

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

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4 Emma Loftus*^{a,b,c}, Julia Lee-Thorp^a, Melanie Leng^d, Curtis Marean^e, Judith Sealy^f

5 * el485@cam.ac.uk

6 ^a Research Laboratory for Archaeology and the History of Art, School of Archaeology,
7 University of Oxford, 1-2 South Parks Road, OX1 3TG, UK

8 ^b Merton College, University of Oxford, Merton Street, OX1 4JD, UK

9 ^c Present address: McDonald Institute for Archaeological Research, University of Cambridge,
10 Downing Street, CB2 3ER, UK

11 ^d NERC Isotope Geoscience Laboratory Facilities, British Geological Survey, Keyworth,
12 Nottingham NG12 5GG, UK and Centre for Environmental Geochemistry, School of
13 Geography, University of Nottingham, Nottingham NG7 2RD, UK

14 ^e Institute of Human Origins, School of Human Evolution and Social Change, Arizona State
15 University, PO Box 874101, Tempe, AZ, 85287-4101, USA and African Centre for Coastal
16 Palaeoscience, Nelson Mandela University, PO Box 77000, Port Elizabeth, 6031, South Africa

17 ^f Department of Archaeology, University of Cape Town, Private Bag X3, Rondebosch 7701,
18 South Africa

19

20 Abstract

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

44

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

47 1. Introduction

48

49 The southernmost coast of South Africa features the longest known record of coastal hunter-
50 gatherer occupation. This regional record has thus been a focus of some considerable interest
51 for understanding the development of complex behaviours that are typical of modern humans.
52 Researchers have suggested that the topographically and climatically circumscribed southern
53 Cape coast may have been an especially hospitable habitat for African hunter-gatherers
54 through the last glacial cycle, given the broadly stable, relatively aseasonal climate, high
55 diversity of terrestrial plant and animal resources within the broader ecological setting, and
56 access to intertidal marine foods along the highly productive rocky shoreline (Marean, 2010,
57 2014; Compton, 2011). Consequently, archaeological sites in this region have been the focus
58 of numerous studies investigating the significance of a coastal adaptation and shellfishing
59 behaviours (Steele and Klein, 2008; Clark and Kandel, 2013; Dusseldorp and Langejans, 2013;
60 Marean, 2014, 2016; Kyriacou et al., 2015; Will et al., 2015; Jerardino, 2016; Klein and Bird,
61 2016).

62

63 Shellfish are a stable and predictable food resource, available year-round along the south coast
64 where toxic algal blooms (e.g. “red tides”) are unusual, unlike along the west coast (Pitcher
65 and Calder, 2000). Recently, marine molluscs have been posited as a valuable source of key
66 nutrients that are otherwise rare in terrestrial foods. Although the overall importance of
67 shellfish to the diet in terms of calories has been disputed (Clark and Kandel, 2013), shellfish
68 have been identified as valuable packets of protein and nutrients, including iron, iodine and
69 long-chain fatty acids (Cunnane and Crawford 2014; Kyriacou et al. 2016; Parkington 2010).
70 This has led to suggestions that a diet with regular contributions of coastal or lacustrine foods
71 was essential for, first, the development of large-brained hominins (Cunnane and Crawford
72 2014), and second, the maintenance of good health and population viability among modern
73 human hunter-gatherers. Marean (2014, 2015, 2016) advanced an alternative evolutionary
74 model on the significance of coastal habitats which argues that a behavioural adaptation
75 focussed on rich and predictable coastal habitats would have triggered competition and
76 territoriality among populations living along the shoreline, leading ultimately to the uniquely
77 high level of non-kin cooperation observed within our species.

78

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

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

103

104 Seasonality of resource acquisition and site occupation is a key dimension of subsistence
105 behaviour and social organisation among hunter-gatherers (Deacon, 1984a; Kelly, 1995).
106 Seasonal mobility has been an influential framework in southern African archaeology for
107 exploring how hunter-gatherers might best have exploited seasonally fluctuating resources
108 found in different ecozones between coastal and inland environments (Parkington, 1976; Sealy
109 and van der Merwe, 1986; Sealy, 2006). Seasonal versus year-round occupation of coastal
110 localities implies different systems of social organisation, from highly mobile bands at one end
111 of the spectrum to permanently settled groups with defended territories at the other (Sealy,
112 2006). Interpreting the season of site occupation from fragmentary refuse in archaeological
113 sites is far from straightforward. Parkington (1972, 1976) detected contrasting seasonal
114 patterns in LSA faunal assemblages of juvenile seals and rock hyraxes between coastal and
115 inland sites along the west coast of South Africa, and developed a coherent model of coastal
116 winter and inland summer settlement. Contradicting evidence from stable isotope analyses of
117 human skeletal remains however showed that people buried at coastal and inland sites had
118 distinct diets and were therefore not a single population (Sealy and van der Merwe, 1986).
119 Subsequently, Sealy (2006) demonstrated dietary differences between two populations of
120 later LSA humans buried at southern Cape coastal sites at Robberg/Plettenberg Bay and
121 Matjies River, only 14 km apart, suggesting that these groups maintained a territorial boundary
122 between them. This study, along with several others from coastal and riverine areas, indicates
123 that some LSA communities became increasingly settled, at least after c.4 kcalBP (Hall, 1986;
124 Binneman, 1995; Jerardino, 1996, 2010, 2012).

125

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

138

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

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

150

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

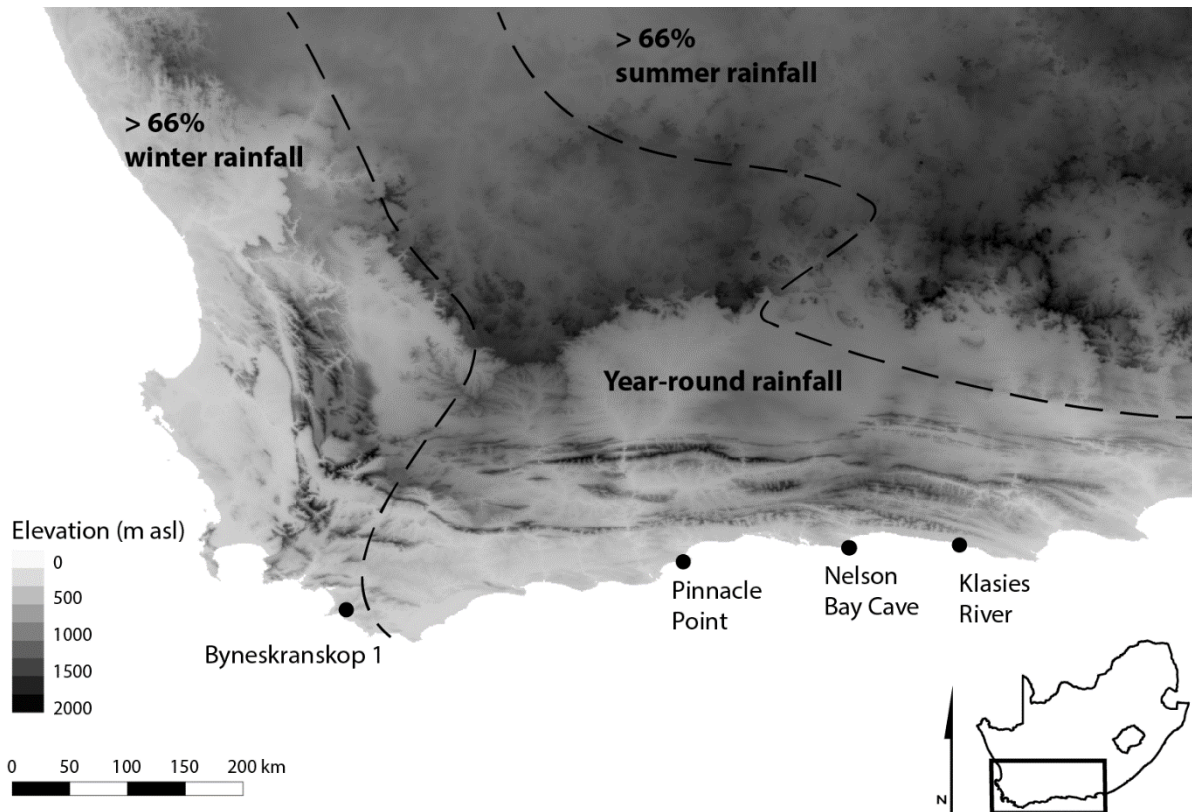
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166 2. Palaeoenvironmental context and archaeological sites

167 2.1 South coast ecology and resources

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

188 past. High numbers of grazing species occurred on the Palaeo-Agulhas Plain in the Pleistocene
189 (Marean et al., 2014; Copeland et al., 2016).
190



191
192
193 **Figure 1 Topographical map of south coast with locations of sites, and approximate limits of**
194 **the summer, winter and year-round rainfall zones indicated (Tyson and Preston-Whyte 2000).**

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

208
209 The modern coastline, part of the Agulhas Marine Province, is a mixture of rocky and sandy
210 shores which boast a wide variety of marine and estuarine resources, including seaweed, fish,
211 shellfish and marine mammals. Much of the coast is subject to high-energy wave action, an
212 important factor in the success of intertidal foraging activities by humans. Marine mammals
213 including seals and whales (whose bulky bones are unlikely to have been transported back to
214 archaeological sites) are another high-value, if unpredictable, marine resource for hunter-

215 gatherers, as a rich source of both protein and fat; seal remains are common in LSA sites along
216 this coastline (Schweitzer and Wilson, 1982; Singer and Wymer, 1982; Deacon, 1984a; Inskeep,
217 1987; Jerardino and Parkington, 1993; Marean et al., 2007).

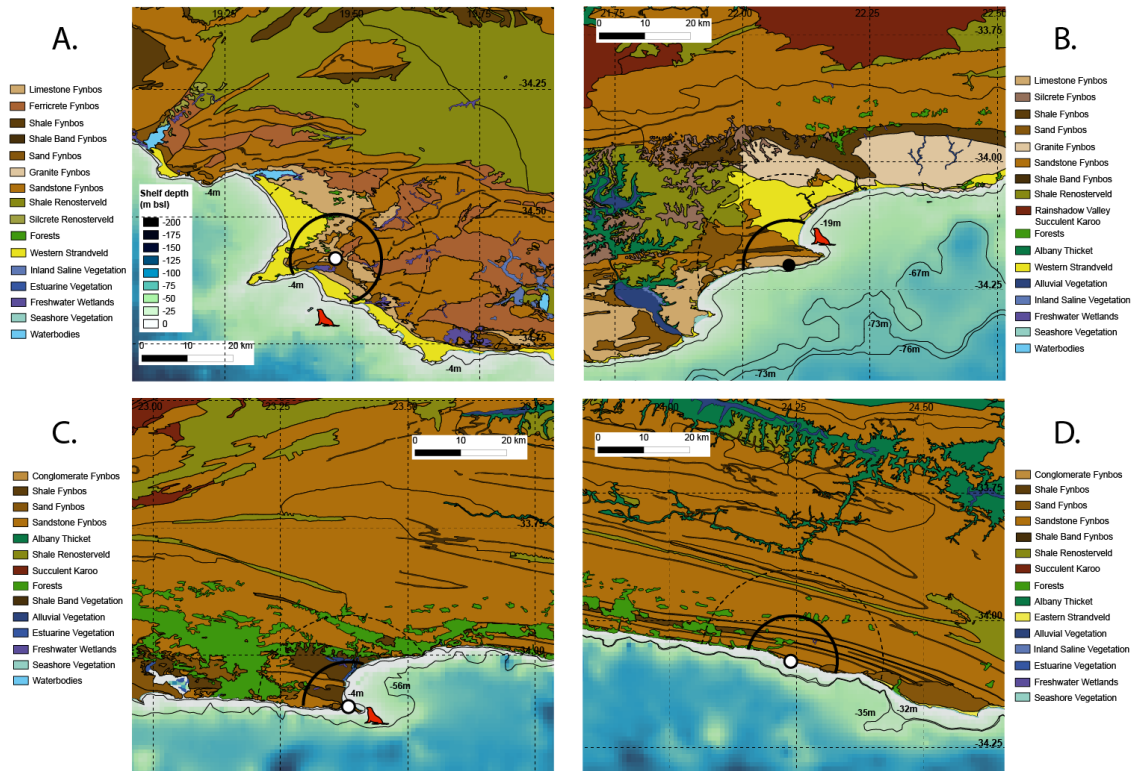
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219 Adjacent to the present coast is the Agulhas Bank, a large, coastal plain that is currently
220 submerged but which was exposed to various degrees during periods of lower global sea levels
221 throughout MIS5-4 (van Andel, 1989; Fisher et al., 2010). Numerous late Pleistocene and
222 Holocene archaeological sites along the coastline of the modern high-sea stand attest to the
223 importance of this coastal shelf region (Compton, 2011). Marean et al. (2014) have proposed
224 that this plain was likely to have been covered with grassy fynbos and thicket vegetation that
225 formed a productive grazing ecosystem supporting large herds of terrestrial herbivores.
226 Importantly for this study, the coastline would have been shifted further out during glacial
227 periods, affecting the sites inhabitants' access to coastal resources. Moreover, the impact of
228 sea level regressions varied along the coastline, as the slope of the coastal shelf steepens
229 towards the east (see Figure 2). Towards the centre and west, where the shelf is shallowest,
230 glacial decreases in sea level of between c. 70 m (average over MIS3 [57-29 ka]) and c. 110 m
231 (average over MIS2 [29-14 ka]) would have resulted in coastlines c. 20 km and c. 70 km further
232 south, respectively, and up to nearly 100 km at the LGM when sea-levels were lowered by
233 120 m (i.e. at Pinnacle Point; Fisher et al. 2010). In contrast, at the eastern extreme of this
234 study, the coastline at Klasies River Main Site was an average of only c. 6 and c. 23 km further
235 out during MIS3 and MIS2, respectively. In addition, changes in the coastal configuration
236 affected the distribution of geological substrates that shape intertidal communities (Jerardino
237 and Marean, 2010), so that certain habitats, such as quartzitic rocks were not present within
238 range of the sites at different times (Cawthra et al., 2015, 2018).

239

240 *2.2 Archaeological context and sites*

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



257
258

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

269 Later Stone Age sites NBC and HRC (see Figure 2C) are both located on the narrow Robberg
270 Peninsula, about 800m apart, and reflect similar environmental conditions. NBC, in particular,
271 is an important site for the regional archaeological sequence, with an LSA technological
272 sequence and good organic preservation (Klein, 1972; Deacon, 1984a; Inskeep, 1987). Shells
273 are abundant in the deposits from the terminal Pleistocene levels (c. 14.5 kcal BP): prior to this,
274 sea-levels were c. 100m below modern levels, with the coastline more than 20 km away. At
275 both sites, the density of identifiable shell increases through time, although assessments of
276 the relative importance of shellfish are confounded by taphonomic and sampling concerns.
277 Shell samples were selected from across the Holocene and terminal Pleistocene levels, which
278 are securely dated by a Bayesian modelled suite of conventional and accelerator radiocarbon
279 dates (Loftus et al., 2016). Radiocarbon dates from HRC show that the part of the sequence
280 investigated thus far spans only a couple of thousand years in the late Holocene (Kyriacou,
281 2009). Today, the Robberg Peninsula and surrounding region is largely vegetated by fynbos,
282 with extensive patches of forest within 20 km, and freshwater and estuarine wetlands present
283 in the adjacent bay. A Cape fur seal breeding colony present on the peninsula itself is likely to
284 have been a highly attractive resource to hunter-gatherers: seal remains are found throughout
285 the LSA levels at NBC and Sealy (2006) suggests that elevated $\delta^{15}\text{N}$ values measured in later
286 LSA human skeletons from Robberg and nearby locations likely reflect regular access to marine
287 mammals.

288
289 BNK1 (Figure 2A) is located c. 400 km west of NBC, at the current boundary between the year-
290 round and winter rainfall zones. The deposits extend from the terminal Pleistocene through to
291 the late Holocene, although well-preserved shells are found only in the upper levels
292 (Schweitzer and Wilson, 1982). The chronology of this site is well constrained by a Bayesian
293 model of AMS and conventional radiocarbon dates (Loftus et al., 2016). The site is located in a
294 patchwork of fynbos vegetation types, with numerous small patches of forest and freshwater
295 wetlands within 20 km. Along the coastline is a stretch of strandveld vegetation. Today, a seal
296 colony is located at an offshore island; this or a similar colony may have provided occasional
297 washed up seals, as their bones are found at low frequencies throughout the BNK deposits.

298
299 The terminal Pleistocene and Holocene archaeological record of the south coast records
300 sweeping changes in the technological record of the south coast region (Deacon, 1978, 1984b).
301 At c. 14 kcalBP in the southern Cape (Loftus et al., 2016), late Pleistocene microlithic
302 assemblages were replaced by the early Holocene macrolithic Oakhurst, characterised by
303 unretouched artifacts made largely on coarse quartzite raw materials. Judging by the numbers
304 of sites and volumes of deposits at this time, the Oakhurst techno-complex appears to have
305 occurred at a time of moderate to high population density along the south coast (Sealy, 2016).
306 The Oakhurst was replaced by the microlithic Wilton at c. 8 kcalBP (Lombard et al., 2012),
307 featuring standardised retouched tools made from fine-grained rocks that may reflect the
308 greater importance of long distance contact among smaller populations, possibly in response
309 to challenging environmental conditions (Wadley, 1989; Sealy, 2016). Faunal remains include
310 more small game and more marine resources (Klein, 1972). In the southern Cape, a macrolithic
311 industry characterised by crude, unstandardized quartzitic artefacts and abundant bone
312 artifacts replaces the Wilton at c. 4 kcalBP. Numerous lines of evidence suggest that population
313 densities were high during the post-Wilton, with increasingly settled populations at least in
314 some areas and indications of “intensification” in the archaeological subsistence record,
315 including increased exploitation of marine foods such as fish (Inskeep, 1987; Sealy, 2006,

316 2016). Although these industries display considerable geographic variation, the technological
317 framework is considered useful for outlining broad trends across southern Africa, and has
318 shaped much of southern African LSA research in the last few decades. In this study, the LSA
319 *T. sarmaticus* samples are aggregated by depositional context and attribution within this broad
320 technocomplex framework.

321

322 Middle Stone Age sites Klasies River Main Site (KRM: Figure 2D), on the Tsitsikamma coastline,
323 is a site complex that contains extensive deposits spanning tens of thousands of years from the
324 last interglacial to c. 55 ka, with overlying Holocene layers (Singer and Wymer, 1982; Deacon
325 and Geleijnse, 1988; Wurz, 2002). The Klasies River sites have produced some of the earliest
326 evidence for anatomically modern humans and complex behaviours in southern Africa
327 (Rightmire and Deacon, 2001). The deposits are dated by a variety of methods (e.g. optically
328 stimulated luminescence [OSL], electron-spin resonance and U-Th dating), but are generally
329 constrained only very broadly to periods within MIS5-3. Shell samples come only from MIS5
330 aged deposits and samples are aggregated according to the technological units identified by
331 Wurz (2002). At the base of the sequence, c. 115-108 ka (MIS5e) (Feathers, 2002), are the
332 “MSA I” levels, characterised by long, thin points and blades. The subsequent “MSA II” levels
333 are divided into “MSA II Lower” (c. 101-90 ka) and “MSA II Upper” (c. 85 ka) phases, and are
334 characterised by the production of Levallois-like points¹. The site is usually described as being
335 located within a fynbos dominated landscape, with only small patches of forest nearby (see
336 Figure 2D). However, a recent comprehensive survey of vegetation within 5 km of KRM found
337 that in fact the surroundings are a complex mosaic of predominantly thicket, forest and coastal
338 vegetation elements, and only occasional fynbos contributions (van Wijk et al., 2017). The
339 authors attribute the discrepancy between this survey and the broad-scale SANBI map to the
340 extremely varied terrain around the site that supports a much greater diversity of vegetation
341 types, especially thicket microhabitats on steep sheltered slopes. The survey recorded a high
342 proportion of useful plants, including edible and medicinal plants. The relatively steep offshore
343 coastal profile means that the coastline would not have been very far away during the
344 occupation periods studied here. Studies of the archaeological shells show that although nearly
345 forty species of marine molluscs were collected, the MSA I and MSA II units are dominated by
346 brown mussels (*Perna perna*), *Turbo sarmaticus*, limpets (*Patellidae sp.*) and, a sandy shore
347 species, white mussel (*Donax serra*) (Thackeray, 1988). Changes in the frequencies of different
348 species through time are attributable to sea level-driven changes in the coastal environment,
349 especially the occurrence of inter-tidal habitats, such as rocky or sandy shores (Thackeray,
350 1988; Langejans et al., 2017).

351

352 Pinnacle Point 5-6 (PP5-6: Figure 2B) is part of a complex of rockshelters and caves in sea-facing
353 cliffs adjacent to Mossel Bay. Research undertaken as part of the South African Coastal
354 Paleoclimate, Paleoenvironment, Paleoecology, and Paleoanthropology project has ranged
355 widely beyond the cave sites, with interdisciplinary studies of the ancient and modern
356 landscape and detailed palaeoenvironmental reconstructions (e.g. Fisher et al. 2010; De Vynck
357 et al. 2016a, 2016b; Singels et al. 2016; Bar-Matthews et al. 2010; Marean, 2010). The PP5-6
358 deposits, dated by a comprehensive suite of OSL dates and Bayesian modelling, validated by
359 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.

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

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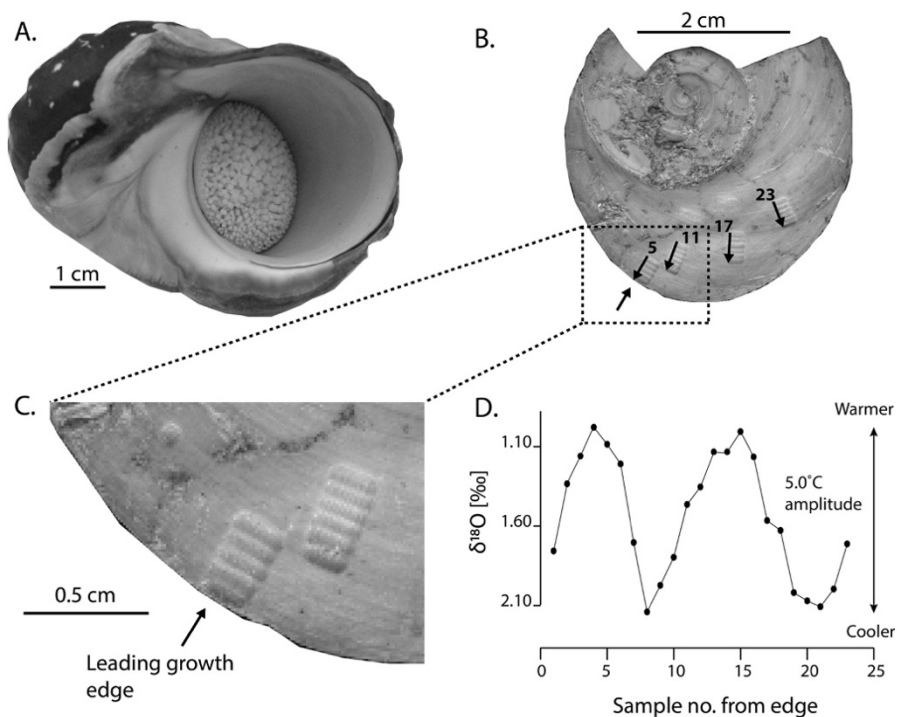
370 3. Materials and methods

371

372 3.1 *Turbo sarmaticus* shell selection

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

383



384

385

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

390 The operculum is precipitated as aragonite, a metastable form of CaCO₃. Aragonite is known
391 to be susceptible to dissolution and recrystallization to more thermodynamically stable calcite
392 over time, whereby the original isotopic composition may be altered. Moreover, aragonite
393 preservation can be highly patchy across the exposed surfaces of individual opercula.
394 Aragonite and calcite are readily distinguished using Fourier transform infrared spectroscopy
395 and x-ray diffraction, and the detection of calcite in these opercula provides an unambiguous
396 indication of recrystallization. We used an FTIR-ATR based method (Loftus et al. 2015) capable
397 of detecting even small amounts of calcite (< c. 5 wt%) that requires small amounts of
398 powdered CaCO₃ (c. 0.5 mg) for analysis, which can be recovered for stable isotope analysis.
399 Thus, each shell sample destined for δ¹⁸O analysis can be pre-assessed for diagenesis,
400 permitting a highly-resolved evaluation of recrystallization across the entire drilling path.

401
402 Upon an initial pre-screening using this FTIR-ATR method, archaeological opercula with intact
403 growth edges were sampled at high-resolution using a New Wave Merchantek micromill with
404 tungsten carbide dental burrs (0.8 mm – overlapping of samples allows for c. 0.6 mm
405 resolution), following the surface growth increments (Figure 3B and C). Every 4th or 5th milled
406 sample (i.e. 2 - 3 mm) was assessed with FTIR-ATR: if recrystallisation was detected along the
407 drilling path then the series of powdered samples continuing past the altered patch were
408 discarded. Approximately a fifth of the milled samples from all sites were discarded in this way.
409

410 3.2 Interpreting season of harvest

411 A recent study of modern *T. sarmaticus* shells collected from Mossel Bay showed that *T.*
412 *sarmaticus* precipitate their shells in equilibrium with δ¹⁸O_{water}, (Galimberti et al., 2017), with
413 formation temperatures best reconstructed using the Grossman and Ku (1986)
414 palaeotemperature equation for aragonitic foraminifera and molluscs (as modified by Hudson
415 and Anderson (1989) to account for the 0.2‰ difference between SMOW and average marine
416 water):

$$417 T(^{\circ}\text{C}) = 19.7 - 4.34 * (\delta^{18}\text{O}_{\text{aragonite}} - \delta^{18}\text{O}_{\text{water}})$$

418 where δ¹⁸O_{water} is 0.53‰, as established by modern measurements at Mossel Bay (adjacent to
419 the Pinnacle Point site; Galimberti et al., 2017). While individual shells do not necessarily
420 capture the full annual temperature amplitude of an *in situ* daily SST recorder, mean
421 measurements across an assemblage of shells capture the average SST conditions well
422 (Galimberti et al., 2017; Loftus et al., 2017).
423

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

437 estimations per archaeological level, additional shells were sampled only at the growth edge
 438 (4 milled samples) to characterise SST conditions just prior to death. The final analytical
 439 samples from each shell are interpreted with reference to the annual SST range from each
 440 archaeological unit to interpret the season of harvest.

441

442 **Table 1 New season of harvest reconstructions, based on serial $\delta^{18}\text{O}$ measurements (‰ PDB)**
 443 **for modern *Turbo sarmaticus* opercula, live-collected from Mossel Bay. The inter-quartile**
 444 **ranges for the entire dataset are: first quartile (winter) = +1.07‰ – +0.58‰; interquartile**
 445 **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 |

446

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

458

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

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

472

473 3.3 Stable isotope analyses and corrections

474 Carbonate samples showing minimal amount of calcite (as described above) were analysed on
475 one of three systems - a Kiel Device coupled to a Delta V Advantage isotope mass spectrometer
476 in the Earth Science Department, University of Oxford (external reproducibility of 0.10‰ for
477 $\delta^{18}\text{O}$); an automated Thermo GasBench II device, coupled to a Thermo Delta V Advantage
478 isotope mass spectrometer at the Division of Archaeological, Geographical and Environmental
479 Sciences of the University of Bradford (external reproducibility of 0.30‰ for $\delta^{18}\text{O}$); and a
480 Multiprep device coupled to a GV Isoprime isotope mass spectrometer at the NERC Isotope
481 Geosciences Facilities at the British Geological Survey, Keyworth (external reproducibility of
482 $<0.10\text{‰}$ for $\delta^{18}\text{O}$). In each case CO_2 was produced by 100% phosphoric acid hydrolysis, and the
483 solid-gas fractionation of the samples is corrected using an aragonite specific factor with
484 appropriate corrections for reaction temperature: 1.00906 at 71°C [Kiel and Gasbench],
485 1.00854 at 90°C [Isoprime]; Kim et al., 2007). The samples were calibrated against internal
486 calcite standards calibrated in turn to international standards (NBS19: $\delta^{18}\text{O} = -2.20\text{‰}$). Results
487 are reported in the delta-notation relative to V-PDB, according to the equation:

$$488 \delta^{18}\text{O} (\text{‰}) = \left\{ \left(\frac{R_{\text{SAMPLE}}}{R_{\text{STANDARD}}} \right) - 1 \right\} \times 1000,$$

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

490

491 Molluscan CaCO_3 $\delta^{18}\text{O}$ is a function of both formation temperature and oceanic $\delta^{18}\text{O}$ and so
492 $\delta^{18}\text{O}$ values must be corrected for the large shifts in global oceanic $\delta^{18}\text{O}$ across the last glacial
493 cycle. While there is no regional record of $\delta^{18}\text{O}$ that spans the entire period of interest, the
494 high-energy wave dynamics of this coastline ensure thorough water mixing, therefore the
495 global stack of Waelbroeck et al. (2002) is applied. The ages for each shell were determined
496 with reference to their context in the archaeological deposits and the error of the correction
497 is a result of the age uncertainty of the sample in each case. See Table 2 for the age and
498 correction applied to shells from each archaeological unit. In total, 104 archaeological shells
499 (1302 $\delta^{18}\text{O}$ determinations) were analysed (Table 2: 40 opercula from the three LSA sites (25
500 from NBC, 2 from HRC, 13 from BNK), and 64 from the MSA sites (34 from PP5-6 and 30 from
501 KRM).

502

503 4. Results

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

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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 Karkanis 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 | DDBS | 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 | 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 |

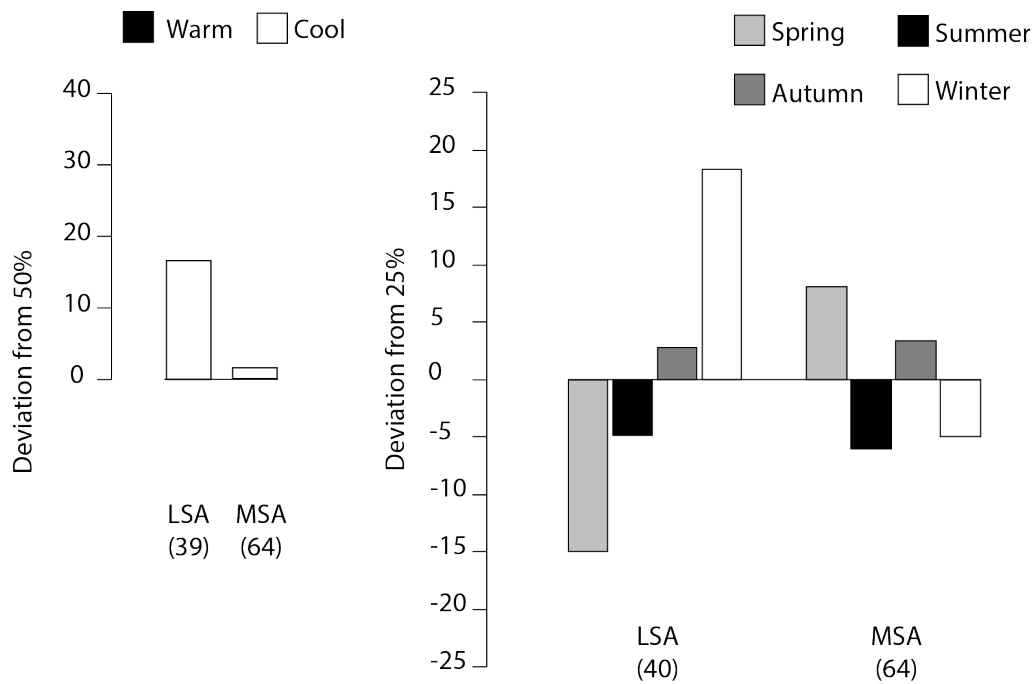
522

523 For example, in Figure 4, a cool season signal is overrepresented in the LSA dataset by 18% (i.e.
 524 68% of the shells were harvested during the cool season). Based on the quarterly method of
 525 interpretation, winter is overrepresented by 18% (i.e. 43% of the shells were harvested in
 526 winter alone), while virtually no shells were collected in spring (only 1 out of 36). However, the
 527 expected frequencies for summer and autumn collection during the LSA are approximately as
 528 hypothesised if equal throughout the year, at c. 25% each. Figure 5A shows a graph of the same
 529 type for the LSA dataset from NBC according to the post-Wilton, Wilton and Oakhurst
 530 archaeological divisions (the patterns from the two Robberg peninsula sites do not differ
 531 significantly from those observed at BNK, and samples from these sites have been aggregated).
 532 The Oakhurst assemblage shows more cool season deaths, and the Wilton and post-Wilton
 533 show a more equal cool and warm season signal. The post-Wilton, Wilton and Oakhurst
 534 quarterly and semi-annual seasonal distributions are not statistically different from one
 535 another.

536
 537 **Table 3 Semi-annual and quarterly seasonal harvesting results summarised for the Later and**
 538 **Middle Stone Age sites, and by archaeological level (individual shell results provided in SM,**
 539 **with the seasonal limits for interpretation). Totals may differ slightly between the two**
 540 **methods of analysis because no attribution is made when a sample value falls exactly at one**
 541 **of the seasonal category boundaries.**

| Site | Level | Semi-annual | | Quarterly seasons | | | | Total | |
|------|---------------|-------------|------|-------------------|--------|--------|--------|-------|----|
| | | cool | warm | spring | summer | Autumn | winter | | |
| | All LSA | 26 | 13 | 4 | 8 | 11 | 17 | 40 | |
| LSA | 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 |
| | All MSA | 33 | 30 | 21 | 12 | 19 | 13 | 64 | |
| MSA | | All PP5-6 | 22 | 11 | 9 | 5 | 11 | 9 | 34 |
| | PP | 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 |
| | MSAII | upper | 5 | 7 | 8 | 1 | 2 | 1 | 12 |
| | | lower | 5 | 7 | 3 | 3 | 4 | 2 | 12 |
| | | MSAI | 1 | 5 | 1 | 3 | 1 | 1 | 6 |

542

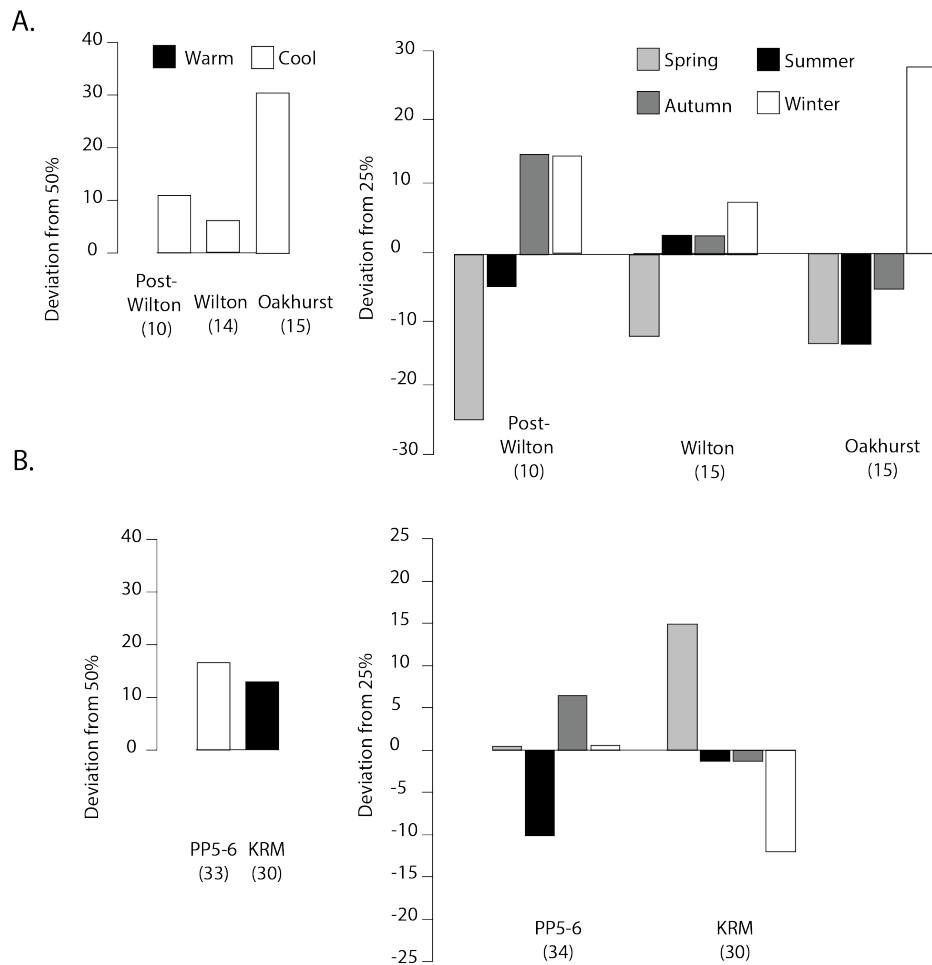


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544

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

550 The overall pattern in the MSA, inferred from both KRM and PP5-6 combined, appears
 551 relatively aseasonal. However, this generalisation masks significant inter-site and inter-period
 552 differences, discussed in more detail below. A comparison of the data for the two MSA sites,
 553 KRM and PP5-6, shows more warm season *T. sarmaticus* deaths in the KRM assemblage
 554 compared to more cool season deaths in PP5-6 (Figure 5B). The semi-annual and quarterly
 555 patterns observed at PP5-6 are statistically different from those observed at KRM ($p=0.02$ and
 556 $p=0.03$, respectively, Chi-squared comparison with Williams correction for small sample sizes),
 557 although the sizes of the effects are small (Cramér's $V = 0.22$ and 0.26 , respectively). The MSA
 558 and LSA quarterly seasonal distributions are statistically different from each other, but again
 559 the effect is small ($p=0.02$, Chi-squared comparison with Williams correction for small sample
 560 sizes, Cramér's $V = 0.30$).

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565

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

570

571 5. Discussion

572 5.1 Later Stone Age shellfishing seasonality

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

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

598
599 While the south coast is relatively aseasonal, with less marked annual variation in temperature
600 and rainfall compared to surrounding regions, there is evidence for seasonal shifts in the
601 availability of important classes of food resources other than shellfish, including plants with
602 underground storage organs, most palatable in late summer and autumn (Deacon, 1976), and
603 other marine foods. The Cape fur seal birthing season is tightly focussed over a few weeks in
604 late November and early December (i.e. summer), but mortality spikes nine months later when
605 the juveniles are weaned and must leave the rocks to find food: many die of exhaustion (in
606 August to October, i.e. late winter and spring) (Klein and Cruz-Urbe, 1996). Klein and Cruz-
607 Urbe argue that, in general, the age range of seals from LSA sites, including NBC, indicates that
608 coastal hunter-gatherers targeted these juvenile seals, and they suggest that LSA hunter-
609 gatherers timed coastal visits to coincide with late winter and spring. In fact, the age range of
610 seals from NBC itself is not very tightly clustered, and instead indicates a broader seasonal
611 range in which seals were eaten (see J. Deacon, 1984: 431). This likely reflects year-round
612 access by local hunter-gatherers to the land-based seal colony on Robberg Peninsula itself and
613 perhaps others; there was a historically documented colony on the tidally-accessible Beacon
614 Island located in Plettenberg Bay. However, seal colonies do fluctuate seasonally in size, as the
615 animals spend more of their time feeding at sea during autumn and winter, whereas they are
616 largely land-based during the spring and summer breeding season (Oosthuizen and David,
617 1988), making better targets of both juvenile and adult seals. Relatedly, a report on the
618 incidence of whale strandings in modern times recorded a significant number of stranded
619 whales on the southern African coast, which were most common from August to December
620 (i.e. centring on spring) (Smith and Kinahan, 1984). Assuming greater numbers of whales prior
621 to commercial hunting, and given the enormous amount of food represented by a whale
622 carcass, strandings may have been an important spring bonanza for hunter-gatherers.

623
624 A strategy whereby the coastal occupants switched within the year from one source of marine
625 *protein* (i.e. marine shellfish) to different sources that are only seasonally abundant (i.e.
626 juvenile and breeding seals, whale wash-ups), could explain both the underrepresentation of
627 spring-harvested shellfish and the overrepresentation of winter-harvested shells at NBC and
628 BNK. Potentially, shellfish were one of the few reliable sources of protein during winter, while
629 in spring and summer hunter-gatherers had more ready access to other marine protein sources
630 such as seals and whale carcasses. Certainly, the $\delta^{15}\text{N}$ values of mid-to-late Holocene LSA
631 hunter-gatherers buried on Robberg and nearby reflect the consumption of considerable
632 amounts of high-trophic level marine foods (Sealy, 2006). Together, these lines of evidence

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

635
636 When assessed by archaeological period, the LSA shellfishing assemblages reveal some small
637 shifts in the seasonality across the Oakhurst, Wilton and subsequent post-Wilton (Figure 5A).
638 Although the small sample sizes warrant caution here, the magnitude of any differences
639 between the three archaeological periods is small. Given the profound shifts that are evident
640 in technological, cultural and other subsistence records (i.e. Deacon, 1984; Inskeep, 1987),
641 alongside evidence for shifts in both total population size and the degree of territoriality across
642 the Holocene (Sealy, 2006, 2016), we expected to observe more marked shifts in the
643 seasonality of shellfishing, identified as a highly suitable activity for intensification. The
644 directions of the observed shifts are also opposite to expectations based on population size –
645 the period for which we have the most secure evidence of large, more territorial populations
646 (the post-Wilton) exhibits more strongly seasonal patterning than the preceding Wilton, when
647 population numbers were regionally depressed. This suggests that when people were more
648 densely packed on the landscape, subsistence activities were more structured within an annual
649 framework to optimise seasonal surfeits and scarcities.

650
651 Of course, the shellfish assemblages found within the archaeological sites represent only those
652 shells brought back to the site, and not the shellfish eaten elsewhere. To exclude the possibility
653 that our conclusions are confined to one species, it would be useful to investigate shellfishing
654 seasonality among other well-preserved species that are common in the sites, including those
655 from different habitats, such as the sandy shore-dwelling white mussel, to establish if similar
656 patterns emerge. In fact, the earliest application of serial isotope sampling to marine shells
657 ever was undertaken by Nicholas Shackleton on shell material from Nelson Bay Cave to identify
658 the season of harvest (Shackleton, 1973). He sampled fifteen *Patella* (now *Scutellastra*)
659 *tabularis* limpet shells from the Wilton levels to investigate seasonal timing of harvest and
660 likewise concluded that the shells were largely harvested during the cooler, winter months.
661 This is an encouraging confirmation that the pattern comprehensively demonstrated here for
662 *T. sarmaticus* in fact reflects the broader subsistence strategy, and not just the targeting of a
663 single species.

664 665 *5.2 Middle Stone Age shellfishing seasonality*

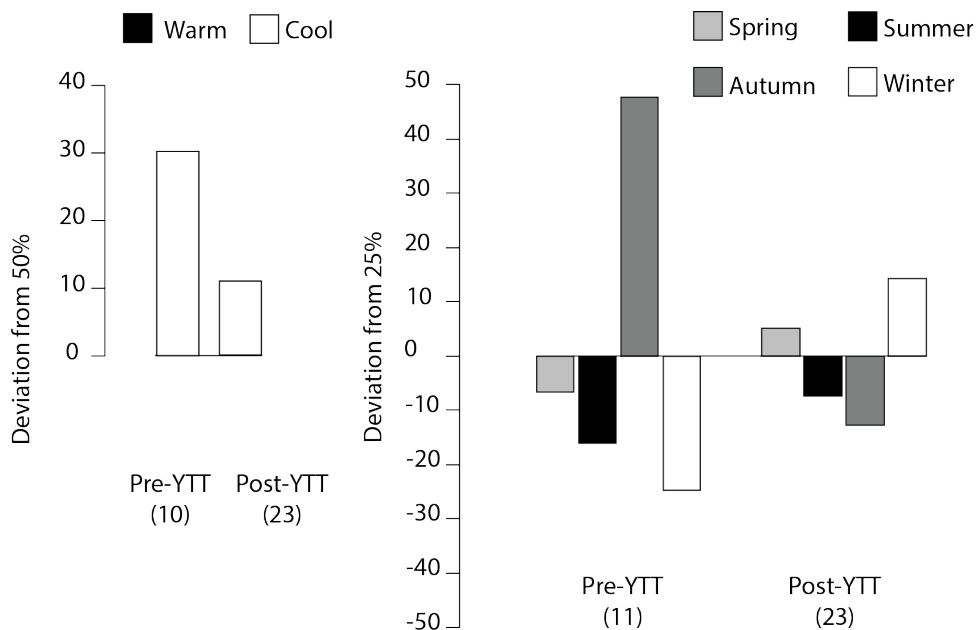
666 Taken all together, the entire dataset of 104 shells demonstrates marked differences in
667 shellfishing behaviours between the MSA and LSA. However, upon closer examination, the
668 apparent year-round pattern observed in the aggregated MSA dataset (Figure 4) reflects the
669 averaging of two very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

676
677 The overall pattern at KRM conforms to expectations, insofar as the fewest number of shells
678 were harvested in winter, the least optimal season, although there are fewer than expected
679 summer harvested shells, assuming this was the most optimal season for shellfishing.

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

701
702 The seasonality pattern at PP5-6 differs from that at KRM, with summer underrepresented and
703 autumn overrepresented. However, it is apparent on closer inspection that this pattern is a
704 consequence of the averaging of two quite different seasonality patterns *within* the PP5-6
705 dataset, although neither corresponds closely with that observed at KRM. A recent study at
706 PP5-6 detected cryptotephra shards from the Toba volcanic eruption in Sumatra, well-dated
707 at proximal deposits to c. 74 ka, just prior to the onset of fully glacial conditions in MIS4 (Smith
708 et al., 2018). The Toba isochron is found above the ALBS samples in this study.
709 Geoarchaeological analysis of the PP5-6 sediments indicate that environmental changes
710 related to the onset of MIS4, including the retreat of the coastline, began with the shift from
711 LBSR to ALBS (a rapidly accumulated dune deposit), with unit SADBS occurring well within
712 MIS4. The archaeological sequence from LBSR to SADBS reveals a shift from low- to high-
713 intensity occupation (Karkanas et al., 2015). Figure 6 shows the combined results of units LBSR
714 and ALBS (n=11), prior to and during the MIS5-4 transition, with those from the overlying MIS4
715 units SADBS and OBS1 (n=22) (again, the small sample sizes for this comparison warrant
716 caution). The comparison reveals subtly different seasonal patterning (although not
717 statistically significant), with the earlier period dominated by autumn harvesting (almost 8 out
718 of 11 shells were collected in autumn), while the later period shows evidence for increased
719 winter harvesting (9 out of 22 shells).

720



721
722

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

726 It appears then that people timed their shellfishing activities differently during MIS5 and the
727 MIS5-4 transition than subsequently during MIS4. The coastline is projected to have been
728 relatively close to the site during the deposition of LBSR and the brief period represented by
729 ALBS, but subsequently retreated rapidly to >10 km away between c. 74 ka and c. 71 ka (Fisher
730 et al., 2010), the limit of a hunter-gatherer's daily foraging range (e.g. Jerardino and Marean,
731 2010). Unit SADBS features a technological shift from preceding units, with an unnamed stone
732 tool technology characterised by heat-treated microlithic backed bladelets similar to
733 microlithic tools from Holocene LSA sites (Brown et al., 2012), which the PP5-6 excavators
734 suggest were made to be hafted as part of projectile weapons, perhaps arrows or atlatl darts.
735 Further, Wilkins et al. (2017) showed that several features of the lithic technology at PP5-6
736 changed with the onset of MIS4 along the south coast, including raw material usage and
737 reduction intensity. The authors attribute these technological changes to increasing
738 populations, more intense site occupation, and decreased residential mobility that was a
739 consequence of landscape and environmental shifts accompanying the onset of glacial
740 conditions. As global sea-levels dropped, the expanded coastal plain is argued to have hosted
741 large populations of migratory ungulates, briefly offering the PP5-6 occupants a rich diversity
742 of both terrestrial and marine resources, before the coastline receded beyond foraging range
743 (Wilkins et al., 2017).

744

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

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

756

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

769

770 Yet, the patterns observed at PP5-6 appear to have been broadly stable, insofar as the
771 inhabitants appear to have preferred the cooler months for shellfishing over long periods,
772 regardless of sea-level. Galimberti (2010) investigated the seasonality of *T. sarmaticus*
773 harvesting from older MIS5 deposits at the sites PP9B (114 ± 5ka) and PP13B (units LRS: 114-
774 106ka, and URS and SBS: 98-92ka), within the Pinnacle Point complex of caves. The small
775 assemblage (n=13) from this study reveal a marked cool season signal for harvesting, with only
776 3 out of 13 shells harvested during the warm months of the year. This pattern is similar to that
777 observed in the more recent deposits at PP5-6, and quite unlike the broadly contemporaneous
778 MIS5 assemblage from KRM (see Figure 5B). This difference in seasonality between the two
779 locations along the south coast implies that MSA hunter-gatherers employed contextual
780 strategies for shellfish harvesting within the same greater ecosystem, perhaps according to
781 differences in the seasonal abundance of different resources such as plant foods and game.
782 Despite both areas being classed as largely fynbos (see Figure 2), the area around KRM today
783 includes more thicket-type vegetation, with a variety of plant communities due to the varied
784 small-scale topography of the slopes around KRM (van Wijk et al., 2017). This type of
785 vegetation yields plant foods year-round and so is less seasonally restrictive for foragers than
786 fynbos or renosterveld (De Vynck et al., 2016). Moreover, variation in the angle of the coastal
787 shelf would accommodate a wider coastal plain in front Pinnacle Point than at KRM when sea-
788 levels began to lower after MIS 5e, which may account for the differing seasonality patterns at
789 these locations. Clearly, additional research in mapping spatial trends in resource availability
790 and ecological seasonality within the south coast, as opposed to treating the region as
791 unvarying all along its length, will contribute greatly to understanding the important
792 differences between these archaeological sites.

793

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

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

805

806 *5.3 Global Comparisons*

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

818

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

829

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

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

849
850

851 6. Conclusion

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

862

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

876

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