

Title: Seasonal scheduling of shellfish collection in the Middle and Later Stone Ages of southern Africa

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Abstract

This study assesses the seasonal scheduling of shellfish harvesting among hunter-gatherer populations along the southernmost coast of South Africa, based on a large number of serial oxygen isotope analyses of marine mollusc shells from four archaeological sites. The south coast of South Africa boasts an exceptional record of coastal hunter-gatherer occupation spanning the Holocene, the last glacial cycle and beyond. The significance of coastal adaptations, in this region in particular, for later modern human evolution has been prominently debated. Shellfishing behaviours are an important focus for investigation given the dietary and scheduling implications and the abundant archaeological shell remains in numerous sites. Key to better understanding coastal foraging is whether it was limited to one particular season, or year-round. Yet, this has proven very difficult to establish by conventional archaeological methods. This study reconstructs seasonal harvesting patterns by calculating water temperatures from the final growth increment of shells. Results from two Later Stone Age sites, Nelson Bay Cave (together with the nearby Hoffman's Robberg Cave) and Byneskranskop 1, show a pronounced cool season signal, which is unexpected given previous ethnographic documentation of summer as the optimal season for shellfishing activities and inferences about hunter-gatherer scheduling and mobility in the late Holocene. Results from two Middle Stone Age sites, Klasies River and Pinnacle Point 5-6, show distinct seasonal patterns that likely reflect the seasonal availability of resources in the two locations. The Pinnacle Point 5-6 assemblage, which spans the MIS5-4 transition, records a marked shift in shellfishing seasonality at c. 71 ka that aligns with other indications of archaeological and environmental change at this time. We conclude that the scheduling and intensity of shellfishing in this region is affected by a suite of factors including environmental and cultural drivers, rather than a single variable, such as population growth.

Key words: Middle Stone Age, Later Stone Age, shellfishing, oxygen isotopes, seasonality, sclerochronology

1. Introduction

The southernmost coast of South Africa features the longest known record of coastal hunter-gatherer occupation. This regional record has thus been a focus of some considerable interest for understanding the development of complex behaviours that are typical of modern humans. Researchers have suggested that the topographically and climatically circumscribed southern Cape coast may have been an especially hospitable habitat for African hunter-gatherers through the last glacial cycle, given the broadly stable, relatively aseasonal climate, high diversity of terrestrial plant and animal resources within the broader ecological setting, and access to intertidal marine foods along the highly productive rocky shoreline (Marean, 2010, 2014; Compton, 2011). Consequently, archaeological sites in this region have been the focus of numerous studies investigating the significance of a coastal adaptation and shellfishing behaviours (Steele and Klein, 2008; Clark and Kandel, 2013; Dusseldorp and Langejans, 2013; Marean, 2014, 2016; Kyriacou et al., 2015; Will et al., 2015; Jerardino, 2016; Klein and Bird, 2016).

Shellfish are a stable and predictable food resource, available year-round along the south coast where toxic algal blooms (e.g. “red tides”) are unusual, unlike along the west coast (Pitcher and Calder, 2000). Recently, marine molluscs have been posited as a valuable source of key nutrients that are otherwise rare in terrestrial foods. Although the overall importance of shellfish to the diet in terms of calories has been disputed (Clark and Kandel, 2013), shellfish have been identified as valuable packets of protein and nutrients, including iron, iodine and long-chain fatty acids (Cunnane and Crawford 2014; Kyriacou et al. 2016; Parkington 2010). This has led to suggestions that a diet with regular contributions of coastal or lacustrine foods was essential for, first, the development of large-brained hominins (Cunnane and Crawford 2014), and second, the maintenance of good health and population viability among modern human hunter-gatherers. Marean (2014, 2015, 2016) advanced an alternative evolutionary model on the significance of coastal habitats which argues that a behavioural adaptation focussed on rich and predictable coastal habitats would have triggered competition and territoriality among populations living along the shoreline, leading ultimately to the uniquely high level of non-kin cooperation observed within our species.

A feature of the southern African record of coastal occupation is the apparent increase in intensity of shellfishing after the post-glacial rise in sea-level with the appearance of open-air “megamiddens” around the coast in the Holocene, during the Later Stone Age (LSA) period. An observed decline in the average size of several shellfish species from Middle Stone Age (MSA) to LSA sites in general, on both the south and west coasts, has been attributed solely to human predation pressure (Klein, 2001; Klein et al., 2004; Steele and Klein, 2009; Klein and Steele, 2013). The authors attribute these size decreases and the increase in shell deposits to an intensification in subsistence behaviours that is indicative of sweeping changes in cognition or social organisation between the MSA and LSA (Steele and Klein, 2009). However, taphonomic considerations are relevant for understanding this record, as open-air middens near to fluctuating shorelines are highly susceptible to erosion, and even within rock shelters shell remains are vulnerable to dissolution, leaving little indication of their original abundance (e.g. Karkanas et al. 2015). Shellfish from MSA and LSA sites generally date to the Pleistocene and Holocene respectively, suggesting possible environmental factors, such as water temperature and nutrient availability, in the size decrease (Teske et al., 2007; Sealy and

Galimberti, 2011). Non-environmental factors, such as changes in the division of labour amongst hunter-gatherers, may also be implicated, as larger individuals live lower in the intertidal zone, where collecting is more dangerous (McLachlan and Lombard, 1980). There is strong evidence for a coastal adaptation amongst hunter-gatherers along the south coast from as far back as c. 110 ka in MIS5 (Singer and Wymer, 1982; Marean, 2014), indicating that the behavioural capacities were in place well before the LSA. Growing evidence for complex spatial and temporal technological patterns observed among sites across southern Africa increasingly challenge the MSA/LSA distinction, and the consequent grouping of different sites within these periods, as useful heuristics (Mitchell, 2008).

Seasonality of resource acquisition and site occupation is a key dimension of subsistence behaviour and social organisation among hunter-gatherers (Deacon, 1984a; Kelly, 1995). Seasonal mobility has been an influential framework in southern African archaeology for exploring how hunter-gatherers might best have exploited seasonally fluctuating resources found in different ecozones between coastal and inland environments (Parkington, 1976; Sealy and van der Merwe, 1986; Sealy, 2006). Seasonal versus year-round occupation of coastal localities implies different systems of social organisation, from highly mobile bands at one end of the spectrum to permanently settled groups with defended territories at the other (Sealy, 2006). Interpreting the season of site occupation from fragmentary refuse in archaeological sites is far from straightforward. Parkington (1972, 1976) detected contrasting seasonal patterns in LSA faunal assemblages of juvenile seals and rock hyraxes between coastal and inland sites along the west coast of South Africa, and developed a coherent model of coastal winter and inland summer settlement. Contradicting evidence from stable isotope analyses of human skeletal remains however showed that people buried at coastal and inland sites had distinct diets and were therefore not a single population (Sealy and van der Merwe, 1986). Subsequently, Sealy (2006) demonstrated dietary differences between two populations of later LSA humans buried at southern Cape coastal sites at Robberg/Plettenberg Bay and Matjies River, only 14 km apart, suggesting that these groups maintained a territorial boundary between them. This study, along with several others from coastal and riverine areas, indicates that some LSA communities became increasingly settled, at least after c.4 kcalBP (Hall, 1986; Binneman, 1995; Jerardino, 1996, 2010, 2012).

Modern ethnographic and ecological research provides additional insights into the feasibility and organisation of a coastal hunter-gatherer adaptation and shellfishing behaviours. De Vynck et al. (2016a) demonstrated, first, that rocky shore shellfishing along the south coast can be a highly productive subsistence activity, comparable to some of the most productive hunting or plant-focussed strategies amongst ethnographically observed hunter-gatherers, and second, that tidal and weather conditions markedly affect shellfish foraging yields along the high-energy and quite dangerous south coast. During rough sea conditions, experienced foragers collected significantly less shellfish than during calm conditions. Modern wave and weather records for the south coast indicate that the average swell is least during the summer months (December, January and February), with the smallest number of windy days compared to other seasons (see online repository for Southern African Data Centre for Oceanography: <http://sadco.csir.co.za>), suggesting that summer is the optimal season for shellfishing.

This project provides an exceptionally long perspective of shellfishing seasonality from a single coastline that can be assessed for both temporal and geographical trends in the context of

existing detailed archaeological and coastal environmental records. Serial oxygen isotope sampling of marine mollusc shells allows the reconstruction of seasonal sea surface temperature (SST) profiles during the period of shell growth, a valuable seasonal climate archive in temperate environments (e.g. Loftus et al. 2017). By comparing the SST of the final growth increment, just prior to death, with the annual SST range, we can establish the season in which the animal was harvested (e.g. Shackleton, 1973; Mannino et al., 2003; Prendergast et al., 2016). Here we explore the annual scheduling of harvest of the rocky shore species *Turbo sarmaticus* from five geographically and temporally spaced archaeological sites that together span key periods across the last glacial cycle.

First, we set out to examine broad patterns in shellfishing behaviours between the Middle and Later Stone Age. Evidence of LSA hunter-gatherer territoriality from Nelson Bay Cave and modern studies of shellfishing efficiency along the south coast lead us to hypothesize that LSA hunter-gatherers would access shellfish resources year-round, or preferentially during summer when the weather conditions are most suitable for shellfish collection. Differences in shellfish assemblages between these periods (i.e. in size and species representation) suggest that harvesting intensity increased in the LSA, which we hypothesise would result in a less seasonal harvesting pattern through time. Second, we examine shellfishing strategies within the MSA and LSA assemblages, both between sites and across periods of broader climatic, technological and/or economic change: between the early Holocene macrolithic Oakhurst, mid-Holocene microlithic Wilton and late Holocene macrolithic post-Wilton technocomplexes, and across the MIS5-4 transition. We hypothesise that the marked technological shifts evident in the lithic record signify broader subsistence changes that will also be reflected in the seasonal scheduling of shellfishing.

2. Palaeoenvironmental context and archaeological sites

2.1 South coast ecology and resources

The southern Cape lies between the two dominant seasonal precipitation regimes of southern Africa: the summer-rainfall climate that dominates the eastern and northern parts of the subcontinent grades into a Mediterranean-like, winter-rainfall climate in the south-west (see Figure 1; Tyson and Preston-Whyte 2000). Consequently, the south coast receives rainfall year-round, although with a gradient of rainfall seasonality along its length from east to west. The south coast is part of the Greater Cape Floristic Region (GCFR) which overlaps well with the area that receives significant winter rain (Born et al., 2007), and has exceptionally high levels of plant diversity and endemism, especially contrasted with the tropical vegetation biomes (e.g. Grassland, Savanna, Desert) which surround the region (Cowling et al., 1997b). The GCFR includes fynbos, renosterveld, strandveld, and succulent karoo vegetation with smaller interdigitated pockets of subtropical thicket and afrotemperate forest (Cowling et al., 1997a). Thicket vegetation is identified as having a very high proportion of edible species in this region, and fynbos and renosterveld also provide abundant edible resources (Deacon, 1993; De Vynck et al., 2016; Singels et al., 2016). A fire-adapted flora, fynbos has relatively few trees but is notably rich in geophytes (plants with underground storage organs) (Proches et al., 2006), which are a valued food resource for hunter-gatherers (Deacon, 1993; Singels et al., 2016). Although the region is presently depauperate in large mammal fauna, archaeological, historical and modelling studies indicate that prior to the arrival of Europeans the fauna included buffalo, eland, red hartebeest, black rhinoceros, zebras and the now-extinct blue antelope (Schweitzer and Wilson, 1982; Singer and Wymer, 1982; Inskeep, 1987; Boshoff and Kerley, 2001) in the

past. High numbers of grazing species occurred on the Palaeo-Agulhas Plain in the Pleistocene (Marean et al., 2014; Copeland et al., 2016).

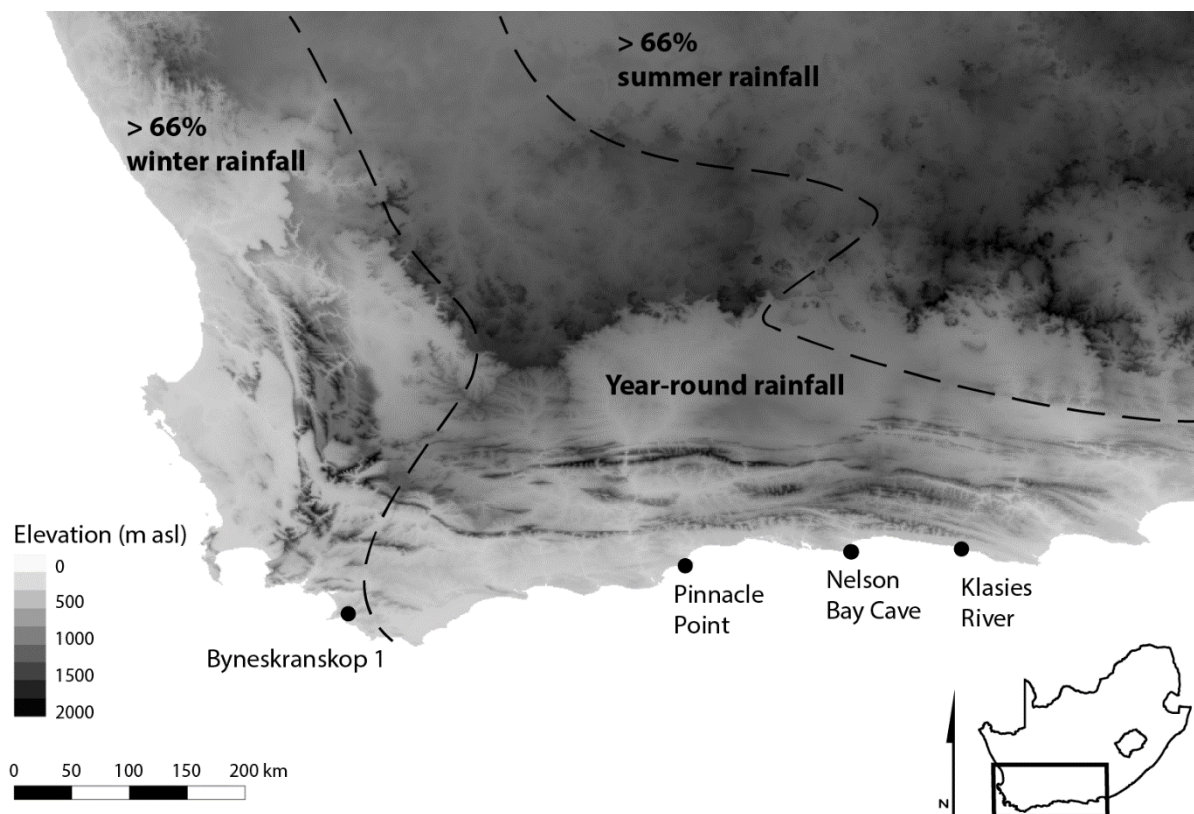


Figure 1 Topographical map of south coast with locations of sites, and approximate limits of the summer, winter and year-round rainfall zones indicated (Tyson and Preston-Whyte 2000).

Along the south coast, the GCFR is oriented east-west, between the coastline and the Cape Fold Mountains that bound the region to the north and separate the lower-lying GCFR from the interior highlands. A marked trend of increasing plant species diversity and endemism from east to west is attributed to more stable winter rainfall conditions across the Pleistocene in the western core of the CFR compared to easterly regions, because of longitudinal shifts in the summer and winter rain-bearing systems (Cowling and Lombard, 2002; Cowling et al., 2015). The western GCFR appears to have been largely stable in the past at the biome level in response to climate change (Meadows et al., 2010; Quick et al., 2011; Valsecchi et al., 2013). Moreover, a key determinant for vegetation patterning is the underlying bedrock and resultant soils: renosterveld is found on nutrient-rich shale-derived soils, while fynbos occurs on the more common low nutrient soils that form on quartzite and limestone (Cowling et al., 1997a). Thicket and afromontane forest occur in valleys and the cooler, wetter parts of the region, respectively, where they are protected from fire.

The modern coastline, part of the Agulhas Marine Province, is a mixture of rocky and sandy shores which boast a wide variety of marine and estuarine resources, including seaweed, fish, shellfish and marine mammals. Much of the coast is subject to high-energy wave action, an important factor in the success of intertidal foraging activities by humans. Marine mammals including seals and whales (whose bulky bones are unlikely to have been transported back to archaeological sites) are another high-value, if unpredictable, marine resource for hunter-

gatherers, as a rich source of both protein and fat; seal remains are common in LSA sites along this coastline (Schweitzer and Wilson, 1982; Singer and Wymer, 1982; Deacon, 1984a; Inskeep, 1987; Jerardino and Parkington, 1993; Marean et al., 2007).

Adjacent to the present coast is the Agulhas Bank, a large, coastal plain that is currently submerged but which was exposed to various degrees during periods of lower global sea levels throughout MIS5-4 (van Andel, 1989; Fisher et al., 2010). Numerous late Pleistocene and Holocene archaeological sites along the coastline of the modern high-sea stand attest to the importance of this coastal shelf region (Compton, 2011). Marean et al. (2014) have proposed that this plain was likely to have been covered with grassy fynbos and thicket vegetation that formed a productive grazing ecosystem supporting large herds of terrestrial herbivores. Importantly for this study, the coastline would have been shifted further out during glacial periods, affecting the sites inhabitants' access to coastal resources. Moreover, the impact of sea level regressions varied along the coastline, as the slope of the coastal shelf steepens towards the east (see Figure 2). Towards the centre and west, where the shelf is shallowest, glacial decreases in sea level of between c. 70 m (average over MIS3 [57-29 ka]) and c. 110 m (average over MIS2 [29-14 ka]) would have resulted in coastlines c. 20 km and c. 70 km further south, respectively, and up to nearly 100 km at the LGM when sea-levels were lowered by 120 m (i.e. at Pinnacle Point; Fisher et al. 2010). In contrast, at the eastern extreme of this study, the coastline at Klasies River Main Site was an average of only c. 6 and c. 23 km further out during MIS3 and MIS2, respectively. In addition, changes in the coastal configuration affected the distribution of geological substrates that shape intertidal communities (Jerardino and Marean, 2010), so that certain habitats, such as quartzitic rocks were not present within range of the sites at different times (Cawthra et al., 2015, 2018).

2.2 Archaeological context and sites

Shell samples were obtained from five archaeological sites that span c. 500 km of the southernmost coast of South Africa (see Figure 1), and key periods of the last glacial/interglacial cycle, including the terminal Pleistocene/Holocene transition, and the transition between MIS5 and 4. A primary goal of this study is to contrast shellfishing behaviours between the MSA and LSA: to this end, samples were selected from the LSA levels at Nelson Bay Cave (NBC)(Deacon, 1984a; Inskeep, 1987), Hoffman's/Robberg Cave (HRC) and Byneskranskop 1 (BNK1), and the MSA levels of Pinnacle Point 5-6 and Klasies River main site. All five sites are caves or rock-shelters located at the modern coastline, except BNK1 which today lies c. 7 km inland. Deposits are mostly a series of human occupation layers interbedded with varying amounts of aeolian sands and roof and cliff derived sediment, and each site contains large assemblages of lithic tools and well-preserved shell and faunal remains. They are valuable repositories of both environmental and archaeological information, and individually have been the focus of intense study. The sites were excavated over the last four decades and the shells used here were obtained mostly from museum collections. Precise three-dimensional co-ordinates for each shell are available only at PP5-6, where excavations led by Curtis Marean are ongoing.

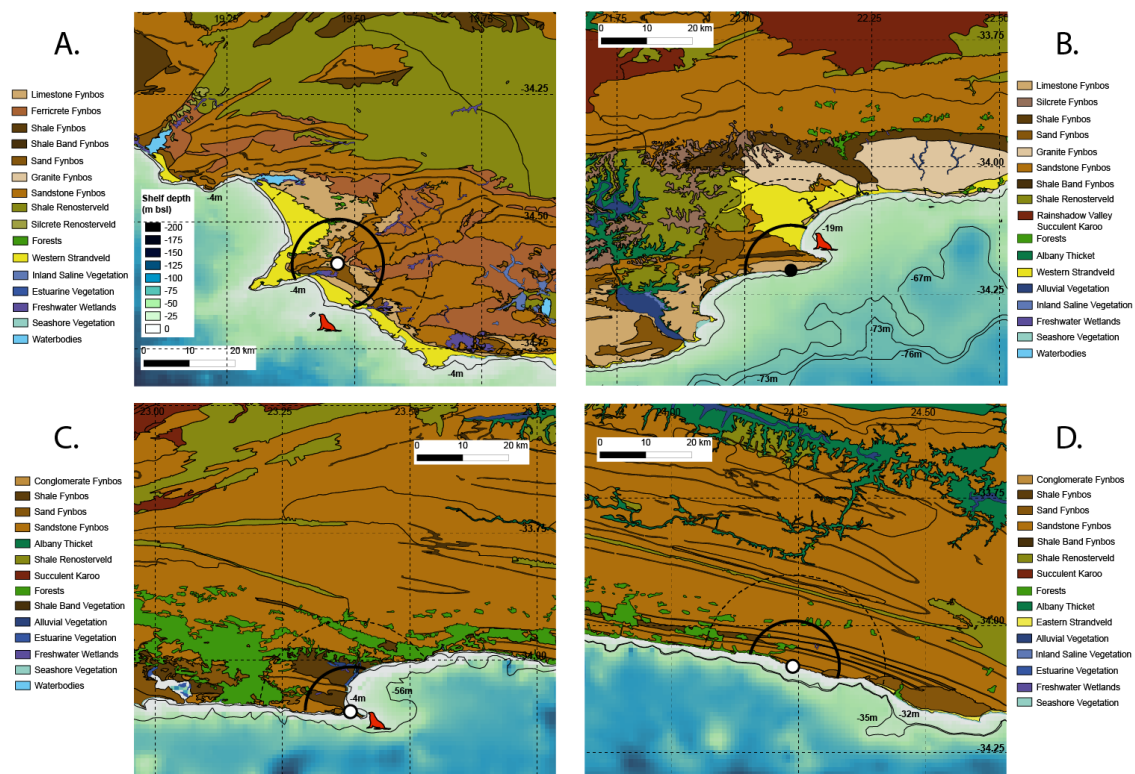


Figure 2 Vegetation and offshore bathymetric maps for the locations around each of the four sites, clockwise from west to east along the coast: A Byneskranskop 1, B Pinnacle Point 5-6, C Nelson Bay Cave (and adjacent Hoffman's Robberg Cave), and D Klasies River Mouth. The thick and dashed line circles represent 10 km and 20 km radii around each site, respectively. The vegetation data are simplified from the National Vegetation Map Project (South African National Biodiversity Institute, 2012), with fynbos vegetation communities in shades of brown. Also indicated are averaged offshore contours (metres below sea level), approximating the position of the coast during the various periods of occupation at each site (see Table 2 for the timing of sea level position at each site). The location of modern seal colonies is indicated by the red icon.

Later Stone Age sites NBC and HRC (see Figure 2C) are both located on the narrow Robberg Peninsula, about 800m apart, and reflect similar environmental conditions. NBC, in particular, is an important site for the regional archaeological sequence, with an LSA technological sequence and good organic preservation (Klein, 1972; Deacon, 1984a; Inskeep, 1987). Shells are abundant in the deposits from the terminal Pleistocene levels (c. 14.5 kcal BP): prior to this, sea-levels were c. 100m below modern levels, with the coastline more than 20 km away. At both sites, the density of identifiable shell increases through time, although assessments of the relative importance of shellfish are confounded by taphonomic and sampling concerns. Shell samples were selected from across the Holocene and terminal Pleistocene levels, which are securely dated by a Bayesian modelled suite of conventional and accelerator radiocarbon dates (Loftus et al., 2016). Radiocarbon dates from HRC show that the part of the sequence investigated thus far spans only a couple of thousand years in the late Holocene (Kyriacou, 2009). Today, the Robberg Peninsula and surrounding region is largely vegetated by fynbos, with extensive patches of forest within 20 km, and freshwater and estuarine wetlands present in the adjacent bay. A Cape fur seal breeding colony present on the peninsula itself is likely to have been a highly attractive resource to hunter-gatherers: seal remains are found throughout the LSA levels at NBC and Sealy (2006) suggests that elevated $\delta^{15}\text{N}$ values measured in later LSA human skeletons from Robberg and nearby locations likely reflect regular access to marine mammals.

BNK1 (Figure 2A) is located c. 400 km west of NBC, at the current boundary between the year-round and winter rainfall zones. The deposits extend from the terminal Pleistocene through to the late Holocene, although well-preserved shells are found only in the upper levels (Schweitzer and Wilson, 1982). The chronology of this site is well constrained by a Bayesian model of AMS and conventional radiocarbon dates (Loftus et al., 2016). The site is located in a patchwork of fynbos vegetation types, with numerous small patches of forest and freshwater wetlands within 20 km. Along the coastline is a stretch of strandveld vegetation. Today, a seal colony is located at an offshore island; this or a similar colony may have provided occasional washed up seals, as their bones are found at low frequencies throughout the BNK deposits.

The terminal Pleistocene and Holocene archaeological record of the south coast records sweeping changes in the technological record of the south coast region (Deacon, 1978, 1984b). At c. 14 kcalBP in the southern Cape (Loftus et al., 2016), late Pleistocene microlithic assemblages were replaced by the early Holocene macrolithic Oakhurst, characterised by unretouched artifacts made largely on coarse quartzite raw materials. Judging by the numbers of sites and volumes of deposits at this time, the Oakhurst techno-complex appears to have occurred at a time of moderate to high population density along the south coast (Sealy, 2016). The Oakhurst was replaced by the microlithic Wilton at c. 8 kcalBP (Lombard et al., 2012), featuring standardised retouched tools made from fine-grained rocks that may reflect the greater importance of long distance contact among smaller populations, possibly in response to challenging environmental conditions (Wadley, 1989; Sealy, 2016). Faunal remains include more small game and more marine resources (Klein, 1972). In the southern Cape, a macrolithic industry characterised by crude, unstandardized quartzitic artefacts and abundant bone artifacts replaces the Wilton at c. 4 kcalBP. Numerous lines of evidence suggest that population densities were high during the post-Wilton, with increasingly settled populations at least in some areas and indications of “intensification” in the archaeological subsistence record, including increased exploitation of marine foods such as fish (Inskeep, 1987; Sealy, 2006,

2016). Although these industries display considerable geographic variation, the technological framework is considered useful for outlining broad trends across southern Africa, and has shaped much of southern African LSA research in the last few decades. In this study, the LSA *T. sarmaticus* samples are aggregated by depositional context and attribution within this broad technocomplex framework.

Middle Stone Age sites Klasies River Main Site (KRM: Figure 2D), on the Tsitsikamma coastline, is a site complex that contains extensive deposits spanning tens of thousands of years from the last interglacial to c. 55 ka, with overlying Holocene layers (Singer and Wymer, 1982; Deacon and Geleijnse, 1988; Wurz, 2002). The Klasies River sites have produced some of the earliest evidence for anatomically modern humans and complex behaviours in southern Africa (Rightmire and Deacon, 2001). The deposits are dated by a variety of methods (e.g. optically stimulated luminescence [OSL], electron-spin resonance and U-Th dating), but are generally constrained only very broadly to periods within MIS5-3. Shell samples come only from MIS5 aged deposits and samples are aggregated according to the technological units identified by Wurz (2002). At the base of the sequence, c. 115-108 ka (MIS5e) (Feathers, 2002), are the “MSA I” levels, characterised by long, thin points and blades. The subsequent “MSA II” levels are divided into “MSA II Lower” (c. 101-90 ka) and “MSA II Upper” (c. 85 ka) phases, and are characterised by the production of Levallois-like points¹. The site is usually described as being located within a fynbos dominated landscape, with only small patches of forest nearby (see Figure 2D). However, a recent comprehensive survey of vegetation within 5 km of KRM found that in fact the surroundings are a complex mosaic of predominantly thicket, forest and coastal vegetation elements, and only occasional fynbos contributions (van Wijk et al., 2017). The authors attribute the discrepancy between this survey and the broad-scale SANBI map to the extremely varied terrain around the site that supports a much greater diversity of vegetation types, especially thicket microhabitats on steep sheltered slopes. The survey recorded a high proportion of useful plants, including edible and medicinal plants. The relatively steep offshore coastal profile means that the coastline would not have been very far away during the occupation periods studied here. Studies of the archaeological shells show that although nearly forty species of marine molluscs were collected, the MSA I and MSA II units are dominated by brown mussels (*Perna perna*), *Turbo sarmaticus*, limpets (*Patellidae sp.*) and, a sandy shore species, white mussel (*Donax serra*) (Thackeray, 1988). Changes in the frequencies of different species through time are attributable to sea level-driven changes in the coastal environment, especially the occurrence of inter-tidal habitats, such as rocky or sandy shores (Thackeray, 1988; Langejans et al., 2017).

Pinnacle Point 5-6 (PP5-6: Figure 2B) is part of a complex of rockshelters and caves in sea-facing cliffs adjacent to Mossel Bay. Research undertaken as part of the South African Coastal Paleoclimate, Paleoenvironment, Paleoecology, and Paleoanthropology project has ranged widely beyond the cave sites, with interdisciplinary studies of the ancient and modern landscape and detailed palaeoenvironmental reconstructions (e.g. Fisher et al. 2010; De Vynck et al. 2016a, 2016b; Singels et al. 2016; Bar-Matthews et al. 2010; Marean, 2010). The PP5-6 deposits, dated by a comprehensive suite of OSL dates and Bayesian modelling, validated by the presence of the Younger Toba cryptotephra to between ~92-49 ka, are well constrained:

¹ Although *T. sarmaticus* opercula were excavated from the overlying Howieson's Poort levels, these could not be located in museum collections.

the ages of shell samples are estimated according to the depositional units, which are each dated to within a few thousand years (Karkanas et al., 2015; Smith et al., 2018). Analyses of the lithic (Brown et al., 2009, 2012; Wilkins et al., 2017) and faunal assemblages from PP5-6 are ongoing. Today, the site is located within a patchwork of fynbos, renosterveld and strandveld vegetation, but the coastal shelf here is shallow, and the coastline would have retreated rapidly and dramatically at the start of MIS4. Marean et al. (2014) hypothesise that the expanded coastal plain in front of the site would have featured highly productive grasslands that benefited from rich soils and a bimodal annual rainfall regime, supporting herds of large herbivores.

3. Materials and methods

3.1 *Turbo sarmaticus* shell selection

Turbo sarmaticus (common name 'alikeukel' or 'giant periwinkle') is a large gastropod endemic to the southern and eastern coasts of South Africa (Figure 3A). Out of the multiple species found in southern coast archaeological sites, this species was chosen to investigate shellfishing behaviours because the dense, compact operculum preserves comparatively well in archaeological sites, and the species ranks highly as a molluscan prey choice (Dusseldorp and Langejans, 2013). Consequently, *T. sarmaticus* opercula are well-represented in south coast archaeological assemblages. The opercula display visible growth increments across their inner surfaces (Figure 3B) and as the species occupies the lower littoral (intertidal) and sublittoral regions (to depths of approximately 8m; Branch et al., 2007), it is nearly always submerged, and so a good candidate for palaeotemperature reconstruction.

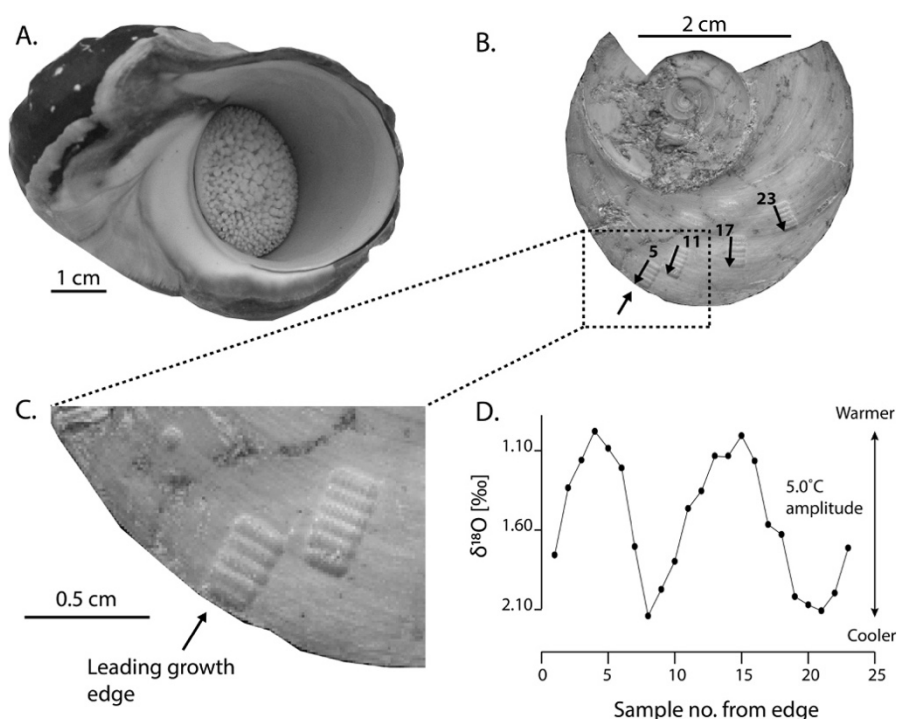


Figure 3A) *Turbo sarmaticus* shell with operculum retracted, 3B) surface of a broken, c. 71 ka archaeological operculum from PP5-6, showing the discontinuous sampling pattern (23 micromilled samples in total), 3C) close up of the growth edge of operculum in B, and 3D) measured $\delta^{18}\text{O}$ values from this operculum, which shows the seasonal SST range of c. 5°C.

The operculum is precipitated as aragonite, a metastable form of CaCO_3 . Aragonite is known to be susceptible to dissolution and recrystallization to more thermodynamically stable calcite over time, whereby the original isotopic composition may be altered. Moreover, aragonite preservation can be highly patchy across the exposed surfaces of individual opercula. Aragonite and calcite are readily distinguished using Fourier transform infrared spectroscopy and x-ray diffraction, and the detection of calcite in these opercula provides an unambiguous indication of recrystallization. We used an FTIR-ATR based method (Loftus et al. 2015) capable of detecting even small amounts of calcite ($< c. 5 \text{ wt}\%$) that requires small amounts of powdered CaCO_3 ($c. 0.5 \text{ mg}$) for analysis, which can be recovered for stable isotope analysis. Thus, each shell sample destined for $\delta^{18}\text{O}$ analysis can be pre-assessed for diagenesis, permitting a highly-resolved evaluation of recrystallization across the entire drilling path.

Upon an initial pre-screening using this FTIR-ATR method, archaeological opercula with intact growth edges were sampled at high-resolution using a New Wave Merchantek micromill with tungsten carbide dental burrs (0.8 mm – overlapping of samples allows for $c. 0.6 \text{ mm}$ resolution), following the surface growth increments (Figure 3B and C). Every 4th or 5th milled sample (i.e. $2 - 3 \text{ mm}$) was assessed with FTIR-ATR: if recrystallisation was detected along the drilling path then the series of powdered samples continuing past the altered patch were discarded. Approximately a fifth of the milled samples from all sites were discarded in this way.

3.2 Interpreting season of harvest

A recent study of modern *T. sarmaticus* shells collected from Mossel Bay showed that *T. sarmaticus* precipitate their shells in equilibrium with $\delta^{18}\text{O}_{\text{water}}$ (Galimberti et al., 2017), with formation temperatures best reconstructed using the Grossman and Ku (1986) palaeotemperature equation for aragonitic foraminifera and molluscs (as modified by Hudson and Anderson (1989) to account for the 0.2‰ difference between SMOW and average marine water):

$$T(^{\circ}\text{C}) = 19.7 - 4.34 * (\delta^{18}\text{O}_{\text{aragonite}} - \delta^{18}\text{O}_{\text{water}})$$

where $\delta^{18}\text{O}_{\text{water}}$ is 0.53‰ , as established by modern measurements at Mossel Bay (adjacent to the Pinnacle Point site; Galimberti et al., 2017). While individual shells do not necessarily capture the full annual temperature amplitude of an *in situ* daily SST recorder, mean measurements across an assemblage of shells capture the average SST conditions well (Galimberti et al., 2017; Loftus et al., 2017).

The opercula of *T. sarmaticus* present challenges for high-resolution sampling as the surface growth increments are only a few millimetres thick, and cannot be sectioned or polished prior to drilling. Opercula are also relatively slow growing. In this study, we drilled closely spaced samples using a micromill, which enables improved spatial and depth control to follow the growth increments (Loftus et al. 2017) compared to previous studies of this species (e.g. Henshilwood, 1995, 2008; Galimberti et al., 2017). This study rotated the sampling direction in discrete increments to accommodate the periodically shifted growth axis of the opercula (see Figure 3B and C), so that each sample is taken perpendicular to the direction of growth. This approach avoids flattening sample spacing near the edge, which is the focus of interest. Several shells from each level (a minimum of 3) were sampled over a year or more of the animal's life, and these "long sequences" were aggregated to define the full annual range of SSTs for each archaeological period (Figure 3D), as reported earlier to reconstruct seasonal near-shore SSTs across the last glacial period (Loftus et al. 2017). To increase the number of seasonal

estimations per archaeological level, additional shells were sampled only at the growth edge (4 milled samples) to characterise SST conditions just prior to death. The final analytical samples from each shell are interpreted with reference to the annual SST range from each archaeological unit to interpret the season of harvest.

Table 1 New season of harvest reconstructions, based on serial $\delta^{18}\text{O}$ measurements (‰ PDB) for modern *Turbo sarmaticus* opercula, live-collected from Mossel Bay. The inter-quartile ranges for the entire dataset are: first quartile (winter) = +1.07‰ – +0.58‰; interquartile range (autumn and spring) = +0.58‰ - -0.35‰; final quartile (summer) = -0.35‰ - -1.05‰.

Date collected	Season collected	Edge $\delta^{18}\text{O}$ (‰)	$\delta^{18}\text{O}$ (‰) 2	$\delta^{18}\text{O}$ (‰) 3	$\delta^{18}\text{O}$ (‰) 4	Final trajectory	Reconstructed season	Reconstructed cool/warm
Nov 2006	spring/warm	+0.38	+0.60	+1.04	+0.76	warming	spring	cool
Dec 2006	summer/warm	-0.80	-0.60	-0.01	-0.31	warming	summer	warm
Jan 2007	summer/warm	-0.68	-0.52	-1.05	+0.04	warming	summer	warm
Jan 2007	summer/warm	-0.49	+0.14	+0.68	+0.50	warming	summer	warm
Feb 2007	summer/warm	-0.07	+0.57	+0.22	+0.06	warming	autumn	warm
Mar 2007	autumn/warm	-0.35	-0.41	-0.43	-0.39	cooling	autumn	warm
Apr 2007	autumn/warm	+0.64	+0.45	+0.47	-0.10	cooling	winter	cool
May 2007	autumn/cool	+0.78	+0.23	-0.01	-0.09	cooling	winter	cool
Jun 2007	winter/cool	+1.07	+0.52	-0.22	-0.34	cooling	winter	cool
Aug 2007	winter/cool	+0.74	+0.84	+0.71	+0.42	warming	winter	cool

The data from Galimberti et al. (2017) showed that season of the final growth increment can be accurately established based on a modified method of Mannino et al. (2003) that distinguishes just two final “seasons”: cool (more positive $\delta^{18}\text{O}$ values) and warm (more negative $\delta^{18}\text{O}$ values). However, the Galimberti et al. (2017) study employed a lower-resolution sampling methodology using a hand-operated drill, and reported only partial success in capturing the quarterly seasons of growth (i.e. spring, summer, autumn, winter). Additional modern shells (different to those from the Galimberti study) were sampled for this study to establish whether *T. sarmaticus* opercula reliably record season of death when sampled with the higher-resolution method using a micromill (Table 1). Samples were analysed at the NERC Isotope Geosciences Facilities at the British Geological Survey (see below for details of analyses).

Table 1 shows $\delta^{18}\text{O}$ edge values for ten opercula, indicating the season in which each was collected and the quarterly season of death as reconstructed by the edge value, with summer and winter represented by the first and final quartiles of the total set of $\delta^{18}\text{O}$ values respectively, and the intermediate seasons, spring and autumn, distinguished by the trajectory of the final samples (i.e. whether SSTs were warming (spring) or cooling (autumn) towards death), following Mannino et al. (2003). These results demonstrate that the new sampling method captures quarterly and semi-annual season of death in most instances (70% and 80% accuracy, respectively). One operculum collected fresh in late summer (February) reflects an autumn season of collection in the isotopic composition, while a further two opercula collected

in autumn (April and May) indicate that they were collected in winter. Both methods of interpretation (quarterly and semi-annual) are presented for the archaeological results, as the choice of interpretation affects comparative sample sizes and statistical comparisons between archaeological units.

3.3 Stable isotope analyses and corrections

Carbonate samples showing minimal amount of calcite (as described above) were analysed on one of three systems - a Kiel Device coupled to a Delta V Advantage isotope mass spectrometer in the Earth Science Department, University of Oxford (external reproducibility of 0.10‰ for $\delta^{18}\text{O}$); an automated Thermo GasBench II device, coupled to a Thermo Delta V Advantage isotope mass spectrometer at the Division of Archaeological, Geographical and Environmental Sciences of the University of Bradford (external reproducibility of 0.30‰ for $\delta^{18}\text{O}$); and a Multiprep device coupled to a GV Isoprime isotope mass spectrometer at the NERC Isotope Geosciences Facilities at the British Geological Survey, Keyworth (external reproducibility of <0.10‰ for $\delta^{18}\text{O}$). In each case CO_2 was produced by 100% phosphoric acid hydrolysis, and the solid-gas fractionation of the samples is corrected using an aragonite specific factor with appropriate corrections for reaction temperature: 1.00906 at 71°C [Kiel and Gasbench], 1.00854 at 90°C [Isoprime]; Kim et al., 2007). The samples were calibrated against internal calcite standards calibrated in turn to international standards (NBS19: $\delta^{18}\text{O} = -2.20\text{‰}$). Results are reported in the delta-notation relative to V-PDB, according to the equation:

$$\delta^{18}\text{O} (\text{‰}) = \left\{ \left(\frac{R_{\text{SAMPLE}}}{R_{\text{STANDARD}}} \right) - 1 \right\} \times 1000,$$

where R_{SAMPLE} and R_{STANDARD} is the $^{18}\text{O}/^{16}\text{O}$ ratio of the sample and reference materials.

Molluscan CaCO_3 $\delta^{18}\text{O}$ is a function of both formation temperature and oceanic $\delta^{18}\text{O}$ and so $\delta^{18}\text{O}$ values must be corrected for the large shifts in global oceanic $\delta^{18}\text{O}$ across the last glacial cycle. While there is no regional record of $\delta^{18}\text{O}$ that spans the entire period of interest, the high-energy wave dynamics of this coastline ensure thorough water mixing, therefore the global stack of Waelbroeck et al. (2002) is applied. The ages for each shell were determined with reference to their context in the archaeological deposits and the error of the correction is a result of the age uncertainty of the sample in each case. See Table 2 for the age and correction applied to shells from each archaeological unit. In total, 104 archaeological shells (1302 $\delta^{18}\text{O}$ determinations) were analysed (Table 2: 40 opercula from the three LSA sites (25 from NBC, 2 from HRC, 13 from BNK), and 64 from the MSA sites (34 from PP5-6 and 30 from KRM)).

4. Results

The semi- and quarter-annual season-of-harvest designations for all 104 shells are summarised by site and archaeological unit in Table 3 (see SM for the final $\delta^{18}\text{O}$ values, seasonal ranges and season-of-harvest designation for each shell). Figure 4 compares the normalised deviations between the inferred MSA and LSA seasons of collection and the null hypothesis of equal distributions throughout the year, i.e. a semi-annual (50%:50%) cool:warm season distribution (a more conservative interpretation) and a quarterly (25%:25%:25%:25%) spring:summer:autumn:winter distribution. As the 50%:50% pattern will be mirrored, only the positive seasonal deviation is plotted. However, with the quarterly interpretation, this method of graphical presentation makes it clear which season is favoured at the expense of others. The data is displayed as percentages to aid visual comparison across the different sized groups.

Table 2 All sample contexts, corrections for global changes in oceanic $\delta^{18}\text{O}$ averaged across the age range for each context (based on Waelbroeck et al., 2002), and the numbers of samples analysed. BNK, NBC and HRC sub-contexts distinguished with B, N and H, respectively. Calibrated radiocarbon dates for NBC and BNK1 from Loftus et al. (2016), and for HRC in Kyriacou (2009). OSL ages for PP5-6 in Karkanas et al. (2015) and Smith et al. (2018), KRM dated with various methods, see Wurz (2002).

Site	Context	Sub-contexts	Date (ka)	$\delta^{18}\text{O}$ correction (%)	No. of opercula	No. of $\delta^{18}\text{O}$ samples
BNK, NBC & HRC	Post-Wilton	B_1_Eva	1.7-1.9	0	3	18
		B_4_Dud	3.7-4.0	0	2	29
		N_EIII	2.5	0	3	35
		H_RR_P	4.0-4.3	0	2	34
BNK & NBC	Wilton	B_5_Inge	3.9-6.1	0.03	2	28
		B_6_Hilary	6.1-6.6	0.04	3	25
		B_9_Mort	6.4-7.4	0.06	3	40
		N_Ivan	4.9-6.6	0.03	2	33
		N_Glen	5.9-7.0	0.06	1	20
		N_RiceA	6.8-9.2	0.15	4	37
NBC	Oakhurst	RiceB	9.2-9.7	0.21	4	48
		Jake	9.5-11.4	0.3	4	79
		BSBJ	10.9-11.9	0.48	2	46
		GSL	12.0 - 14.9	0.75	5	73
PP5-6	DBCS		65-59	0.54	1	20
	OBS1		72-66	0.64	5	80
	SADBS		73-68	0.57	15	179
	ALBS		74 ka	0.43	7	81
	LBSR		89-75 ka	0.28	6	78
KRM	MSA II Upper		c. 80 - 85	0.27	12	124
	MSA II Lower		c. 90 - 95	0.27	12	128
	MSA I		c. 115-120	0.30	6	67
Total					104	1302

For example, in Figure 4, a cool season signal is overrepresented in the LSA dataset by 18% (i.e. 68% of the shells were harvested during the cool season). Based on the quarterly method of interpretation, winter is overrepresented by 18% (i.e. 43% of the shells were harvested in winter alone), while virtually no shells were collected in spring (only 1 out of 36). However, the expected frequencies for summer and autumn collection during the LSA are approximately as hypothesised if equal throughout the year, at c. 25% each. Figure 5A shows a graph of the same type for the LSA dataset from NBC according to the post-Wilton, Wilton and Oakhurst archaeological divisions (the patterns from the two Robberg peninsula sites do not differ significantly from those observed at BNK, and samples from these sites have been aggregated). The Oakhurst assemblage shows more cool season deaths, and the Wilton and post-Wilton show a more equal cool and warm season signal. The post-Wilton, Wilton and Oakhurst quarterly and semi-annual seasonal distributions are not statistically different from one another.

Table 3 Semi-annual and quarterly seasonal harvesting results summarised for the Later and Middle Stone Age sites, and by archaeological level (individual shell results provided in SM, with the seasonal limits for interpretation). Totals may differ slightly between the two methods of analysis because no attribution is made when a sample value falls exactly at one of the seasonal category boundaries.

Site		Level	Semi-annual		Quarterly seasons				
			cool	warm	spring	summer	Autumn	winter	Total
LSA		All LSA	26	13	4	8	11	17	40
	NBC, HRC, BNK	Post-Wilton	6	4	0	2	4	4	10
	NBC, BNK	Wilton	8	6	2	4	4	5	15
	NBC	Oakhurst	12	3	2	2	3	8	15
MSA		All MSA	33	30	21	12	19	13	64
	PP	All PP5-6	22	11	9	5	11	9	34
		DBCS	1	0	0	1	0	0	1
		OBS1	2	3	2	1	0	2	5
		SADBS	6	11	5	2	3	7	17
		ALBS	0	4	1	0	4	0	5
		LBSR	2	4	1	1	4	0	6
	KRM	All KRM	11	19	12	7	7	4	30
		MSAIIupper	5	7	8	1	2	1	12
		MSAIIlower	5	7	3	3	4	2	12
MSAI		1	5	1	3	1	1	6	

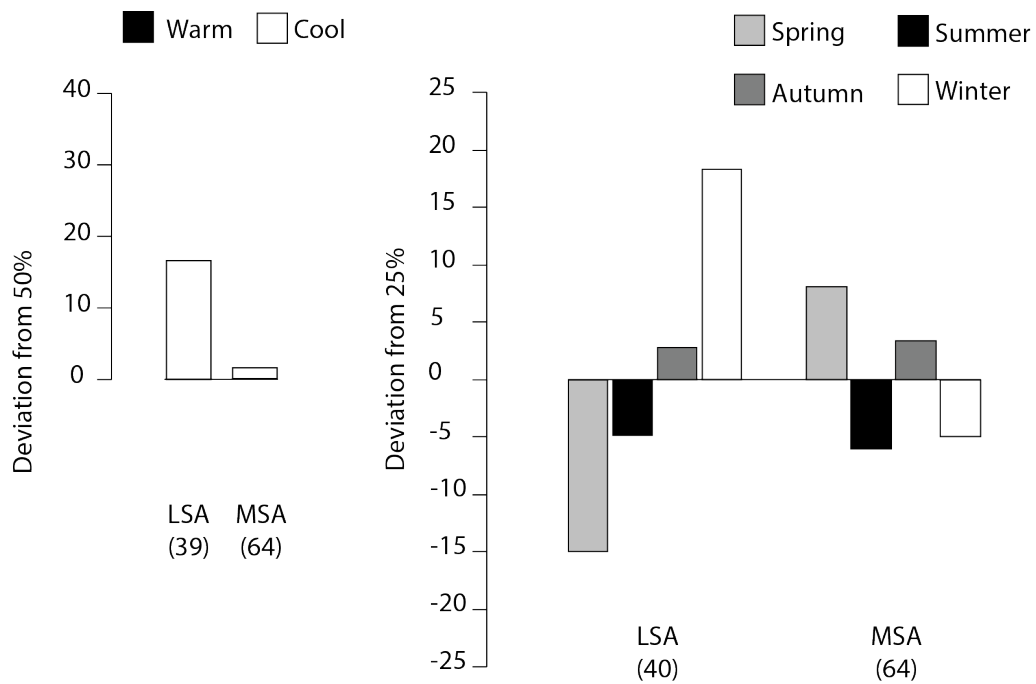


Figure 4 Deviations of seasonal assessments of shell harvesting from hypothesised equal distributions throughout the year, compared between the Middle and Later Stone Ages. On the left, the data are interpreted with a semi-annual seasonal division and on the right the data are interpreted according to a quarterly seasonal division, equated with the four common seasons.

The overall pattern in the MSA, inferred from both KRM and PP5-6 combined, appears relatively aseasonal. However, this generalisation masks significant inter-site and inter-period differences, discussed in more detail below. A comparison of the data for the two MSA sites, KRM and PP5-6, shows more warm season *T. sarmaticus* deaths in the KRM assemblage compared to more cool season deaths in PP5-6 (Figure 5B). The semi-annual and quarterly patterns observed at PP5-6 are statistically different from those observed at KRM ($p=0.02$ and $p=0.03$, respectively, Chi-squared comparison with Williams correction for small sample sizes), although the sizes of the effects are small (Cramér's $V = 0.22$ and 0.26 , respectively). The MSA and LSA quarterly seasonal distributions are statistically different from each other, but again the effect is small ($p=0.02$, Chi-squared comparison with Williams correction for small sample sizes, Cramér's $V = 0.30$).

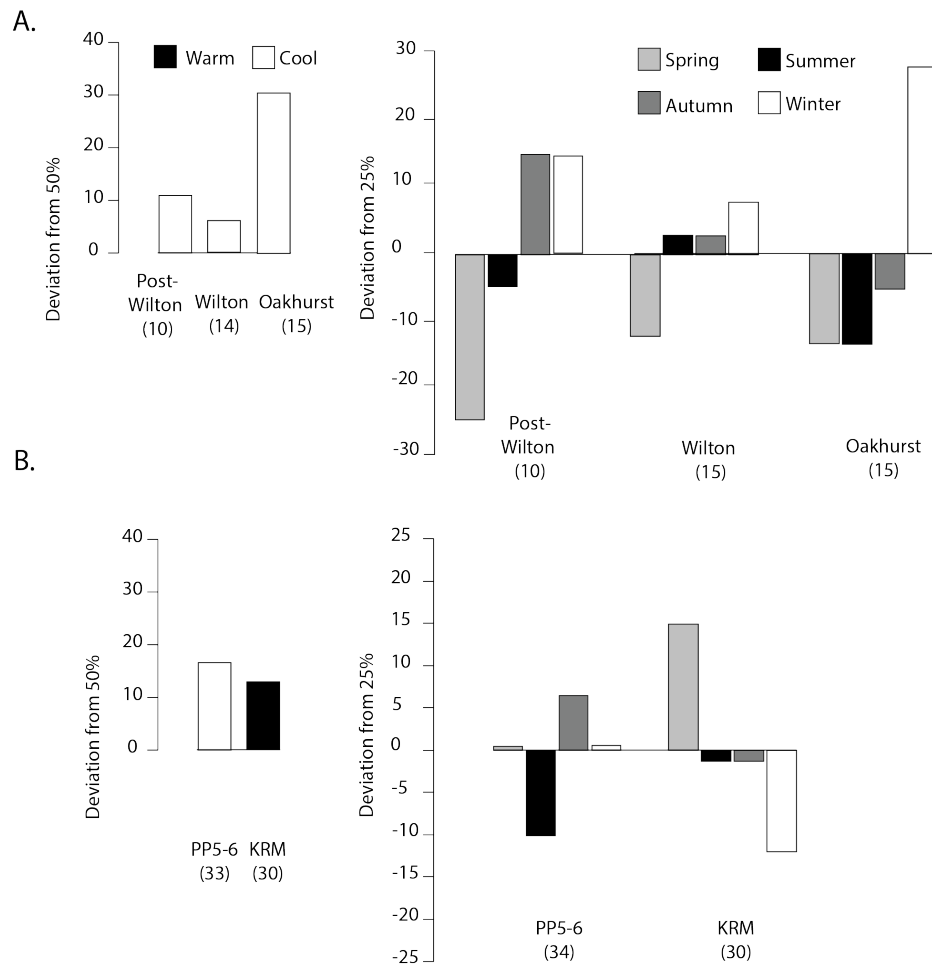


Figure 5 Deviations of seasonal assessments of shell harvesting compared A. between the post-Wilton (late Holocene), Wilton (mid-Holocene) and Oakhurst (early Holocene and terminal Pleistocene) assemblages at NBC, and B. between MSA sites PP5-6 and KRM, from hypothesised equal distributions throughout the year. See Figure 4 for interpretation.

5. Discussion

5.1 Later Stone Age shellfishing seasonality

Klein and Steele (2013) showed that the average sizes of *T. sarmaticus* opercula and the shells of other marine molluscs from Holocene LSA contexts are substantially smaller than shells from MSA contexts, which they interpret as indicating that marine shellfish were under higher predation pressure at this time. During at least some periods during the LSA (i.e. the Oakhurst and post-Wilton), several lines of evidence indicate that populations appear to have been comparatively large, and densely packed on the landscape (Hall, 1986; Jerardino, 2010, 2012; Sealy, 2016), with particular indications of reduced residential mobility during the late Holocene post-Wilton (Sealy, 2006). A high degree of territoriality and limited annual movements led us to hypothesise that these periods of higher population density would be characterised by year-round shellfish collection, as the coastal occupants would have had access to the shoreline year-round and could have harvested shellfish opportunistically throughout the year. This would align with the evidence for reduced size during the Holocene LSA. Yet, the isotope data reveal a seasonal pattern of shellfish harvesting that does not fit these expectations, and is indeed the opposite of our expectations. The total LSA dataset

reveals marked seasonality, with shellfish harvesting concentrated in the cooler months of the year. This tendency is most pronounced during the early Holocene, when LSA foragers clearly preferentially harvested *T. sarmaticus* during the cooler months of the year, and only rarely during the spring months (only four shells out of 40 across all three periods are identified as having been harvested during spring). This does not appear to correspond to either ease of access of intertidal resources (best in summer) or to ecological considerations related to *T. sarmaticus*: gonad development for the species peaks during spring/early summer and body composition analyses show that the animal has highest protein values during this time (McLachlan and Lombard, 1980). Yet McLachlan and Lombard (1980) also note that the foot is the main part of the animal that is eaten (at least by modern consumers), and this body part is little affected by the seasonal reproductive cycle.

While the south coast is relatively aseasonal, with less marked annual variation in temperature and rainfall compared to surrounding regions, there is evidence for seasonal shifts in the availability of important classes of food resources other than shellfish, including plants with underground storage organs, most palatable in late summer and autumn (Deacon, 1976), and other marine foods. The Cape fur seal birthing season is tightly focussed over a few weeks in late November and early December (i.e. summer), but mortality spikes nine months later when the juveniles are weaned and must leave the rocks to find food: many die of exhaustion (in August to October, i.e. late winter and spring) (Klein and Cruz-Urbe, 1996). Klein and Cruz-Urbe argue that, in general, the age range of seals from LSA sites, including NBC, indicates that coastal hunter-gatherers targeted these juvenile seals, and they suggest that LSA hunter-gatherers timed coastal visits to coincide with late winter and spring. In fact, the age range of seals from NBC itself is not very tightly clustered, and instead indicates a broader seasonal range in which seals were eaten (see J. Deacon, 1984: 431). This likely reflects year-round access by local hunter-gatherers to the land-based seal colony on Robberg Peninsula itself and perhaps others; there was a historically documented colony on the tidally-accessible Beacon Island located in Plettenberg Bay. However, seal colonies do fluctuate seasonally in size, as the animals spend more of their time feeding at sea during autumn and winter, whereas they are largely land-based during the spring and summer breeding season (Oosthuizen and David, 1988), making better targets of both juvenile and adult seals. Relatedly, a report on the incidence of whale strandings in modern times recorded a significant number of stranded whales on the southern African coast, which were most common from August to December (i.e. centring on spring) (Smith and Kinahan, 1984). Assuming greater numbers of whales prior to commercial hunting, and given the enormous amount of food represented by a whale carcass, strandings may have been an important spring bonanza for hunter-gatherers.

A strategy whereby the coastal occupants switched within the year from one source of marine protein (i.e. marine shellfish) to different sources that are only seasonally abundant (i.e. juvenile and breeding seals, whale wash-ups), could explain both the underrepresentation of spring-harvested shellfish and the overrepresentation of winter-harvested shells at NBC and BNK. Potentially, shellfish were one of the few reliable sources of protein during winter, while in spring and summer hunter-gatherers had more ready access to other marine protein sources such as seals and whale carcasses. Certainly, the $\delta^{15}\text{N}$ values of mid-to-late Holocene LSA hunter-gatherers buried on Robberg and nearby reflect the consumption of considerable amounts of high-trophic level marine foods (Sealy, 2006). Together, these lines of evidence

point towards a marine-focussed subsistence strategy at NBC, with the annual breeding cycle of seals playing an important role.

When assessed by archaeological period, the LSA shellfishing assemblages reveal some small shifts in the seasonality across the Oakhurst, Wilton and subsequent post-Wilton (Figure 5A). Although the small sample sizes warrant caution here, the magnitude of any differences between the three archaeological periods is small. Given the profound shifts that are evident in technological, cultural and other subsistence records (i.e. Deacon, 1984; Inskeep, 1987), alongside evidence for shifts in both total population size and the degree of territoriality across the Holocene (Sealy, 2006, 2016), we expected to observe more marked shifts in the seasonality of shellfishing, identified as a highly suitable activity for intensification. The directions of the observed shifts are also opposite to expectations based on population size – the period for which we have the most secure evidence of large, more territorial populations (the post-Wilton) exhibits more strongly seasonal patterning than the preceding Wilton, when population numbers were regionally depressed. This suggests that when people were more densely packed on the landscape, subsistence activities were more structured within an annual framework to optimise seasonal surfeits and scarcities.

Of course, the shellfish assemblages found within the archaeological sites represent only those shells brought back to the site, and not the shellfish eaten elsewhere. To exclude the possibility that our conclusions are confined to one species, it would be useful to investigate shellfishing seasonality among other well-preserved species that are common in the sites, including those from different habitats, such as the sandy shore-dwelling white mussel, to establish if similar patterns emerge. In fact, the earliest application of serial isotope sampling to marine shells ever was undertaken by Nicholas Shackleton on shell material from Nelson Bay Cave to identify the season of harvest (Shackleton, 1973). He sampled fifteen *Patella* (now *Scutellastra*) *tabularis* limpet shells from the Wilton levels to investigate seasonal timing of harvest and likewise concluded that the shells were largely harvested during the cooler, winter months. This is an encouraging confirmation that the pattern comprehensively demonstrated here for *T. sarmaticus* in fact reflects the broader subsistence strategy, and not just the targeting of a single species.

5.2 Middle Stone Age shellfishing seasonality

Taken all together, the entire dataset of 104 shells demonstrates marked differences in shellfishing behaviours between the MSA and LSA. However, upon closer examination, the apparent year-round pattern observed in the aggregated MSA dataset (Figure 4) reflects the averaging of two very different seasonal patterns at KRM and PP5-6 (Figure 5B). This suggests that, rather than a sweeping contrast between the MSA and LSA assemblages, the distinctions lie between sites and that to understand the seasonal patterning of shellfish harvesting, we need to consider variations in the resources available at these different sites during the periods of occupation. The shells from KRM generally date to MIS5, a more clement climatic period, while those from PP5-6 date from late MIS5 and across the MIS5-4 interglacial/glacial transition.

The overall pattern at KRM conforms to expectations, insofar as the fewest number of shells were harvested in winter, the least optimal season, although there are fewer than expected summer harvested shells, assuming this was the most optimal season for shellfishing.

Generally, KRM shows a strong warm season signal and only four out of 30 shells are identified as having been harvested in winter, while nearly half are identified as having been collected during spring. Today, there is no seal colony anywhere along the coastline near KRM, and reconstructions of the locations of seal rookeries before the arrival of Europeans indicate that it is unlikely that one was ever located very near to the site (Rand, 1972; Marean, 1986 - although these assessments predated the van Andel (1989) reconstruction of glacial-era sea levels). Yet, seal remains are relatively common throughout the KRM deposits, and, based on the near-absence of vulnerable younger seals, have been interpreted as wash-ups of older seals, rather than actively hunted from land-based colonies, where a broader age range would be represented. Moreover, a shift in the age-profile, from older seals in MSA I and MSA II Lower to more juvenile seals in MSA II Upper levels, has been interpreted as reflecting a shift in the seasonality of site occupation, from summer, when adult seal wash-ups are more frequent, to spring, when juveniles are more vulnerable (Marean, 1986). Interestingly, the majority of shells from MSA II Upper (8 out of 12) reflect a spring harvesting signal, while summer is the most frequent season for the admittedly small samples of shells from the combined earlier two levels, all of which is consistent with Marean's interpretation of the occupational sequence. However, this indicates that at KRM hunter-gatherers exploited shellfish alongside seals, as opposed to focussing on seals. This patterning may simply reflect the greater abundances of seals in those sites with nearby and/or mainland colonies (i.e. PP5-6, NBC), where seals can be expected to have been more abundant and more predictably available. It may also indicate KRM was not habitually occupied during the winter months during MIS5.

The seasonality pattern at PP5-6 differs from that at KRM, with summer underrepresented and autumn overrepresented. However, it is apparent on closer inspection that this pattern is a consequence of the averaging of two quite different seasonality patterns *within* the PP5-6 dataset, although neither corresponds closely with that observed at KRM. A recent study at PP5-6 detected cryptotephra shards from the Toba volcanic eruption in Sumatra, well-dated at proximal deposits to c. 74 ka, just prior to the onset of fully glacial conditions in MIS4 (Smith et al., 2018). The Toba isochron is found above the ALBS samples in this study. Geoarchaeological analysis of the PP5-6 sediments indicate that environmental changes related to the onset of MIS4, including the retreat of the coastline, began with the shift from LBSR to ALBS (a rapidly accumulated dune deposit), with unit SADBS occurring well within MIS4. The archaeological sequence from LBSR to SADBS reveals a shift from low- to high-intensity occupation (Karkanas et al., 2015). Figure 6 shows the combined results of units LBSR and ALBS (n=11), prior to and during the MIS5-4 transition, with those from the overlying MIS4 units SADBS and OBS1 (n=22) (again, the small sample sizes for this comparison warrant caution). The comparison reveals subtly different seasonal patterning (although not statistically significant), with the earlier period dominated by autumn harvesting (almost 8 out of 11 shells were collected in autumn), while the later period shows evidence for increased winter harvesting (9 out of 22 shells).

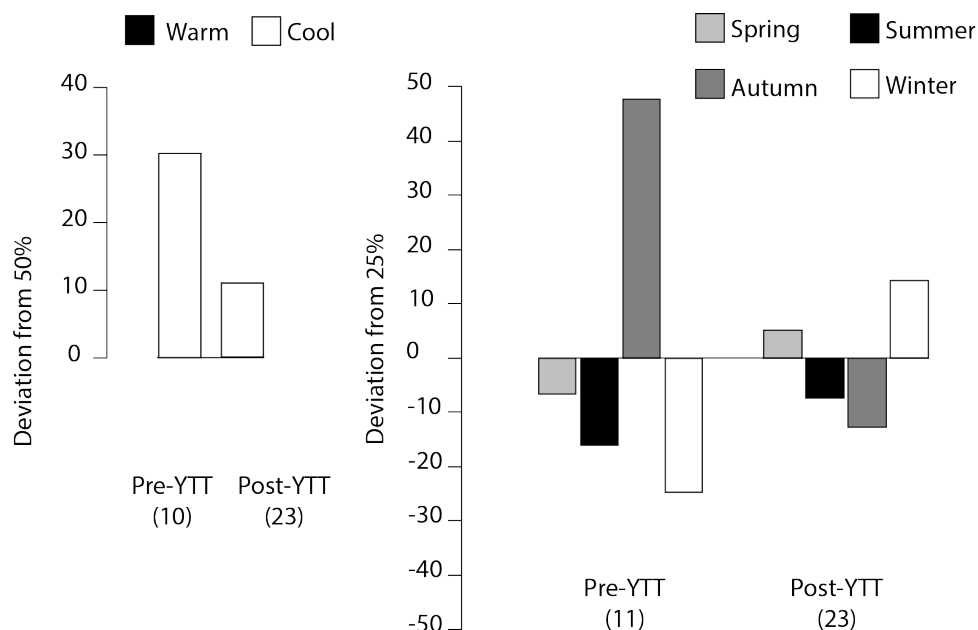


Figure 6 Deviations of seasonal assessments of shell harvesting compared between archaeological units LBSR and ALBS (pre-Toba) and units SADBS and OBS1 (post-Toba), from hypothesised equal distributions throughout the year. See Figure 4 for interpretation.

It appears then that people timed their shellfishing activities differently during MIS5 and the MIS5-4 transition than subsequently during MIS4. The coastline is projected to have been relatively close to the site during the deposition of LBSR and the brief period represented by ALBS, but subsequently retreated rapidly to >10 km away between c. 74 ka and c. 71 ka (Fisher et al., 2010), the limit of a hunter-gatherer's daily foraging range (e.g. Jerardino and Marean, 2010). Unit SADBS features a technological shift from preceding units, with an unnamed stone tool technology characterised by heat-treated microlithic backed bladelets similar to microlithic tools from Holocene LSA sites (Brown et al., 2012), which the PP5-6 excavators suggest were made to be hafted as part of projectile weapons, perhaps arrows or atlatl darts. Further, Wilkins et al. (2017) showed that several features of the lithic technology at PP5-6 changed with the onset of MIS4 along the south coast, including raw material usage and reduction intensity. The authors attribute these technological changes to increasing populations, more intense site occupation, and decreased residential mobility that was a consequence of landscape and environmental shifts accompanying the onset of glacial conditions. As global sea-levels dropped, the expanded coastal plain is argued to have hosted large populations of migratory ungulates, briefly offering the PP5-6 occupants a rich diversity of both terrestrial and marine resources, before the coastline receded beyond foraging range (Wilkins et al., 2017).

Reconstructions of seasonal sea surface temperatures based on the long $\delta^{18}\text{O}$ sequences of shells across these units show a c. 2°C increase in the intra-annual temperature range from ALBS to SADBS. This greater range is argued elsewhere to reflect reduced seasonal upwelling driven by the rain-bearing wind systems, and so to record a drying trend in the summer rainfall region between MIS5 and MIS4 (Loftus et al., 2017). These multiple lines of evidence for environmental and archaeological shifts suggest that PP5-6 inhabitants responded to climate changes and the dramatic reorganisation of the landscape between MIS5 and MIS4 in ways

that are reflected in the shellfishing seasonality data. The apparent absence of shellfishing activities in SADBS during summer and autumn may suggest that the Pinnacle Point occupants diverted their attention to other, more profitable resources and/or moved away from the site entirely during this half of the year.

The newly exposed coastal plain would perhaps have offered novel subsistence opportunities such as herds of game that may have migrated seasonally from east to west along the summer-winter rainfall gradient of this coastline (Marean et al., 2014). Hunter-gatherers may have invested greater time and resources in seasonal hunting of terrestrial animals, but continued to rely upon shellfish for large parts of the year during the cooler months when large mammals moved away from their summer grazing grounds. This suggestion is consistent with the lithic evidence for more efficient projectile tools during this level, which have been argued to be highly effective hunting weapons (Brown et al., 2012). Again, similar to the situation in the LSA where pronounced seasonality is evident, this may indicate that MSA hunter-gatherers living at the onset of the last glacial optimised their subsistence activities by ranking seasonally restricted resources more highly when they are available, relative to those that are available year-round.

Yet, the patterns observed at PP5-6 appear to have been broadly stable, insofar as the inhabitants appear to have preferred the cooler months for shellfishing over long periods, regardless of sea-level. Galimberti (2010) investigated the seasonality of *T. sarmaticus* harvesting from older MIS5 deposits at the sites PP9B (114 ± 5 ka) and PP13B (units LRS: 114-106ka, and URS and SBS: 98-92ka), within the Pinnacle Point complex of caves. The small assemblage ($n=13$) from this study reveal a marked cool season signal for harvesting, with only 3 out of 13 shells harvested during the warm months of the year. This pattern is similar to that observed in the more recent deposits at PP5-6, and quite unlike the broadly contemporaneous MIS5 assemblage from KRM (see Figure 5B). This difference in seasonality between the two locations along the south coast implies that MSA hunter-gatherers employed contextual strategies for shellfish harvesting within the same greater ecosystem, perhaps according to differences in the seasonal abundance of different resources such as plant foods and game. Despite both areas being classed as largely fynbos (see Figure 2), the area around KRM today includes more thicket-type vegetation, with a variety of plant communities due to the varied small-scale topography of the slopes around KRM (van Wijk et al., 2017). This type of vegetation yields plant foods year-round and so is less seasonally restrictive for foragers than fynbos or renosterveld (De Vynck et al., 2016). Moreover, variation in the angle of the coastal shelf would accommodate a wider coastal plain in front Pinnacle Point than at KRM when sea-levels began to lower after MIS 5e, which may account for the differing seasonality patterns at these locations. Clearly, additional research in mapping spatial trends in resource availability and ecological seasonality within the south coast, as opposed to treating the region as unvarying all along its length, will contribute greatly to understanding the important differences between these archaeological sites.

A final observation on the differences between the MSA and LSA assemblages notes that a winter-dominated harvesting strategy during the LSA may contribute to the size differences observed between MSA and LSA assemblages of *T. sarmaticus* shells (Klein and Steele, 2013). Younger (and smaller) *T. sarmaticus* individuals live higher in the intertidal range, migrating down the shore into cooler, deeper waters as they age and their tolerance of temperature

shifts decreases (McLachlan and Lombard, 1980; Foster, 1997). Since shellfish harvesting is more difficult and dangerous during rough weather conditions that are more frequent in winter, people may have systematically exploited smaller *T. sarmaticus* that lived higher on the shore as a consequence of shellfishing in rougher conditions. However, this explanation would not account for similar declines in size among limpet species that were also observed by Klein and Steele.

5.3 Global Comparisons

Marine shellfishing has been found to have been a cool season activity for hunter-gatherers living in diverse ecological contexts around the world. At the Haua Fteah, Libya, Prendergast et al. (2016) observed a shift from a year-round pattern during the Late Glacial to a strongly winter dominated signal in the terminal Pleistocene and early Holocene. Across various early Mesolithic sites in Italy, studies have observed a trend for cool season harvesting, which the authors proposed reflects the seasonal availability of other resources, including plant foods and large mammals (Colonese et al., 2011a). And during the Upper Palaeolithic at Ksâr 'Akil near the Levantine coast, marine shells were similarly collected preferentially during the cooler months of the year (Bosch et al., 2017). Prendergast et al. (2016) thus suggest that for prehistoric peoples in these environments, marine molluscs were important foods primarily during the lean season when other foods were scarce.

Similar patterns are seen elsewhere in very different environments around the world. Along the Beagle Channel in Tierra del Fuego, winter-harvested shells likewise dominate shellfish collections at various prehistoric sites, perhaps reflecting an aggregation-dispersal settlement pattern in this region (Colonese et al., 2011b, 2012). A study of several residential and specialist shellfishing processing locations of complex hunter-gatherers of the Pacific Northwest coast of Canada revealed that shellfishing for butter clams was most likely to occur during spring and autumn, less so during winter, and very rarely during summer, when salmon was abundant (Burchell et al., 2012). Along the coastline of the arid Farasan Islands in Saudi Arabia, shellfish were collected preferentially during the drier summer and autumn months, when plant foods were less available (Hausmann and Meredith-Williams, 2017).

In contrast to the Mediterranean shoreline, where molluscan biomass would have been generally limited, and shellfish could not have been a primary food resource throughout the year, marine productivity along the south coast of South Africa is comparatively high and resources are amenable to prolonged harvesting (Branch et al., 2007), as attested by the formation of dense shell middens over comparatively short periods during the Holocene (McGrath et al., 2015). Thus, shellfish *could* have been collected year-round, and yet MSA and LSA hunter-gatherers repeatedly chose to schedule shellfishing activities within defined seasons. During the earlier part of this long record, at KRM during MIS5, people harvested shellfish during the warmer months, suggesting that they took advantage of the improved summertime weather conditions and largely avoided shellfishing during the cooler months when it was more difficult and dangerous. Yet, during the MIS5-4 transition at PP5-6, during an episode of dramatic landscape reorganisation and climate change, people concentrated their shellfishing activity during the cooler months of the year, suggesting that these resources played a specific role in the annual scheduling of subsistence activities. A similar pattern is observed in the LSA, during periods when it is thought that people lived at the coast throughout the year. The model we have proposed is that, at certain times, people relied on shellfish as an

important source of protein and essential nutrients for those times of the year when they were not engaged in procuring other, more highly-ranked protein resources, such as migrating terrestrial mammals or seals and whales.

6. Conclusion

No single period or site across the Middle or Later Stone Age demonstrates a year-round collection pattern for shellfish – what seems at first to be a year-round pattern during the MSA actually reflects the averaging of more complex patterning across sites and through time. Shellfishing may have been a more opportunistic activity during the MSA at KRM, given that few shells indicate that people harvested *T. sarmaticus* during winter, the most difficult season for shellfishing. However, by the MIS5-4 transition, during a major reorganisation of the coastal landscape and a time of sudden climate shifts, shellfishing at PP5-6 may have been integrated more systematically into the utilization of available resources on the landscape, to optimise the most highly valued seasonally-restricted resources, reflected in more focussed harvesting of shellfish during the cooler part of the year.

The marked cool season signal across the LSA is unexpected, given that other lines of evidence strongly indicate that hunter-gatherers were living permanently at the coast for at least some of this period (e.g. the post-Wilton). This strong pattern of seasonality, especially as it falls during times of the year considered to have been *less* optimal for shellfishing, indicates that LSA hunter-gatherers' subsistence behaviours were highly structured with respect to shellfish and to other coastal resources, and that shellfish was not a staple food throughout the year. Yet, the consistency in Holocene shellfishing seasonality, against the backdrop of otherwise large technological and subsistence shifts, supports interpretations of shellfishing as a mainstay of Later Stone Age coastal hunter-gatherer economic activities. The pronounced seasonality of shellfishing at various times throughout both the MSA and LSA records also confirms interpretations of shellfishing as one subsistence strategy within a highly organised coastal adaptation, and suggests that LSA and MSA hunter-gatherers might have been heavily reliant on shellfish at particular times of the year.

Acknowledgements

This work was supported by the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation of South Africa (grant no 84407); Clarendon Fund, University of Oxford; a Quaternary Research Association New Research Worker's Award, the Palaeontological Scientific Trust and a NERC Isotopes Geosciences Facilities Steering Committee Award (grant number IP-1543-0515). Permissions for export and sampling were obtained from the curator of the archaeological collections at Iziko Museum, Heritage Western Cape (case number 14072110GT0730E) and the Eastern Cape Provincial Heritage Resources Agency (permit number 2/2/APM-PERMIT/14/09/003). Grateful acknowledgments to Sarah Wurz for help accessing the collections from KRM, and Peter Ditchfield and Christopher Day for help with analyses. We thank Zenobia Jacobs for providing specific modelled age estimates. Excavations at PP5-6 were carried out with financial support from the National Science Foundation (BCS-0524087, BCS-1138073 and BCS-1460376), Hyde Family Foundations, and the Institute of Human Origins (IHO) at Arizona State University. CWM also acknowledges assistance from the Dias Museum, Mossel Bay, and permits issued by SAHRA and HWC.

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