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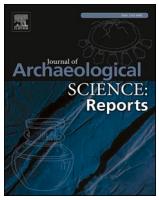

Shellfish gathering during MIS 5c-d at Klasies River main site and Blombos Cave, southern Cape, South Africa: An inter-assemblage comparison

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ABSTRACT

Klasies River main site and Blombos Cave, both situated in the southern Cape, South Africa, provide new insights on shellfish harvesting behaviour during MIS 5c-d. This is a period linked to the MSA II Lower or Mossel Bay techno-complex. The shellfish assemblage composition at Klasies River main site and Blombos Cave are somewhat different and fluctuation in species representation occurs through time at each site. For example, at Klasies River main site, *Turbo sarmaticus* and *Perna perna* are predominant while some of the lesser represented species include *Diloma sinensis* and *Burnupena cincta limbosa*. *T. sarmaticus* dominates the Blombos Cave shellfish assemblage followed by *Cymbula oculus*, *P. perna*, *Dinoplax gigas*, and *Scutellastra argenvillei*. The coastal habitat at both sites were generally rocky with smaller sandy shores during some periods, especially in layers Black Occupational Soils Three (Klasies River main site) and CJ (Blombos Cave). Sea surface temperatures were relatively colder than today in the southern Cape during this period. *T. sarmaticus* individuals are larger at Blombos Cave than at Klasies River Main site and there are clear differences in the ratio of *T. sarmaticus* shell weight to opercula weight at Klasies River main site compared to Blombos Cave. Size differences may be explained by climatic or environmental factors, and contrasting ratios may have resulted from different processing strategies at these two sites. Alternatively, the Klasies River deposits may have been subjected to more intensive post depositional processes influencing the preservation of the shell.

1. Introduction

Subsistence behaviour in the Middle Stone Age (MSA) of Africa comprised mainly of hunting and gathering of terrestrial resources and, becoming apparent from Marine Isotope Stage (MIS) 6 onwards, coastal resources such as shellfish are found in some deposits.

Coastal adaptation *sensu lato* means the occupation of coastal environments and the regular use of marine/aquatic resources (e.g., Erlandson and Fitzpatrick, 2006; Jerardino, 2016; Klein and Bird, 2016; Will et al., 2016). Early evidence for coastal subsistence is characterised by marine resources such as fish, sea mammals and birds, molluscs, and crustaceans (Avery et al., 2008; Dusseldorp and Langejans, 2013; Marean, 2014; Will et al., 2019) at archaeological sites along the coasts of South Africa. In some cases, it has led to the formation of shell middens (Jerardino, 2016) especially in the latter part of human prehistory. A shell midden constitutes deposits of shells accumulated by human beings through foraging activities for subsistence needs. Non-human agents also accumulated shells and these do not qualify as shell middens (Claassen, 1998; Jerardino, 2016). Shell middens also contain other foraged resources such as terrestrial vertebrates, seals, seabirds, and plants.

From a global perspective, early evidence of shellfish collecting appears in the MSA and Mousterian occupations during MIS 6 (Stiner, 1993; Jerardino and Marean, 2010; Ramos-Muñoz et al., 2016; Marean, 2010; Will et al., 2019; Will, 2020) involving *Homo sapiens* and Neanderthals. However, the rise of sea levels during the MIS 5e would have destroyed many localities pre-dating MIS 6 (Marean et al., 2007), hence evidence for systematic shellfish gathering before this time is scarce (Erlandson, 2001; Fisher et al., 2010; Will et al., 2016).

Evidence of marine mollusc exploitation for food during the MSA/Mousterian is summarised in Table 1 (although this is not an exhaustive list). On the Mediterranean coast of northern Africa, sites with marine

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shell remains include Contrebandiers Cave (Steele and Álvarez-Fernández, 2011), El Mnasra Cave (Campmas et al., 2016) and El Harhoura 2 (Stoetzel et al., 2014) in Morocco (Table 1). At the junction of northern Africa and southern Europe, Benzú Rockshelter (Ramos-Muñoz et al., 2016) probably contains one of the earliest evidence of shellfish collection. It has shellfish associated with lithic artefacts and bones recovered from ca. 250 ka (Ramos-Muñoz et al., 2016). Whether these shells were collected for food is unclear, as preservation is poor. In Europe, Mousterian sites with evidence of shellfish harvesting by Neanderthals include Grotta dei Moscerini (Moscerini Cave) in Italy (Stiner, 1993, 1994), the Vanguard and Gorham's Caves on Gibraltar (Stringer et al., 2008; Fa et al., 2016), Bajondile Cave (MIS 6) and Cueva de los Aviones in Spain (Zilhão and Villaverde, 2008; Cortés-Sánchez et al., 2011), and Üçagizli Cave II in Turkey (Stiner, 2009). Limpets (cf. *P. vulgata*) and mussels of the Genus *Mytilus* (cf. *M. galloprovincialis*) dominate on the Atlantic and Mediterranean coasts of North Africa and southern Europe at these early sites.

In South Africa, MSA sites are present along the south and west coasts. The south coast sites with preserved shellfish include Klasies River main site (Deacon and Geleijnse, 1988), Blombos Cave (Henshilwood et al., 2001), Pinnacle Point Cave 13B (Jerardino and Marean, 2010), and Klipdrift Shelter (Henshilwood et al., 2014) (Table 1). On the west coast of South Africa MSA sites with evidence of shellfish gathering are Sea Harvest (Volman, 1978), Hoedjies Punt (Kyriacou et al., 2015; Tribolo et al., 2022), Diepkloof Rock Shelter (Steele and Klein, 2013), and Ysterfontein 1 (Klein et al., 2004; Avery et al., 2008; Niespolo et al., 2021) (Table 1). It has been suggested that ca. 100,000–110,000 years ago may have been an important period that captures the transition to more intensive coastal subsistence on the Cape coast and that this is linked to more successful adaptations and social strategies (Marean, 2014; Will et al., 2016, 2019). However, given that new data indicate systematic shellfish foraging prior to this period, for example at Ysterfontein, Hoedjies Punt and Klasies River (Niespolo et al., 2020; Tribolo et al., 2022; Wurz et al., 2022), and that higher interglacial sea levels play a role in what can be recorded, this hypothesis needs further investigation.

The brown mussel *P. perna* and alikreukel *T. sarmaticus* dominate the south coast sites but with a significant presence of limpets and the giant chiton *D. gigas* at some sites (Table 1). Limpets and the black mussel (*Choromytilus meridionalis*) are most common on the Atlantic west coast of South Africa. Shellfish not only inform on subsistence behaviour but are also proxies for coastal environments, local sea surface temperatures (Ainis et al., 2014; Langejans et al., 2017), and biogeographical regions (Kilburn and Rippey, 1982).

Shellfish complemented subsistence strategies and likely took place during spring low tides and may not have been a central subsistence activity (Klein and Bird, 2016). This is because the calorific contribution of terrestrial resources (small and large mammals, and plant foods) is higher than that of shellfish (Bocherens, 2009; Jerardino, 2010; Salazar-García et al., 2013; Stiner, 2013). The tidal cycle, the distance from the site to the shore affected amounts of shellfish collected, and the extractive technology employed would have played a role (Jerardino, 2016; Klein and Bird, 2016). Accessing the shore for collecting shellfish is largely limited to the times when tides recede exposing mollusc

Table 1
Shellfish foraging during the Middle Stone Age (Africa) and Middle Palaeolithic (Europe).

Site name	Layers/cultural designation	Region and Country	Marine Isotope Stage	Total MNI/NISP	Main shellfish species	Reference(s)
Klasies River	MSA I to MSA III	South coast, South Africa	5–3 (115–43 ka)	MNI = 12051	*Perna perna; Turbo sarmaticus*	Langejans et al., 2012
Blombos Cave	MSA ll, Still Bay	South coast, South Africa	MIS 5–4 (100–72 ka)	MNI = 9013	*Turbo sarmaticus; Perna perna*	Henshilwood et al., 2001; Langejans et al., 2012
Pinnacle Point 13B		South coast, South Africa	MIS 6–5 (174–90 ka)	MNI = 771	*Donax serra; Perna perna*	Jerardino and Marean, 2010
Klipdrift Shelter	Howiesons Poort	South coast, South Africa	MIS 4 (66–60 ka)	MNI = 999	*Dinoplax gigas*	Henshilwood et al., 2014
Herolds Bay Cave	?	South coast, South Africa	MIS 5 (120–80 ka)	n.d.	*Perna perna*	Brink and Deacon, 1982
Sea Harvest	?MSA	West coast, South Africa	MIS 5 (128–74 ka)	MNI = 212	*Cymbula granatina; C. oculus*	Volman, 1978
Hoedjies Punt	AHI, AHII, AHIII	West coast, South Africa	MIS 5 (130–115 ka)	MNI = 840	*Cymbula granatina; Choromytilus meridionalis*	Kyriacou et al., 2015
Ysterfontein 1	Lower-Middle-Upper Units	West coast, South Africa	MIS 5 (115–71 ka)	MNI = 10336	*Choromytilus meridionalis; Cymbula granatina*	Klein et al., 2004; Avery et al., 2008; Niespolo et al., 2021
Diepkloof rock shelter	Several	West coast, South Africa	MIS 5 (110–50 ka)	*Gm = 3132.5	Limpets & mussels	Steele and Klein, 2013
Contrabandiers Cave	Aterian, Mousterian	Atlantic coast, Morocco	MIS 5	MNI = 2661	*Patella vulgata*	Steele and Álvarez-Fernández, 2011
El Mnasra Cave	Unit 8 (layers 7, 6 & 5)	Atlantic coast, Morocco	MIS 5 (117—105 ka)	NISP = 201	*Patella* sp.; *Mytilus* sp.	Campmas et al., 2016
El Harhoura 2	Aterian	Atlantic coast, Morocco	MIS 5–4 (130–40 ka)	n.d.	*Mytilus* sp.; *Patella* sp.	Stoetzel et al., 2014
Benzú rockshelter		Straits of Gibraltar, North Africa	MIS 6–4 (254–70 ka)	MNI = 68	*Patella* sp.	Ramos-Muñoz et al., 2016
Grotta dei Moscerini		Mediterranean coast, Italy	MIS 5–4 (115–65 ka)	MNI = 616	*Mytilus galloprovincialis; Calista chione*	Stiner, 1993, 1994
Vanguard Cave	Units C & D	Gibraltar	MIS 3 (55–45 ka)	NISP = 149	*Mytilus galloprovincialis*	Stringer et al., 2008
Gorham's Cave	Level 4	South-east coast, Gibraltar	MIS 3 (>28 ka)	MNI = 38	*Patella* sp.; *Mytilus* sp.	Stringer et al., 2008; Fa et al., 2016
Bajondillo Cave	Bj19, Bj18, B17	Alboran coast, Spain	MIS 6–3 (150–65 ka)	NISP = 162	*Bitynia tentaculata; Rumina decollata; Mytilus galloprovincialis*	Cortés-Sánchez et al., 2011
Cueva de los Aviones	Levels IV – I	Murcia, Spain	MIS 5, 3	MNI = 391	*Patella* sp.; *Mytilus* sp.	Zilhão and Villaverde, 2008
Üçagizli Cave II	Layers D-A	Hatay coast, Turkey	MIS 5–3 (50–40 ka)	MNI = 1779	*Patella* spp.; *Monodonta lineata & M. turbinata*	Stiner, 2009

*No MNI or NISP values available, hence weight data used here.

species (Jerardino, 2016). The tidal cycle allows foragers to access molluscs during daily tidal lows twice a day, especially during spring low tides (Jerardino, 2016; Klein and Bird, 2016). This has been observed in ethnographic research and experimental observations from coastal areas including in southern and southeastern South Africa, Arnhem Land, and the Merriam Islands (Bigalke, 1973; Lasiak, 1992; Mehan, 1982; Bird and Bird, 1997; Bird et al.,2004; Jerardino, 2016). It has been suggested that shellfish collection implies a mastery of the perception of and use of tidal movements including by MSA people (Marean et al., 2014). This might imply a sophisticated degree of cognition in terms of forward planning and record keeping that continued to LSA times (Jerardino et al., 2014; Jerardino & Navarro, 2021).

The distance from the shore to the site probably affected amounts of shellfish collected and brought to the site and the number of days the coast was visited (Jerardino, 2016). Ethnographic literature (Bigalke, 1973; Bigalke and Voigt, 1973; Lasiak, 1993; Kyle et al., 1997) indicates that modern shellfish collectors could travel distances of up to 12 km and groups living closer to the coast tend to visit more often than those living far away (Mehan, 1982; Siegfried et al., 1985). During the MIS 5 MSA at Klasies River main site and Blombos Cave distances from the sites to the coast may have been within a 5 km periphery (Fisher et al., 2010; Langejans and Dusseldorp, 2017). For other MSA sites and periods, however, more variable distances to nearby shorelines occurred. Compared to LSA shellfish collectors, MSA people seem to have visited the coast more sporadically, collecting a somewhat narrower range of shellfish species during low tides (Jerardino, 2016).

Jerardino (2016) discusses shellfish collection techniques and its implications for tracing its use as a systematic food resource. Recent collectors of shellfish used their hands to collect mussels, winkles, and whelks while species such as limpets, chitons, and abalone were removed by stick, rock, bone, or iron levers (Budack, 1977; Jerardino, 2016). Snorkelling equipment was also used by researchers to collect experimental samples (Bruton et al., 1991). Prehistoric MSA shellfish collectors would have faced similar situations, and they could have used simple technologies such as sticks or even rocks that cannot be noticed in the archaeological record to remove limpets and chitons such as those represented in the southern Cape sites mentioned in this study (see also De Vynck et al., 2019).

Shellfish may have contributed crucial dietary nutrients (Parkington, 2010; Cunnane and Stewart, 2010; Kyriacou et al., 2014) and it may have played a major role in the diet of coastal dwellers (De Vynck et al., 2019). Shellfish is a good source of polyunsaturated fatty acids (Broadhurst et al., 2002; Parkington, 2010) necessary for the development and maintenance of the human brain. This may have been crucial in human brain development (Brenna and Carlson, 2014; Broadhurst et al., 1998, 2002; Cunnane, 2010; Parkington, 2010) leading to evolutionary advantages as it may have assisted the reproductive success of MSA people staying close to the coasts (Parkington, 2010; Will et al., 2016, 2019). However, this hypothesis needs to be considered against the background that the human brain evolved in nonaquatic settings as well (Klein and Bird, 2016).

Here, we compare shellfish exploitation during the early MIS 5, from two well-known southern Cape MSA sites, Klasies River main site and Blombos Cave (Fig. 1) found within the Cape Floristic Region. Both these sites play important roles in understanding early human development globally. Previous publications on shellfish subsistence (e.g., Voigt, 1982; Thackeray, 1988; Langejans et al., 2012, 2017; Dusseldorp and Langejans, 2013) at these two sites are temporally more extensive than this study and covered MIS 5–3. The Klasies River main site data from MIS 5 for the 100,000–110,000-year period was limited, and came from a small area where cave 1 and cave 1A intersects, AA43 (Fig. 2), excavated by Deacon. Here we examine Klasies River main site shellfish from recently excavated discrete layers from the middle of cave 1, the Witness Baulk, and similarly aged but somewhat younger layers from Blombos Cave from the MIS 5c-d time frame. Our aim is to investigate how shellfish exploitation and environments compare across and within sites to provide a more in-depth perspective of this important period on the Cape coast.

2. The context of the data

2.1. Klasies River main site

Klasies River main site has been investigated since the late 1960 s with the first excavations by Wymer (Singer and Wymer, 1982) followed by Deacon (Deacon and Geleijnse, 1988), and subsequently by Wurz et al. (2018,2022). Klasies River main site (34°,06′S, 24°,24′E) is situated along the Tsitsikamma coast in the southern Cape, South Africa. The site consists of four closely positioned caves and overhangs and occurs is at the end of a coastal platform which is 13 km wide and rising from 40 to 250 m above sea level towards the slopes of the Tsitsikamma Mountains (Deacon and Geleijnse, 1988:6). The two caves (Caves 1 and 2) and associated overhangs (Cave 1A and 1B) collectively contain 21 m of deposits with palaeoanthropological and archaeological materials (Singer and Wymer, 1982; Deacon and Geleijnse, 1988; Wurz et al., 2018, 2022).

During the MSA, humans occupied the Klasies River main site caves

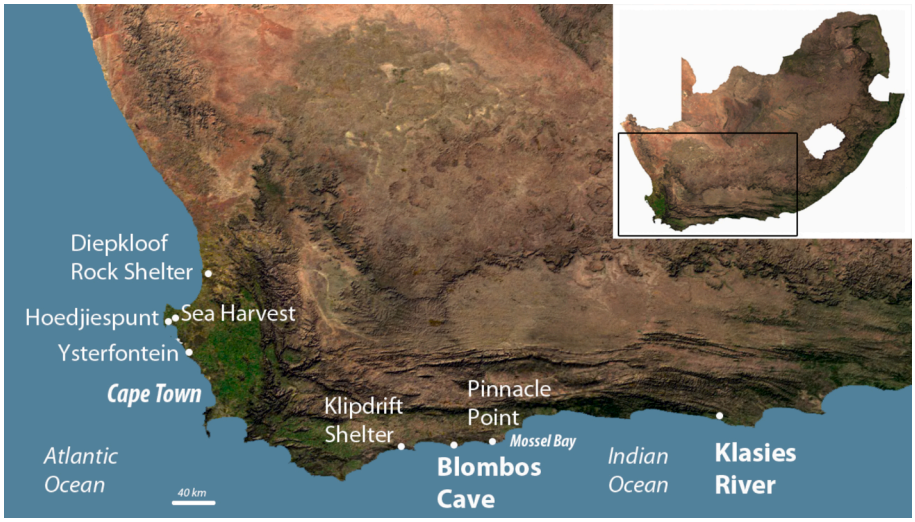

Fig. 1. Location of Klasies River and Blombos Cave in southern Cape coast context.

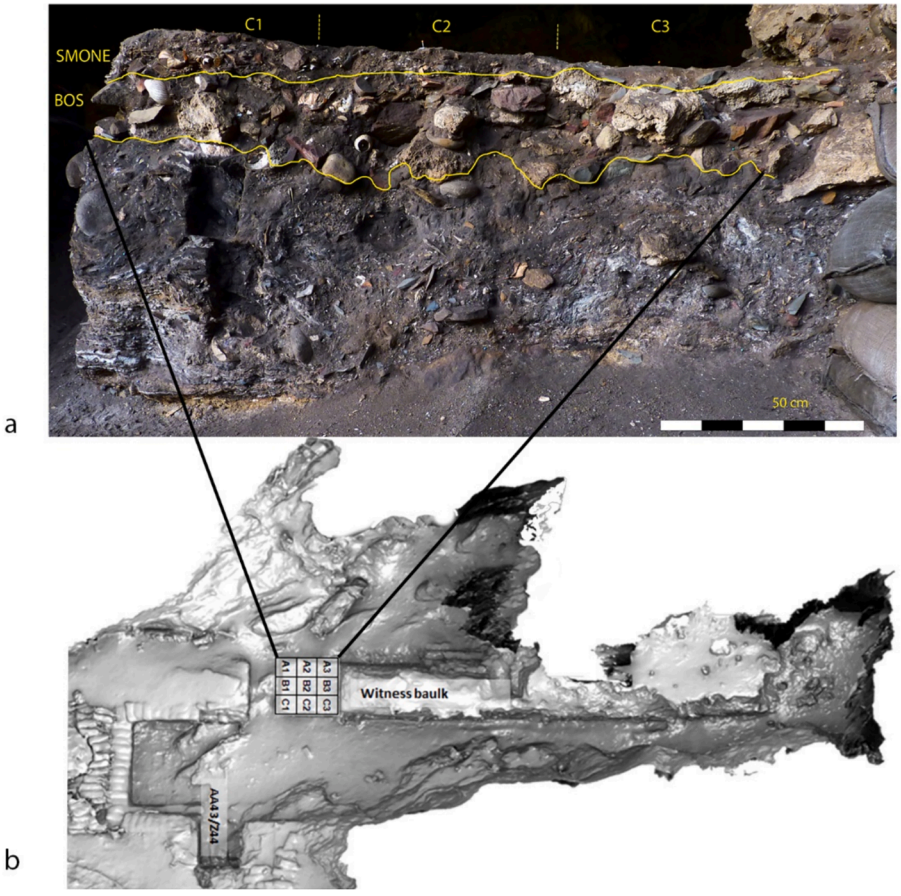

Fig. 2. (a) Eastern profile of the witness baulk in cave 1, layers shell midden one (smone) and black occupational soils (bos); (b) ground plan of cave 1 showing the witness baulk and squares excavated (a1–c3).

between c. 120 and 43 ka (Grine et al., 2017; Reynard and Wurz, 2020) with evidence for hunting and gathering, fishing and shellfish collecting (Thackeray, 1988; Rightmire and Deacon, 1991; van Niekerk, 2011; Langejans et al., 2012; Wurz et al., 2018, 2022; Brenner et al., 2022). Singer and Wymer described the stratigraphy in several layers, from Layer 40 to 1, and Deacon grouped these into several members and sub-members, including the Light Brown Sand (LBS) at the base, followed by the Shell and Sand (SAS), Rock Fall (RF), and Upper Member. The layers that we discussed here fall within Deacon's SAS member of Cave 1 that he divided into the SAS Lower, Upper, and Wedge sub-members (Wurz et al., 2018; Morrissey et al., 2022). The SAS member is broadly associated with an age bracket between 126 ka and 85 ka (Wurz et al., 2022) and contains lithics designated as the MSA II or Mossel Bay technocomplex (MSA II/Mossel Bay Lower and MSA II/Mossel Bay Upper) (Wurz, 2002; Table 2). Shellfish data analysed in this paper come from the SASL sub-member, associated with MSA II Lower (Table 2), with its deposits dating to between 100 ka and older than 110 ka (Wurz et al., 2022; Fig. 2). Previously Deacon excavated a large shellfish sample from the Witness Baulk from the overlying SASU and SASW sub-members, that relate to a younger phase of MIS 5 that is currently under analysis

Table 2
Summarised stratigraphy of the layers analysed for Blombos Cave and Klasies River main site.

Site name	Layer analysed	Age	Cave 1 Witness Baulk Deacon (not excavated)	Cave 1A AA43 Deacon (excavated)	Singer & Wymer Cave 1 (excavated apart from the Witness Baulk)
Blombos Cave	CH CI CIB CIBh2 CJ CK/CL CM CN/CO CP CPA	Between 78 and 100 ka			
Klasies River Main Site*	Shell Midde One	ca.100 ka	SASL sub-member	SAS member base	Layer 17a
	Black Occupational Soils One & Two	Older than 110 ka	SASL sub-member	SAS member base	Layer 17b
	Black Occupational Soils Three	Older than 110 ka	SASL sub-member	SAS member base	Layer 17b

*Klasies River main site excavated layers are shown against their equivalents of previous excavators.

(see Reynard and Wurz, 2020 for the stratigraphy of the SASW and SASU sub-members).

The Klasies River main site shellfish analysed here are from the recent excavations by Wurz of the Witness Baulk in cave 1 (Fig. 2). Wurz continued the excavation of the Witness Baulk, from where Deacon stopped his excavations in 1995, at the base of the SASU sub-member. These layers from the SASL sub-member include the Shell Midden One and the Black Occupational Soils divided into three spits: Black Occupational Soils One, Black Occupational Soils Two, and Black Occupational Soils Three (Wurz et al., 2018; Fig. 2). These layers are the thickest in square C1 in the easternmost part of the Witness Baulk, and significantly thin out towards the west.

Shell Midden One is equivalent to Singer and Wymer's (1982) layer 17a (Table 2) and its thickness varies from at least 5 mm in squares A1-3 to 15 cm in square C1. It is a shell rich layer associated with disintegrated smaller tufa blocks, leached ashes (no hearths), and charcoal specks intermingled with fauna and lithics. It is a shell midden layer where the matrix is embedded with shells. The Black Occupational Soils layers (1–3) are equivalent to Singer and Wymer's Layer 17b and this unit is more extensive. Substantial winnowing of the soil matrix occurred, and the palimpsests of deposits represent 'occupational soils' (see also Singer and Wymer, 1982:26). The colour of the soil in this layer is somewhat darker than that from Shell Midden One, and moister with higher clay content, especially towards the Black Occupational Soils Three. A detailed study of the soils is in progress. The Black Occupational Soils layers differ further from Shell Midden One in the higher occurrence of tufa blocks, some very large, including many stalagmite structures which have been sampled for dating (Wurz et al., 2022).

The Black Occupational Soils One – Three contain well preserved shellfish, lithics and fauna. In these layers some quartzite blocks show evidence of colour changes and fractures indicating exposure to fire (e.g., Bentsen and Wurz, 2017; Bentsen and Wurz, 2019). U-series dates on speleothem material from Black Occupational Soils Three associated with a hiatus after the deposition of this layer, indicate ages of between 110 ka and 106 ka. The Black Occupational Soils layers are thus older than 110 ka (Wurz et al., 2022). Shell Midden One is a different phase of occupation and is somewhat younger than the Black Occupational Soils layers, dating to MIS 5c (106–93 ka) (Wurz et al., 2018). The data discussed here is from all the squares excavated from the Witness Baulk, squares A1, A2, A3, B1, B2, B3, C1, C2 and C3 (Fig. 2). Recently, the shellfish from only square C1 at Shell Midden One – Black Occupational Soils Three layers was discussed within the context of lithic technology (Brenner et al., 2022). This paper thus provides the full representation of shellfish exploitation at Klasies River main site from all the squares excavated by Wurz.

2.2. Blombos Cave

Blombos Cave (34°25′ S, 21°13′ E) excavations by Henshilwood began in 1992 and are ongoing (Henshilwood et al., 2001; Henshilwood and van Niekerk, 2018). Blombos Cave is a small cave situated in a steep solution and wave-cut calcrete cliff close to the Indian Ocean that contains 2–3 m of MSA deposits. The MSA sequence dates from 100 ka to 70 ka (Jacobs et al., 2020; Henshilwood and van Niekerk, 2018) with evidence of hunting-gathering, fishing and shellfish collecting (Henshilwood et al., 2001, 2011; van Niekerk, 2011; Langejans et al., 2012). The MSA deposits comprise four phases of occupation from the top of the sequence, M1, M2 Upper, M2 Lower, and M3 (Henshilwood et al., 2001, 2011; Jacobs et al., 2020). The oldest human occupation phase at Blombos Cave, M3, dating from 100 ka to 80 ka (Fig. 3), is the focus of this paper.

At Blombos Cave, we present data from the M3 layers (CP–CH) (Table 2), from squares and quadrants E4, E5a and b, F4, F5, F6a and b, and H6a. Layers CP to CH date to between 100 and 78 ka (Jacobs et al., 2020; Fig. 3). We selected these layers to provide a sequence from >110,000 years ago to 78,000 years ago, linking the ages of the newly excavated sample from Klasies River main site and the Blombos Cave layers. The excavation protocols were similar, and thus similar data is available. Layers CH to CJ are light to medium brown sands with significant variations in shell quantities. Layers CK to CP consist of sands with thin carbonaceous partings and low frequencies of shell and artefacts (Henshilwood et al., 2001, 2011; Haaland et al., 2021). Brenner et al., (2022, Table 7) used published data from Henshilwood et al. (2001) for the entire M3 phase to compare to the Klasies River main site sample above. Here we provide the detailed data per layer for the layers of the M3 broadly contemporary with the Klasies River main site layers.

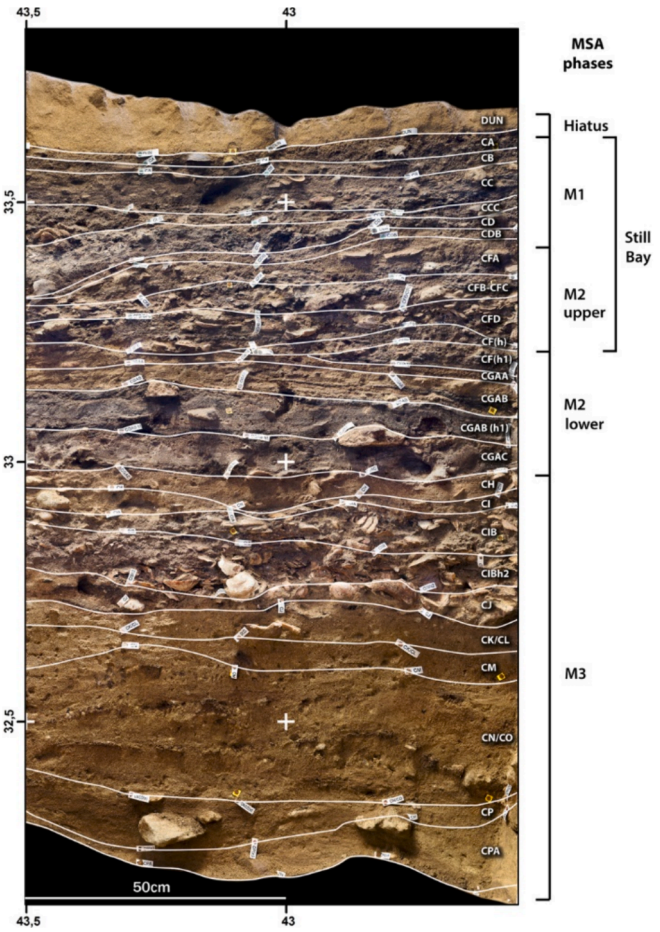

Fig. 3. South section of Blombos Cave profile. The shellfish from the M3 phase (layers CH to CP) were analysed in this study. Image courtesy of Magnus Haaland.

3. Method and sample

Shellfish <2 cm are not traditionally considered as food items (Jerardino, 1993; Klein and Steele, 2013; Henshilwood et al., 2014) but rather as molluscs that have been brought to the sites incidentally, attached to bigger shells, or used for ornamental purposes. However, some analysts (e.g., Langejans et al., 2017) consider that some of these 'incidental' small shells could have been collected by children and brought to the site. Here we do not consider that the smaller shells' contents were eaten and exclude them from this study. Shellfish were identified to species level where possible. *Oxystele* fragments from Blombos Cave could not all be identified to species level and thus they are presented as *Oxystele* spp. Specimens that could not be identified were labelled as "Ind. Species."

Minimum number of individuals (MNI) was calculated, and shell weight was recorded. The maximum diameters of *T. sarmaticus* opercula were measured using digital callipers. Limpets and *P. perna* specimens

were not measured using standard procedure (Jerardino et al., 2008) as no complete pieces were found or were too fragile in the case of specimens from Klasies River main site layers. The lengths of limpets and black mussels could not be estimated according to the procedure used by Jerardino and Navarro (2008) due to the fragmented nature of the shells. In terms of comparing overall contribution of each species, we use both MNI and weight values because: (i) infrequent species may be underrepresented when only MNI is used (Langejans et al., 2013) and, (ii) post-depositional damage can affect the MNI counts (Henshilwood, 2008). Some limpet specimens were not identified to species level at Klasies River main site because they were too fragmented and are presented here as unidentified limpets.

The total MNI values for *T. sarmaticus* were based on counting apices and opercula and the higher/highest value was used to determine the MNI. The weight for this species includes both the opercula and shell. The MNI values for whelks and topshells (*Oxystele sinensis*, *Burnupena cincta limbosa*, and *Bullia digitalis*) – were calculated by counting the columella or apices. Apices were used to determine the MNI values of the abalone *Haliotis midae*, Venus ear *H. spadicea*, and the limpets (*Scutellastra chochlear*, *S. argenvillei*, *S. longicosta, S. tabularis, S. barbara, Cymbula granatina,* and *C. oculus*). For *D. gigas*, MNI values were obtained by separately counting the front, middle (the number of middle plates divided by six), and the rear plates. The highest value of the three categories gave the MNI. The hinges of bivalves or mussels, *P. perna*, black mussel *Choromytilus meridionalis*, ribbed mussel *Aulacomya ater*, and white mussel *Donax serra*, were counted and divided by two to get the MNI counts. Because of poor preservation (e.g., see Fig. 4) it was difficult to determine the sides of the hinges of bivalves and this strategy may have somewhat underestimated or overestimated their MNIs.

4. Results

4.1. Shellfish densities: Klasies River main site and Blombos Cave

Although we compare the densities of shells through the layers and between the two sites, we use this strategy with caution as it has its drawbacks. Jerardino (2016:218–219) highlights that it assumes that matrix composition remains unchanged over time, depositional rates are constant, and that the preservation of archaeological remains is the same over different sites.

At Klasies River main site the highest density of shellfish is in Shell Midden One (46.7 kg/m^3) followed by Black Occupational Soils One and Two (27.1 kg/m^3) while Black Occupational Soils Three is the least dense, 22.0 kg/m^3 (Table 3). It was observed that the shellfish densities from square C1 (Brenner et al., 2022) are much higher than squares C2 and C3 for the Shell Midden One and Black Occupational Soils One and Two layers. This is because square C1 captured the edge of shell midden deposit concentrated toward the eastern part of the cave (Singer and Wymer, 1982: Fig. 3.23).

At Blombos Cave, layer CI (which comprises of sublevels CIA, CIB, CIBh2, HiCI, and CIH1) has the highest density of shellfish (159.7 kg/m^3) followed by layer CJ (96.5 kg/m^3), and CH (60.9 kg/m^3) (Fig. 5). Comparatively, except for the lower layers, some Blombos Cave M3/MSA II layers discussed here have noticeably higher densities of shellfish than those of Klasies River main site (Fig. 5).

4.2. Species composition during MSA II at Klasies River main site and Blombos Cave

A total of 18 species of edible marine molluscs from Klasies River main site and Blombos Cave are presented in terms of MNI and weight (Table 4). Fifteen species are present at each site.

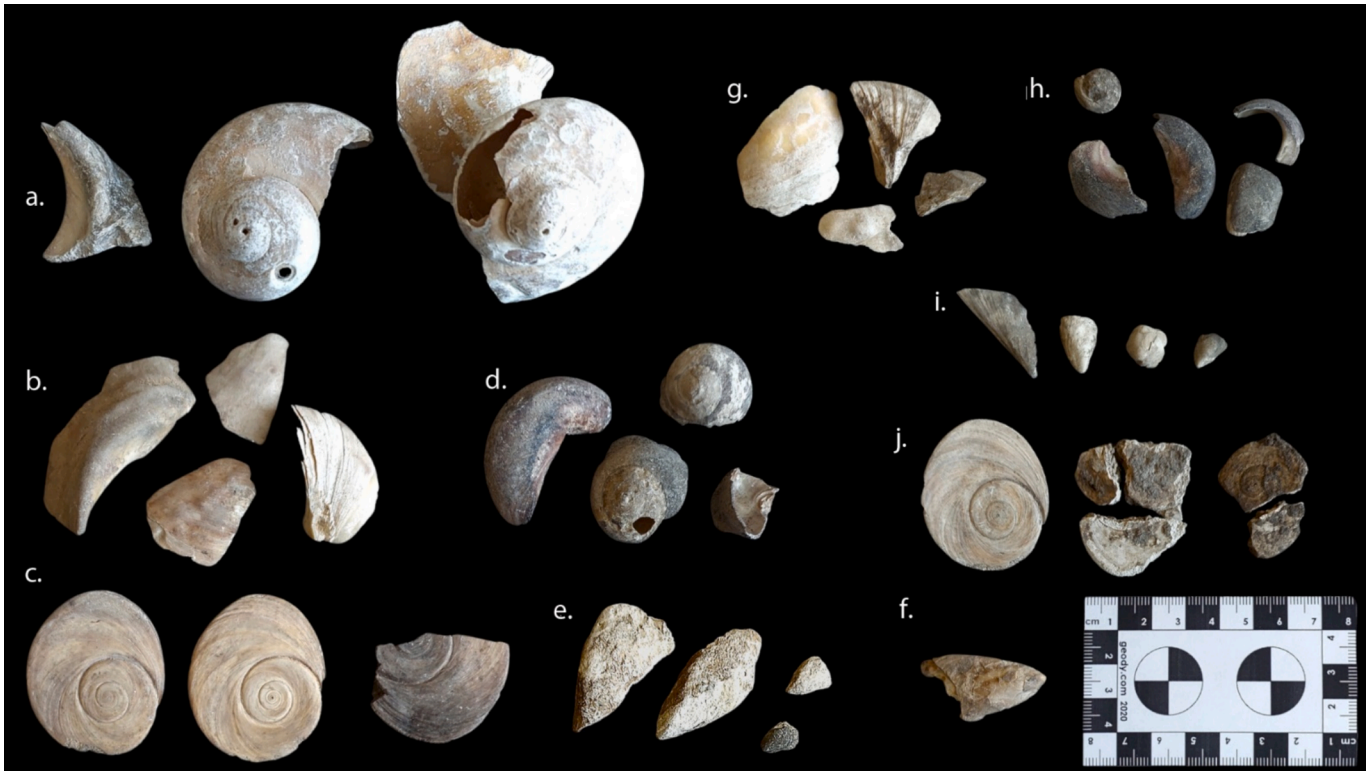

Fig. 4. Representation of the condition of preservation of the shells from Blombos Cave and Klasies River main site analysed for this study. Shells from Blombos Cave: a. *Turbo sarmaticus shell* (layer CIA); *b. Turbo sarmaticus shell* (layer CIBh2); c. *Turbo sarmaticus* opercula (layer CIBh2); d. *Oxystele spp.* (layer CIBh2); e. *Perna perna* (layer CIA), f. *Perna perna* (layer CIBh2). Shells from Klasies River main site: g. *Turbo sarmaticus shell*; h. *Oxystele sinensis*; i. *Perna perna*; j. *Turbo sarmaticus opercula* (layer Black Occupational Soils One). Image courtesy of Carl Holmes and Alexandra Pearson.

Table 3
Shellfish densities during the MSA II Lower layers at Blombos Cave and Klasies River main site.

Site	BBC				KRM		
Layer	CH	CI	CJ	CK-CP	SMONE	BOS One + Two	BOS Three
Shellfish weight in g	29748.2	102741.8	22521.6	3744.0	2523,9	2116,6	5500.1
Volume of deposits (liters)	488.4	643.5	233.4	377.0	54.1	78.0	249.8
Density (kg/m^3)	60.9	159.7	96.5	9.9	46.7	27.1	22.0

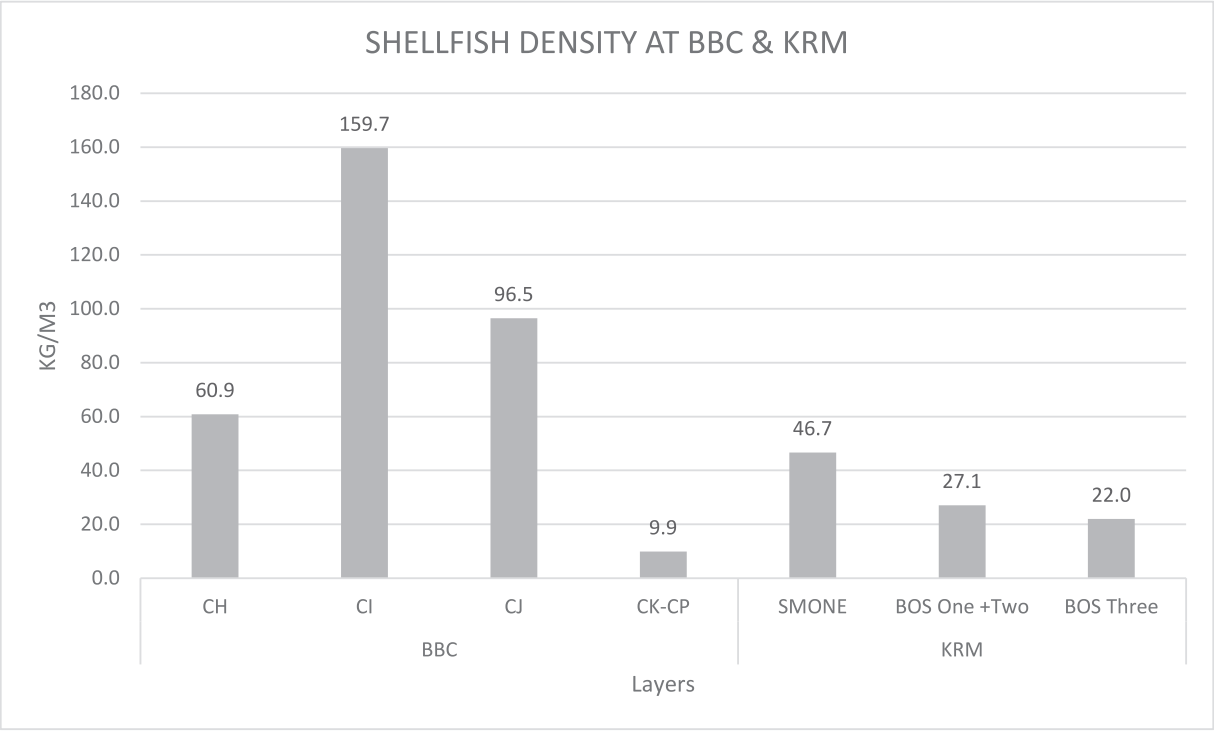

Fig. 5. Shellfish density of the MSA II Lower layers at Blombos Cave and Klasies River main site.

A total MNI of 1380 and weight of 10140.6 g (~10.1 kg) have been analysed at Klasies River main site. At Klasies River main site data for Black Occupational Soils One and Two layers have also been combined as these spits are similar and the difference between them is not clear (Brenner et al., 2022). The raw figures of MNI and weight have also been presented as percentage frequencies of both these values for each layer or group (Table 5). These percentage frequencies are calculated based on layer/group total.

Blombos Cave MNI totals are 3613 and weigh 158755.6 g (c. 159 kg). Because of the rarity of shellfish data in six lowermost layers of Blombos Cave (CK, CL, CM, CN, CO, and CP), these have been combined into CK-CP group/layers.

In terms of MNI, the four most dominant species in the analysed Klasies River main site layers are *P. perna*, *T. sarmaticus*, *O. sinensis*, and *B. cincta limbosa*. The dominance of these species however fluctuates from layer to layer (Table 5; Figs. 6 and 7). For example, *T. sarmaticus* (42.3 % MNI, 52.8 % weight) dominates during Shell Midden One followed by *P. perna* (39.7 % MNI, 22.1 % weight) and *B. cincta limbosa* (4.2 % MNI, 0.5 % weight). In Black Occupational Soils One and Two, *T. sarmaticus* constitutes 34.1 % and 44.7 % of MNI and weight respectively followed by *P. perna* (27.7 % MNI, 24.0 % weight), *O. sinensis* (12.7 % MNI, 5.5 % weight), and *B. cincta limbosa* (8.9 % MNI, 3.2 % weight).

In Black Occupational Soils Three, contributions of *T. sarmaticus* (24.3 % MNI, 30.6 % weight) and *P. perna* (30.0 % MNI, 26.7 % weight) are almost equal. The next most numerous species in this layer is *O. sinensis* (19.2 % MNI, 8.4 % weight) followed by *B. cincta limbosa* (11.9 % MNI, 3.9 % weight) (Table 4). This is followed by unidentified limpet species and *C. oculus*. *D. serra*, *S. longicosta*, *S. argenvillei* and *S. cochlear* are minimally represented in the sequence. *H. midae* occurs in almost equal proportions in MNI for layers Shell Midden One and Black Occupational Soils One and Two (Fig. 6).

There is a spike of *H. midae* in Shell Midden One in terms of weight (Fig. 7). *S. cochlear*, *S. tabularis* and *S. barbara* are not represented at Shell Midden One and only marginally present at the Black Occupational Soils layers (Table 4). *A. ater* is rare and only found in Shell Midden One and Black Occupational Soils Three. *B. digitalis* is one of the rare species at Klasies River main site and only found in Black Occupational Soils Three.

In the Blombos Cave M3 layers, *T. sarmaticus* dominates the assemblage both in terms of MNI and weight values. Other species (*C. oculus*, *P. perna*, *D. gigas*, *S. argenvillei*, *C. granatina*, and *Oxystele* spp.) are moderately represented (Table 5). The contribution of *P. perna* is more visible in terms of MNI (Table 5) whereas its weight suggests that it is marginally represented. This is because the shells of this species are comparatively lighter than most other species. There are fluctuations of species through time/layers.

In the youngest layer (CH) at Blombos Cave, *T. sarmaticus* contributes 32.4 % and 55.4 % in terms of MNI and weight respectively followed by *C. oculus* (24.3 % MNI, 12.0 % weight), *P. perna* (16.3 % MNI, 1.2 % weight), *S. argenvillei* (8.4 % MNI, 9.3 % weight), *C. granatina* (6.1 % MNI, 3.2 % weight), and *D. gigas* (5.5 % MNI, 9.3 % weight). In layer CI, *T. sarmaticus* contributes 34.7 % MNI and 56.7 % weight, followed by *C. oculus* (15.8 % MNI, 8.9 % weight), *D. gigas* (12.1 % MNI, 12.3 %

Table 4
MNI and weight values (in grams) of shellfish species at Blombos Cave (BBC) and Klasies River main site (KRM) MSA II Lower.

Site	BBC										KRM							
Layer	CH		CI		CJ		CK-CP		BBC Total		SMONE		BOS One + Two		BOS Three		Total KRM	
Species	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g
Dinoplax gigas	44	2760	267	12,586	74	3633	6	138	391	19,117	1	0,2	6	12,5	10	31	17	43,7
Turbo sarmaticus	259	16,467	767	57,999	170	10,364	65	2405	1261	87,235	132	1331,5	123	945,6	172	1682,2	427	3959,3
C. meridionalis	1	0,68	1	1					2	1,68								
Cymbula oculus	194	3557	350	9119	64	1648,3	20	388	628	14712,3	8	87,6	12	197,2	23	675,3	43	960,1
Oxystele sinensis/spp.	25	304	104	1862	38	831	2	33	169	3030	7	11,2	46	116,9	136	463,9	189	592,0
Donax serra	1	0,5	1	2					2	2,5	6	8,2	5	5,2	8	35,4	19	48,8
Perna perna	130	343	232	665	14	30,3	13	54	389	1092,3	124	557,8	100	507,3	212	1466,4	436	2531,5
Cymbula granatina	49	949	159	2848	27	555	4	69	239	4421								
C. oculus/granatina	2	538	1	1551	1	406	1	14	5	2509								
Haliotis midae	6	1602	27	4741	7	1619	5	394	45	8356	6	381,8	8	72,31	7	34,6	21	488,8
Haliotis spadicea	6	68	6	42	1	8	1	4	14	122								
Scutellastra argenvillei	67	2759	229	9148	70	2728	5	175	371	14,810	2	39,3	5	13,07	5	31,53	12	83,9
Scutellastra tabularis			1	52					1	52			2	66,7			2	66,7
B. cincta limbosa											13	11,7	32	68,3	84	213	129	293,1
Scutellastra longicosta			1	3	2	25			3	28	4	2,6	5	13,9	7	62,6	16	79,1
Aulacomya ater	1	1,1	2	5,8			1	1	4	7,8	1	1,1			4	2,1	5	3,2
Scutellastra barbara													1	1,7			1	1,7
Scutellastra cochlear	1	5	2	8					3	13					4	5,6	4	5,6
Unidentified limpets											8	90,8	16	95,9	34	793,8	58	980,5
Bullia digitalis															1	2,6	1	2,6
Species ind.	13	394	59	2109	8	674	6	69	86	3246								
Total	799	29748,2	2209	102,742	476	22521,6	129	3744	3613	158,756	312	2523,9	361	2116,6	707	5500,1	1380	10140,6

weight), *P. perna* (10.5 % MNI, 0.6 % weight), *S. argenvillei* (10.4 % MNI, 8.9 % weight), and *C. granatina* (7.2 % MNI, 2.8 % weight) (Table 4).

In layer CJ, T. *sarmaticus* constitutes 35.7 % MNI and 46.0 % of weight. This is followed by *D. gigas* (15.5 % MNI, 16.1 % weight), *S. argenvillei* (14.7 % MNI, 12.1 % weight), *C. oculus* (13.4 % MNI, 7.3 % weight), and *C. granatina* (5.7 % MNI, 2.5 % weight). In the oldest group of layers (CK-CP), *T. sarmaticus* contributes more than 50 % both in terms of MNI (50.4 %) and weight (64.2 %) (see also Figs. 8 and 9) followed by *C. oculus* (15.5 % MNI, 10.4 % weight), *P. perna* (10.4 % MNI, 1.4 % weight), *D. gigas* (4.7 % MNI, 3.7 % weight), *S. argenvillei* (3.9 % MNI, 4.7 % weight), and *C. granatina* (3.1 % MNI, 1.8 % weight).

Generally, *T. sarmaticus* shows higher proportions of MNI and weight in the lowermost six layers (CK-CP) than in other layers (Figs. 8 and 9). Proportions of *D. gigas* are higher in the middle layers (CJ and CI) relative to the uppermost CH and lowermost CK-CP layers (Figs. 8 and 9). *P. perna* (2.9 % MNI, 0.1 % weight) shows a sharp decline in layer CJ as opposed to its contributions in the layers above and below this. In terms of weight, *C. granatina* progressively increases towards the upper part of the occupation sequence (Fig. 9). *H. midae* represents >5 % of weight in each layer although its maximum contribution is 10.5 % in layer CK-CP (Table 5). One of the rare species, *A. ater*, is found in layers CK-CP (Figs. 8 and 9). Other rare species include *S. tabularis*, *S. longicosta*, *S. cochlear*, *H. spadicea*, *D. serra*, and *C. meridionalis* (Figs. 8 and 9).

Inter-site comparison shows that *T. sarmaticus* dominates both assemblages in terms of MNI and weight when the data for the various layers are combined as seen in the total columns (Table 5). At Klasies River main site, this species constitutes slightly less than one third (30 %) of the total in terms of MNI while it is above one third (39.0 %) in terms of weight. At Blombos Cave the frequencies of this species are higher compared to Klasies River main site, 34.9 % MNI and 54.9 % weight. Proportions of *D. gigas* and *C. oculus* are higher at Blombos Cave than at Klasies River main site layers (Table 5).

On the other hand, *P. perna* is better presented at Klasies River main site than at Blombos Cave. *D. serra*, *S. longicosta* and *S. tabularis* are marginally present at both Klasies River main site and Blomos Cave assemblages. The cold-water endemic species (*C. granatina*) of the Western Cape coast (Kilburn and Rippey, 1982) is represented at Blombos Cave but not at Klasies River main site from the analysed sample. *C. meridionalis* and *H. spadicea* are present at Blombos Cave but absent at Klasies River main site. *B. cincta limbosa* and *B. digitalis* are only represented at Klasies River main site. The number of species collected varies between 10 and 15 in the layers studied. When species that contribute very little (less than 100 g) to the assemblages are removed, the number of species per layer at Klasies River main site range between 5 and 3, and 5 and 8 at Blombos Cave, with the most species present in CI and CH at Blombos Cave and in Black Occupational Soils layers at Klasies River main site.

4.3. *Turbo sarmaticus opercula size*

The summary statistics of the *T. sarmaticus* opercula sizes at Klasies River main site and Blombos Cave are presented in Table 6 and Fig. 10. At Klasies River main site, measured specimens come from layers Shell Midden One, Black Occupational Soils Two, and Black Occupational Soils Three. The summary statistics (Table 6) show that the median values for Klasies River main site layers are almost equal (36.9 mm for layer Shell Midden One; 37.9 mm for Black Occupational Soils Two; and 38.3 mm for Black Occupational Soils Three).

At Blombos Cave variation between layers is minimal, varying between 42 and 44 mm, and show a slight increase in size from the lowermost layers to the uppermost CH. Fig. 10 shows that there are more outliers in layers CH and CI at Blombos Cave than in other layers.

To examine the degree of difference of *T. sarmaticus* opercula sizes within and between the two assemblages, a nonparametric Mann-Whitney *U* test was used (Table 7). Klasies River main site layers are

Table 5
Percentage frequencies of MNI and weight values (in grams) per layer of marine shellfish assemblages from Klasies River main site (KRM) and Blombos Cave (BBC) MSA II layers.

Site	BBC										KRM							
Layer	CH		CI		CJ		CK-CP		BBC Total		SMONE		BOS One + Two		BOS Three		Total KRM	
Species	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g	MNI	g
Dinoplax gigas	5,5	9,3	12,1	12,3	15,5	16,1	4,7	3,7	10,8	12,0	0,3	0,0	1,7	0,6	1,4	0,6	1,2	0,4
Turbo sarmaticus	32,4	55,4	34,7	56,5	35,7	46,0	50,4	64,2	34,9	54,9	42,3	52,8	34,1	44,7	24,3	30,6	30,9	39,0
C. meridionalis	0,1	0,0	0,0	0,0					0,1	0,0								
Cymbula oculus	24,3	12,0	15,8	8,9	13,4	7,3	15,5	10,4	17,4	9,3	2,6	3,5	3,3	9,3	3,3	12,3	3,1	9,5
Oxystele sinensis/spp.	3,1	1,0	4,7	1,8	8,0	3,7	1,6	0,9	4,7	1,9	2,2	0,4	12,7	5,5	19,2	8,4	13,7	5,8
Donax serra	0,1	0,0	0,0	0,0					0,1	0,0	1,9	0,3	1,4	0,2	1,1	0,6	1,4	0,5
Perna perna	16,3	1,2	10,5	0,6	2,9	0,1	10,1	1,4	10,8	0,7	39,7	22,1	27,7	24,0	30,0	26,7	31,6	25,0
Cymbula granatina	6,1	3,2	7,2	2,8	5,7	2,5	3,1	1,8	6,6	2,8								
C. oculus/granatina	0,3	1,8	0,0	1,5	0,2	1,8	0,8	0,4	0,1	1,6								
Haliotis midae	0,8	5,4	1,2	4,6	1,5	7,2	3,9	10,5	1,2	5,3	1,9	15,1	2,2	3,4	1,0	0,6	1,5	4,8
Haliotis spadicea	0,8	0,2	0,3	0,0	0,2	0,0	0,8	0,1	0,4	0,1								
Scutellastra argenvillei	8,4	9,3	10,4	8,9	14,7	12,1	3,9	4,7	10,3	9,3	0,6	1,6	1,4	0,6	0,7	0,6	0,9	0,8
Scutellastra tabularis			0,0	0,1					0,0	0,0			0,6	3,2			0,1	0,7
B. cincta limbosa											4,2	0,5	8,9	3,2	11,9	3,9	9,3	2,9
Scutellastra longicosta			0,0	0,0	0,4	0,1			0,1	0,0	1,3	0,1	1,4	0,7	1,0	1,1	1,2	0,8
Aulacomya ater	0,1	0,0	0,1	0,0			0,8	0,0	0,1	0,0	0,3	0,0			0,6	0,0	0,4	0,0
Scutellastra barbara													0,3	0,1			0,1	0,0
Scutellastra cochlear	0,1	0,0	0,1	0,0					0,1	0,0					0,6	0,1	0,3	0,1
Uidentified limpets											2,6	3,6	4,4	4,5	4,8	14,4	4,2	9,7
Bullia digitalis															0,1	0,0	0,1	0,0
Species ind.	1,6	1,3	2,7	2,1	1,7	3,0	4,7	1,8	2,4	2,0								
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

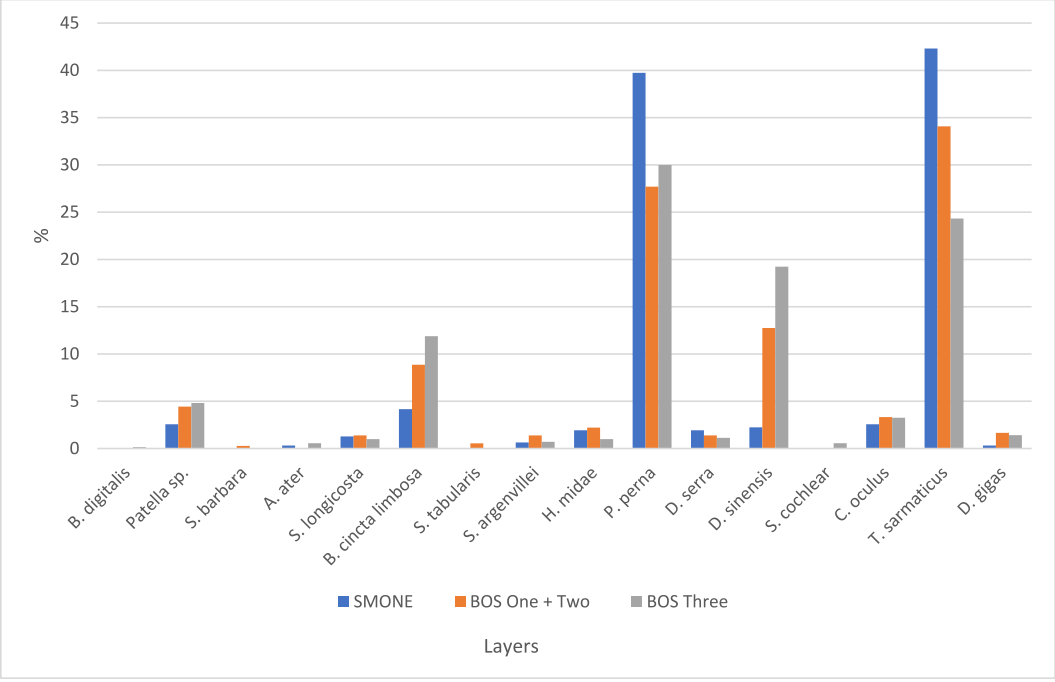

Fig. 6. Percentage frequencies of shellfish MNI at Klasies River main site MSA II Lower layers. Patella sp. refers to fragments of limpets that could not be identified to genus or species.

compared with one another, e.g., between Shell Midden One and Black Occupational Soils Two and then compared against those of Blombos Cave. The layers of the latter site are also compared with each other. The results show that there is no significant difference in opercula lengths within the Klasies River main site layers. However, the differences between the opercula sizes of the Klasies River main site and Blombos Cave layers are significant (Table 7).

While opercula lengths in most of the layers at Blombos Cave show no significant differences, those from the topmost layer CH and the lowest layers CK-CP are significantly different (Table 7). At Klasies River main site the median shows a minor decrease in size from the lowermost layer, Black Occupational Soils Three, to the topmost layer, Shell Midden One while at Blombos Cave this pattern is reversed; the median increases upwards (Table 6).

4.4. *Turbo sarmaticus* shell over opercula ratios

Whole fresh *T. sarmaticus* shells typically weigh approximately 10 times more than the opercula (Millic, unpublished data, personal communication). The weight ratios of *T. sarmaticus* shell over opercula

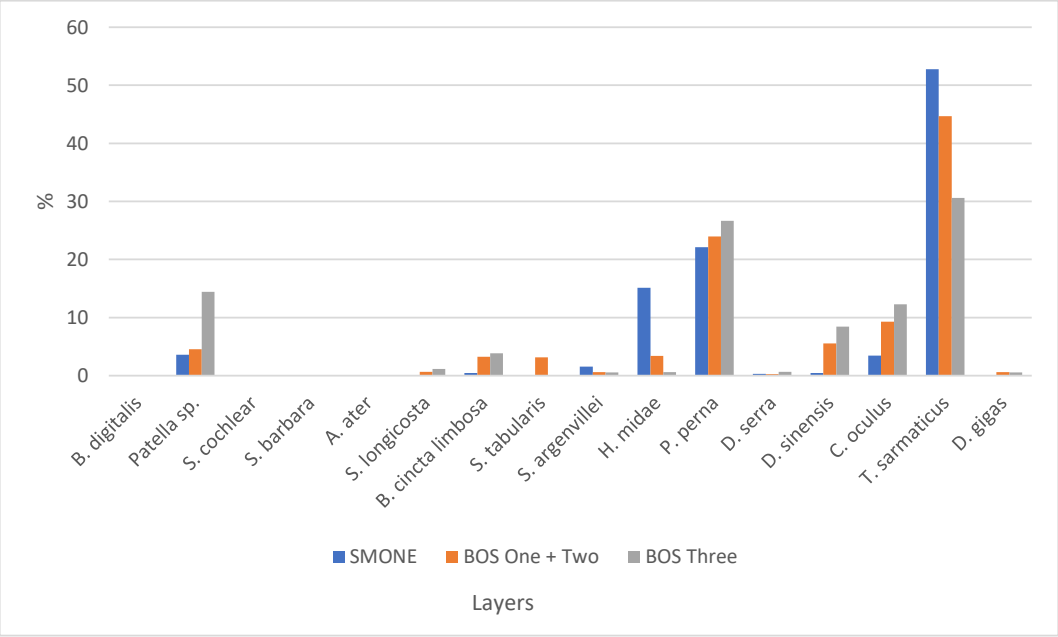

Fig. 7. Percentage frequencies of shellfish weight at Klasies River main site MSA II Lower layers. 'Limpet' refers to fragments of limpet that could not be identified to genus or species.

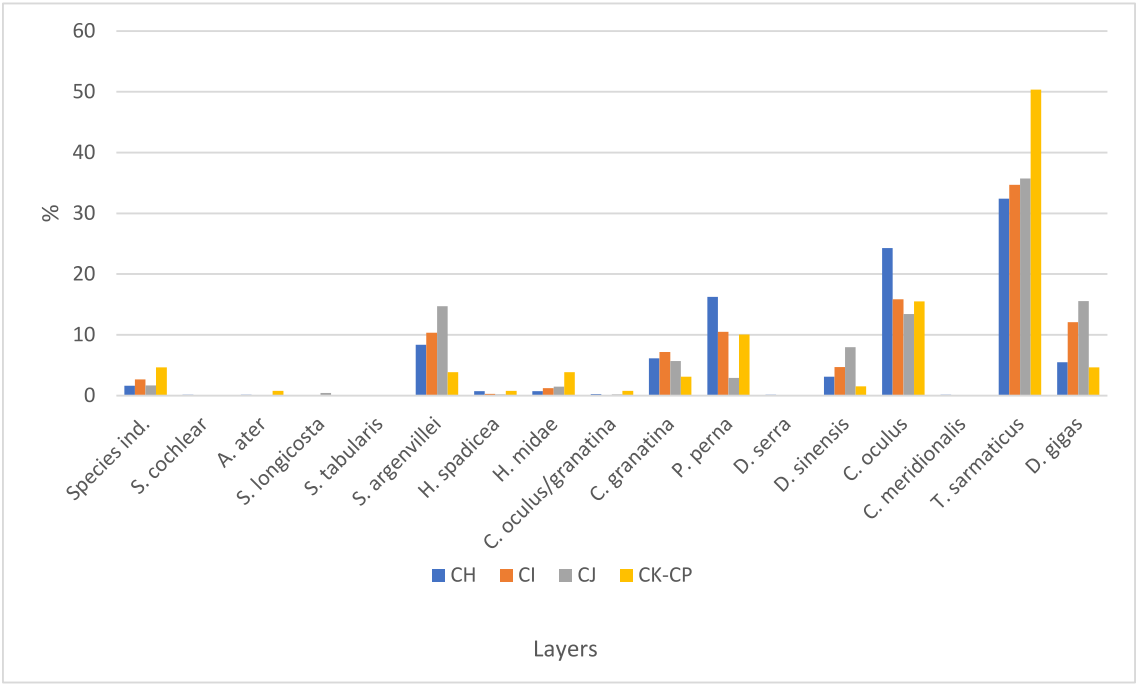

Fig. 8. Percentage frequencies of shellfish MNI at Blombos Cave MSA II Lower layers.

(see also Henshilwood et al., 2001) indicate that shells occur in higher quantities than opercula in all layers, especially in layer CI, at Blombos Cave (Fig. 11). This is consistent with higher ratios of shells over opercula for the whole Blombos Cave M3 assemblage (Henshilwood et al., 2001). At Klasies River main site, the ratios of shells are lower than opercula (Fig. 11).

5. Discussion

5.1. Coastal palaeoenvironments/climates

The results from the present study suggest that coastal environments consisted of mosaic rocky shorelines in both early MIS 5 samples at Klasies River main site and Blombos Cave as also suggested by previous studies (Langejans et al., 2012, 2017; Thackeray, 1988). On the other hand, there was an extensive sand beach at Pinnacle Point Cave 13B which made *D. serra* thrive there during MIS5c-d period especially during the Upper and Lower Roof Spall layers (see Jerardino and

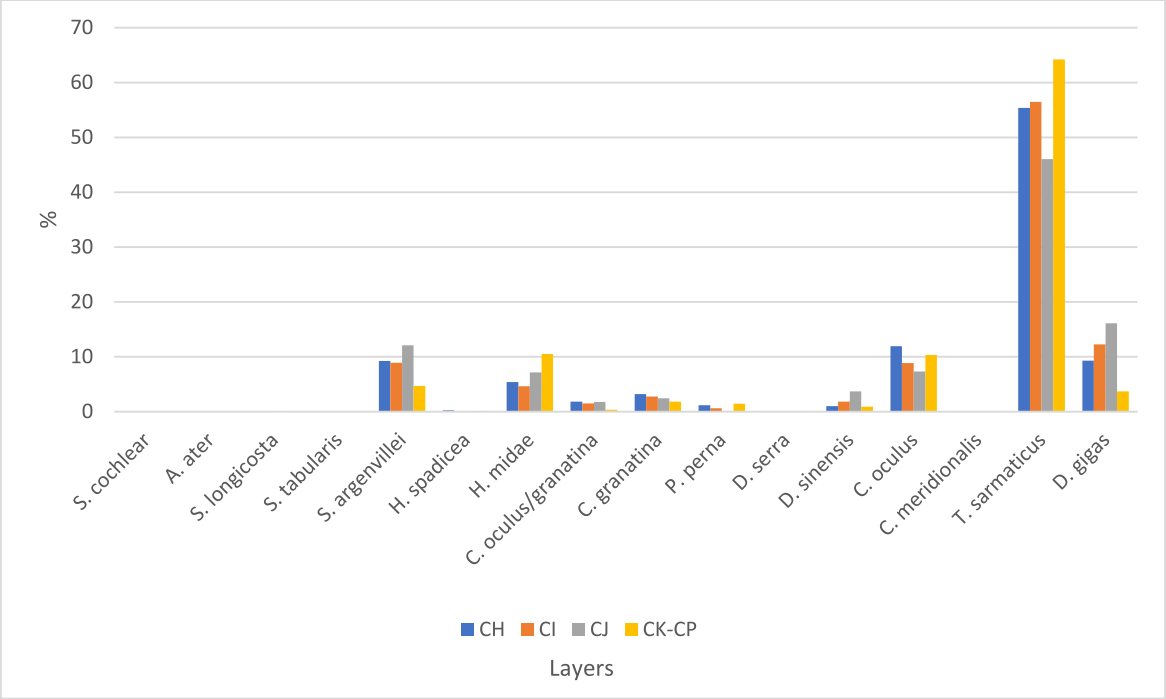

Fig. 9. Percentage frequencies of shellfish weight at Blombos Cave MSA II Lower layers.

Table 6
Summary statistics of the *Turbo sarmaticus* opercula measurements for Blombos Cave (BBC) and Klasies River main site (KRM) MSA II Lower layers.

Site name	BBC				KRM		
Variables/ Layers	CH	CI	CJ	CK-CP	SMONE	BOS Two	BOS Three
Mean	43.2	43.4	42.5	40.6	36.4	37.6	38.1
Median	44	44	43	42	36.7	37.9	38.4
Standard Deviation	6.2	5.7	5.6	6.6	4.3	3.9	4.6
Range	36	33	29	33	19.5	18.2	23.1
Minimum	17	22	24	17	27.2	28.0	23.6
Maximum	53	55	53	50	46.7	46.2	46.7
Frequency	117	283	106	41	67	55	86
Confidence Level (95.0 %)	1.1	0.7	1.1	2.1	1.0	1.0	1.0

Marean, 2010: Table 2). There were few rocky shores present at Pinnacle Point Cave 13B during MIS 5 (Jerardino and Marean, 2010).

The dominant presence of *T. sarmaticus* at Klasies River main site and Blombos Cave throughout the sequences suggests wave inundated rocks between the lower intertidal and subtidal zones of the shore (Bruton et al., 1991) where this species thrives. The presence of this species further suggests aeolianite (lithified beach sand usually softer than Table Mountain Sandstone) intertidal habitat type. Aeolianite shores contain extensive, flat, wave-cut platforms with shallow pools (De Vynck et al., 2019).

Although rare, the presence of *S. tabularis* and *S. barbara* which occupy infratidal rocks covered by seaweed, *Ralfsia*, and on rocks on low spring tide level respectively (Kilburn and Rippey, 1982) indicates further that the shore was rocky. These mosaic rocky habitats were present throughout MSA II Lower layers at all the three southern Cape sites discussed here.

The lower-most layer at Klasies River main site discussed in this study, Black Occupational Soils Three, contains relatively minimal proportions of *T. sarmaticus* compared to the other layers, but note that this layer was subjected to significant post depositional alteration (Wurz et al., 2022). This and other species such as *D. gigas*, *B. cincta limbosa*, and *H. midae* indicate an exposed rocky shore (Bruton et al., 1991) which extended towards the upper part of the sequence as indicated by the relative increase of *T. sarmaticus*, *D. gigas*, and *H. midae* (Figs. 6 and 7; Langejans et al., 2017). An exposed rocky shore is indicated by the presence of *P. perna*, *C. cochlear*, *O. sinensis*, *S. argenvillei*, *S. longicosta* and *A. ater* and this environmental setting also extended towards the topmost Shell Midden One as suggested by the increase of *P. perna* (Table 5).

An exposed shore as indicated by *P. perna* and other species (*C. meridionalis*, *O. sinensis*, *S. argenvillei*, *S. longicosta* and *A. ater*) occurred in the BBC sequence for most of the layers (Fig. 8). The pattern of a rocky shoreline, particularly aeolianite cliffs, with a sandy substrate is also indicated by the presence of rock hyrax and Cape dune molerat during MSA II layers at Blombos Cave, which thrive in such coastal environments (Badenhorst et al., 2016).

Generally, shoreline ecology at Klasies River main site (Voigt, 1982:162), and Blombos Cave was rocky throughout the sequence as indicated by many intertidal and rock-loving species present.

The results of the current study indicate that sea surface temperature was likely lower at Blombos Cave than at Klasies River main site for the period under discussion. Cold sea surface temperature (as indicated by *C. granatina*) is clear particularly for layers CH and CJ (Fig. 8). Sea surface temperature may have also been colder in the lowermost layers (CK-CP) which have a small presence of *C. granatina*. However, data from Voigt (1982) show that there are *C. granatina* at Klasies River main site in layers contemporaneous to MSA II, hence sea surface temperature may have been cooler than today at some point during the MIS5c-d. The sampling strategy in Voigt's study consisted of selecting only some excavated material for analysis, and furthermore, it is not possible to clearly link her results to this study. As Pinnacle Point Cave 13B is situated between Klasies River and Blombos Cave (Fig. 1) similar sea surface temperature may have prevailed in the whole of the southern coast, South Africa.

Another question addressed in this study is whether the change of shellfish species through time represents human choices or environmental changes. As noted above, rocky-shore-loving species dominate

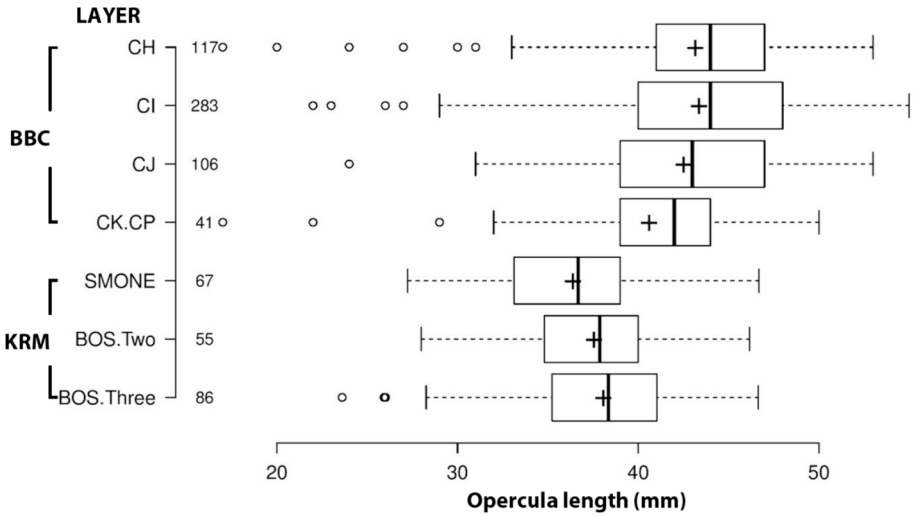

Fig. 10. Boxplots summarising *Turbo sarmaticus* opercula measurements for the MSA II Lower layers at Klasies River and Blombos Cave (layers from each site arranged from oldest to youngest). Numbers along the layer names indicate sample size. Whiskers extend data points from first and third quartiles. The median is represented by the line near the centre of the box. Dots represent outliers (values that are far from the median). The cross sign represents sample means. Boxplots are constructed on http://shiny.chemgrid.org/boxplotr/).

Table 7
Mann-Whitney U Test results of *Turbo sarmaticus* opercula, calculated at https://www.socscistatistics.com/tests/mannwhitney/default2.aspx.

Layers compared	Z-score	U-value	Significance	P-value
SMONE vs BOS Two	−1.20318	6300	Not significant, $p < 0.05$	0.23014
SMONE vs BOS Three	0.83488	9740.5	Not significant, $p < 0.05$	0.40654
BOS Two vs BOS Three	−0.39893	8763	Not significant, $p < 0.05$	0.68916
SMONE vs CH	−4.21006	5065.5	Significant, $p < 0.05$	<0.00001
BOS Two vs CI	4.11379	11405.5	Significant, $p < 0.05$	<0.00001
BOS Three vs CJ	−3.69712	6375	Significant, $p < 0.05$	<0.00022
CH vs CI	−0.25431	16287.5	Not significant, $p < 0.05$	0.80258
CH vs CJ	1.36029	5546	Not significant, $p < 0.05$	0.17384
CH vs CK-CP	2.79241	1694	Significant, $p < 0.05$	0.00528
CI vs CJ	1.28015	13734.5	Not significant, $p < 0.05$	0.20054
CJ vs CK-CP	1.57439	1808	Not significant, $p < 0.05$	0.11642

the layers at Klasies River main site and Blombos Cave for the period investigated, while Pinnacle Point Cave 13B indicates a sandy beach. However, this analysis shows that *T. sarmaticus* is more prevalent especially at Blombos Cave while *P. perna* proportions at Klasies River main site were sometimes as much as those of *T. sarmaticus*.

There are fluctuations of the dominant species through time. We argue that these changes in shellfish species are influenced by changes in seashores (habitat changes) that were probably due to rising or lowering sea levels (e.g., Ryano et al., 2019). Sea level retreats during this time would have resulted in sandy beaches as postulated by Jerardino and Marean (2010). The effort spent collecting one species may differ from another (Jerardino and Marean, 2010), but processing strategies are likely to be influenced by available species (Langejans et al., 2012). Jerardino and Marean (2016) also argue that shellfish species fluctuations may have been influenced by environmental changes at Pinnacle Point Cave 13B. By MIS 5c, wind and current activity at Pinnacle Point Cave (Cawthra et al., 2020) may have been responsible for the formation of a sand beach there during Upper and Lower Roof Spall layers suggested by the presence of *D. serra* (Jerardino & Marean, 2010).

5.2. Site function and occupational patterns

Although coastal habitats remained broadly similar during the early MIS 5, there is a clear difference between shellfish density and lithic density at Klasies River main site and Blombos Cave. The deposits from Klasies River main site discussed here contain lower shellfish and higher lithic densities than the Blombos Cave M3 deposits (Brenner et al., 2022: Table 7). The distance to the coast at Klasies River main site at c. 100 ka was modelled to be around 1.2 km, and at 110 ka it is estimated to be

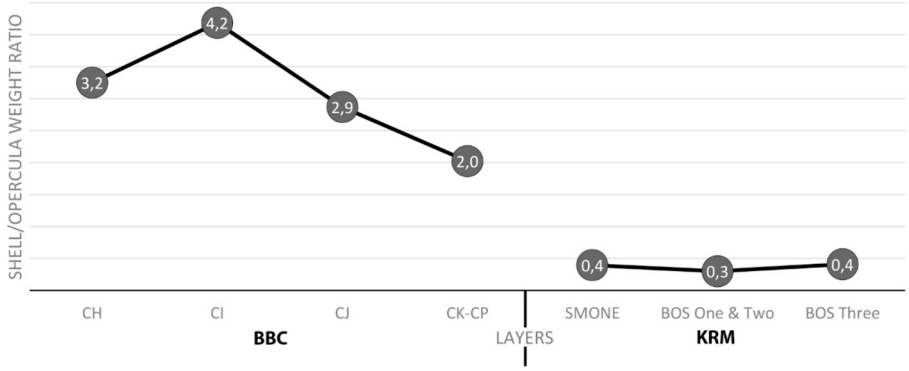

Fig. 11. Ratios of *Turbo sarmaticus* shell weights over opercula weights at Blombos Cave and Klasies River main site.

3.2 km (Langejans and Dusseldorp, 2017). The beginning of M3 phase around 100 ka at Blombos Cave (CP to CK layers) suggests minimal exploitation of shellfish, minimal occupation, or perhaps longer distance from the coast to the site. For the other phases, especially CJ and CI, higher densities of shellfish occur (Fig. 5). Distances from the coast to the cave have been estimated to be around 2.33–4.10 km (Fisher et al., 2010: Table 2) or 1.5 and 4 km (Dusseldorp and Langejans, 2013: Table 2) during M3 phase/MSA II Lower. Jacobs et al., (2020:18) estimate the coastline was c. 3.5 km from the present shoreline at the lowest sea level during this phase. Both sites would have been within 5 km of the coast during the early MIS 5. However, the density values of the Blombos Cave assemblages suggests that it was probably closer to the coast during the peak of M3 phase than the earlier phases at Klasies River main site discussed here. Hence, the pattern of collection was probably influenced by the short distance from the collection area (Fisher et al., 2010) due to rising sea level.

There were possibly different processing patterns. As shown in Fig. 11 and Table 4, there are clear differences in the ratio of *T. sarmaticus* shell weight to opercula weight at Klasies River main site compared to Blombos Cave. The Klasies River main site opercula are smaller (Fig. 10) and the comparative weights are less. This may indicate that some of the *T. sarmaticus* at Klasies River main site were deshelled at, or nearby, the collection area before they were brought to the cave while at Blombos Cave deshelling may have taken place at the cave (see Henshilwood et al., 2001; De Vynck et al., 2019). Alternatively, the shells at Klasies River main site may have decomposed more rapidly leaving mainly the denser calcitic opercula, and fragments of the thicker shells, for example the columella (Fig. 4). Additionally, deshelling on site at Blombos Cave and away from the site at Klasies River main site may indicate that distance from the coast to the site was closer at the former site than at the latter site.

Although Pinnacle Point Cave 13B has much lower densities of shellfish than the other two southern Cape sites, as Jerardino and Marean (2010) argue, this could be due to differences in the patterns of occupation of the site, the rates in which sediments formed, and site proximity to the coast during the MIS5c-d. It is also possible that this site was further from the coast than the other two southern Cape localities. Overall, MSA II layers at Pinnacle Point 13B (Shelly Brown Sand to Lower Roof Spall) shows an increase in shellfish collection through time indicating that this practice appears to have become more common.

5.3. Collection pressure and T. Sarmaticus opercula size

Collection pressure on marine invertebrates has been compared and debated for shellfish assemblages between two successive periods, the MSA and LSA. Scholars opined that small sizes of shellfish during the LSA indicate intensive harvesting and therefore higher human population numbers (e.g., Klein et al., 2004; Klein and Steele, 2013).

Here we only compare shellfish sizes of *T. sarmaticus* opercula (Fig. 10) collected in a broadly contemporaneous period, MSA II Lower techno-complex. As no opercula data is available for Pinnacle Point Cave 13B, *T. sarmaticus* size discussion is only based on Klasies River main site and Blombos Cave.

Although both occupations took place during MIS 5c-d, Klasies River main site deposits are somewhat older than Blombos Cave ones. *T. sarmaticus* are larger at Blombos Cave than at Klasies River main site. This shows that variability in MSA opercula sizes exists, and the scenario suggested by Klein et al. (2004) and Klein and Steele (2013) is not always confirmed with observations of *T. sarmaticus* opercula.

Alternatively, size difference between the *Turbo* community at Klasies River main site and Blombos Cave may be related to palaeoclimatic/environmental conditions. Different natural factors affect the growth of *T. sarmaticus* (Bruton et al., 1991) and the shoreline conditions near Klasies River main site may not have been optimal for the growth of the turban shells during this time. That environmental factors affected *T. sarmaticus* growth remains a hypothesis until further independent palaeoenvironmental evidence can be obtained. It may also be possible that harvesting at Blombos Cave happened at punctuated episodes over long periods of years and collectors accessed larger *Turbo*.

6. Conclusions

In this study, we have examined the shellfish assemblages from Klasies River main site and Blombos Cave during MIS 5c-d, for the MSA II Lower layers, c. > 110–90 ka. We have discussed subsistence patterns, commented on shoreline ecology, and compared *T. sarmaticus* opercula size and weight between the assemblages. We highlight the following main findings.

The targeted shellfish species at the two sites differ in some respects. At Blombos Cave the main species include *D. gigas*, *T. sarmaticus, C. oculus, P. perna*, *C. granatina*, and *S. argenvillei*. At Klasies River main site *T. sarmaticus* and *P. perna* are dominant in most layers. Klasies River main site, Blombos Cave, and Pinnacle Point Cave13B contain significant amounts of shellfish remains during MIS 5. However, quantities of marine shells from LSA contexts are larger than those from MSA contexts, as the densities of shells are one order of magnitude lower in the latter sites (cf. Jerardino, 2016). Nonetheless, the shellfish remains from the Middle Stone Age assemblages discussed here indicate that shellfish subsistence was not an opportunistic activity but reflect intentional and planned behaviour by MSA coastal communities during MIS 5 (Marean, 2014). Further investigation of coastal assemblages that are securely dated to MIS 6 may extend this pattern.

Both Klasies River main site and Blombos Cave show fluctuations through time in open and closed rocky shores as indicated by the relative dominance of the species favouring such habitats. Sea surface temperatures were likely similar in the southern Cape sites, but colder than today. This does not rule out the possibility of localised variations in temperature. *T. sarmaticus* opercula are significantly larger at Blombos Cave than at Klasies River main site and we suggest that these differences are either naturally induced or due to human harvesting pressure. Environments for the growth of the turban shell may have been more favourable at Blombos Cave than at Klasies River main site. The relative *T. sarmaticus* shell to opercula weights are less at Klasies River Main Site than at Blombos Cave. This may indicate that shell processing took place onsite at Blombos Cave while at the Klasies River main site it may have been done away from the site. Such behaviour may have been influenced by the distance to the shore, but it is also a possibility that the Klasies River shell was more extensively impacted by post depositional alteration.

This detailed comparison involved the MIS 5c-d period for which it has been argued that evidence for the relative increase of shellfish consumption occurs on the southern Cape coast. However, more research is needed to support such an inference, and localised patterns in subsistence and coastal ecologies occurred during this time frame.

CRediT authorship contribution statement

Kokeli P. Ryano: . Karen L. van Niekerk: Writing – review & editing, Formal analysis, Data curation. **Christopher S. Henshilwood:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition. **Sarah Wurz:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data relating to this article are included within it except raw data on *T. sarmaticus* opercula lengths which is available on a separate excel sheet on request.

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