed the simulated boxplots in Fig. 2 to indicate that they are only approximations.

Figs. 2–4 support the following fundamental conclusions: (i) south coast MSA goat's eye limpets, Argenville's limpets, and Cape turban shells are significantly larger than their LSA counterparts; (ii) among the Klasies River MSA samples, for each species, the Howieson's Poort (HP) specimens tend to be the largest, but the Cape turban shells and perhaps the goat's eye limpets are even larger at Blombos Cave; and (iii) the largest LSA limpets and Cape turban shells come from deposits that formed before 5 ka at Nelson Bay.

Combined with the large size of west coast MSA limpets that we have reported previously (22), the large size of south coast MSA goat's eye limpets, Argenville's limpets, and turban shells supports our inference that MSA people collected rocky intertidal gastropods less intensively than their LSA successors, and the most economic explanation is that MSA populations were appreciably smaller. By extension, the especially large sizes of the shells from the Klasies River Howieson's Poort and from the Blombos MSA layers imply especially small populations. In addition, the relatively small size of the LSA limpets and turban shells postdating 5 ka supports our suggestion that LSA population size increased when regional climate turned moister.

Finally, we note that like the rocky intertidal gastropods in Figs. 2–4, tick shells (*Nassarius kraussianus*) are larger in the Blombos Cave MSA layers than in historic south coast samples (35, 57). This may not be relevant to our research question, however, because tick shells are tiny scavengers in estuarine grass beds, and stone age people collected them not for food but either for bead manufacture or incidentally on grasses introduced for bedding.

Summary and Conclusion

We have shown that goat's eye limpets, Argenville's limpets, and Cape turban shells from MSA sites on the south coast of South Africa tend to be significantly larger than their LSA counterparts. The size contrast closely resembles the one we previously demonstrated between MSA and LSA granite limpets, granular limpets, and Argenville's limpets from west coast sites. On both coasts, the MSA sites formed mainly during the Last Interglacial (MIS 5) and the LSA sites mainly during the Present Interglacial (MIS 1). The intertidal shellfish communities on the two coasts differed in the same way throughout both interglacials, implying both a persistent contrast in intertidal environments and fundamental environmental similarity between the interglacials. The most conspicuous difference between them was in their human inhabitants—MSA people during the Last Interglacial and LSA people during the Present Interglacial. We lack numeric estimates for the average size of currently unexploited rocky intertidal gastropods on the south coast, but on the west coast they tend to be larger than their MSA counterparts (22), which suggests that the question should be not why MSA gastropods are so large but why LSA specimens are so small. The most parsimonious explanation is that relative to MSA people, LSA foragers exploited gastropods more intensively, probably because LSA populations were significantly larger. Among the factors that could have promoted larger LSA populations, the most important was probably the routine addition of fishing to the foraging repertoire. On both coasts, LSA sites are the oldest to provide implements that are

readily interpretable as fishing gear (58), and the number of fish bones in LSA sites, both absolutely and relative to mammal bones, is many times greater than in MSA sites (e.g., ref. 20).

Demographic modeling from mitochondrial DNA diversification has been used to suggest that the Still Bay and Howieson's Poort MSA variants emerged at times when African populations had become especially large, increasing the number of potential innovators and decreasing the likelihood that innovations would be lost by chance (7). However, our data suggest that Still Bay and Howieson's Poort populations were no larger than other MSA populations and might even have been smaller. A recent comprehensive attempt to estimate effective past population size from multiple genetic loci of living humans also fails to support significant fluctuation within the MSA interval (11), although genetic reconstructions can provide only a global perspective. In contrast, archaeological proxies such as shellfish size can monitor changes in human population densities at a regional level.

There is the further problem that whatever explains Still Bay and Howieson's Poort novelties, the European Mousterian, produced by Neanderthals, provides similar sporadic evidence for precocious LSA- or Upper Paleolithic-like behaviors (59–62). Most archaeologists see no relevance in this, because human fossils and genetics indicate that the Neanderthals did not invent the Upper Paleolithic. However, if it could be shown that they did, it would be easy to argue that the Mousterian also sometimes signals the initial flickering of fully modern behavior.

Our most fundamental conclusion is that whatever cognitive abilities underlay Still Bay and Howieson's Poort innovations, they did not enhance human ability to survive and reproduce. Only the Out-of-Africa expansion that occurred roughly 60–50 ka confirms such enhancement, and the underlying factor then is likely to have been the development of forager cultures that not only more closely resembled historic ones in technological complexity but that maintained this complexity more or less continuously. Mumba Cave, Tanzania (63), and especially Border Cave, South Africa (64, 65), have provided artifacts that demonstrate such complexity and its uninterrupted persistence only after 60–50 ka. Most South African coastal sites that formed between 60 and 12 ka are now on the drowned continental shelf and are probably badly degraded (66), even if they could be located. However, if it is possible to locate a relevant site on an African coast adjacent to a much narrower or steeper shelf, we predict that it will show an abrupt decline in average gastropod size at or shortly after the advent of the LSA. In the meantime, sites on other African coasts, perhaps above all in northwest Africa, can be used to investigate the possibility that MSA gastropods were generally larger than those in later sites and thus to check our suggestion that MSA population growth did not underlie innovation. Alternative explanations, particularly for the blossoming of innovation at the MSA/LSA interface, include the pressure of late Pleistocene climatic fluctuations (67) and changes in the human genome that ancient DNA analyses promise to reveal (68).

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