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Environment versus behaviour: Zooarchaeological and taphonomic analyses of fauna from the Still Bay layers at Blombos Cave, South Africa

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ABSTRACT

Zooarchaeological data offer a unique opportunity to examine both palaeoenvironmental and behavioural trends using single datasets. In this study, we combine taphonomic and palaeoecological analyses of the faunal remains from recent excavations from the Still Bay layers at Blombos Cave to explore subsistence behaviour during this significant period in behavioural modernity. The c. 77-72 ka Still Bay is linked to innovative technology and the expression of complex cognition but is often lumped together as a homogenous entity. Here, we assess subsistence strategies within the Still Bay at Blombos Cave by examining zooarchaeological data from each layer. We investigate temporal changes during this techno-complex in an attempt to place subsistence behaviour within a paleoecological context. Our results show significant differences in surface modification frequencies between the early and middle/later Still Bay phases. Large and medium-sized ungulates were processed differently and filleting was probably an important activity. The data show that changes in shellfish density from the early to later Still Bay correspond to changes in ungulate representation. This may be due to changing environmental conditions around Blombos or shifting foraging strategies. This shift may also be associated with transport decisions for larger mammals. We discuss mobility patterns and the connection between subsistence strategies, environmental change and occupational intensity during the Still Bay levels at Blombos Cave.

1. Introduction

The Middle Stone Age (MSA), between ∼ 320 000 years ago (ka) to ∼ 30 ka, was a significant period in the anatomical and behavioural evolution of *Homo sapiens* (Deino et al., 2018; Wadley, 2015). An important focus of MSA research is the development of modern human behaviour – a suite of traits such as enhanced working memory, symbolism and sophisticated technology that define modern people (Henshilwood and Marean, 2003; Henshilwood and Dubreuil, 2011; Wynn and Coolidge, 2011). Two techno-complexes in the southern African record were probably key periods in this development: the Still Bay (SB) and Howiesons Poort occurring from Marine Isotope Stage (MIS) 5a through 4. The Howiesons Poort is associated with innovative technology such as the possible use of bow-and-arrows (Lombard and Phillipson, 2010), insecticides (Lennox and Bamford, 2015) and bedding (Wadley et al., 2011). The SB is generally dated to earlier than the Howiesons Poort and is also linked to complex behaviour (Jacobs et al., 2008). One of the most notable SB sites is Blombos Cave (BBC) along the southern Cape coast of South Africa, where this period has been

dated to between c. 77-72 ka (Jacobs et al., 2012). Shell-beads, engraved ochre, possible abstract ochre drawings, pressure-flaked bifacial points and finely crafted bone tools recovered in the SB layers at BBC suggest that modern human behaviour occurred in that region well before humans moved out of Africa between c. 60 and 50 ka (Henshilwood et al., 2002, 2004; 2018; d'Errico and Henshilwood, 2007; Mourre et al., 2010; Henn et al., 2012). The SB is thus an important marker in human development and a useful period through which to explore complex behavioural change in the Pleistocene.

An important means of understanding complex behaviour is through zooarchaeological analyses. Faunal remains are often used to infer environmental conditions (e.g., Klein, 1980, 1983; Klein and Cruz-Uribe, 2000; Clark and Plug, 2008; Clark, 2013) and taphonomic studies can yield critical information on subsistence behaviour by informing on transport decisions, exploitation strategies and processing patterns. However, relatively few faunal assemblages recovered from Late Pleistocene sites in southern Africa have been taphonomically analysed (but see Thompson, 2010; Thompson and Henshilwood, 2011; Faith, 2013a; Reynard et al., 2016a) which means that, at many sites,

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we are unable, confidently, to deconstruct subsistence strategies. Zooarchaeology is therefore an essential component in examining both palaeoecology and past human behaviour. By exploring subsistence strategies through taphonomic analyses we are better able to situate behaviour within a palaeoenvironmental context.

The relationship between environment and behaviour has framed much of the research concerning the Pleistocene (Butzer, 1964; Deacon, 1989; Foley, 1995; Klein, 2000; McBrearty and Brooks, 2000; Ash and Gallup, 2007; Compton, 2011; Faith, 2011; Weaver et al., 2011; McCall and Thomas, 2012; Saltré et al., 2016; Hillestad-Nel and Henshilwood, 2016; Reynard et al., 2016b). While some studies suggest that the prevailing environment played a key role in subsistence and behavioural trends (Ambrose and Lorenz, 1990; Wroe et al., 2013; Faith, 2011; Ziegler et al., 2013; Chase et al., 2018), other research suggests that other factors were more significant (Klein, 1995; Laland and Brown, 2006; Rector and Verrelli, 2010; Roberts et al., 2016; Saltré et al., 2016). Indeed, the links between modern human behaviour and the environment in which it evolved is complex. For example, as cognition developed and working memory improved, humans employed more innovative subsistence strategies – such as remote capture – that involved long-term planning and complex technology (Wadley, 2010). Yet, while remote capture involves sophisticated technology such as the use of snares and the ability to predict long-term animal behaviour, its effectiveness is probably linked to suitable environmental conditions that favour a prevalence of small mammals and small, size class 1 bovids. This is particularly relevant in the scrubland environment of the southern Cape with its predominance of small fauna.

The Cape Floristic Region (CFR) in the southwestern Cape of South Africa is a distinctive ecosystem encompassing a diverse array of endemic plants (Cowling, 1992; Cowling and Lombard, 2002; Bergh et al., 2014). Vegetation is dominated by *fynbos* – an evergreen, sclerophyllous shrub – and mean annual precipitation in the vicinity BBC is ~380 mm (Mucina and Rutherford, 2006). Its temperate climate and the availability of ample food resources such as geophytes (Deacon, 1993; Proches et al., 2005), shellfish (Jerardino and Marean, 2010; Langejans et al., 2012; Kyriacou et al., 2014), and small and large fauna (Klein, 1980; Skinner and Chimimba, 2005; Faith, 2011; Thompson and Henshilwood, 2014a) has led some researchers to suggests that the CFR may be linked to the development of complex behaviour in southern Africa during the Late Pleistocene (Marean, 2010; Parkington, 2010; Compton, 2011). Because of the broad, gentle slope of the Agulhas Bank – the continental shelf off the southern Cape coast – sea level fluctuations would have had significant effects on the southern Cape environment during glacial and interglacial periods (Van Andel, 1989; Fisher et al., 2010). Shifts in land availability in the southern Cape may have influenced prey selection patterns and the exposed terrain of the Agulhas Bank would have formed a southern coastal plain (SCP; Compton, 2011) which could have acted as a possible refugium for hominin and ungulate populations during periods of shoreline regression (Fisher et al., 2010; Compton, 2011; Faith and Behrensmeyer, 2013; Marean et al., 2014). Questions therefore arise as to the extent that temporal environmental conditions in the CFR played in incentivizing foraging patterns during the SB in the southern Cape.

Our understanding of subsistence patterns during the SB is almost exclusively derived from BBC fauna. Previous research has shown that larger bovids are more common than smaller, size 1 bovids in the SB layers at BBC (Thompson and Henshilwood, 2011). Thompson and Henshilwood (2014a, 2014b) also show that, although large-bodied ungulates are prevalent in the SB, tortoises were a common resource then. They argue, further, that there was a shift in subsistence patterns from a focus on small bovids in the M3 phase and earlier SB, to one that emphasised high-return large bovid hunting in the later SB. We are still uncertain of the extent (and causes) of these changes. Much of this could be related to how we assess the SB. With the exception of Discamps and Henshilwood (2015), our understanding of subsistence behaviour in the SB is based on lumped data for the entire SB sequence.

The implication of this is that the SB is an unchanging, consistent period. The idea of the SB as a homogenous entity has been re-assessed by some researchers (Villa et al., 2009; Porraz et al., 2013; Wurz, 2013; Soriano et al., 2015) and recent studies have highlighted both regional and temporal variation within the SB (e.g., Archer et al., 2015). Bifacials points, for example, were shaped and used differently at various sites (Lombard et al., 2010; Soriano et al., 2015). Soriano et al. (2015, pp. 40) argue that SB assemblages show extensive discontinuity and cannot be considered a homogenous set. It is reasonable to assume that variability in technology may be linked to changes in subsistence patterns. In fact, variation in the lithic technology of the SB may be reflected in subsistence behaviour (Lombard and Clark, 2008; Kandel et al., 2016). Discamps and Henshilwood (2015) argue that grouping faunal data in the SB can result in a loss of detailed information and they show a range of variability both temporally and spatially during the SB period. Furthermore, given that the SB may have occurred during the transition from MIS 5a to 4, it is likely that environmental conditions changed through the SB. We thus still need to explore if or how these changing environments affected subsistence behaviour at that time. Environmental conditions may also affect prey selection patterns and it is feasible that both would influence mobility. It is therefore necessary to investigate the SB at the refined, layer-specific level to address these issues and to unpack the complex links between behaviour and environment.

This study explores whether such patterns exist and if temporal changes through the SB could be related to subsistence variability. The aim of this research is threefold. First, on a broad level, it seeks to add to our knowledge of subsistence behaviour and environmental conditions during the SB at BBC. Second, our aim is to explore zooarchaeological changes in the SB based on refined analysis of the layers within this techno-complex. We must note, however, that small samples sizes can sometimes render that objective unattainable. Third, we wish to examine the relationship between environmental conditions and subsistence behaviour. Are they linked, and if so, to what extent? By assessing both taphonomic and palaeoenvironmental indicators using the same faunal sample, we are better able to link data at a more explicit level and explore variability through time to investigate the connection between foraging behaviour and environmental conditions.

2. Blombos Cave

2.1. Site background

BBC is ~300 km east of Cape Town and 25 km west of the town of Still Bay (Fig. 1). It is located at 34°25′S, 21°13′E ~100 m from the shore of the Indian Ocean and 34.5 m above sea level. The entrance to the cave occurs in a wave-cut cliff formed in calcified sediments of the Bredasdorp Group geological formation. Table Mountain Sandstone of the Cape Supergroup forms the basal layer of the caves about 4–6 m below the surface deposits under Bredasdorp Group sediments (Henshilwood et al., 2001a). These sediments consist of shelly conglomerate and marine sands of the De Hoopvlei Formation which is overlain by the aeolian sands of the Pliocene-aged Wankoe Formation that represents the volumetric bulk of the Bredasdorp Group (Malan, 1989). Sediments within the cave lie on large blocks of calcarenite rockfall that have caused the deposits to undulate from back to front. A 'wrapping effect' has occurred as sediments slump and drape in response to the basal rockfall (Henshilwood et al., 2001a). Ground waters rich in $CaCO_3$ (calcium carbonate) percolate through the cave roof and walls, creating an environment suited to the preservation of bone and shell, particularly near hearths and ash deposits (Henshilwood, 2005). The surface area of BBC is divided into metre squares and 0.5 m quadrates. Compared to other MSA cave sites in the southern Cape such as Pinnacle Point and Klasies River, the interior of the cave is relatively small: the surface area of the cave floor is ~55 m² behind the drip line. The mouth of the cave was virtually sealed off by dune sand when
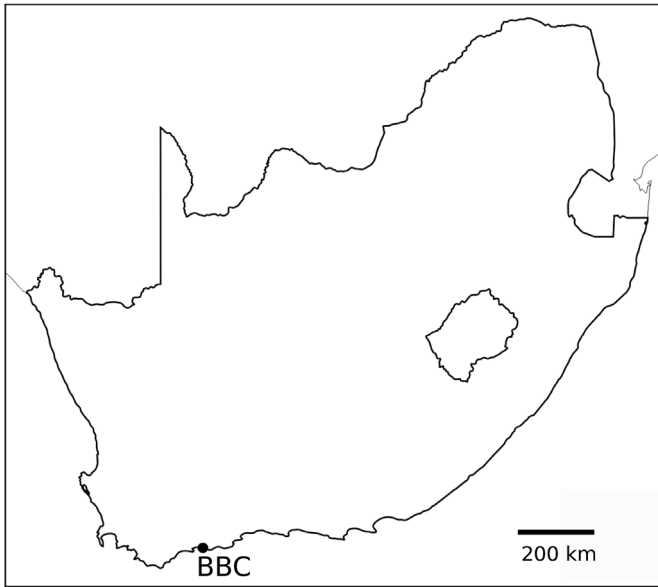
Fig. 1. Blombos Cave (BBC) along the southern Cape coast of South Africa.

excavations began. Excavations started in 1991 with regular seasonal excavations continuing to the present.

2.2. Stratigraphy

The stratigraphic sequence consists of three Later Stone Age and four MSA occupation phases. The MSA layers are divided into four phases: the M1 just below BBC Hiatus; the upper and lower M2; and the M3 at the bottom (Fig. 2). The M1 phase consist of medium brown sands containing lenses of shell, stone and bone, and many small, basin-shaped hearths (Henshilwood et al., 2001b; Henshilwood, 2005). The M1 and upper M2 phases contain SB points, and end and side scrapers (Goodwin and Van Riet Lowe, 1929; Henshilwood et al., 2001a). These phases also contain engraved ochre plaques, perforated shell beads, formal bone tools and an engraved bone fragment and a possible ochre drawing (Henshilwood and Sealy, 1997; Henshilwood et al., 2001a, 2001b; 2002, 2004, 2018; d'Errico et al., 2005, d'Errico and Henshilwood, 2007). Three human teeth were also recovered (Grine et al., 2000; Grine and Henshilwood, 2002). These are the layers that encompass the SB period and that are analysed in this study. The lower M2 phase is generally less dense than the M1 or upper M2 and contains small amounts of flakes, blades and cores, a few pieces of ochre and hearths. No shell beads, SB points or bone tools were recovered from this phase (Henshilwood et al., 2001a).

The M1 phase consists of Layers CA, CB, CC, CCC, CD, CDA and CDB. The upper M2 phase consists of Layer CF, CFA, CFB/CFC and CFD. In this paper, layers are combined for statistical purposes. Thus, Layers CFA, CFB/CFC and CFD are grouped into Layer CF, CDA and CDB are grouped as CD, and CC and CCC are combined as Layer CC. We define the 'early' SB as Layer CF (or the upper M2 phase), the 'middle' SB as CD and CC (the lower M1 phase) and the 'later' SB as CB and CA (the upper M1 phase).

2.3. Dating

The SB levels at Blombos Cave have been dated using various methods, including optically stimulated luminescence (OSL), thermo-luminescence (TL) and electron spin resonance (ESR) (Henshilwood et al., 2002; Jones, 2001; Jacobs et al., 2003a, 2003b, 2006; Tribolo et al., 2005, 2006). BBC hiatus overlaying the M1 phase was dated by OSL to 69 ± 5 and 70 ± 5 ka (Henshilwood et al., 2002; Jacobs et al., 2003a, b, 2006). An OSL age of 72.7 ± 3.1 ka was obtained for the
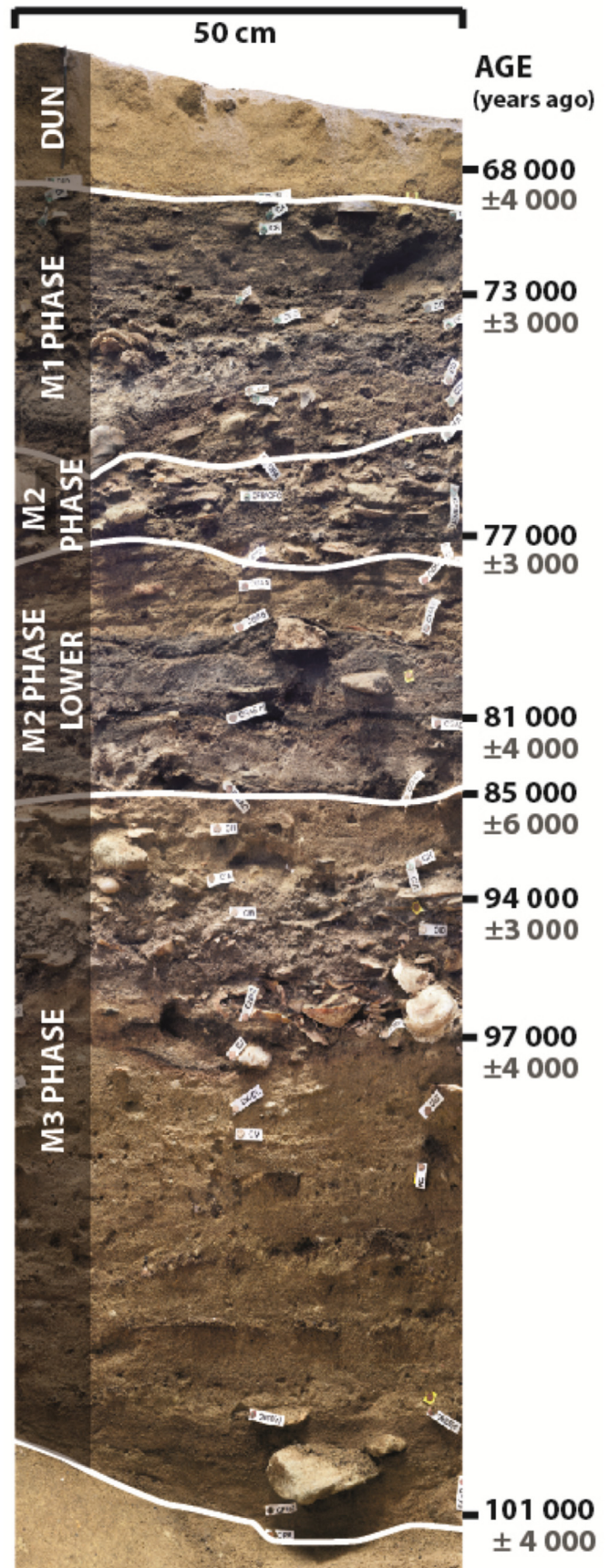

Fig. 2. Stratigraphy and optically stimulated luminescence (OSL) dates for Blombos Cave. The Still Bay consists of the M1 Phase and Upper M2 Phase.
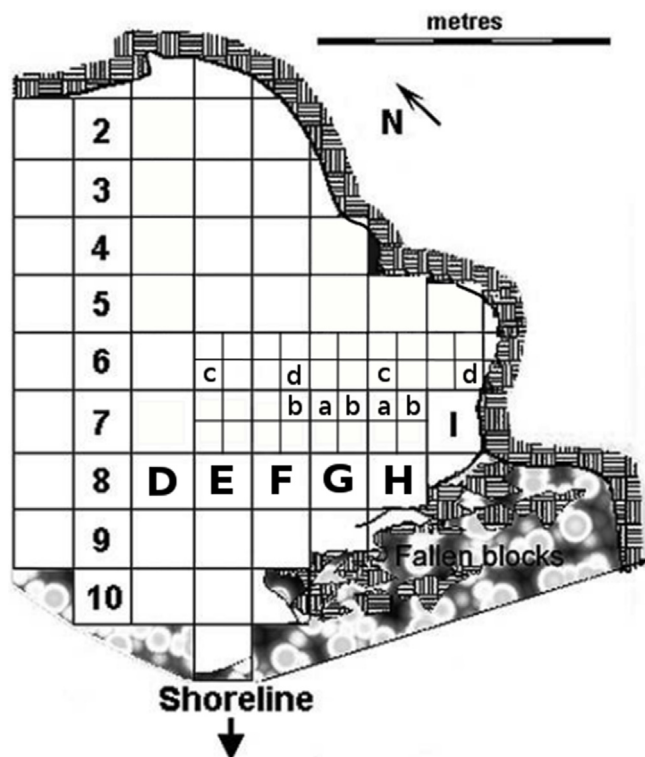
Fig. 3. Site map of Blombos Cave. Lowercase letters represent squares examined in this study.

Table 1
Classification of skeletal groups.

Skeletal group	All elements	High survival only
Head	Cranium, mandible, hyoid, horncores	Cranium, mandible, horncores
Forelimb	Scapula, humerus, radius, ulna	Humerus, radius, ulna
Hindlimb	Innominate, femur, patella, tibia	Femur, tibia
Distal limb	Carpals, tarsals, metapodia	Metapodia
Extremities	Phalanges, sesamoids	–

upper part of the M1 phase (Jacobs et al., 2003a, b). TL ages for the M1 phase are 74 ± 5 and 78 ± 6 ka (Tribolo et al., 2006). The OSL age for the upper M2 layers is 76.8 ± 3.1 ka (Jacobs et al., 2006). The SB levels were resampled for OSL dating in 2010 with the new ages dated from 75 to 72 ka (Jacobs et al., 2012). Based on these dating results and those obtained using the TL method, we suggest that 76 ka should be regarded as the *terminus post quem* for the SB levels at BBC.

3. Materials and methods

Faunal remains were assessed following Driver (2005) and Klein and Cruz-Uribe (1984) using the comparative faunal collections of the Ditsong National Museum of Natural History (formerly the Transvaal Museum) in Pretoria. We analysed identified faunal remains, and long-bone fragments not identified to element, recovered from the 2011 and 2013 excavation seasons (Fig. 3). Out of the 6673 mammalian and tortoise specimens identified, a total of 656 specimens (9.8%) could be assigned at least to the class level. Taxa, element, skeletal portion, side, state of epiphyseal fusion and types of surface modification were recorded for all specimens. Faunal specimens were assessed for surface modification following standard criteria (Behrensmeyer, 1978; Blumenschine and Selvaggio, 1988; Fisher, 1995; Blumenschine et al., 1996) using a Nikon binocular light microscope (10–40× magnification) under oblique, unidirectional, incandescent lighting. Following Thompson et al. (2017), we use only midshafts of long bones when documenting surface modification. Our study also includes unidentified long bone midshafts (cf. Reynard et al., 2016a). The lengths of all faunal specimens were classed as code 1 (0–0.9 cm), code 2 (1–1.9 cm), code 3 (2–2.9 cm), etc.

Teeth, astragali and distal phalanges were used to identify specimens to genus or species. Bovid post-cranial remains are categorised to size class based on Brain (1974). Indeterminate mammal remains that could only be consigned to element (e.g., cranial and vertebral fragments) were assigned to 'very small', 'small', 'medium' or 'large' indeterminate mammal size classes. Very small mammal are species

smaller than the Cape dune molerat (*Bathyergus suillus*), small mammals ranging in size from the Cape dune molerat up to and including size 1 bovids, medium mammals correspond to size 2 bovids, large mammals to size 3 bovids and larger. We differentiate between 'Large mammal' and 'Large ungulate'. Large mammal includes all specimens identified to element (including taxonomically indeterminate elements), while 'Large ungulate' remains comprise identified size 3, 4 and 5 bovids, and perissodactyls and exclude indeterminate large mammal elements such as cranial, rib and vertebral specimens. Because of the general lack of large carnivore remains in our sample (cf. Henshilwood et al., 2001a), most 'medium mammal' specimens probably belong to size 2 bovids. Tortoise remains were tallied but not included in our analysis. We 'normalize' the number of identified specimens (NISP) to adjust for the expected frequency that a particular skeletal element should occur in the complete carcass of an ungulate (see Reynard et al., 2016a). Skeletal-parts of ungulates are categorised into five skeletal groups: the head, forelimb, hindlimb, distal limbs and extremities (Table 1). Where density mediated attrition has affected element representation, only high-survival elements (skulls and long-bones) are used in our classification of skeletal-groups (cf. Marean and Cleghorn, 2003). Because skull bones and long bones occur in pairs (cf. Clark, 2013), we use raw NISP values to demonstrate whether skeletal-groups in ungulates were affected by density-mediated attrition.

We also measure ungulate richness and diversity. Ungulate diversity is associated with environmental productivity and may be linked to precipitation and/or moisture availability (Thackeray, 1980; Faith, 2013b). Richness is usually described by the number of ungulate taxa (NTAXA) within an assemblage. Because NTAXA is affected by sample size, residual analyses were also conducted. This was then compared to Fisher's alpha (α), a measure of diversity relatively insensitive to sample size discrepancies (Magurran, 2004; Faith, 2013b). Due to a lack of assessable teeth, specimens with epiphyseal plates such as phalanges, long-bones and vertebrae fragments were examined for indicators of age. Bone with fused epiphyses are categorised as adult, while those that are 'unfused' or 'recently-fused' are classed as juvenile. For a specimen to be examined, at least one end should have an epiphysis. We were able to assess 205 specimens for epiphyseal fusion.

4. Results

4.1. Taphonomic history

4.1.1. Fragmentation

The extent of the fragmentation of bone assemblages relate to site preservation or anthropogenic processes. Bone density-mediated attrition is therefore critical when evaluating the taphonomic history of an assemblage. Generally, both medium-sized and large ungulates at BBC are affected by bone density-mediated attrition (Table 2). Size 1 bovids are not affected, probably due to a combination of taphonomic influences (e.g., larger ungulate elements are more likely to fragment because long bones with narrower diameters, such as those from smaller elements or species, tend to resist fragmentation better than those with larger diameters [Johnson, 1985; Marean, 1991]) or behavioural patterns such as transport strategies (entire carcasses were transported back to the home-base). Following Marean and Cleghorn (2003), if only

Table 2
Spearmans' rank-order correlation between skeletal-element abundance (normed NISP) of medium and large ungulates and 'high survival' element bone densities (caribou and wildebeest data in Lam et al., 1999). Medium mammal and Size 2 bovids compared to caribou data. Large mammals compared to wildebeest data. Significant values emboldened.

Sample	Blombos Cave	
	r_s	p
Medium mammal[a] (all elements)	**0.376**	**0.045**
Size 2 bovid[a] (high survival)	0.437	0.103
Larger mammal[b] (all elements)	**0.353**	**0.038**
Larger mammal[b] (high survival)	0.282	0.256

[a] Medium mammal comprises size 2 bovids and indeterminate 'medium mammal' remains.

[b] Larger mammal equals size 3, 4 & 5 bovids, perissodactyls and indeterminate 'large mammal' remains. See Table 2 for the definition of high-survival elements. BMD values were assigned to proximal, medial & distal portions of long-bone & rib, and to the densest portions of vertebrae, scapulae, pelves & mandibles.

high-survival elements – i.e., the skull and long-bones – are included in the analysis, taphonomic attrition is less likely to affect skeletal-part profiles.

Fragment lengths for unidentified long-bone fragments are relatively small (mean code = 3.2). Fragment lengths for all faunal specimens through the sequence – including unidentified faunal specimens – indicate that the majority of specimens (n = 997; 43%) are length code 3 (2–2.9 cm long), with 31% (n = 722) of specimens code 2. There is no significant difference in the frequencies of lengths between CA and CB ($\chi^2 = 6.613$; df = 3; $p = 0.0853$), and CB and CC ($\chi^2 = 1.163$; df = 3; $p = 0.7618$) (Fig. 4). However, there are significant differences between CC and CD ($\chi^2 = 81.056$; df = 3; $p < 0.0001$) and CD and CF ($\chi^2 = 22.856$; df = 3; $p < 0.0001$). Layer CD has, proportionally, the smallest fragments, followed by CF.

4.1.2. Surface modification

Percussion marks occur on 15.2% (n = 76) of specimens and are most common in Layer CB (20.2%, n = 17) (Table 3). Cut marks (8%; n = 40) are slightly more prevalent than tooth marks (6.2%; n = 31) but not significantly so ($\chi^2 = 1.228$; df = 1; p = 0.2678) while gnaw marks are rare (0.6%; n = 3). Cut marks are proportionally more common in CB (n = 12; 14.3%) with one cut-marked specimen in CF. Only two specimens – in CA – display gastric-acid etching (n = 2, 2%) and one specimen in CF was weathered.
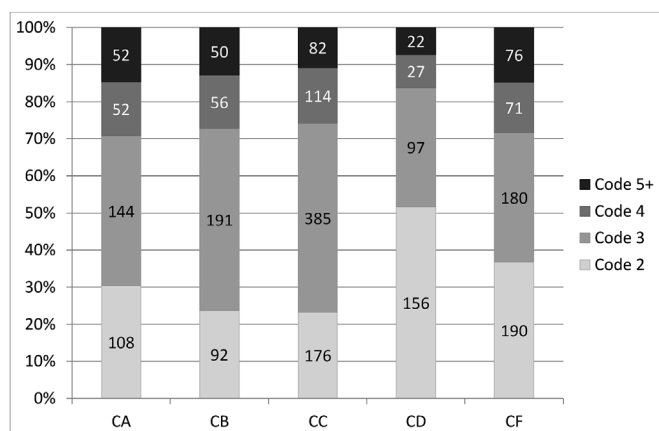
Fig. 4. Fragment lengths through the Still Bay. Code 5+ = Codes 5 and above. Number of specimens in columns.

4.2. Processing activities

On the whole, ungulates were extensively processed at BBC. Cut marks are significantly more common on larger mammals than size 2 bovids (Fig. S1 $\chi^2 = 5.065$; df = 1; p = 0.0244). Cut marks on phalanges may be indicative of skinning but few phalanges at BBC display these marks (n = 3; 5.8% of all phalanges). Only three metapodial fragments display cut marks (4.7% of metapodia of all taxa). Overall, evidence of skinning is not common at BBC but this probably related to sample sizes. Previous research by Thompson (2008) suggests that filleting was common at BBC. Filleting is often implied when cut marks are prevalent on the mid-shafts of long-bones (Dominguez-Rodrigo, 1999; Thompson, 2008; Galán and Domínguez-Rodrigo, 2013). Our study indicates that the mid-shafts of ungulate long-bone are the most common region to exhibit cut marks (7.7% [4/52] of proximal ends, 13.8% [13/94] of shafts and 2.5% [1/40] of distal ends display cut marks). Percussion marks shown in Table 3 may indicate bone marrow extraction. Percussion marks are more likely to occur on ungulate femora (NISP = 10; 40%) and tibiae (NISP = 9; 36%) with no crania, humeri or radio-ulnae displaying evidence of impact marks.

4.2.1. Utility indices

Utility data are influenced by numerous factors: small sample sizes, equifinality in element abundance and/or the use of caribou to extrapolate information on African bovids or other factors such as bone tool manufacturing. Although bone tool production is outside of the scope of this study, 20% (n = 98) of long-bone specimens in our sample were probably bone tools or fragments thereof (Table 3; see also Henshilwood et al., 2001b and d'Errico and Henshilwood, 2007). Despite this, theoretical modelling of nutritional utility is a useful means of inferring transport decisions and understanding foraging behaviour (Morin and Ready, 2013).

We compare utility indices and skeletal-abundance for all elements and high-survival elements (Marean and Cleghorn, 2003). Table 4 shows a range of relationships between element abundance and nutritional utility for small, medium and large ungulates. Because size 1 bovids have not been significantly affected by taphonomic destruction, we did not restrict our analysis to only their high-survival elements. Size 1 bovids are positively correlated with marrow utility. Interestingly, the only significant relationships between medium-size and large mammal abundance and utility indices are when all elements are included in the analysis, and not just high-survival bones. For both medium-size and large mammals, there are inversely proportional correlations between skeletal abundance and meat-drying utility. Evenness index for large mammals at BBC points to a 'bulk' element transport strategy according to Faith and Gordons' (2007) model for a MNE of 50 elements. Medium mammal (size 2) element evenness data are inconclusive. In any case, the correlation between high-survival element abundance and SFUI for both medium and large bovid samples is not significant, militating against any strong evidence for a particular transport strategy (Table 5).

4.3. Mortality profiles

For all identified taxa, slightly more specimens at BBC were noted as juveniles (number of unfused/recently-fused ends [n] = 125; 30.5%) compared to fragments with fused ends or adults (n = 122; 29.8%). There is a significant decrease in juveniles from the upper M2 through the M1 phase ($\chi^2 = 8.579$; df = 2; p = 0.0137) (Fig. 5). There is no significant difference between small mammals and bovid (for adult vs. juvenile: $\chi^2 = 0.0192$; df = 1; p = 0.8898) (Fig. 6a). Carnivores consist of significantly more adult remains compared to bovids ($\chi^2 = 6.353$; df = 2; p = 0.0417) or small mammals ($\chi^2 = 5.211$; df = 2; p = 0.0224).

With regard to bovids, size 2 bovids have the highest proportion of juveniles (n = 23; 56.1%) while size 1 bovids have the most adults

Table 3
Surface modifications on long bones in the Still Bay at Blombos Cave.

Layer	N	Percussion Marks		Cut Marks		Tooth Marks		Gnaw Marks		Acid-etching		Root etching		Weathering		Worked bone[a]	
		n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
CA	100	8	8.0	9	9.0	9	9.0	0	0	2	2	6	6.0	0	0	14	14.0
CB	84	17	20.2	12	14.3	4	4.8	0	0	0	0	7	8.3	0	0	11	13.1
CC	114	22	19.3	9	7.9	6	5.3	0	0	0	0	6	5.3	0	0	34	29.8
CD	97	14	14.4	9	9.3	0	0	0	0	0	0	7	7.2	0	0	11	11.3
CF	106	15	14.2	1	0.9	12	11.3	3	2.8	0	0	6	5.7	1	0.9	28	26.4
Total	**501**	**76**	**15.2**	**40**	**8.0**	**31**	**6.2**	**3**	**0.6**	**2**	**0.4**	**32**	**6.4**	**1**	**0.2**	**98**	**19.6**

[a] Worked bone are abraded specimens that have possibly been intentionally polished (based on Reynard, 2014).

Table 4
Spearmans' rank-order correlation between skeletal-abundance (nNISP) and Standardised Food Utility Indices (SFUI), Meat Utility Indices (MUI), Unsaturated Marrow Indices (UMI) and Meat Drying Indices (MDI) for all elements and high-survival elements. Indices data from Metcalfe and Jones (1988) and Morin and Ready (2013). Size 1 bovids compared to sheep data, medium mammal and size 2 bovids compared to caribou, and large mammal compared to bison data. Emboldened values are significant (p < 0.05).

Samples	UMI		MDI	
	r	p-value	r	p-value
Size 1 bovid (all elements)	**0.688**	**0.0134**	−0.452	0.0518
Medium mammal (all elements)	0.643	0.1194	**−0.732**	**0.0068**
Size 2 bovid (high survival)	0.427	0.3390	−0.340	0.3702
Large mammal (all elements)	**0.857**	**0.0015**	**−0.625**	**0.0043**
Large mammal (high survival)	0.493	0.3333	0.029	0.9833

| **Samples**	**MUI**		**SFUI**	
	r	p-value	r	p-value
Size 1 bovid (all elements)	−0.155	0.5274	−0.226	0.1997
Medium mammal (all elements)	−0.556	0.0604	−0.357	0.1914
Size 2 bovid (high survival)	0.021	0.9572	−0.366	0.3333
Large mammal (all elements)	0.171	0.4836	−0.093	0.7124
Large mammal (high survival)	0.232	0.6722	0.422	0.3456

Medium mammals comprise size 2 bovids and indeterminate 'medium mammal' remains. Larger mammal comprise size 3, 4 & 5 bovids, perissodactyls and indeterminate 'larger mammal' remains.

Table 5
Skeletal element evenness (embolden) for size 2 bovid and large mammals at Blombos Cave.

Elements	Size 2 bovid	Large mammal
Crania	39	1
Mandibles	10	11
Humerus	2	5
Radius	7	7
Ulna	2	5
Metacarpal	4.5	7
Femur	3	11
Tibia	4	10
Metatarsal	5.5	8
Total	77	65
Element evenness	**0.751**	**0.949**
Spearman's rho	−0.366	0.422
Transport strategy	Inconclusive	Bulk?

Larger mammal comprise size 3, 4 & 5 bovids, perissodactyls and indeterminate 'large mammal' remains.

(n = 50; 53.2%) (Fig. 6b). There are significant differences in neonates, juveniles and adults between size 1 and 2 bovids ($\chi^2 = 17.749$; df = 2; p = 0.00014). Large mammals have equal proportions of juveniles and adults (for both: n = 13; 40.6%) and there is no significant difference in age classes between size 2 bovids and large mammals ($\chi^2 = 2.381$;
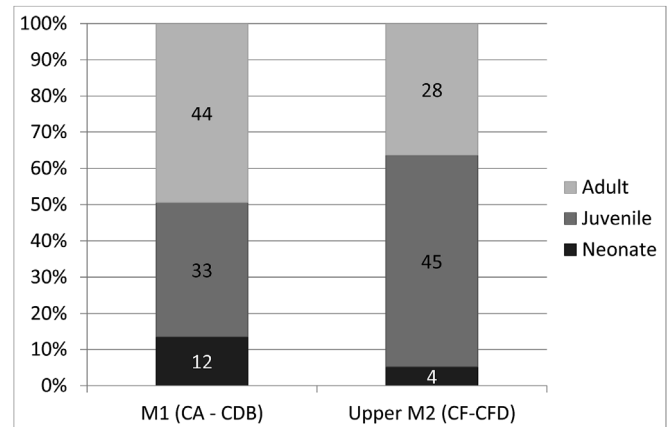
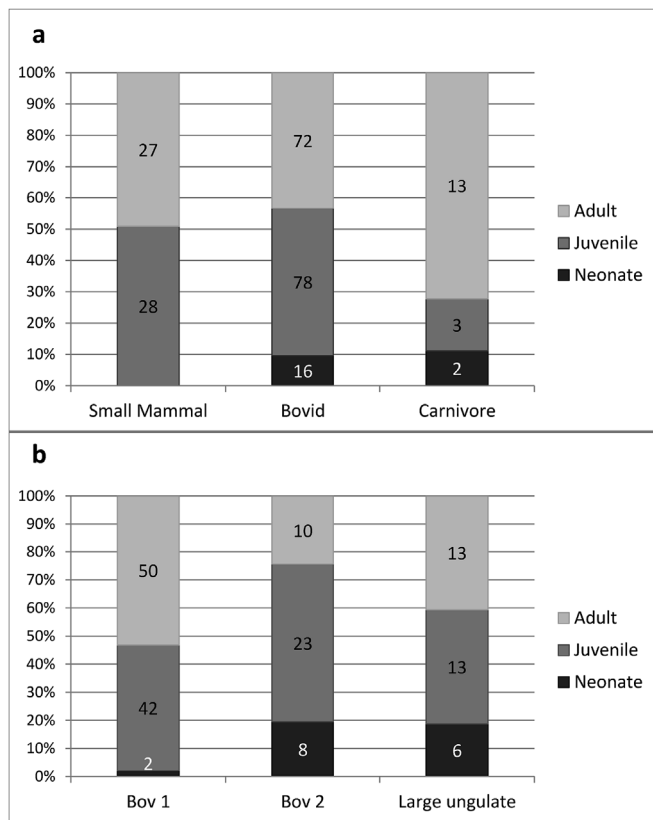**Fig. 5.** Faunal mortality profiles in the Still Bay at Blombos Cave.

df = 2; p = 0.304). There are no significant differences in adults and juveniles between small mammals and size 1 bovids ($\chi^2 = 0.381$; df = 2; p = 0.5369) or between small mammals and size 2 bovids ($\chi^2 = 2.988$; df = 2; p = 0.0839).

4.4. Skeletal-part profiles

To assess skeletal-part profiles, we only use high-survival elements since ungulates are affected by density-mediated attrition (Table 2). The data presented in Fig. 7 are raw NISP values because all high-survival elements – including crania and mandibles – are paired (see Reynard et al., 2016a).

Medium mammals (Fig. 7a) and size 1 bovids (Fig. S2) are dominated by skull remains. Skulls are significantly more common than long-bones for medium mammals compared to size 1 bovids (Fig. S3; $\chi^2 = 14.83$; df = 1; p = 0.0001). Generally, large mammal crania are rare (Fig. S4) with skulls from medium mammals significantly more common than those of large mammals ($\chi^2 = 27.940$; df = 1; p < 0.0001 for skulls and high-survival post-cranial elements between medium and large mammals). The proportion of crania and mandibles is also significantly different between medium and large mammals ($\chi^2 = 18.910$; df = 1; p < 0.0001).

The prevalence of large mammal long bones is probably because large mammals yield more meat and marrow. On the whole, fewer elements of medium mammals were recovered than either large mammals or size 1 bovids. There are proportionally more skull remains of size 2 than size 1 bovids. This may be the result of identification bias: skull fragments were easier to categorise as size 2 than size 1 bovids due to the difficulty in discerning hyrax and other small mammals from some small bovids. Size 1 skull specimens may therefore be under-estimated. Layer CD generally has few post-cranial remains relative to the other layers. Fisher's exact tests show no significant differences between skulls and long-bones through the layers. The variability in skeletal-parts may be the result of the general lack of medium mammal remains

Fig. 6. Mortality profiles for (a) mammalian taxonomic groups, and (b) ungulate size classes in the Still Bay at Blombos Cave. Small mammals comprise identified lagomorphs, Cape dune mole rat and hyrax remains and excludes small carnivores. Carnivore excludes seal. Large ungulate comprise identified size 3, 4 & 5 bovids, and perissodactyls. Number of assessed ends in columns.

Fig. 7. Distribution of (a) medium mammal, and (b) large mammal skeletal-parts in the Still Bay at Blombos Cave.

mentioned earlier. Size 2 elements are especially lacking in CA and CB (Fig. 7a).

For large mammals, skull remains are generally not common throughout the SB sequence and post-cranials are proportionally more prevalent (Fig. S4). Proximal limbs are more common than distal limbs (Fig. 7b) probably because these are more meat and marrow-bearing elements than the extremities. As with medium mammals, few large mammal remains occur in CD. Fisher's exact tests suggest no significant differences between skeletal regions of large mammals between most layers.

4.5. Taxonomic and palaeoenvironmental assessment

Tortoise is the most prevalent taxon (cf. Thompson and Henshilwood, 2014b) but small mammals are also relatively common at (NISP = 79; 46.8% of taxa identified to genus) (Table 6). Size 1 bovids such as steenbok/Cape grysbok (*Raphicerus* sp.) are the most common ungulates. Large ungulates such as eland (*Tragelaphus oryx*) and the long-horned buffalo (*Syncerus antiquus*) were also identified. Due to the relatively small sample size of identified taxa, the mammalian fauna identified by Klein and Cruz-Uribe in Henshilwood et al. (2001a) is also presented (Table 6). Cape fur seal are noticeably more common in their assemblage, as are eland and rhinoceros. Other taxa identified by Klein and Cruz-Uribe but not in our sample include hippopotamus (*Hippopotamus amphibious*) and bluebuck (*Hippotragus leucophaeus*) (see Henshilwood et al., 2001a for a detailed list of fauna identified).

In terms of mammals, size 1 bovids are the most numerous taxa followed by small mammals. Large ungulates dominate CB while size 1 bovids are more common in CF (Fig. 8a). Small mammals are relatively common in CD. There are significant difference in the proportion of
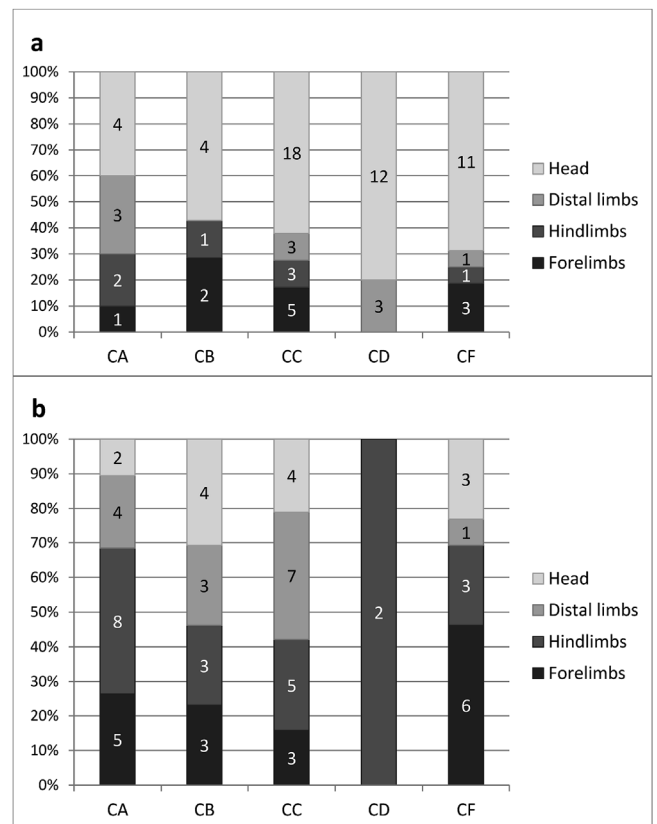
taxa between CC and CD ($\chi^2 = 16.818$; df = 4; p = 0.0021) and between CD and CF ($\chi^2 = 28.710$; df = 4; p < 0.00001) which probably relate to the substantial decrease in size 1 bovids from CF to CD and the increase in large ungulates from CD to CC. Browsers are prevalent throughout the sequence but are significantly more common in CF (CF vs. all other layers for browers and mixed-feeders/grazers: Fisher's exact test, p = 0.0037) (Fig. 8b). Mixed-feeders/grazers become more common in the later SB (CC-CA).

There is generally an exponential relationship between the number of taxa in an assemblage and sample size: as sample sizes increase, taxa become more abundance (Lyman, 2008). In our dataset, ungulate NTAXA is significantly correlated to log transformed ungulate NISP ($r_s = 0.85714$; p = 0.0137). To account for sample size discrepancies, we conduct a residual analysis. Positive residual values indicate more taxa than predicted by the regression, while negative residuals indicate fewer species than expected. Fisher's alpha is significantly correlated to residuals, which suggest that both metrics have similar estimates of richness and diversity. Residual values are the most positive in CC and lowest in CF (Table 7). Fisher's alpha, likewise, reflects this trend.

5. Discussion

In the following sections, we first discuss how the data relate to the Still Bay assemblage as a whole and then, where possible, explore diachronic changes within the Still Bay based on layers or phases.

5.1. Subsistence behaviour

Taphonomic data from our sample and that analysed by Thompson (2008; Thompson and Henshilwood, 2011) suggest that, although humans were the dominant accumulators, carnivores had a significant effect on the BBC assemblage. The SB at BBC was thus likely a 'human

Table 6
Number of identified specimens (NISP) at Blombos Cave (BBC). 'Total Identified' include tortoise. ULBF = unidentified long-bone fragments.

Order	Taxa	Common Name	CA	CB	CC	CD	CF	Total	KC M1[a]	KC M2[a]
Chelonii	*Testudinidae*	Tortoise	1397	539	899	756	1665	5256		
	Chersina angulata	Angulate tortoise	97	65	127	63	127	479		
Lagomorpha	*Lepus* sp.	Hare	2	–	–	–	1	3	25	15
	Lepus capensis	Cape hare	–	–	–	1	–	1	11	4
Rodentia	*Bathyergus suillus*	Cape dune molerat	3	–	8	6	3	20	419	303
	Hystrix sp.	Porcupine	–	1	–	–	–	1	1	–
Carnivora	*Herpestes* sp.	Mongoose	–	–	1	–	1	2	3	4
	Arctocephalus cf. pusillus	Cape fur seal	2	–	13	1	5	21	126	32
	Felis lybica	African wildcat	1	–	–	–	–	1	16	1
	Felis caracal/serval	Caracal/serval	–	–	1	1	1	3	–	–
	Vulpes chama	Cape fox	–	–	–	–	5	5	–	–
Hyracoidea	*Procavia capensis*	Rock hyrax	1	4	7	11	25	48	169	190
Perissodactyla	*Rhinicerotidae* indet.	Rhinoceros	1	1	–	–	–	2	16	6
	Equus sp.	Zebra	1	–	–	–	–	–	–	–
Ruminantia	*Tragelaphus oryx*	Eland	–	3	1	–	–	4	48	8
	Syncerus caffer	African buffalo	–	–	2	–	1	1	2	–
	Syncerus antiquus	Giant buffalo	–	–	1	1	–	2	–	–
	Pelea capreolus	Grey (Vaal) rhebok	–	–	1	–	1	2	6	2
	Raphicerus sp.	Steenbok/grysbok	8	2	5	3	34	52	111	51
	Oreotragus oreotragus	Klipspringer	1	–	2	–	2	5	–	–
	Sylvicapra grimmia	Grey duiker	1	–	1	–	–	2	–	2
	Alcelaphini indet.	Hartebeest or wildebeest	–	–	–	–	1	1	5	–

Taxa	Common Name	CA	CB	CC	CD	CF	Total	KC M1[a]	KC M2[a]
Bovidae indet.	Bov I	12	8	26	13	62	121	382	360
	Bov I/II	–	–	1	1	4	6		
	Bov II	12	5	17	17	13	64	74	51
	Bov II/III	2	–	2	1	–	5		
	Bov III	8	5	10	2	11	36	91	50
	Bov III/IV	5	7	9	4	7	32		
	Bov IV	5	5	6	2	10	28	183	58
	Bov IV/V	1	–	–	3	–	4		
	Bov V	–	2	2	–	–	4		
	Large ungulate	–	2	2	–	4	8		
Carnivora indet.	Small carnivore	–	–	1	–	3	4		
	Medium carnivore	2	–	–	2	2	6		
Mammal indet.	Very small mammal	3	6	19	8	21	57		
	Small mammal	17	18	47	23	57	162		
	Medium mammal	27	21	75	16	30	169		
	Large mammal	4	16	16	3	14	53		
	Very large mammal	–	1	1	–	–	2		
Total Identified		1613	711	1301	938	2110	6673	1729	1167
Total ULBF		76	70	88	85	71	390		
Total Unidentified		4350	3541	8887	3516	5703	25997		
Grand Total		5942	4257	10149	4476	7757	32581		

[a] KC M1 & KC M2 = BBC M1 & M2 layers analysed by Klein& Cruz-Uribe (Henshilwood et al., 2001a).

first' faunal assemblage where humans were the primary collectors of the remains, followed by animal scavenging (Fig. S4; Blumenschine, 1988). In the early SB (Layer CF), we see evidence of more animal involvement in the assemblage compared to the middle and later SB. Fragmentation data show that CD and CF have the smallest specimens. The data in Fig. 4 suggest that CF and CD are different to the later SB (CC-CA) and these differences may represent changes in site formation history. Layer CD is an especially interesting layer given the fragmentation data and the lack of ungulate remains there, but the particulars of CD will be discussed later.

Skeletal element evenness data indicate that the bulk of large mammal remains were likely transported back to the BBC home-base. Evenness values also suggest that medium-sized mammals were treated differently from large mammals implying that most size 2 mammals were processed in the field. This could also be related to filleting. If filleting was an important activity at BBC – and cut mark data indicate it was – then this may suggest a subsistence strategy reliant on meat-storage. The likely drying of mussel meat on the south-western Cape coast in the Late Holocene also attests to the importance of storage by hunter gatherers (Henshilwood et al., 1994). Filleting is an important phase in meat-storage and in equatorial and subequatorial regions,

drying meat is essential to meat storage. In fact, we may see evidence of meat drying in our utility data. The data for all elements indicate significant inverse correlations between skeletal abundance and meat-drying indices (MDI) which may occur when skeletal-parts are left behind after high-utility elements are transported to other locations (Friesen, 2001, pp. 329). However, the significantly correlated utility values in Table 5 are derived from all elements and not high-survival elements. It is therefore likely that taphonomic destruction would have had a major effect on these data and it would be problematic to use it to infer transport decisions (Faith and Thompson, 2018). Still, other data also point to evidence of meat-drying. Indeed, what the evenness and cut mark data may suggest is that meat – especially from size 2 bovids – may have been taken from BBC to be consumed elsewhere. Since BBC was probably not a kill-site (Henshilwood et al., 2001a), it could mean that prey was first transported to the cave, processed, and then moved to other locales.

5.2. Mortality profiles

Neonate and juveniles are generally more common for size 2 bovids and large ungulates than for size 1 bovids. The similarity in age profiles
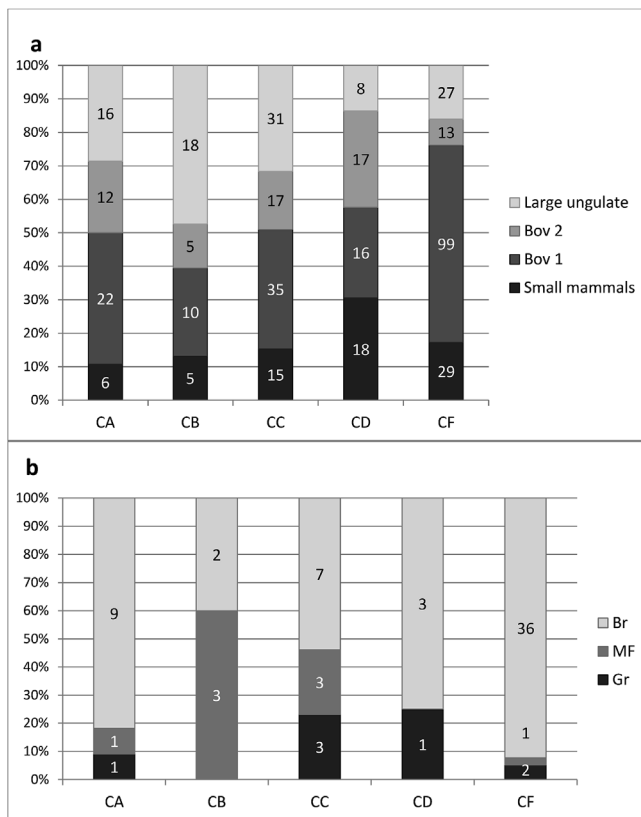
Fig. 8. (a) Distribution of taxonomic groups in the Still Bay at Blombos Cave. Large ungulate comprise identified size 3, 4 & 5 bovids, and perissodactyls. Small mammals comprise identified lagomorphs, Cape dune mole rat and hyrax remains and excludes small carnivores. (b) Ungulate dietary preference in the Still Bay at Blombos Cave. Br = browsers; MF = mixed-feeders; Gr = grazers.

Table 7
Richness (NTAXA), residuals and diversity values for the Still Bay at Blombos. BBC = our Blombos Cave data; KC BBC = fauna from M1 and M2 Phases analysed by Klein and Cruze-Uribe in Henshilwood et al.(2001a).

Dataset	NTAXA	NISP	Residuals	Fishers α
CA	5	12	0.413	3.217
CB	3	6	−0.152	2.387
CC	6	11	1.594	5.401
CD	2	4	−0.313	1.592
CF	4	33	−2.685	1.192
BBC	9	66	0.881	2.815
KC BBC	12	379	0.263	2.359

between large ungulates and size 2 bovids, and the difference between these and size 1 bovids may point to different accumulation techniques (Fig. 6b). The mortality data from BBC may indicate that medium and large bovids were hunted along similar lines, or at least during similar seasons. In contrast to size 2 and large ungulates, small mammals and size 1 bovids have a very few neonate remains, and their age profiles appear very similar (Fig. 6). This may imply either different hunting techniques or that non-human bone collectors played a role in their accumulation. It is possible that small mammal and size 1 bovid accumulation may have occurred through remote capture techniques such as trapping or snaring. The presence of carnivores in the assemblage may reinforce this possibility since these animals are more likely to be captured in traps than through encounter hunting (Wadley, 2010). Given the relative prevalence of tooth marks at BBC, it is also feasible the small mammal/size 1 bovid mortality profiles may be the result of scavengers. In all likelihood, it may have been a combination of both.

The significant difference in mortality profiles between carnivores on the one hand, and bovids and small mammals on the other, suggest different strategies in their accumulation. Generally, small mammals and bovids have a similar mortality distribution consisting of a relatively large number of juveniles (Fig. 6a). Some studies have suggested that the significant number of bovid and seal juvenile remains at BBC may be due to seasonality (e.g., Faith and Thompson, 2013; Dusseldorp and Langejans, 2015). The decrease in juveniles from the early SB (CF) through the later SB (M1 phase), for example, could be linked to seasonal occupations driven by bovid calving. Carnivore remains, on the other hand, are generally adult-dominated which could point to a different strategy. If these carnivore bones were the remains of scavengers using BBC as lairs then we would expect to find more juvenile and neonate remains (Kuhn et al., 2010). Even though no cut marks were observed on them, the prevalence of matured specimens makes it possible that these carnivore remains are the result of hunting for skins.

5.3. Transport decisions

Skeletal parts profiles are useful in exploring transport distances. To investigate variation in transport distances, we examine the proportions of skulls to post-cranial remains of ungulates. Research on modern foragers suggests that the proportion of ungulate skulls to post-cranials decline as foraging distances increases (O'Connell et al., 1988). Similarly, the ratio of crania to mandibles may also depend on transport distances (Speth and Clark, 2006). Mandibles – which contain some marrow and the tongue – are more likely to be removed from the skull at the kill-site with increasing foraging distances while the heavier cranium is left behind. If the proportion of skulls/crania is a function of foraging range then the lack of skull bones at BBC – and crania in particular – is indicative of increased transport distances for larger bovids during the SB. In our sample, 19.7% (n = 13) of high-survival elements in the large mammal assemblage are skull specimens. Furthermore, cranial specimens are also substantially less common than mandibular remains in the large mammal assemblage compared to the medium mammal collection (Figs. S3 and S4). The distributions of large mammal skeletal-parts are not significantly different through the SB layers, with the exception of layer CD. Very few large ungulate elements were recovered in this layer and it is possible this may relate to lower occupational intensity at that time (Reynard and Henshilwood, 2018) but this will be discussed later.

5.4. Palaeoenvironment

Research suggests that marine regressions from the early to the later SB coincided with a changing environment (Fisher et al., 2010; Hillestad-Nel and Henshilwood, 2016). Fisher et al. (2010) show that, from ~85 to 75 ka (likely during the upper and lower M2), the shoreline off BBC averages between 2 and 4 km away from the site. Their model indicates that, by c. 72 ka, (the M1 phase) the sea retreated to over 15 km which suggests a gradual marine regression through the SB. Yet our data show shellfish density dropping significantly from CF to CD, then increasing gradually to CB (Fig. 9). Shellfish data are sometimes used as a proxy for distances to shorelines with lower shellfish densities signifying regressed shorelines at coastal sites (Fisher et al., 2010; Marean, 2010; Reynard et al., 2016b). Optimal foraging models also propose that lower sea levels would result in a drop in shellfish density (Dusseldorp and Langejans, 2013). The discrepancy between Fisher et al.'s model and our shellfish data suggests one of two things. Either marine regression through the SB may not have been a gradual but rather a punctuated process and other geomorphological or environmental factors may have affected short-term sea level fluctuations during that time (Caputo, 2007), or the shellfish densities reflect the influence of additional factors such as taphonomic processes or site-use intensity (see Reynard and Henshilwood, 2018).

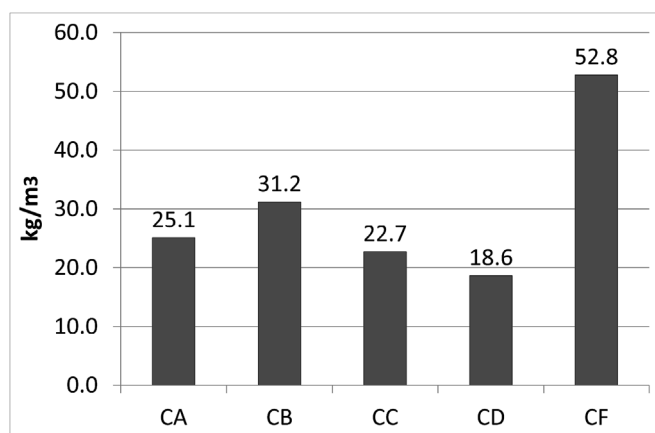If these shellfish data correspond to shoreline fluctuations then it

Fig. 9. Shellfish density per volume in the Still Bay at Blombos Cave. Data courtesy of Karen van Niekerk and from Henshilwood et al. (2001a).

may raise important paleoenvironment considerations. There is a significant inverse correlation between grazers and shellfish density during the SB ($r_s = -0.900$; $p = 0.0374$). If this reflects marine regression then it suggests that as sea levels retreated, the area surrounding BBC became more grass-dominated (Figs. 8band 9). This implies that cooler temperatures associated with glacial periods (and receding sea levels) are linked to an increase in grasslands during the SB. If shellfish density per layer does *not* correspond to shoreline regression then it may reflect changing mobility patterns during the SB. The correlation between grazers and shellfish density could be a function of foraging decisions where increased mobility is linked to less shellfishing and an increase in the exploitation of larger, more gregarious ungulates. Given that taphonomic processes, depositional rates, and environmental factors all affect shellfish density volumes (Jerardino, 1995, 2016; Ricciardi and Bourget, 1999), it is likely that the changing shellfish densities through the SB sequence are, at least in part, a result of environmental trends, site formation processes and occupational patterns.

The increase in larger ungulates from the early to later SB and the corresponding decrease in size 1 bovids and smaller mammals may reflect ungulate communities' reaction to the changing availability of the exposed SCP. Fluctuating shorelines would have affected ungulate populations and human access to large, grazing herds (Faith and Behrensmeyer, 2013). Changing vegetation would also result in shifts in species compositions and bovid communities. In the area surrounding BBC, the vegetation of the immediate coastal belt generally consists of typical lowland *fynbos* with grassier *renosterveld* further inland (Bergh et al., 2014). As sea levels fluctuate, and dependent on the soil type, this band of *fynbos* may track the coastline. The result could be that the area surrounding near-coastal MSA sites may switch from bushy to grassy and *vice versa* (Faith and Behrensmeyer, 2013). This may be what is documented at BBC. Taphonomic data also point to different foraging – and possibly mobility – strategies in the early SB (Reynard and Henshilwood, 2018). This could be related to the influence shellfish had on subsistence strategies and may speak to seasonality (Jew et al., 2013). For example, *Haliotis midae* and *Scutellastra argenvillei* occur more frequently at BBC than predicted by foraging models and their exploitation may be the result of seasonal visits to the site (Langejans et al., 2012).

Ungulate diversity and/or richness may be associated to primary environmental productivity and precipitation (Coe et al., 1976; Thackeray, 1980; Radloff, 2008; Faith, 2011, 2013b). There is generally more ungulate diversity as precipitation increases in low to medium-rainfall environments with precipitation up to ~750 ml/year, declining thereafter (Olff et al., 2002). Residual and diversity values in Table 7 suggest that precipitation may have been lower in the early SB (CF) and

relatively higher in the middle period (CC). What this could mean is that periods of marine regression coincided with more rainfall, which would suggest that glacial periods were wetter in the southern Cape. This supports research by Chase (2010) who has argued that the cooler MIS 4 is linked to more humid conditions in the southwestern Cape brought about by a shift in subtropical circulatory systems. However, the contrasting diversity values between CC and CF could also be linked to the availability of land on the SCP. Researchers have suggested that large grazing ungulate communities would likely migrate to the exposed areas of the SCP as sea levels retreat (Compton, 2011; Faith, 2011). A decline in ungulate richness could therefore be linked to a loss of suitable grassy habitats resulting from rising sea levels (Brink and Lee-Thorp, 1992; Marean, 2010; Faith, 2011).

5.5. Temporal trends during the Still Bay

The significant differences in surface modification frequencies between the early SB (CF) and later SB phases (CA-CB) probably relates to occupational patterns. Our research suggests that, although CC and CF were both probably high occupational phases, these periods reflected different occupational trends with one being a more intense, longer-term phase and the other showing evidence of more frequent, multiple occupations (Reynard and Henshilwood, 2018). Changes in occupational patterns during the SB may also be linked to mobility patterns. Residential mobility occurs when groups move between different residential camps whereas logistical mobility describes groups, based at a central home-base, who embark on logistical trips to outlying camps (Binford, 1980). Binford (1980) also suggests that dispersed solitary resources are best exploited through residential mobility, while gregarious, predictable resources (occurring in relatively low densities) may best be exploited using logistical mobility (see also Dusseldorp, 2014). We may therefore be seeing changes in mobility patterns from the early to the middle/later SB at BBC. This, in turn, may reflect shifting foraging strategies possibly based on changing availability of faunal resources.

The significantly different subsistence trends evident in CD may be when these changes occurred. CD yields the most fragmented faunal specimens (Fig. 4). This could indicate evidence of increase processing and imply that CD was a high occupation period. However, CD has significantly more small mammals and size 1 bovid remains than other layers, so smaller fragments could be a result of smaller fauna. Furthermore, both macro-taphonomic data (Reynard and Henshilwood, 2018), and micromorphological and geoarchaeological research (Haaland, 2017) show that CD was a low-intensity occupational phase with occupations becoming more intense in a later period (CC). This is interesting since, if CD was a low-occupational period, we would expect higher frequencies of tooth marked bone there, yet it has no tooth-marked long bone fragments. What may be at play here are depositional issues and changes in site formation processes. Discamps and Henshilwood (2015) note that lateral variability is relative extensive in the SB layers and, given the small number of ungulate long bones recovered in CD, tooth mark frequencies would vary. It is also possible that environmental conditions played a role and CD represents a period of resource stress resulting from environmental change. This is also the layer that yields the least shellfish densities which suggest either lower occupational intensity or increased marine regressions. Less intense occupations may have, in turn, encouraged changes in foraging and mobility patterns. Whatever the case, Layer CD represents a change between the early and later SB phase and more work needs to be done in exploring this period.

The data show significant differences in environmental conditions between the browse-dominated early (Layer CF) and the grassier middle/later SB (CA-CD) (Hillestad-Nel and Henshilwood, 2016). This may be related to the shift from MIS 5a to 4 since the SB at BBC seems to have occurred during this transition (Hillestad-Nel and Henshilwood, 2016 but see Chase, 2010 who argues that the SB encompassed MIS 4).

Prey selection would have been affected by this changing environment and may be linked to raw material procurement strategies. Silcrete sources are not found in the near vicinity of BBC (Villa et al., 2009). Yet silcrete is more common in the later than the earlier SB which suggests shifting mobility patterns as the environment changes (Henshilwood et al., 2001a; Reynard and Henshilwood, 2017, pp. 124). Indeed, foraging distances may have been affected by environmental conditions. There is a significant inverse correlation between the proportion of grazers present in the assemblage and the proportion of large mammal skulls ($r_s = -0.900$; $p = 0.0374$; Figs. 7band 8b) which also suggests that, as the terrain became more grass-dominated, the distances embarked on to hunt these large mammals increased. Increasing transport distances could be a product of the expanding SCP during periods of marine regression. The early SB probably coincided with a closer shoreline and occupations at BBC may have been influence by shoreline regressions. In fact, visits to BBC – especially during the early SB period – may have been seasonal and influenced by bovid calving. Thompson and Henshilwood (2014b) suggest that site abandonment at BBC may be associated with a marine regression and the resultant over-exploitation of key local resources such as tortoise. They also argue that increasing evidence for symbolically-mediated ornamentation and SB hunting-tools may be connected to resource stress linked in part to environmental change.

6. Conclusion

In this paper we explore subsistence patterns during the SB at BBC and examine the links between subsistence behaviour and the palaeoenvironment. We find significant differences in surface modification frequencies between the early SB (Layer CF) and middle and later SB phases (Layers CD-CA) which is probably associated with occupational patterns. Large mammals were processed differently to size 2 mammals which may be related to the availability of ungulate size classes near BBC during the SB but is possibly a reflection of specific subsistence strategies. Filleting was likely an important activity at BBC (cf. Thompson, 2008) and may be linked to expansive mobility patterns. Mortality data suggest that small mammals and size 1 bovids may have been accumulated along similar lines through remote capture, or by scavengers or both. Our faunal sample complements other studies (e.g., Henshilwood et al., 2001a; Thompson and Henshilwood, 2014b; Hillestad-Nel and Henshilwood, 2016) which suggests a change from bushy habitats in the early SB (Layer CF) to probably more grassy environments in the later SB (CC – CA). This is documented by a shift from smaller animals such as size 1 bovids and small mammals in CF to larger bovids in CA.

Our research also suggests that marine regressions from the early to later SB correspond to shifting vegetative zones. Ungulate richness and diversity is lowest in the early SB (CF) and highest in the middle period (CC) which may also reflect a change in environmental conditions. A shift to grass-dominated conditions may be linked to possible increases in transport distance for large mammals from the early to late SB. Prey selection is therefore probably associated with the prevailing environment. These shifts in human prey selection and, possibly, mobility patterns, however, may be more consistent with how faunal communities respond to changing environmental conditions than independent human behavioural choices.

Occupational intensity may have had a significant effect on subsistence behaviour during the SB. Mortality data, for example, suggest that seasonality may have influenced when BBC was occupied during the SB. Reynard and Henshilwood (2018) have suggested that Layer CC in the middle SB was an intensely or frequently occupied period and, in this study, CC also yields the richest ungulate sample. Another intensely or frequently occupied period at BBC – Layer CF in the early SB – corresponds to a significant *drop* in ungulate richness and diversity. This implies that site-use intensity at BBC may have been affected by environmental conditions in the SB.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2018.10.040.

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