

COASTAL RESOURCES AND NUTRITION AMONG MIDDLE STONE  
AGE HUNTER-GATHERERS IN THE SOUTHWESTERN CAPE

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KYRKAT001

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## PLAGIARISM DECLARATION

This work has not been previously submitted in whole, or in part, for the award of any degree. It is my own work. Each significant contribution to, and quotation in, this dissertation from the work or works of other people has been attributed, and has been cited and referenced.

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Katharine Kyriacou

**Signature**

**Date:** 11 November 2014

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## ABBREVIATIONS

AA	Arachidonic acid
ACO	Archaeology Contracts Office
ALA	$\alpha$ -linolenic acid
AMS	Accelerator Mass Spectrometry
BP	Before Present
BSB	Brandsebaai
DHA	Docosahexaenoic acid
DFM	Dunefield Midden
DRI's	Dietary Reference Intakes
EFA's	Essential fatty acids
EPA	Eicosapentaenoic acid
ESR	Electron Spin Resonance
HDP	Hoedjiespunt
KA	Thousand years ago
LA	Linoleic acid
LCP's	Long-chain polyunsaturated fatty acids
LP	Lipoprotein
LSA	Later Stone Age
MIS	Marine Isotope Stage
MNI	Minimum Number of Individuals
MSA	Middle Stone Age

MtDNA

Mitochondrial DNA

MYA

Million years ago

PUFA

Polyunsaturated fatty acid

RDA's

Recommended Dietary Allowances

TAG

Triacylglycerol

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## ABSTRACT

This thesis presents new information on the macronutrient, micronutrient and fatty acid content of marine and terrestrial resources available to Middle Stone Age hunter-gatherers in the southwestern Cape, and examines the role of coastal and terrestrial foods in the diets of early modern humans in the region. The collection, consumption and systematic discard of intertidal molluscs by prehistoric people is firmly attested by the presence of shellfish residues at archaeological sites dating to the Last Interglacial (120 000 years ago) at Klasies River Mouth, Blombos Cave, Hoedjiespunt and Sea Harvest, or earlier (164 000 years ago) at Pinnacle Point. The incorporation of marine foods into the diet is one of several forms of innovative behaviour characteristic of the Middle Stone Age. Classification of fossil hominin remains from key sites in southern Africa as anatomically modern further marks the Middle Stone Age as a crucial stage in the evolution of our species. The apparent link between coastal resources, innovative behaviour and anatomical modernity is tantalising, and in need of further exploration.

The nutrient content of one hundred and twenty three samples from a range of marine and terrestrial animals and plants known or presumed to have been eaten by Middle Stone Age hunter-gatherers in the southwestern Cape was measured using spectrophotometry and gas chromatography. When interpreted against existing knowledge on prehistoric subsistence strategies and ecology, these results provide a quantitative framework within which the relative utility of marine and terrestrial resources as a nutritional substrate for encephalising humans is evaluated. While terrestrial foods would have provided prehistoric people with sufficient energy and trace elements, sources of long-chain polyunsaturated fatty acids would have been limited. Marine foods, including intertidal mussels and limpets, are rich in the two most important omega-3 fatty acids found in the human brain, namely eicosapentaenoic and docosahexaenoic acid. The inclusion of coastal resources, particularly sessile, abundant, predictable and easily collected marine molluscs, in the diet would have been highly advantageous for groups of early modern humans in the vicinity of the Atlantic west coast. Pregnant and lactating women and very young children, who have some of the highest requirements for brain-specific nutrients, are likely to have benefitted the most.

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## CHAPTER ONE

### INTRODUCTION

The Middle Stone Age (MSA), a period in human prehistory dating from at least two hundred thousand to forty thousand years ago (ka) has long been recognised as one of the most interesting stages in the evolution of our genus. Evidence from the fossil record and genetic studies indicates that anatomically modern *Homo sapiens* emerged in Africa between 200 and 100ka. Archaeological remains consistent with the adoption of numerous innovative and novel behaviours appear shortly thereafter at several securely-dated sites on the subcontinent (Henshilwood and Dubreuil 2011; Shea 2011; Jacobs *et al.* 2008; Mellars 2006; Marean *et al.* 2004, 2007; Henshilwood and Marean 2003; Parkington 2003, 2010; McBrearty and Brooks 2000). The consumption of marine resources, notably intertidal shellfish, as well as marine mammals, some birds, and in rarer cases, fish, is one of these innovations, and represents a considerable broadening in the subsistence base of early modern humans. Shellfish residues and the remains of other marine taxa appear in archaeological contexts from 164ka, and are a component of coastal sites throughout the Middle Stone Age (Marean 2010; Marean and Jerardino 2010; Marean *et al.* 2004, 2007; Parkington 2010). While the absence of shellfish remains predating Marine Isotope Stage 6 does not mean that molluscs were never eaten during earlier times, the occurrence of well-defined middens dominated by food refuse from mussels and limpets, and to a lesser extent sea birds, fish and seals, attests to more regular consumption and systematic discard (Marean *et al.* 2007; Parkington 2003, 2010). The acquisition and consumption of terrestrial animals is also apparent. Faunal remains from a variety of small to very large terrestrial taxa represent flexible and dynamic strategies including scavenging, hunting and remote trapping or snaring.

Material cultural remains including standardised and stylised lithic artefacts, bone tools, perforated marine shells and incised ostrich eggshell fragments and ochre are among the strongest indicators or markers of modern behaviour (Henshilwood and Dubreuil 2011; Jacobs *et al.* 2008; Mellars 2006; Henshilwood and Marean 2003; McBrearty and Brooks 2000). Behavioural or cognitive modernity is an essential aspect of debates surrounding the development and emergence of fully modern human beings. As an intangible quality, it is

difficult to define and to measure and detect in the archaeological record. Modern behaviour is often conflated with humans' unique ability to communicate by means of seemingly arbitrary symbols, exemplified by the origin and use of language (Shea 2011; Henshilwood and Marean 2003; McBrearty and Brooks 2000). A burgeoning awareness of and capacity for symbolic communication seems implicit in fragments of utilised and engraved ochre, incised ostrich eggshell, and perforated and/or curated sea shells from Middle Stone Age archaeological contexts in the southwestern Cape (Texier 2010, 2013; Parkington 2010; Marean *et al.* 2007; Henshilwood and Marean 2003; Henshilwood *et al.* 2001 a and b; McBrearty and Brooks 2000). Furthermore, bifacial stone points and backed pieces from the Still Bay and Howieson's Poort industries, respectively, which appear to pre-empt the complex and composite stone tools characteristic of the Later Stone Age, could only be manufactured by following a deliberate and premeditated reduction process. Their presence in the artefactual assemblages from numerous Middle Stone Age sites throughout southern Africa appears to indicate increased technological proficiency.

In contrast to the vague concept of behavioural modernity, behavioural variability, as Shea (2011) defines it, is quantitative and more easily identified in the archaeological record. It is evident in the manufacture of a wide range of objects, some of which have symbolic connotations, using a variety of raw materials; the pursuit of increasingly flexible subsistence strategies; and the reorganisation of economic activities and domestic space. Archaeological remains associated with novel and innovative behaviours are particularly visible and appear to be clustered in sites and occupation layers or horizons dating to the Still Bay (77ka) and Howiesons Poort industries (59ka) industries, and are often discussed in relation to them (Henshilwood and Dubreuil 2011; Jacobs *et al.* 2008; Mellars 2006). These material expressions of complex behaviour are thought to reflect the increased intelligence of modern humans. A number of theories have been put forward to account for and explain the cognitive changes and shifts that occurred in humans between 280 and 40ka. Richard Klein has argued for a neural reorganization or mutation, possibly linked to the genetic predisposition for language, no earlier than 60-50ka. Other researchers (Henshilwood and Marean 2003; McBrearty and Brooks 2000) make the case for the gradual and cumulative adoption of modern behaviours and traits throughout the Middle Stone Age. From around 60ka, genetically and anatomically modern humans were beginning to

disperse from Africa into Eurasia (Henshilwood and Dubreuil 2011; Jacobs *et al.* 2008; Mellars 2006). A more detailed review of the archaeological literature on Middle Stone Age subsistence strategies and behaviour is presented in Chapter Two of this thesis.

Encephalisation, or the increase in brain relative to body size, is an energetically and metabolically costly process, and would have required high quality, energy-dense diets rich in macronutrients, micronutrients and essential fatty acids (Kuipers *et al.* 2010; Broadhurst *et al.* 2002; Aiello and Wheeler 1995). Not surprisingly, nutrition figures prominently in most scenarios for human evolution. Earlier models emphasised big-game hunting in savannah environments. Protein consumed in the form of muscle tissue from terrestrial ungulates was originally considered the most important nutrient and defining characteristic of high quality diets (Ben-Dor *et al.* 2011; Speth 2010; O'Connell *et al.* 2002; Aiello and Wheeler 1995). Current models increasingly acknowledge the importance of fat, and especially long-chain polyunsaturated fatty acids, for the development of the human brain (Kuipers *et al.* 2010; Speth 2010; Broadhurst *et al.* 2002; Cordain *et al.* 2000). As the muscle tissue of most wild terrestrial ungulates is very lean, fat-rich brain tissue, blubber and bone marrow would have been important lipid sources for prehistoric humans (Ben-Dor *et al.* 2011; Kuipers *et al.* 2010; Speth 2010; O'Connell *et al.* 2002; Broadhurst *et al.* 2002; Cordain *et al.* 2000).

A recent shift in emphasis sees the potential of marine and aquatic resources as a source of essential micronutrients, vitamins and omega 3 fatty acids collectively referred to as brain-specific nutrients (Crawford 2010; Cunnane 2010; Cunnane and Crawford 2014; Kuipers *et al.* 2010; Muskiet and Kuipers 2010). Researchers including Crawford, Stewart and Kuipers have proposed that the evolution of our genus in East Africa took place in a water-land ecosystem rich in protein, fat, micronutrients and polyunsaturated fatty acids from a combination of aquatic and terrestrial food resources (Kuipers *et al.* 2010; Muskiet and Kuipers 2010; Stewart 2010). Fossil hominins and associated faunal and lithic remains are frequently discovered on the margins of inland lakes. Lacustrine environments would have provided the earliest members of our genus with subsistence in the form of aquatic plants, shellfish and fish. Some of the earliest evidence for the exploitation of freshwater fish derives from Koobi Fora and Olduvai Gorge, where the remains of catfish have been dated to 1.5 mya (Braun *et al.* 2010; Stewart 2010).

Marine resources are ascribed an important role in the evolution of anatomically modern humans living along the coast of southern Africa. Marean (2010) and colleagues (2004, 2007) suggest that a diet composed of shellfish and corms from iridaceous plants would have sustained small populations of early *H. sapiens* living at Pinnacle Point, Mossel Bay, during Marine Isotope Stage (MIS) 6. This would have been a glacial cycle characterised by harsh environments and cool, dry conditions in which intertidal molluscs and the underground storage organs of plants would have been among the few available resources of protein and carbohydrates, respectively (Marean *et al.* 2007). Parkington (2003) notes the contrast between the highly productive marine ecosystems and relatively poor terrestrial ones in the vicinity of Middle Stone Age shell middens in the southwestern Cape. Upwelling of nutrient rich cold waters from the Benguela current sustains large populations of intertidal shellfish. Marine mammals and birds in the form of wash-ups would have presented an additional opportunity for subsistence. Faunal remains from Middle Stone Age shell middens located in the southwestern Cape suggest exploitation of a number of small terrestrial animals such as tortoises, dune molerats and hyraxes, as well as ostrich eggs, in conjunction with shellfish collecting. Dependence on large terrestrial bovids is not as strongly indicated in the assemblages from sites including Sea Harvest, Hoedjiespunt, Ysterfontein and Diepkloof Rock Shelter (Steele and Klein 2013; Avery *et al.* 2009; Klein *et al.* 2004; Parkington 2003). Underground storage organs from iridaceous plants indigenous to the Cape *fynbos* biome might have been a source of seasonally available energy in the form of carbohydrates (Parkington 2001, 2003, 2010).

There has been a growing realisation among researchers that simple and abundant marine resources rich in polyunsaturated fatty acids and essential micronutrients would have presented a distinct nutritional advantage for early modern humans living in coastal environments (Crawford 2010; Cunnane 2010; Erlandson 2010; Parkington 2010). Women and children in particular would have benefited from subsistence strategies geared towards the collection and consumption of sessile, abundant and predictable marine molluscs. Pregnant and lactating women have an especially high demand for omega-3 fatty acids, as well as essential micronutrients like iodine and iron. Children, too, have specific nutritional requirements related to growth and development. The last trimester of pregnancy, and first two years of life, are the most critical times for human neurological development. Pregnant

and lactating women and young children are therefore key players in scenarios for the emergence of anatomically modern, large-brained humans; meeting their requirements for brain-specific nutrition would have been crucial. Prehistoric women and children are unlikely to have been active participants in the tracking and hunting of large terrestrial prey, and may not have had early access to fat-rich portions of game such as organs, bone marrow and brains (Crawford 2010; Cunnane 2010; Erlandson 2010; Parkington 2003, 2010; Broadhurst *et al.* 2002; Cordain *et al.* 2000). Foraging for intertidal shellfish would have presented women and children with an ideal economic opportunity for obtaining the brain-specific nutrients they required.

Several models for prehistoric or “palaeo” diets have attempted to reconstruct the “dietary niche” (Kuipers *et al.* 2010; Muskiet and Kuipers 2010; Broadhurst *et al.* 2002; Cordain *et al.* 2000; Eaton *et al.* 1997) of our genus, often with a view to understanding and addressing modern health concerns. Given the research linking marine and aquatic foods rich in essential fatty acids and trace elements with the emergence of large-brained, anatomically modern humans, this thesis suggests that simple marine resources would have been one of the best and most accessible sources of brain-specific nutrients for Middle Stone Age hunter-gatherers living in the southwestern Cape. In this study, new information on the nutrient content of a range of marine and terrestrial resources known or presumed to have been eaten by the Middle Stone Age inhabitants of this region is presented. The littoral zone along the Atlantic west Cape and adjacent Cape Folded Mountain Belt represents a key area in the study of emerging modern humans in southern Africa. Some of the earliest shell middens (120ka) have been preserved in this region (Will *et al.* 2013; Parkington 2003; Volman 1978). One of these, Hoedjiespunt 1, was re-excavated in 2011; the expanded shellfish assemblage, which I analysed, is discussed in Chapter Four of this thesis. Furthermore, the extreme seasonality of the winter-rainfall Cape fynbos biome sets this region apart from other parts of the subcontinent inhabited by prehistoric people.

The edible tissues of more than four dozen indigenous plants, intertidal shellfish, marine mammals and birds, aquatic amphibians, and terrestrial vertebrates and insects available to prehistoric hunter-gatherers in the southwestern Cape were analysed, and their nutrient content quantified (Chapter Five). As a result, several generalisations can be made

regarding the distribution of essential nutrients in marine and terrestrial foodwebs. Protein and essential micronutrients are fairly abundant and evenly distributed in marine and terrestrial resources. However, marked differences in the fat and, especially, fatty acid content of different edible components of marine and, to a greater extent, terrestrial vertebrates, and of aquatic and terrestrial resources, would have had important implications for groups of early modern people.

Information on the nutrient content of marine and terrestrial foods is examined *vis a vis* patterns in the ethnographic and archaeological record to better understand the role of marine resources in the diets of Middle Stone Age hunter-gatherers in the southwestern Cape. Previous archaeological research explores the temporal and spatial relationships between archaeological sites, prehistoric people and potential food resources (Parkington 1972, 1976, 2001). In this thesis, the nutritional landscape serves as a theoretical construct and analytical device in terms of which the distribution of not just resources, but of essential nutrients within these resources, and the way in which prehistoric hunter-gatherers may have interacted with them, is investigated and explored. The results of quantitative nutrient analyses are integrated into the existing ecological, archaeological and ethnographic framework of this well-documented region.

Finally, some nutritional challenges and constraints inherent in particular subsistence and settlement strategies are identified and competing scenarios extrapolated for Middle Stone Age hunter-gatherers are evaluated (Chapter Six). While terrestrial resources contain sufficient energy, essential micronutrients and omega-6 fatty acids to have met short- and longer-term nutrient requirements, marine and aquatic foods are rich in long-chain omega-3 polyunsaturated fatty acids and other brain-specific nutrients, and would have supported groups of encephalising humans along the southwestern Cape coast. Mobility between the coast and surrounding hinterland would provide a means of integrating marine and terrestrial resources in prehistoric diets, and of overcoming the challenges and limitations associated with exclusively marine or terrestrial foods and environments.

## CHAPTER TWO

### THE SOUTH AFRICAN MIDDLE STONE AGE: A LITERATURE REVIEW

#### 2.1. INTRODUCTION

The South African Middle Stone Age, dating from 200 000 to 40 000 (ka), encompasses several critical developments in the emergence of our species. Some of the earliest fossil remains of anatomically modern humans have been recovered from Middle Stone Age sites in South and East Africa, including Klasies River Mouth, Die Kelders Cave 1, Pinnacle Point 13a and 13b, Border Cave, Equus Cave, Omo and Laetoli in Tanzania (Rightmire 1989; Klein 1989; Deacon 1989; Marean *et. al.* 2004). These fossil remains are highly fragmentary, consisting mostly of crania and teeth; were difficult to date prior to the use of optically stimulated thermoluminescence; and often not recovered *in situ* (Marean *et al.* 2004; Klein 1989; Rightmire 1989). Nevertheless, they display a mixture of features consistent with a transition from archaic to increasingly modern forms, and, at least at some sites, are strongly associated with the Middle Stone Age (Marean *et. al.* 2004; McBrearty and Brooks 2000; Rightmire 1989).

Genetic evidence further supports the emergence of anatomically modern *H. sapiens* in Africa between 200 and 100ka. The results of studies of mitochondrial DNA in modern populations are especially convincing. According to Stoneking and Cann (1989), all mitochondrial DNA in extant humans derives from a single ancestral population living in Africa 200ka. An African origin for *H. sapiens* is based on the identification of mitochondrial DNA (mtDNA) types, and comparison of genetic variability in extant populations. Of the 34 mtDNA types recognised, seven are exclusively African, while the remainder also contain African types. African populations are also the most diverse and are therefore of the greatest antiquity, as genetic mutations accrue over time. A date of 200ka for the emergence of *H. sapiens* is based on the rate of evolution in mtDNA and amount of sequence divergence (Stoneking and Cann 1989; Cann *et al.* 1987). Anatomically modern humans then migrated out of Africa and into Eurasia, where they replaced indigenous populations of Neanderthals, probably because of some behavioural advantage. They were dispersed throughout the globe by 35ka (Henshilwood and Marean 2003; McBrearty and Brooks 2000).

The evolution of modern behaviour, which may have been rooted in biological changes as genes promoting the capacity for such behaviour were selected for in early populations of *H. sapiens* (d'Errico and Henshilwood 2007), is much more difficult to define and detect. Much of what we call modern behaviour is premised on the capacity for symbolic communication (Henshilwood and Dubreuil 2011; Shea 2011). The ability to attach symbolic meanings to material objects makes symbolic behaviour visible to archaeologists. Among the artefacts recognised as stores of cultural meaning are personal ornaments such as beads and stylised stone and bone tools (d'Errico and Henshilwood 2007; Henshilwood and Marean 2003). Some of the earliest examples of these objects were recovered from the securely dated Middle Stone Age levels of Blombos Cave on the southern Cape coast. Excavations at this site yielded bone artefacts, deliberately perforated *N. kraussianus* shells and two fragments of ochre engraved with slightly different geometric designs (Henshilwood *et al.* 2009; d'Errico and Henshilwood 2007; d'Errico *et al.* 2005). Standardised, stylised stone artefacts representing two precocious lithic industries known as the Still Bay and Howiesons Poort, have been documented at numerous Middle Stone Age sites throughout South Africa (Henshilwood and Dubreuil 2011; Jacobs and Roberts 2008; McBrearty and Brooks 2000). Certain changes in foraging and subsistence strategies, including the exploitation of new resources from different environments, improved hunting ability and increased foraging ranges, are also identified as indicators of modern behaviour. Faunal remains from numerous Middle Stone Age sites attest to this (Henshilwood and Marean 2003; McBrearty and Brooks 2000).

In the light of this evidence, most archaeologists reject the dichotomy between anatomical and behavioural modernity, and argue that they evolved together during the African Middle Stone Age. Prior to the 1990s, it was generally accepted that modern behaviour is a relatively recent phenomenon which emerged suddenly and simultaneously in Europe around 40ka. According to this point of view, the African Middle Stone Age and European Middle Palaeolithic alike are characterised by relatively simple and static lithic technologies and subsistence strategies, and absence of bone and shell artefacts, personal ornaments and art. A small but not insignificant minority of researchers continue to adhere to this model, arguing that early anatomically modern humans living in southern Africa during the Middle

Stone Age were not behaviourally or culturally modern. The few examples of artefacts indicative of symbolic behaviour recovered from Middle Stone Age sites such as Blombos are dismissed as being intrusive from younger Later Stone Age (LSA) layers (Klein 1989).

The majority of researchers assert that *H. sapiens* living in southern Africa were capable of fully symbolic behaviour by at least 75ka. They suggest that certain modern behaviours were adopted on a trial basis. Innovations which conferred a demonstrable advantage, for example, the exploitation of abundant and easily collected food resources, or manufacture of more effective stone tools, then became more permanent. This explanation is more parsimonious than one which separates biological from cultural evolution, and accounts for the piece-meal appearance of material cultural remains associated with modern behaviour in the archaeological record (Henshilwood and Dubreuil 2011; Henshilwood and Marean 2003; McBrearty and Brooks 2000). Many of the artefacts regarded as evidence for symbolic behaviour are particularly vulnerable to diagenesis, and may have been deleted from the archaeological record. Alternatively, people may simply have elected not use organic materials such as bone as raw materials for tools, even though they were familiar with its potential (Henshilwood and Marean 2003; Deacon 1989). Furthermore, the significantly greater time-span represented by the Middle Stone Age deposits and compaction of sediments in archaeological sites means that there is much less time-resolution for this period than for the Later Stone Age (Henshilwood and Marean 2003; McBrearty and Brooks 2000). The proliferation of complex technologies during the Later Stone Age may be a product of intensification rather than an indication of superior cognition or symbolic behaviour. Growing populations coupled with environmental deterioration may have prompted people to increase their productivity by manufacturing specialized toolkits or incorporating different food resources into their diets (Henshilwood and Marean 2003; McBrearty and Brooks 2000).

## 2.2 COASTAL FORAGING: INNOVATIONS AND LIMITATIONS

Archaeologists rely on material traces left behind by prehistoric people as a means of reconstructing their lifeways. The exploitation of coastal resources is firmly attested by the presence of shellfish and other marine food residues at several securely dated Middle Stone Age sites on the subcontinent. The absence of evidence for a particular kind of behaviour is not necessarily evidence of its absence. Thus, the lack of marine faunal remains predating the Middle Stone Age does not mean that coastal foods were completely ignored by the earlier inhabitants of the southwestern Cape. Marine resources may have been occasionally consumed and haphazardly discarded along the shoreline in such a way that no material traces were left (Parkington 2003). Evidence for coastal foraging predating the Last Interglacial would also have been vulnerable to erosion and wave action (Marean *et al.* 2004, 2007; Klein *et al.* 2004), and may have been deleted from the archaeological record. The accumulation of shell midden deposits in the Middle Stone Age is consistent with a shift towards more regular and systematic exploitation of marine resources, and may reflect a reorganisation of settlement patterns to focus on the shoreline (Parkington 2003)

The earliest evidence to date for the exploitation of marine resources derives from site 13b at Pinnacle Point, Mossel Bay. The archaeological deposits in this site were preserved during the Last Interglacial as the cave is located 15m above current sea level. Excavations conducted by Curtis Marean and colleagues over the last several years yielded shellfish remains dating to 164ka (Marean *et al.* 2004, 2007). The presence of whale barnacles indicates that dead whales were scavenged for their meat and fat. The faunal assemblage is atypical of other Middle Stone Age sites in the region, in that the remains of small mammals and tortoises, which are usually abundant, are not as well represented. A lithic assemblage dominated by relatively small flakes, blades and points manufactured on fine-grained raw materials and diagnostic of the Mossel Bay industry, and numerous fragments of red ochre, were also recovered from this site. Two hominin fossils, including a cranial fragment and incisor “intermediate between mid Pleistocene hominins and modern humans” were found *ex situ*. The degree of fossilisation evident on the bones and lack of Later Stone Age deposits at the site indicate that they are part of the Middle Stone Age deposits (Marean *et.*

*al.* 2004, 2007). Systematic excavation and optically stimulated luminescence dating of these sites is still ongoing.

Prior to the fairly recent excavations at Pinnacle Point, Klasies River Mouth, located on the Tsitsikama coast in the southern Cape, was the site with the earliest evidence for marine foraging. Extensive fieldwork carried out at the Klasies River Main Site in 1967 and 1968 yielded large samples of marine and terrestrial fauna, Middle Stone Age artefacts and fragmentary human remains (Deacon 2008; Wurz 2008). Further excavations carried out in 1984 were aimed at refining the stratigraphy at dating of the deposits, which were comprised of three distinct members or units which accumulated between 115 and 53ka, and obtaining an additional, unselected sample of archaeological material. Shifts in lithic technology, from the production of regular quartzite blades and elongated points, to Levallois flakes, to small backed segments and crescents characteristic of the Howiesons Poort industry, are documented (Deacon 2008; Wurz 2008). Fluctuations in the intensity of shellfish exploitation are also indicated, and are attributed to changing sea levels which would have placed the shore at too great a distance from the site for efficient marine foraging during the Howiesons Poort period. Human teeth recovered from the oldest member varied in respect to size but had crown dimensions similar to those observed in living African populations (Rightmire and Deacon 2001).

Shellfish residues dating to the Last Interglacial (130ka) were also found at Blombos Cave, located near Still Bay on the southern Cape coast. This site contains Middle and Later Stone Age deposits separated from each other by a layer of sterile aeolian sand. The earliest of the Middle Stone Age levels, dated to 125ka by means of optically stimulated luminescence and thermoluminescence, is dominated by the remains of marine molluscs, large fish, dolphins and seals. These would have been made accessible to the inhabitants of the site by the high sea levels characteristic of the Last Interglacial (d'Errico and Henshilwood 2007; Lombard 2007; Henshilwood *et al.* 2001a and b). More than twenty pieces of shaped, modified or worked bone were recovered from a stratigraphic layer (M2) dating to 82ka. The alkalinity of the deposit matrix at Blombos Cave facilitated the preservation of these artefacts (d'Errico and Henshilwood 2007; Henshilwood *et al.* 2001a and b). The youngest of the MSA layers (M1), dating to 75-77ka, yielded large numbers of stone artefacts manufactured on

non-local, fine-grained silcrete. Many of these were bifacial points typical of the Still Bay industry. Large quantities of ochre, including two deliberately engraved pieces, were also recovered from this stratigraphic layer, as well as 41 perforated *N. kraussianus* shells and an engraved bone fragment. The cultural material recovered from M1 and M2 provides some of the most convincing evidence in the argument for the development of behavioural modernity in southern Africa during the Middle Stone Age (d'Errico and Henshilwood 2007; Lombard 2007; Henshilwood *et. al.* 2001a and b). Nine human teeth were also recovered from the Middle Stone Age deposits at Blombos Cave, but were too worn to be classified as anatomically modern (Henshilwood *et. al.* 2001b).

Die Kelders Cave 1, located near Walker Bay on the southwestern Cape coast, is another site containing archaeological, faunal and human remains from separate Middle and Later Stone Age occupations. The deposits consist of alternating layers of occupational debris and wind-blown aeolian sand. The site was first excavated by Schweitzer between 1969 and 1973. He focused on the Later Stone Age material recovered from the youngest of seventeen "lithological layers" discerned within the cave. The remainder of the deposits, which accumulated during the Middle Stone Age, were explored on a limited scale during Schweitzer's initial excavation (Marean *et. al.* 2000; Feathers and Bush 2000). In the course of three field seasons in 1992, 1993 and 1995, Avery, Grine, Klein and Marean conducted renewed excavations to the east and west of Schweitzer's trench in order to enlarge the sample of material from the Middle Stone Age, and further elucidate the stratigraphy and dating of the Middle Stone Age deposits (Marean *et. al.* 2000).

The renewed excavations at Die Kelders yielded 27 human fossils, mostly derived from subadult individuals. Electron Spin Resonance dates of 70ka were obtained for ten enamel samples from six different teeth recovered from the deposit (Grine 2000; Schwartz and Rink 2000). Luminescence dates from five sand samples place the Middle Stone Age occupation of the site to between 60 and 70ka during the early part of the Last Glaciation (Feathers and Bush 2000). The faunal assemblage from Die Kelders is dominated by the remains of mammals and tortoises. While the shellfish from the Middle Stone Age layers of the site were too poorly preserved to be properly analysed, their presence within the deposits

confirms that they were being collected and eaten by the site's inhabitants by at least 60ka (Klein 2000).

Shellfish residues and other marine faunal remains dating to the MSA are not restricted to the southern Cape, and have been recovered at several sites on the Atlantic west coast. Two open air middens located near Saldanha Bay yielded some of the earliest evidence for the systematic exploitation of marine fauna in the region. These sites, namely Sea Harvest and Hoedjiespunt I, were first discovered by Avery, Klein and Tankard in 1973. Faunal remains and artefacts were collected from the surface of the deposits during several follow-up visits by Avery, Klein and Volman (Volman 1978). The site of Hoedjiespunt 1, which consists of a number of shellfish and artefact bearing horizons capped by calcrete, is one of several localities on the Hoedjiespunt Peninsula containing archaeological and palaeontological remains. Excavations conducted at the site by Parkington and colleagues in the 1990s produced a shellfish assemblage dominated by limpets, with some contribution from black mussels. The remains of other marine and terrestrial fauna, notably penguins, seals and tortoises, are also represented. Large quantities of ostrich eggshell fragments were also found. Relatively informal lithic artefacts manufactured on locally occurring quartz, as well as some pieces of ochre, were recovered (Volman 1978; Berger and Parkington 1995). Human molars derived from undisturbed shelly sand at the bottom of the archaeological deposit fall within the range of variation expected in modern *H. sapiens* (Berger and Parkington 1995). Uranium series dates place the occupation of the site to before 74ka, most likely between 110-120ka (Volman 1978; Berger and Parkington 1995).

The site of Sea Harvest, located 1.3km away from Hoedjiespunt 1, yielded a sample of intertidal shellfish similar in composition to those recovered from the latter site and much younger middens along the Atlantic coast. These represent the remains of marine molluscs collected from the nearby shore and consumed and discarded at the site. The shellfish and other faunal remains are thought to have accumulated as a result of short, repeated episodes of occupation (Volman 1978). Lithic artefacts from Sea Harvest were undoubtedly MSA in character, were manufactured on fine-grained raw materials and included flakes, blades and utilised or retouched pieces (Volman 1978). Unusually large quantities of ostrich eggshell were also recovered from Sea Harvest. Ostrich eggshell fragments from two separate

samples yielded radiocarbon dates older than 40ka. It is likely that the occupation of Sea Harvest dates to the terminal part of the Last Interglacial during Oxygen Isotope Stage 4 (Volman 1978).

Archaeological evidence for marine foraging along the Atlantic coast during the Middle Stone Age has been augmented by the recovery of a large sample of material from the site of Ysterfontein. This rock shelter, located adjacent to the harbour in the town of Ysterfontein, was partially exposed by contractors during the 1980s. Parkington and colleagues collected material from the exposed surface in 1998 and 1999. Systematic excavations began in 2002 under the direction of the Archaeology Contracts Office at the University of Cape Town, and concluded in 2008. The chronology and dating of the deposits is still unresolved (Avery *et al.* 2008). An Accelerator Mass Spectrometry radiocarbon date places the top of the sequence to before 46ka. The deposit probably postdates 115ka, as storm surges during the preceding period would have flushed out any older material. Artefact typology suggests a date older than 70ka. It is most likely that the archaeological deposits within the shelter accumulated during MIS5c, between 70-110ka (Avery *et al.* 2008; Klein *et al.* 2004; Halkett *et al.* 2003).

Excavations at Ysterfontein yielded a large collection of lithic artefacts comprised primarily of unretouched Middle Stone Age flakes manufactured on fine-grained silcrete, and the debitage associated with their production. Scraper retouch and denticulate flakes are not uncommon. The precocious Still Bay and Howiesons Poort industries found at southern Cape coastal sites are completely absent. This may indicate that the Middle Stone Age deposits at Ysterfontein predate these industries. Still Bay points and backed microliths associated with the Howiesons Poort are also not represented at Hoedjiespunt 1 and Sea Harvest. The non-lithic artefactual assemblage from Ysterfontein further resembles those from the aforementioned two sites in that worked bone implements are lacking. While the sample from Ysterfontein is much larger, the faunal remains from all three sites are very similar. Intertidal mussels and limpets are particularly well represented, as are the remains of certain species of mammals, birds, tortoises and snakes. The large quantity of ostrich eggshell fragments recovered from this site is also remarkable (Avery *et al.* 2008; Klein *et al.* 2004; Halkett *et al.* 2003).

The analysis of food residues from the aforementioned sites has enabled archaeologists to reconstruct the subsistence strategies of some of the earliest coastal foragers in human prehistory. The remains of marine molluscs are often the most abundant component of the archaeological deposits at these sites, suggesting that they were of considerable dietary importance (Steele and Klein 2008). Marean and Parkington, among others, propose that marine resources played a significant role in the emergence of anatomical and behavioural modernity during the African Middle Stone Age. Parkington (2003) emphasises the difference between the highly productive coastal ecosystem and the relatively poor terrestrial one in the southwestern Cape. Upwelling of the cold waters of the Benguela current ensures an abundant supply of nutrients for primary production by marine organisms, increasing productivity at all levels of the coastal ecosystem. The wealth of marine resources and paucity of terrestrial ones favoured a shift toward coastal foraging in the region. The collection and consumption of marine resources, which contain essential fatty acids and other brain-specific nutrients, went hand in hand with the development of modern anatomy, behaviour and cognition (Parkington 2003, 2010). Marean *et al.* (2007) propose that shellfish were incorporated into the diets of MSA hunter-gatherers living at Pinnacle Point in response to the harsh climatic conditions associated with MIS6. They go so far as to assert that without these predictable, nutritious and accessible resources, human populations are unlikely to have survived. Marean and his colleagues regard the inclusion of shellfish into the diet of MSA hunter-gatherers as one of the last of such additions prior to the domestication of animals and plants.

Several broad patterns in MSA peoples' marine foraging strategies have been discerned and interpreted by archaeologists. The shellfish assemblages from Hoedjiespunt 1, Sea Harvest and Ysterfontein are dominated by black mussels (*Choromytilus meridionalis*) and three limpet species, *Cymbula granatina*, *Scutellastra argenvillei* and *Scutellastra granularis*. Granite limpets (*C. granatina*) are more abundant than granular (*S. granularis*) and Argenville's (*S. argenvillei*) limpets in Middle Stone Age shellfish assemblages. *C. granatina* are large, and occur in larger numbers in the mid-intertidal zone, where they are visible and accessible at all stages of the tidal cycle. *S. argenvillei*, which can grow even larger than *C. granatina*, inhabits the lower-intertidal, which is only visible and accessible during spring low tides. *S.*

*granularis* are found in the upper intertidal and are thus always visible and accessible to human collectors, but are considerably smaller than the other two limpets. Black mussels live in dense colonies in the intertidal and subtidal. The preference for large, accessible and abundant shellfish taxa is a recurring attribute of Middle Stone Age faunal assemblages (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004; Volman 1978). Winkles and whelks inhabiting the upper reaches of the shore, and west coast rock lobsters (*Jassus lallandii*) are a common feature at Later Stone Age sites but are absent or rare in Middle Stone Age ones. This may reflect differences in prey choice with regard to the former, and an inability to forage in the subtidal or to recognize crustaceans as potential food items in the case of the latter. Limpets recovered from Middle Stone Age sites are also significantly larger than those from Later Stone Age contexts, as well as modern, unexploited mollusc populations (Avery *et al.* 2008; Steele and Klein 2008). Large, mature individuals are preferentially targeted by modern hunter-gatherers (Meehan 1982), and would have been the first choice of prehistoric collectors. Continued harvesting of adult molluscs by human foragers would eventually drive the average size of shellfish populations down.

Differences in the relative abundance of particular species as well as differences in the mean size of limpets in Middle and Later Stone Age assemblages is regarded as indicative of selective as opposed to intensive exploitation of a limited range of coastal resources by small populations of hunter-gatherers (Avery *et al.* 2008; Steele and Klein 2008). Large mean sizes of tortoise humeri recovered from Middle Stone Age sites mirror the trend observed in limpets, and have been interpreted as additional evidence for low population densities during the Middle Stone Age. Furthermore, no fish remains have been recovered from sites predating 40ka on the Atlantic coast, and the remains of avian fauna are restricted to a few easily captured species. This has led some researchers to conclude that fishing and fowling, which were regularly practised by Later Stone Age hunter-gatherers in the region, were beyond the scope of their Middle Stone Age predecessors.

Evidence from Middle Stone Age sites on the southern Cape coast supports some of the patterns identified in the western Cape, and seems to contradict others. Brown mussels (*Perna perna*), the large alikreukel *Turbo sarmaticus* and several limpet species are the main components of the shellfish assemblages at Pinnacle Point, Blombos Cave and Klasies River

Mouth (Marean *et al.* 2007; Henshilwood 2001 a and b; Thackeray 1988). These are for the most part large, easily accessible and abundant. *T. sarmaticus* opercula are significantly larger in the Middle Stone Age levels of Blombos Cave than in the Later Stone Age ones. This may be the result of environmental or cultural factors, or a combination of both ( Sealy and Galimberti 2011; Henshilwood *et al.* 2001 a and b). Tortoise humeri from the Middle Stone Age deposits at Blombos are also larger than those from the Later Stone Age levels.

Mussels, limpets and tortoises from the Middle Stone Age levels of Klasies River Mouth, and tortoises from the comparable levels of Die Kelders, are larger than specimens from the Later Stone Age (Henshilwood 2001 a and b; Klein and Cruz-Uribe 2000; Thackeray 1988). Seal bones have been recovered from the Middle and Later Stone Age levels at these sites; cut-marks indicate processing by humans (Binford 1984; Klein and Cruz-Uribe 1996). The minimum number and age at death of seals in archaeological deposits are based on counts and measurements of the distal humerus (Klein and Cruz-Uribe 1996). Occupation layers dating to the Later Stone Age contain large quantities of seals aged between nine and eleven months; those dating to the Middle Stone Age contain the remains of either very young, or very old animals characteristic of hyena accumulations (Klein and Cruz-Uribe 1996). Klein and Cruz – Uribe (1996, 2000) attribute the predominance of yearling seals in Later Stone Age deposits to the deliberate scheduling of coastal visits to coincide with the annual weaning of nine-to-eleven-month-old pups, during which they are forced out of off-shore rookeries into open water. Many of them drown and wash up onto nearby beaches, where they would be accessible to prehistoric hunter-gatherers. Middle Stone Age people appear to have overlooked this regularly recurring seasonal phenomenon. Their subsistence and mobility patterns were less focused and more opportunistic (Henshilwood and Marean 2003; Klein and Cruz-Uribe 1996, 2000).

While no fish remains have been recovered from Middle Stone Age sites along the southwestern Cape coast, two southern Cape coastal sites have yielded the remains of fish. At least ten species of fish have been identified in stratigraphic layers dating to the Middle Stone Age at Blombos Cave. Two of these, namely *C. nasutus* and *A. feliceps*, are large deep-sea fish which were probably caught by means of trapping or spearing, not by scavenging for wash-ups on the beach (Henshilwood *et al.* 2001 a and b; McBrearty and Brooks 2000).

This contradicts assertions that Middle Stone Age people lacked the technology or skill to actively acquire deep sea fish. Remains representing 47 families of fish, mostly small estuarine and intertidal-species, were recovered during the 1984-1988 excavations at Klasies River Mouth. The Middle Stone Age inhabitants of the site are one of the possible agents of accumulation (von den Driesch 2004).

Differences in the marine faunal remains from Middle and Later Stone Age assemblages can be interpreted in different ways. Some researchers regard Middle Stone Age people's preference for certain shellfish species over equally and even more accessible ones as evidence for reduced foraging ability. There is, however, an alternative explanation. The exploitation of marginal marine resources by Later Stone Age hunter-gatherers is more likely to have been a matter of necessity than choice. These small molluscs offer relatively little caloric return for the energy expended in collecting them. While Middle Stone Age people were able to ignore them in favour of larger, high-ranking marine resources, expansion in population sizes during the Later Stone Age forced people to broaden their subsistence base to include these items. Economic intensification and long-term population growth among prehistoric hunter-gatherers also accounts for differences in the mean size of molluscs and tortoises (Henshilwood and Marean 2003; McBrearty and Brooks 2000). Furthermore, the absence of fish remains from Middle Stone Age sites is far from universal, and yearling seals would only wash up onto beaches in the vicinity of off-shore rookeries.

### 2.3 HUNTING AND PROJECTILE TECHNOLOGY

Faunal assemblages from Middle Stone Age sites contain a wide range of terrestrial species, including some which are currently extinct. Middle Stone Age sites on the southwestern Cape coast are characterised by an abundance of small mammals and reptiles (Avery *et al.* 2008; Klein *et al.* 2004). Sites in the southern Cape contain substantial remains from large browsing or grazing ungulates. The analysis of these remains has allowed archaeologists to reconstruct Middle Stone Age hunters' interactions with terrestrial game. A number of quantitative and qualitative differences have been identified in terrestrial faunal remains from Middle and Later Stone Age sites. Interpretations of these patterns are as contested as those pertaining to coastal foraging.

Some terrestrial species are better represented in Middle Stone Age faunal assemblages than others. The Minimum Number of Individuals (MNI) of each species present in an archaeological assemblage may be calculated in a number of ways, but is usually based on counts of teeth or particular skeletal elements. Eland (*Taurotragus oryx*) outnumber Cape buffalo (*Syncerus caffer*) at the southern Cape coastal sites of Klasies River Mouth and Die Kelders. Although large, the former species is relatively docile and is known to flee from predators, while the latter is aggressive and likely to mob predators when attacked. Cape buffalo would have been more visible and numerous on the landscape at the time. The abundance of eland relative to buffalo remains at Klasies River Mouth and Die Kelders suggests a preference by Middle Stone Age hunters for docile prey amenable to driving and/or herding, and corresponding reluctance or inability to engage more dangerous animals (Klein and Cruz-Urbe 1996, 2000). This pattern is reversed in faunal assemblages from the Later Stone Age deposits at Nelson Bay Cave and Die Kelders, where the remains of buffalo and other species significantly outnumber those of eland. These differences cannot be attributed to environmental or ecological changes. Klein and Cruz-Urbe (1996,2000) suggest that improvements in hunting technology, particularly the development of the bow and arrow, would have enabled Later Stone Age people to engage and bring down aggressive prey species from a safe distance (Klein and Cruz-Urbe 1996,2000).

Markedly different mortality profiles for eland and buffalo from Middle Stone Age sites serves as additional proof of Middle Stone Age hunters' relative lack of prowess. Age at death for archaeological specimens is established using measurements of the crown height of frequently preserved teeth (Klein and Cruz-Urbe 1996,2000). The remains of very old, and especially very young buffalo outnumber those of prime-aged adults in the Middle Stone Age assemblages from Klasies River Mouth and Die Kelders. This attritional mortality profile is consistent with hunting strategies based on stalking and the picking off weak or vulnerable members of a herd (Milo 1998; Klein and Cruz-Urbe 1996, 2000). The remains of eland are dominated by prime-age adults. Catastrophic mortality profiles, in which individuals of all age classes are present in proportion to their live abundance, are consistent with the driving of herds over cliffs or into natural traps (Milo 1998, Klein and Cruz-Urbe 1996, 2000).

Several researchers have challenged earlier interpretations of patterns in Middle Stone Age faunal assemblages, and assertions that Middle Stone Age people were ineffective hunters. Milo's (1998) microscopic analysis of bovid remains from Klasies River Mouth, and comparison of butchery marks on bones processed by prehistoric and modern hunter-gatherers, refutes an earlier model by Binford (1984). Binford (1984) concluded that large ungulates at this site, which are most frequently represented by crania and lower limb bones, low-ranking portions of a carcass with relatively little meat, were obtained by means of scavenging rather than active hunting. Extensive breakage on metapodials and phalanges and crude hack marks visible to the naked eye are consistent with the extraction of bone marrow and butchery of old carcasses (Binford 1984). Smaller bovids are represented by a wider range of skeletal elements, and have butchery marks resembling those made by modern Nanamuit Eskimos, indicating the processing of meat from fresh kills (Binford 1984). Milo (1998) did not observe significant traces of carnivore damage on the bones of large ungulates, suggesting that humans were the main agents of accumulation. Butchery marks evident on large and small bovids and different skeletal elements indicate that Middle Stone Age hunters enjoyed early and fairly unrestricted access to fairly complete bovids of all age classes. There are also indications that specific processing techniques were applied to particular size classes by groups of hunters in such a way as to extract most of the available nutrition (Milo 1998).

Marean *et al.* (2000) carried out a meticulous and in-depth examination and analysis of the faunal remains from Middle Stone Age layers of Die Kelders. All of the bones, including refitted shaft fragments, were identified to the most precise taxonomic level and skeletal element. The relative abundance of species was determined by means of four different indexes rather than just MNI's, and all surface modifications were examined microscopically and recorded. Eland of all age groups are the best represented species in the assemblage. Percussion- and cut-marks associated with butchery were observed on many of the long-bone shafts; carnivore tooth marks were less common. Marean *et al.* (2000) assert that Middle Stone Age people at this site were engaged in the selective hunting of large, high-ranking prey, and that they enjoyed early access to the meaty, marrow-rich portions of the carcass. Based on the location of carnivore tooth marks on the bones, they suggest that

less desirable portions may have been scavenged by carnivores following disposal by humans (Marean *et al.* 2000).

Faith (2007) conducted statistical analyses of ungulate remains from 51 Middle and 98 Later Stone Age sites in a variety of environmental settings in order to re-evaluate Klein and Cruz-Uribe's (1996, 2000) hypotheses regarding Middle Stone Age people's hunting proficiency. The large assemblage from Klasies River Mouth, which forms the basis of Binford (1984) and Klein and Cruz-Uribe's (1996,2000) interpretations, is excluded. Sampling strategies used during Singer and Wymer's (1982) excavations at this site were biased towards the recovery of large bovids, skewing patterns in the faunal remains. The Middle Stone Age assemblages examined by Faith (2007) were shown to contain more ungulate taxa than the Later Stone Age ones. Eland, buffalo and wild pigs (*Sus scrofa*) were found to be equally abundant in Middle and Later Stone Age assemblages; large ungulates are better represented at Middle Stone Age sites. These findings suggest that Middle Stone Age hunters encountered large, high-ranking prey more frequently and enjoyed greater diet breadth than their Later Stone Age counterparts (Faith 2007).

Several lines of evidence suggest that Middle Stone Age segments and points attached to hafts with adhesives comprised of ochre and plant gum may have been used as hunting weapons (Wadley 2010). Microscopic traces of adhesive substances and animal residues have been identified on backed segments from Sibudu and Rose Cottage Cave. The distribution of adhesives on the backed or blunted portion of these segments, and of animal residues on the unmodified cutting edge, is consistent with the practice of hafting (Lombard 2011; Wadley 2010). Diagnostic impact fractures on backed segments from the Howiesons Poort layers at Sibudu Cave and Umhlatuzana are consistent with their being used as inserts for hand-thrown spears. A similar function has been inferred for Howiesons Poort segments from Klasies River Mouth (Lombard 2011; Wadley 2008). Experimental replicas of segments recovered from Klasies River Mouth, Sibudu and Rose Cottage Cave and used as hunting implements demonstrated that artefacts would have made effective spear tips capable of penetrating animal hides in 85% of cases (Lombard and Phillipson 2010; Lombard and Pargeter 2008).

Impact fractures associated with hunting have been identified on a significant proportion (17% and 21%) of the stone artefacts from two of the three Middle Stone Age occupations at Blombos Cave. This suggests that some of the convergent flakes being produced by Middle Stone Age people were used to tip composite hunting weapons. These would have enabled them to successfully hunt small and large bovids and Cape fur seals (*Arctocephalus pusillus*). Similar impact fractures were observed on only one stone flake from the remaining occupation Layer (M2). This layer yielded the majority of bone artefacts from the site, as well as large quantities of small bovid remains (d'Errico and Henshilwood 2007, Lombard 2007). This may reflect a shift from stone insets to bone points in the manufacture of hunting weapons, and from large to smaller game animals (Lombard 2007).

The presence of eighteen stone inclusions in bovid remains from Klasies River Mouth serves as further, compelling evidence that Middle Stone Age hunters were proficient in the manufacture and use of projectile technology (Milo 1998). A stone tip embedded in one of the cervical vertebra of an extinct giant buffalo is a particularly striking example. All of the other stone tips were also found in portions of the skeleton more likely associated with hunting than butchery. The driving of game into pit traps lined with stone points may have been one of a number of strategies employed by Middle Stone Age hunters (Milo 1998). Other possible methods include trapping and snaring, which may have been employed by Middle Stone Age people at Sibudu to capture small animals such as blue duiker (*Philantomba monticola*). This small bovid is the most abundant species in the faunal assemblage from Sibudu, further indicating that the preference for large ungulates inferred for all Middle Stone Age hunters is far from ubiquitous (Lombard 2011; Wadley 2008).

#### 2.4 MIDDLE STONE AGE MATERIAL CULTURE AND COMPLEX COGNITION

Goodwin and van Riet Lowe (1929) define Middle Stone Age lithic technology, which is characterised by the production of convergent flakes struck from prepared cores with faceted striking platforms, as intermediate between the Early and Later Stone Ages. It is generally described as highly conservative, with little evidence for innovation or change over a long period of time (Thackeray 1989). Two distinctive stone artefact industries stand as exceptions, and are considered by many lithic researchers as precocious or innovative.

The Still Bay and Howiesons Poort industries, respectively, are characterised by the production of leaf-shaped bifacial points and backed segments. These industries, which are evocative of later developments in lithic technology, were originally regarded as innovations brought into the region by immigrants. The Howiesons Poort was erroneously labelled as transitional between the Middle and Later Stone Age (Jacobs and Roberts 2008; Goodwin and van Riet Lowe 1929). Singer and Wymer's (1982) excavations at the southern Cape coastal site of Klasies River Mouth clarified the position of the Howiesons Poort industry within the Middle Stone Age sequence (Lombard and Wurz 2007; Soriano *et al.* 2007; Thackeray 1989).

Dating these Late Pleistocene industries was originally problematic, as both predate 40 000 BP and are beyond the scope of radiocarbon methods (Jacobs and Roberts 2008; Vogel and Beaumont 1972). A number of other techniques including Electron Spin Resonance, Uranium Thorium, Amino Acid Racemisation, Thermoluminescence and Optically Stimulated Luminescence have been used to date them (Tribolo *et al.* 2006). According to Jacobs and Roberts' (2008) chronology, based on Optically Stimulated Luminescence dates from ten Middle Stone Age sites in South Africa, Lesotho and Namibia, the Still Bay dates to 71ka and the Howiesons Poort to 60-65ka. Both industries were relatively short-lived, and occurred synchronously at different sites on the subcontinent (Jacobs and Roberts 2008). The Still Bay and Howiesons Poort represent periods of remarkable inventiveness and innovation marked by the production of sophisticated stone tools as well as bone and shell artefacts; activities which would have required planning, forethought and communication (Lombard and Philipson 2010; Sealy 2009; Jacobs and Roberts 2008). It is not surprising that these objects and industries figure prominently in debates concerning the origin of modern behaviour on the subcontinent.

The Still Bay lithic industry is characterised by the production of finely shaped, bifacially worked lanceolate points from fine-grained raw materials sourced from outcrops located considerable distances from sites (Brown *et al.* 2009; Jacobs and Roberts 2008; d'Errico and Henshilwood 2007; Henshilwood *et al.* 2001a and b). The experimental replication of Still Bay points by Mourre *et al.* (2010) indicates that an early form of pressure flaking may have been applied during the final stage in the reduction process. Pressure flaking, which is

usually associated with the Upper Palaeolithic in Europe and Later Stone Age in Africa, would have allowed toolmakers to produce the thin, narrow, sharp points which are the hallmark of the industry. Patterns of artefact discard at Blombos Cave suggest that this site may have been used as a workshop for the large-scale production of Still Bay points (Henshilwood *et al.* 2001a and b; Villa *et al.* 2009). The large number of unfinished Still Bay points classified as production failures or rejects hints at the steepness of the learning curve and intensity of production (Villa *et al.* 2009). The use of heat treatment as a means of improving the flaking properties of fine-grained silcrete used in the production of Still Bay points appears to have been adopted by stone knappers at Blombos Cave and Pinnacle Point by 75ka, and possibly as early as 164ka at the latter site. Thermoluminescence, archaeomagnetism, gloss analysis and experimental replication show that heating silcrete at high temperatures alters the crystalline matrix of this raw material, allowing it to flake more predictably and evenly. There are no precursors for this technique in the archaeological record of Africa and Eurasia (Mourre *et al.* 2010; Brown *et al.* 2009; Sealy 2009).

A number of other artefacts usually recovered from Later rather than Middle Stone Age sites have been found in association with Still Bay points at Blombos Cave. Fifteen of the twenty eight bone artefacts recovered from this site derive from layers dated to the Still Bay industry. Bone awls and points, which were recovered *in situ* from intact Middle Stone Age deposits and therefore do not represent intrusions from younger Later Stone Age layers, were manufactured on carefully selected and prepared blanks. A few other examples of Middle Stone Age bone tool technology have been found at Peers Cave and Klasies River Mouth (d'Errico and Henshilwood 2007; Henshilwood *et al.* 2001 a and b). Some of the earliest examples of personal ornamentation and "abstract representation" derive from the securely dated Still Bay levels of Blombos Cave (Henshilwood 2005). Two pieces of red ochre decorated with geometric designs, and thirteen additional pieces of incised ochre were found (Henshilwood *et al.* 2009; Cain 2006; Henshilwood 2005). Incised notches were also deliberately applied to a fragment of mammal bone associated with the Still Bay industry. The incisions appear to have been applied in a single sitting and according to a preconceived design (Henshilwood *et al.* 2001a; Cain 2006). A number of researchers regard this as firm evidence for symbolic communication and modern cognition.

Forty nine deliberately perforated *Nassarius kraussinaus* beads recovered from the Still Bay levels of the site are regarded as early examples of personal ornamentation. The shells, which are all adult specimens of roughly the same size, would have been deliberately and systematically collected from estuaries at some distance from the site. Experimental replication shows that they were probably modified by piercing the shell wall through the aperture using a sharp bone point (d'Errico *et al.* 2005). These perforated shells, which were discarded in discrete clusters in the deposit, exhibit use-wear patterns consistent with having been strung and worn. The modification and use of objects for personal adornment is suggestive of self-awareness and -recognition, important components of modern symbolic behaviour (d'Errico and Henshilwood 2007; d'Errico *et al.* 2005).

The Howiesons Poort industry has been recognised at more than twenty sites on the subcontinent (Villa *et al.* 2005). The lithic artefacts which define this industry include small backed blades, trapezes and segments which tend to be larger than the microliths produced during the Later Stone Age (Jacobs and Roberts 2008; Wadley 2008). While backed segments were being produced at Twin Rivers and Kalambo falls in Zambia as early as 200ka, these lack the standardisation evident in the Howiesons Poort (Barham 2002). The Howiesons Poort is further characterised by a marked preference on the part of toolmakers for fine-grained raw materials, some of which could only be sourced at considerable distances from archaeological sites. At Klasies River Mouth and Rose Cottage cave, backed blades and segments were manufactured by direct marginal percussion, an innovative technique with no precursors in the European Middle Palaeolithic. Singer and Wymer's (1982) original suggestion that Howiesons Poort microliths at Klasies River Mouth were used as insets for hunting implements has been born out by research at Sibudu, Umhlatuzana and Rose Cottage Cave. The analysis of micro-residues on stone artefacts from these sites is consistent with the practice of hafting, an innovation previously associated with the Later Stone Age (Lombard 2011; Villa *et al.* 2010; Soriano *et al.* 2007).

The production of compound adhesives used to attach standardised segments to hafts is in itself a strong indicator of complex behaviour and modern cognition (Wadley 2010). The manufacture of effective glues comprised of disparate ingredients, and use of these compounds to create innovative weapons and tools, is a multi-phase process requiring

abstraction, forethought, mental rotation and cognitive fluidity (Lombard 2011; Wadley 2010). Replication of adhesives and composite tools made by the Middle Stone Age inhabitants of Sibudu Cave 70 000 years ago showed that the strongest glues contained red ochre and acacia gum (Wadley *et al.* 2009). Different types of adhesive were applied to segments manufactured out of particular raw materials (Lombard 2011). While dolerite and hornfels were the predominant raw materials used by Middle Stone Age people at Sibudu, some larger, less standardised segments were made from quartz which may have been available close to the site (Wadley 2007, 2008; Delagnes *et al.* 2006). Methods of hafting also vary between different Middle Stone Age sites (Lombard 2011).

While Wadley and Lombard emphasise the practical application of Howiesons Poort lithic technology, Henshilwood (2008) and Wurz (1999) suggest that backed segments may also have served as symbolic objects. The imposition of style on artefacts, in this case the distinctive backed crescents recognised as the *fossil directeur* of the Howiesons Poort industry (Wadley 2007) implies the capacity for symbolic communication (Wurz 1999). Engraved ostrich eggshell fragments recovered in large quantities from Diepkloof Rock Shelter in the southwestern Cape have also been interpreted as evidence for symbolic communication (Texier *et al.* 2010, 2013). The deeply stratified Middle Stone Age sequence at this site is one of few where both the Still Bay and Howiesons Poort techno-complexes have been documented. Thermoluminescence dates for these industries at this site are between 10ka and 50ka older than those for other sites (Tribolo *et al.* 2009). More than four hundred fragments of deliberately incised ostrich eggshell were found, mostly in occupation layers dating to the Howiesons Poort (~60ka). These fragments probably derive from broken drinking containers used and curated by Middle Stone Age hunter-gatherers, and are marked with repetitive and abstract linear motifs similar to those that appear on ochre and bone at other Middle Stone Age sites (Texier *et al.* 2010; Cain 2006). The application of decorative motifs representative of group identity to functional objects marks the beginning of a tradition still practised by contemporary hunter-gatherers, and suggests significant cognitive overlap and affinity between modern and prehistoric people (Texier *et al.* 2010, 2013).

The Still Bay and Howiesons Poort are both precocious, time-restricted industrial complexes within the broader chronological framework of the Middle Stone Age. Numerous explanations have been posited for the punctuated appearance of innovative artefacts and complex behaviours at these particular stages in human prehistory. It has been suggested that warm climatic conditions prevalent during Marine Isotope Stage 5 supported relatively large populations of hunter-gatherers. These large populations were conducive to the types of social learning implicit in Still Bay technology and material culture. This may account for the brief appearance of standardised stone tools and bone and shell artefacts at several southern African sites prior to their widespread emergence during the Later Stone Age (Henshilwood *et al.* 2001a). Alternatively, the Still Bay may represent an adaptive response to harsh environments at the onset of Marine Isotope Stage 4 (McCall 2007). Environmental degradation necessitated the adoption of more extensive mobility patterns to access widely dispersed lithic raw materials and food resources. Objects with culturally mediated symbolic meanings attached to them may have served as a mechanism for exchanging information and minimising risk in challenging circumstances (McCall 2007).

An occupational hiatus of around six thousand years between the Still Bay and the Howiesons Poort is consistent with the movement of people out of previously occupied regions during this time (Henshilwood 2008; Jacobs and Roberts 2008). Technological innovations characteristic of the Howiesons Poort industry may have emerged in response to environmental constraints during the Last Glacial Maximum. Dry and arid conditions caused resources to be widely distributed across the landscape. Increased foraging distances would have facilitated the acquisition of non-local raw material often but not always used for manufacturing backed segments (Cochrane 2008; Ambrose and Lorenz; McCall 2006, 2007; Ambrose and Loranz 1990). Survival in this challenging environment may also have resulted in economic intensification and the development of specialised toolkits (Henshilwood 2008; McCall 2006 and 2007). Backed segments endowed with symbolic meaning may have been used to maintain social relationships based on reciprocal exchange similar to *hxaro* networks among the Kalahari San (Henshilwood 2008; McCall 2006).

There are some inconsistencies in these interpretations. For instance, it can be argued that intensification and specialisation are examples of economically costly behaviour, which would not have been advantageous during times of environmental stress (Minchillo 2006). Furthermore, Marine Isotope Stage 4 was not uniformly cold and dry (Jacobs and Roberts 2008). Patterns of artefact discard at Klein Kliphuis, a Middle Stone Age site located near the Olifants River in the western Cape, are consistent with intensive occupation during this time (Mackay 2010). An increase in the number of sites occupied following a hiatus between the Still Bay and Howiesons Poort may indicate the movement of new groups into the region (Henshilwood 2008). The transition between the Howiesons Poort and post-Howiesons Poort or MSAIII coincided with the onset of Marine Isotope Stage 3. It is sometimes portrayed as an abrupt discontinuity of subsistence and lithic production strategies accompanied by a decline in hunter-gatherers populations (Cochrane 2008; Henshilwood 2008; McCall 2007). Evidence from several sites in diverse regions including Sibudu, Klasies River Mouth, Rose Cottage Cave and Klein Kliphuis is more consistent with continuity and gradual change in response to climatic amelioration (Mackay 2010; Villa *et al.* 2010; Soriano *et al.* 2007; Minchillo 2006).

## 2.5 SUMMARY

The Middle Stone Age has been of interest to archaeologists since it was first defined by Goodwin and van Riet Lowe (1929). Extensive research conducted from the 1970s, but especially over the last two decades, has shown this stage in human prehistory to be characterised by significant change and innovation. Fossils and genetic evidence indicate that Middle Stone Age people were anatomically modern, and were the first members of our species, *Homo sapiens*. Marine resources including shellfish, fish and occasionally seals and birds, were incorporated into the diet of people who left material traces of their coastal foraging activities behind at sites along the Cape coast. Middle Stone Age people also employed a number of effective and flexible strategies and projectile technology to hunt terrestrial game (Lombard 2011). Artefacts with strong affinities to those normally associated with the Later Stone Age, including standardised stone tools, bone artefacts, perforated shells and engraved ochre and ostrich egg shell are material innovations with symbolic connotations. Specific activities inferred for Middle Stone Age hunter-gatherers at

particular sites, notably the manufacture of compound adhesives and composite tools, and heat treatment of lithic raw materials, are consistent with planning, abstract thought and social learning: all attributes of modern cognition.

The appearance of anatomically modern humans, marine foods and numerous material and behavioural innovations during the South African Middle Stone Age warrants further investigation. The possible nutritional underpinnings of coastal foraging, and implications for encephalisation are particularly intriguing. In the following chapters, the nutritional requirements of modern and prehistoric humans will be discussed; patterns in the shellfish assemblages from Middle and Later Stone Age sites in the southwestern Cape will be described; and new information on the nutrient content of marine and terrestrial resources available to the Middle Stone Age inhabitants of the region will be presented. To conclude, a number of competing scenarios for Middle Stone Age subsistence will be evaluated, and the role of marine resources in the emergence of anatomically modern humans will be assessed.

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## CHAPTER THREE

### NUTRITION AND HUMAN EVOLUTION

#### 3.1 INTRODUCTION

Nutrition is a central theme in discussions about human evolution. A high quality diet was of paramount importance to support the dramatic increase in brain size among hominins, which culminated in the emergence of anatomically modern humans by at least 100 ka. Energy-dense, nutrient-rich diets and large-brained hominins evolved together. The consumption of these diets is both a pre-requisite for, and a product of, the high level of encephalisation that distinguishes humans from non-human primates (Leonard *et al.* 2007). The evolution of large brains came at a high price. Brain tissue is metabolically expensive, requiring sixteen times more energy than skeletal muscle and accounting for between 20 and 25% of the basal metabolic rate of adult humans (Leonard *et al.* 2007; Aiello and Wheeler 1995). The allocation of such a large proportion of the energy budget to the brain required corresponding physical changes as a means of compensation. These include a reduction in the size of the gut, another metabolically expensive organ, and the development of less muscular but fatter phenotypes in comparison with other primates. As a result of these changes, members of the increasingly large-brained *Homo* genus became dependent on high quality, easily digested food resources. Animal foods appear to be more suitable in this regard, as opposed to some of the fibrous plant food favoured by non-human primates (Ben-Dor *et al.* 2011; Leonard 2007; Aiello and Wheeler 1995).

Earlier scenarios for human evolution are firmly based on this premise, and are centred on what Speth (2010) has called the "holy trinity" of big-game hunting, meat eating and meat sharing. A number of the physiological and behavioural characteristics that have come to define our genus, including large and complex brains and bipedal locomotion, as well as prolonged juvenility among offspring, food provisioning, nuclear families and a division of labour based on gender, are believed to have emerged for the first time on the African Savannah, in response to dietary changes associated with the hunting and consumption of terrestrial game (Speth 2010; O'Connell *et al.* 2002; Bird and Bliege Bird 2000, 2002). The plausibility of big-game hunting and meat-eating as a driving force in human evolution has

increasingly been called into question over the last few decades (Broadhurst *et al.* 2002; Crawford 2010; Cunnane 2010; Parkington 2003, 2010). This follows the recognition that high protein diets are problematic in a number of respects; that big-game hunting as practiced by modern hunter-gatherers is considerably less important for securing basic subsistence than other economic activities, and may be more important as a mechanism for “costly signalling” and gaining status; that fat rather than protein is a critical nutrient in encephalisation; and that littoral rather than terrestrial environments may have provided early modern humans with the nutrition required for increasingly large and complex brains (Speth 2010; O’Connell *et al.* 2002; Crawford *et al.* 1999).

Marine and aquatic food resources are rich in long chain, polyunsaturated fatty acids required for brain structures and growth (Crawford *et al.* 1999). Consuming small amounts of the simplest marine resources would have provided evolving *H. sapiens* with sufficient preformed docosahexaenoic acid (DHA) and arachidonic acid (AA) for brain growth and function (Crawford 2010; Cunnane 2010). Not very long ago, shellfish were regarded as low-ranking and marginal resources collected by women and children as a last resort during times of nutritional stress or as a supplement to higher ranking food resources procured by men (Erlandson 1988). This view has undergone considerable revision, as the nutritional value of marine resources and their contribution to subsistence has been acknowledged. In this chapter, the main components of the modern human diet, and current understanding of prehistoric hunter-gatherers diets, will be reviewed, and the nutrient requirements of Middle Stone Age hunter-gatherers discussed and determined.

### 3.2 NUTRIENTS IN THE HUMAN DIET

Essential nutrients are substances which must be supplied by the diet directly or in precursor form, as they are not synthesised in the body in adequate amounts (Dwyer 2008). Human diets consist of three energy providing macronutrients, namely carbohydrates, protein and fat. These are consumed in large amounts. While proteins are not stored for future use, their constituent amino acids may be used after proteolysis during starvation. Carbohydrates are stored to a small extent and can rapidly provide glucose from glycogen stored in muscle or liver. In contrast, fat (lipid), which is much more energy-dense, is stored as energy reserve. All fatty acids can serve as substrates for oxidation to provide

energy. Some fatty acids are required for phospholipids in cell membranes and bile while others are transported in lipoprotein (LP) as triacylglycerol (TAG). Polyunsaturated fatty acids (PUFAS) with omega-6 (*n*-6) and omega-3 (*n*-3) double bonds cannot be synthesised by mammals but are essential for health. Micronutrients, including iron, copper, zinc, selenium and iodine are required by the body for growth and function in small amounts, but may critically affect health when deficient. Dietary Reference Intakes (DRI's), which include and subsume the more popular Recommended Dietary Allowances (RDA's), provide a "quantitative benchmark" against which people's nutrient intakes are assessed (Dwyer 2008). Requirements for specific nutrients may change at different stages of the lifecycle, most notably during gestation, infancy, adolescence, pregnancy and lactation. Dietary deficiency diseases occur when supply of specific nutrients are inadequate to meet demands, including the exhaustion of stores which in many instances develop as adaptations.

### 3.2.1 Macronutrients and Water

#### *Water*

Water is the most critical element for human survival. It makes up between 50% and 75% of the human body, depending on age, adiposity and gender, and is present in and around the cells, as well as in the blood vessels and lumen of the gut. Water is lost through defecation, sweating, exhalation and especially urination, and is also produced during the oxidation of food (Sheng 2013; Dwyer 2008). Five hundred millilitres of free water must be ingested each day to offset that which is lost and maintain proper water balance. Infants have a high requirement for water to compensate for the immaturity of their kidneys, and women's requirements increase during pregnancy and lactation (Sheng 2013).

#### *Macronutrients: carbohydrates, protein and fat*

In order for health to be maintained, energy intake must equal output. Macronutrients are oxidised by the human body to provide energy. Carbohydrates, in the form of monosaccharides, disaccharides, oligosaccharides and polysaccharides such as starches and glycogen, represent the main source of glucose in the human diet after infancy. Starches occur as "semicrystalline storage granules in all species of plants" (Leturque and Brot-Laroche 2013:142), the specific structural and chemical composition of which varies between

different species and parts. Simple and complex carbohydrates are broken down into monosaccharide units by an enzyme known as soluble  $\alpha$ -amylase. This digestion process, which is highly efficient, begins in the mouth as food is masticated and mixes with saliva, and is completed in the duodenal lumen. Some plant polysaccharides, including cellulose, hemicellulose and pectin, are nondigestible, and may inhibit the digestion of other polysaccharides. These are known as dietary fibre. In current diets, carbohydrates contribute between 45% and 65% of the average person's energy intake. Carbohydrates are typically consumed in quantities of 250g per day by people in the United States (Leturque and Brot-Laroche 2013). Glycogen is a large polymer of glucose that serves as a source of this saccharide during starvation, but this retains water and has less energy than fat.

Protein plays an important role in growth and development and throughout life. Apart from structural and enzymatic functions, protein is required for the regulation of cellular metabolism, hormonal functions and production of milk in lactating women (Young and Pellett 1987). Protein from the diet consists of essential and other amino acids that can be synthesised *in vivo* (Dwyer 2008; Young and Pellett 1987). Amino acids processed to form glucose and fatty acids are either stored, or metabolised to provide the body with energy. Some intake of amino acids from the diet is essential to replace those lost through degradation. Rates of protein synthesis are highest in infants, and decrease with increasing age (Dwyer 2008; Young and Pellett 1987).

The digestibility and biological value of proteins varies among different sources. Proteins embedded in the cell wall of plants are less accessible to pepsin and pancreatic proteases that digest proteins than those in animal tissue, and are frequently regarded as of lower value. Plant proteins must therefore be combined with other plant or animal proteins to be optimally utilised by the body. Animal proteins are usually but not always of higher biological value, as they contain more of the essential amino acids in sufficient amounts (Dwyer 2008; Young and Pellett 1987). Whilst mastication fragments the food and provides a greater surface area for digestive enzymes, food processing such as cooking may affect the digestibility of proteins as well. Current RDA's for protein are set at 0.6 – 0.8g per kg body weight, with increased requirements during growth, pregnancy and lactation (Dwyer 2008). Diets very high in protein (>50% total energy) are problematic and can produce a negative

energy balance when not offset by the consumption of adequate fat ( Ben-Dor *et al.* 2011; Kuipers *et al.* 2010; Speth 2010). Humans have a physiological ceiling on protein intake because of the limited capacity of the liver to dispose of nitrogen as urea, the main by-product of protein metabolism. Long-term protein intake should not exceed 2g/kg body weight per day, or 35% of total energy (Ben-Dore *et al.* 2011; Speth 2010; Cordain *et al.* 2000; Mann 2000). In the United States of America, 15% of people's energetic requirements derive from protein; diets where between 10% and 14% of people's calories are supplied by this nutrient are considered healthy.

Lipids or fats represent the most important form of concentrated stored energy in all mammals, including humans. Of the several dietary lipids consumed by humans, triacylglycerols are the vast majority (90% or more) and are the primary source of essential fatty acids. Other dietary lipids include cholesterol, cholesteryl esters, plant sterols, plant sterol esters, fat-soluble vitamins, carotenoids and phospholipids (Brannon *et al.* 2013; Dwyer 2008). Lipids from dietary resources are digested by means of a series of co-ordinated processes beginning in the stomach and small intestine and concluding in the enterocyte (Brannon *et al.* 2013.). In the stomach, triacylglycerols are hydrolysed by gastric lipase, an enzyme produced by the gastric mucosa. Between 10% and 25% of fat is digested in the stomach; most of the remainder is subsequently digested in the luminal small intestine by pancreatic lipase.

The products of lipid digestion are then taken up by the enterocyte and exported from the intestinal tract by means of lipid-protein complexes or lipoproteins assembled by the small intestine in a process summarised as exogenous lipid transport. The liver provides endogenous lipid transport to recycle exogenous lipid and to transport TAG and cholesterol synthesised in this organ (Brannon *et al.* 2013). Fats account for 34% of the total energy consumed in current diets in the United States; adult males and females typically ingest 95g and 65g of fat per day, respectively. When the total energy consumed exceeds the immediate energetic demands of individuals, carbohydrates and amino acids are modified to fatty acids which are esterified to glycerol to form triacylglycerol and stored in the adipose tissue (Brannon *et al.* 2013; Dwyer 2008).

### *The physiology of starvation and protein-energy malnutrition*

Starvation occurs when insufficient or no energy-providing nutrients are supplied to adequately offset energy expenditure. Once all carbohydrates are exhausted, ketone bodies are synthesised from non-esterified fatty acids to provide energy. The resting metabolic rate is reduced by 10% to 30% to conserve energy and slow the rate of weight loss, and rates of protein degradation decline in order to preserve the body's protein stores and prevent wasting. Where prolonged starvation is unmitigated, and the adipose deposits depleted, protein degradation increases and body protein is metabolized for energy (Dwyer 2008; Young and Pellett 1987).

#### 3.2.2 Micronutrients

##### *Iron*

Iron is an indispensable micronutrient in the human diet, and performs a number of essential functions. It is a constituent of the haem proteins haemoglobin and myoglobin, which are responsible for the transport and metabolism of oxygen in the human body. Iron is stored as ferritin and haemosiderin in the liver, bone marrow and spleen, and is lost via the gastrointestinal tract and cells shed from the surface of the skin. Due to the toxic nature of iron, its uptake is regulated through a mucosal block and haem is favoured for uptake. Dietary iron must be absorbed in similar quantities to that which is lost in order prevent negative balance and deficiency. Women experience increased iron losses during menstruation and especially pregnancy and parturition, which is why their iron requirements (18-27mg/day) exceed those of adult men (8mg/day). The increased iron requirements of pregnant and lactating women are partially offset by the temporary cessation of menstruation, (amenorrhea) which reduces iron loss for the duration of pregnancy and lactation. Nevertheless, increased dietary iron is required to compensate for that lost by the mother to iron deposition in the fetus, particularly during the second and third trimesters (Crichton 2013). Iron requirements are likely to exceed intake during the first six to eighteen months of postnatal life, which is a time of rapid neural development, and also during adolescence and the onset of menarche in females (Crichton 2013; Beard 2008).

Iron deficiency is the most common and widespread single nutrient disorder in the world today, probably due to our limited capacity to absorb dietary iron. It is recognised as the primary cause of anaemia, and is associated with a number of cognitive abnormalities and disorders. For instance, iron deficiency in utero and during the first six months of postnatal life may significantly impair the development of the central nervous system. Iron has been shown to be essential for “proper neurogenesis and the differentiation of certain brain cells and brain regions” (Beard 2008). Data from human and animal studies have identified several alterations in brain morphology as a result of iron deficiency, notably in the myelination of white matter, the striatum and hippocampus, as well as changes in biochemistry and bioenergetics. Iron deficiency has also been linked to impaired auditory brainstem responses, motor control, learning and memory (Beard 2008), as well as to increased incidence of premature delivery and perinatal mortality. Decreased work performance due to a lack of energy and impaired concentration would have had important consequences in populations dependent on manual labour for their subsistence (Crichton 2013), including hunter-gatherers.

#### *Copper and zinc*

The trace elements copper and zinc are part of numerous enzymes and proteins involved in various biochemical pathways in the human body (Grider 2013). Copper is an essential component of enzyme systems involved in iron metabolism, melanin synthesis and cartilage production, neuropeptide and neurotransmitter synthesis and protection from oxidative stress (Grider 2013; Dwyer 2008). Zinc is associated with enzyme systems involved in protein, DNA and RNA synthesis and metabolism, bone formation, signal transduction and protection from reactive oxygen species (Grider 2013; Dwyer 2008). It is furthermore an absolute requirement for normal spermatogenesis, fetal growth and embryonic development (Dwyer 2008). Shellfish, meat, nuts and legumes are among the best sources of dietary zinc. These two minerals are absorbed throughout the length of the small intestine; excretion is mainly through the faeces, with minimal losses via urine and the skin. The decline of copper and zinc in animals fed experimental diets deficient in these micronutrients suggests that they are probably not stored efficiently to be utilized in times of increased need or decreased dietary availability (Grider 2013).

Copper deficiency is relatively rare, but has been associated with anaemia, growth retardation and mental deterioration (Dwyer 2008). Because of its crucial role in growth regulation, one of the main consequences of zinc deficiency is slow or retarded growth, especially in children and adolescents. This is thought to be a result of disruptions in the biochemical processes that regulate the effect of human growth hormone. Mild zinc deficiency, which results in stunted growth, reduced taste sensation and compromised immune function, has been well documented among adolescents in Iran consuming plant-based diets high in phytates and lacking in zinc. Severe chronic deficiency is associated with hypogonadism and dwarfism (Grider 2013; Dwyer 2008).

### *Iodine*

Iodine is responsible for a single but critically important process in the human body, the synthesis of thyroid hormones thyroxine (T4) and triiodothyronine (T3) which perform a number of metabolic and developmental functions throughout the life cycle (Pearce and Freake 2013; Gunnarsdottir and Dahl 2012). Specifically, thyroid hormones regulate the basal metabolic rate, stimulate the synthesis of fatty acids during macronutrient metabolism, and regulate growth and development. With regard to neurological development and brain maturation, T3 is essential for normal cell migration, myelination and the formation of cortical layers, and neuronal and glial cell differentiation in utero and during infancy. Thus, inadequate thyroid hormone production during the critical periods of gestation and pregnancy may cause serious and irreversible brain damage (Zimmerman 2009; Bernal, Guadaño-Ferraz and Morte 2003).

Iodine is fairly abundant but unevenly distributed in the environment. The majority exists as iodide found in the oceans. Soils in mountainous regions are deficient in iodine, as are those in river deltas and other areas prone to flooding, where iodine in the soil is dissolved and leached out. The iodine content of most food resources is low. Terrestrial plants contain about 1mg of iodine per kg dry weight; the content of terrestrial animals is determined by the amount in the foods they consume. Marine flora and fauna have high amounts of iodine, as they are able to concentrate it from sea water (Pearce and Freake 2013; Zimmerman 2009). Iodine, which is ingested in several chemical forms, is changed to inorganic iodide and rapidly and efficiently absorbed in the stomach and duodenum. In

healthy adults, more than 90% of ingested iodine will be absorbed. Iodine is removed from circulation mainly by the renal system, where the rate of clearance remains fairly constant, and the thyroid, which actively takes up this micronutrient in accordance with its availability. In lactating women, iodine concentrated in the mammary gland is secreted into breastmilk to meet the requirements of the neonate. During pregnancy, iodine requirements are increased by approximately 50% (220 µg/day) in order to compensate for the transfer of thyroxine to the foetus both early in the first trimester when the foetal thyroid system is not fully functional and during later gestation and growth, and for increased renal iodine clearance. While most healthy women have stores of between 15mg and 20mg of iodine in the thyroid to be drawn upon in times of increased need, those in areas of chronic deficiency will have already depleted those stores (Pearce and Freake 2013; Zimmerman 2009).

Iodine deficiency, which results in the diminished capacity to adequately produce thyroid hormones, has a number of adverse affects. The most significant of these is neurological impairment stemming from deficiency during pregnancy and early infancy. The extent of the resultant neurological abnormalities is dependent on the timing and severity of the deficiency. Hypothyroxinaemia in the first trimester of pregnancy, during which the foetus is completely dependent on maternal supply of thyroid hormones and is undergoing rapid neural development, results in irreversible brain damage and mental retardation (Pearce and Freake 2013; Zimmerman 2009). In this form, neurological cretinism causes severe mental retardation, deaf mutism and motor spasticity. The myxedematous form is associated with growth retardation, delayed sexual maturation and less severe mental retardation. Other consequences of inadequate iodine supply during and prior to pregnancy include increased risk of infertility, spontaneous abortion, congenital abnormalities and infant and perinatal abnormalities (Pearce and Freake 2013; Gunnarsdottir and Dahl 2012; Zimmerman 2009). Mild to moderate maternal deficiency has been linked to more subtle cognitive and neurological dysfunction including Attention Deficit and Hyperactivity disorders. Iodine deficiency during childhood has been shown to result in reduced intellectual function and motor skills (Zimmerman 2009)

## Selenium

Selenium plays an important role in metabolism, and was recognised as an essential micronutrient fairly recently. It is a component of the enzyme glutathione peroxidase, which protects proteins, cell membranes, lipids and nucleic acids from oxidant molecules, and may have anticarcinogenic properties. The selenium content of plant foods is determined by the content of the soil in which they grow; thus, the local soil selenium environment will be strongly reflected in the tissues of both animals and plants. Seafood, meat and cereals are the most common sources of selenium in current diets. Selenium is efficiently absorbed from dietary sources; the majority is then taken up by the liver and re-enters the circulatory system as selenoprotein. Selenium deficiency has been associated with Keshan disease, a condition which produces cardiomyopathy. When it occurs simultaneously with iodine deficiency, it may exacerbate the clinical manifestations of cretinism and muscle degeneration (Combs 2013; Dwyer 2011).

### 3.2.3 Essential and polyunsaturated fatty acids

Essential fatty acids (EFAs) are indispensable for human development and physiological function. Individual EFAs are composed of a hydrocarbon chain and a carboxyl group; those with two or more double bonds in the hydrocarbon chain are referred to as polyunsaturated fatty acids (PUFAs). While *n*-6 essential fatty acids are rapidly depleted from tissues in the human body, *n*-3 fatty acids are highly conserved. The parent 18-carbon EFAs of each of these groups, respectively, linoleic acid (LA) and  $\alpha$ -linolenic acid (ALA), can be synthesised by terrestrial plants, the starting point for all fatty acids in the human food chain. LA is the primary PUFA manufactured by terrestrial plants. While small amounts of the parent EFA for the *n*-3 class ALA, are synthesised by some terrestrial plants, the majority is produced by vegetation growing in cold water. Thus, marine food chains are enriched in omega-3 polyunsaturated fatty acids (Orr *et al.* 2013). The simplest human requirements are linoleic (C18:2, *n*-6) and  $\alpha$ -linolenic (C18:3, *n*-3); the more important arachidonic acid can be synthesised *in vivo* from the former and eicosapentaenoic (EPA) and docosahexaenoic from the latter. As EFAs cannot be synthesised by the human body, and the extent to which long-chain polyunsaturated fatty acids (LCP's) can be synthesised from their parent fatty acids is limited, these must be derived from dietary sources (Orr *et al.* 2013; Hornstra 2000).

Linoleic and  $\alpha$ -linolenic acid can both be elongated to longer chains (20 or 22 carbon atoms) and can gain double bonds through a pathway first identified in rats (Figure 3.1). This involves a sequential process of adding two carbon atoms in an acetyl group followed by desaturation.  $\beta$ -oxidation is necessary to return the 24 carbon chain omega-3 EFA to 22 carbons (Orr *et al.* 2013; Burdge and Wootton 2002; Al *et al.* 2000; Hornstra 2000). Linoleic acid serves as the precursor for the most functionally important polyunsaturated omega-6 EFA, arachidonic acid (AA), while  $\alpha$ -linolenic acid serves as a substrate for the synthesis of two vital omega-3 LCPUFAs, eicosapentaenoic acid (EPA; 20:5) and docosahexaenoic acid (DHA 22:6). The elongation and desaturation of *n*-6 and *n*-3 fatty acids occurs along the same enzymatic pathway and there is significant competition between the two families (Al *et al.* 2000). While all EFAs can be oxidised by the human body to provide energy, polyunsaturated fatty acids have a number of unique structural and metabolic functions (Haggarty 2002). Arachidonic acid and, especially, docosahexaenoic acid, are the primary structural phospholipids in the human brain and retina (Orr *et al.* 2013; Carnielli *et al.* 2007; Al *et al.* 2000; Hornstra 2000). The deleterious effects of *n*-6 and *n*-3 fatty acid deficiency have been well demonstrated by animal experiments, and also in humans. Deficiency in LA is associated with poor wound healing and dermatitis, and, in infants and children, failure to grow (Orr *et al.* 2013). Omega-3 deficiency results in compromised visual function and peripheral neuropathy (Orr *et al.* 2013; Innis 2000).

Our metabolic requirement for LCPUFAs can be satisfied in a number of ways, including the consumption of preformed dietary PUFAs, mobilization of PUFAs stored in adipose tissue, and synthesis of long chain polyenes from shorter-chain precursors (Bakewell *et al.* 2006). It is generally accepted that *n*-6 PUFAs can be synthesized in sufficient amounts from dietary LA. Opinions differ, however, as to whether the synthesis of longer-chain *n*-3 PUFAs from ALA and other precursors is sufficient to sustain optimal cognitive and visual function (Orr *et al.* 2013; Carlson and Kingston 2007). Some researchers assert that rapid  $\beta$ -oxidation of ALA and EPA entering the brain renders them inadequate for local DHA synthesis, meaning that dietary DHA is an important source of this LCPUFA in neural tissue. The retina uses

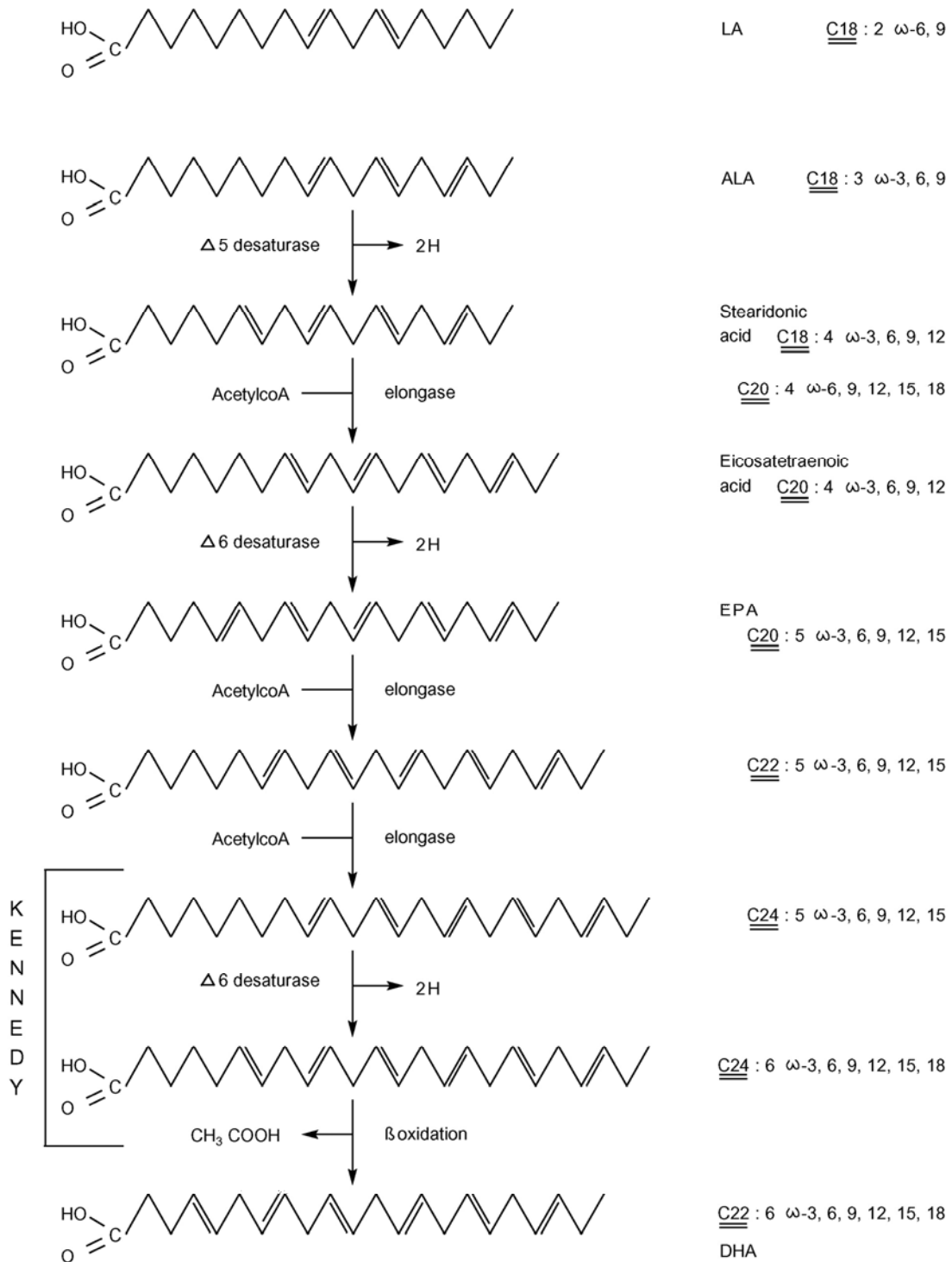


Figure 3.1 The elongation and desaturation of essential fatty acids along a biochemical pathway. Illustration by Neil Rusch.

DHA formed in the liver from shorter-chain precursors (Orr *et al.* 2013). Plourde, Cunnane and colleagues(2007) contend that the conversion of ALA to DHA is very inefficient, and rarely exceeds a ratio of 0.5%. Thus, around 60g of ALA would have to be consumed to obtain 300mg of DHA, making the direct consumption of pre-formed dietary DHA an absolute requirement.

Other researchers argue that the biosynthesis of *n*-3 LCPUFAs, particularly DHA, varies considerably among humans on the basis of a number of biological and other factors, and that the conversion from shorter- to longer-chain *n* - 3 PUFAs can be upregulated by means of physiological mechanisms during periods of critical need (Carlson and Kingston 2007). Several lines of evidence suggest that women may be considerably more efficient at DHA synthesis than men. Stable isotope tracer studies conducted by several investigators show that women of reproductive age (~ 28 years) have a significantly greater capacity to convert the predominant *n*-3 precursor, ALA, as well as EPA, into DHA, than men (Bakewell *et al.* 2006; Burdge and Calder 2005; Burdge 2003; Burdge *et al.*2002; Burdge and Wooton 2002; Pawlosky 2003). While some conversion of ALA into EPA does occur in adult men, further elongation and desaturation into DHA is very low. Thus, the intake of preformed dietary DHA and recycling of DHA conserved within bodily tissues may play a more important role for the maintenance of adequate levels in men than in women (Burdge and Calder 2005; Burdge 2003; Burdge *et al.* 2002; Pawlosky 2003). In adult women, it appears that a lower proportion of ingested ALA is used for  $\beta$  - oxidation; greater amounts of ALA and EPA are transformed into DHA (Bakewell *et al.* 2006; Burdge and Calder 2005).

DHA concentrations in the plasma lipids of young adult female subjects are considerably higher ( $15 \pm 4\%$ ) than those of adult males consuming similar diets. This strongly supports the suggestion that women are more efficient at converting shorter-chain PUFAs into DHA. Higher concentrations ( $10 \pm 4\%$ ) of DHA found in the plasma lipid of women taking the oestrogen-based oral contraceptive pill relative to those not on this regime indicate that exposure to this hormone plays an important role in women's capacity to synthesise this PUFA from its parent fatty acid (Bakewell *et al.* 2006; Burdge and Calder 2005; Giltay *et al.* 2004 a and b; Burdge 2003; Burdge *et al.* 2002). The influence of sex hormones on DHA synthesis is further demonstrated by two interesting studies conducted by Giltay and

associates (2004a and b). In the course of one of these investigations, male-to female transsexuals were randomly assigned to receive either oral ethynyl oestradiol or a placebo, and female-to-male transsexuals were given either testosterone esters or placebos. It was found that while exposure to ethynyl oestradiol increased DHA concentrations in subjects by  $42 \pm 8\%$ , treatment with testosterone esters decreased concentrations by  $22 \pm 4\%$  (Giltay *et al.* 2004a). Another study examined the effect of oestrogen- and/or progesterone-based hormone replacement therapies on AA and DHA concentrations in plasma cholesterol esters in postmenopausal women. Subjects on the different hormonal regimes showed a 6-14% increase in AA, and an even more substantial increase (15-22% in DHA). Pawlosky *et al.* (2003) investigated the effect of different diets on men and women's ability to synthesise DHA from its shorter-chain precursors. In an interesting caveat to the argument around the necessity for preformed DHA, preferably of marine origin, they found that women utilised almost three times more EPA for DHA synthesis than men while both consumed terrestrial, beef-based diets (Figure 3.2). When both sexes subsisted on marine based diets, however, rates of conversion from EPA to DHA were about the same (Pawlosky *et al.* 2003). This indicates that dietary sources of DHA can suppress *de novo* synthesis through a regulatory mechanism. More information on this mechanism could yield further insight into DHA requirement and capacity to synthesise and/or store this important fatty acid.

Women's ability to efficiently convert ALA and EPA into DHA may be of great importance in helping them meet their requirements for the latter LCPUFA where dietary resources are insufficient or lacking, and during times of increased demand, notably pregnancy and lactation (Burdge and Wootton 2002; Al *et al.* 2000; Hornstra 2000). The foetus *in utero* has an absolute requirement for AA and especially DHA for the development of the brain and retina (Haggarty 2004). Fat deposition and neurogenesis in the foetus occur most rapidly during the last trimester, especially the final ten weeks, of pregnancy, making this the most nutritionally demanding time for the mother. While some of the fatty acid structure accrued by the foetus is the result of foetal lipogenesis, most is derived from the mother via placental transfer (Haggarty 2002; 2004; Al *et al.* 2000; Duta – Roy 2000).

The placenta is a barrier through which maternal nutrients, including essential fatty acids, need to cross to the fetus (Figures 3.2 and 3.3A). Fatty acids stored in maternal adipose tissue

are mobilised by the action of placental leptin; they then cross the microvillous and basal membranes by simple diffusion and by the action of fatty acids binding proteins or FABPs (Haggarty 2002). Higher concentrations of AA and DHA in the placenta relative to maternal blood suggest that the placenta may actively select and take up specific  $n-3$  and  $n-6$  fatty acids for export to the foetus (Haggarty 2002, 2004; Duta-Roy 2000). Preferential uptake and transfer may be attributed to selective hydrolysis of TAG by placental lipase, uptake by the microvillous membrane, metabolism within the placenta and the form in which fatty acids are exported to the foetus (Haggarty 2002). It appears, for instance, that the placenta preferentially retains AA, which is required for the production of metabolites, transferring it to the foetus only when this requirement is met. Increasing the concentration of this fatty acid in the maternal circulation thus alters the order of transfer to the foetus to favour DHA, followed by AA, followed by the parent fatty acids ALA and LA (Haggarty 2002).

The LCPUFA status of neonates is related to that of their mothers pre- and post-partum, and has a number of long-term effects. Lower LCPUFA status is associated with multiple and premature births (Al *et al.* 2000). For mothers, normalization of PUFA status following delivery is slow. Supplementation of  $n-3$  and  $n-6$  fatty acids during pregnancy has been shown to be beneficial to both mothers and their infants. The consumption of *trans* fatty acids has been shown to have a deleterious effect on neonatal and maternal PUFA status (Al *et al.* 2000; Hornstra 2000). Although relatively little is known about endogenous LCPUFA synthesis in neonates, all infants, even premature ones, are able to synthesise AA and DHA to some extent (Orr *et al.* 2013; Brenna *et al.* 2009; Carnielli *et al.* 2007; Haggarty 2002).

Neonates are better able to synthesise AA than DHA, making the consumption of preformed DHA important for proper brain development (Haggarty 2002). Breastmilk contains both AA and DHA (Carnielli *et al.* 2007), and is an important source of LCPUFAs for lactating infants (Figure 3.4)

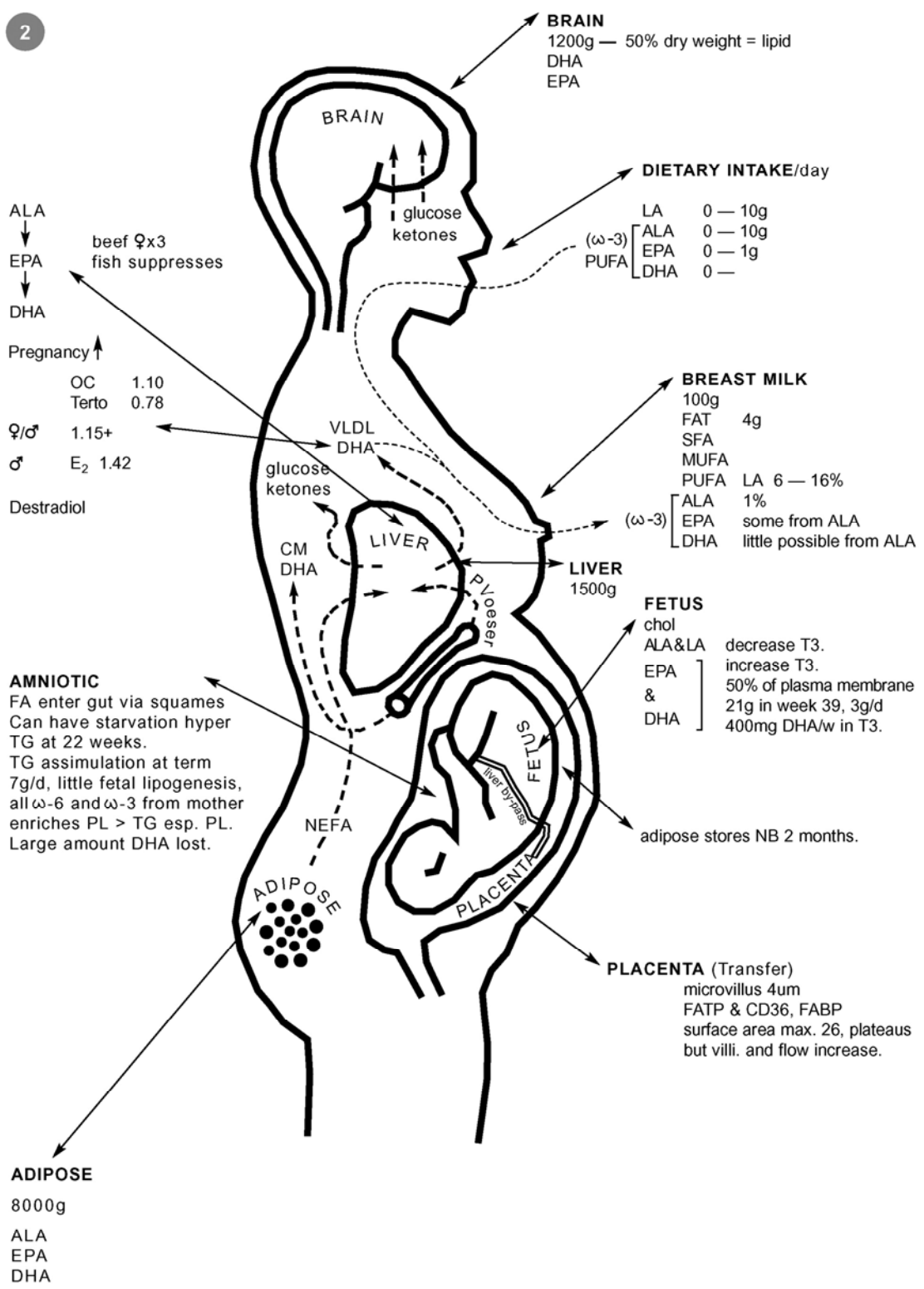


Figure 3.2 Essential fatty acids in pregnant women and the foetus *in utero* (Giltay *et al.* 2004a and b; Pawlosky *et al.* 2003). Illustration by Neil Rusch.

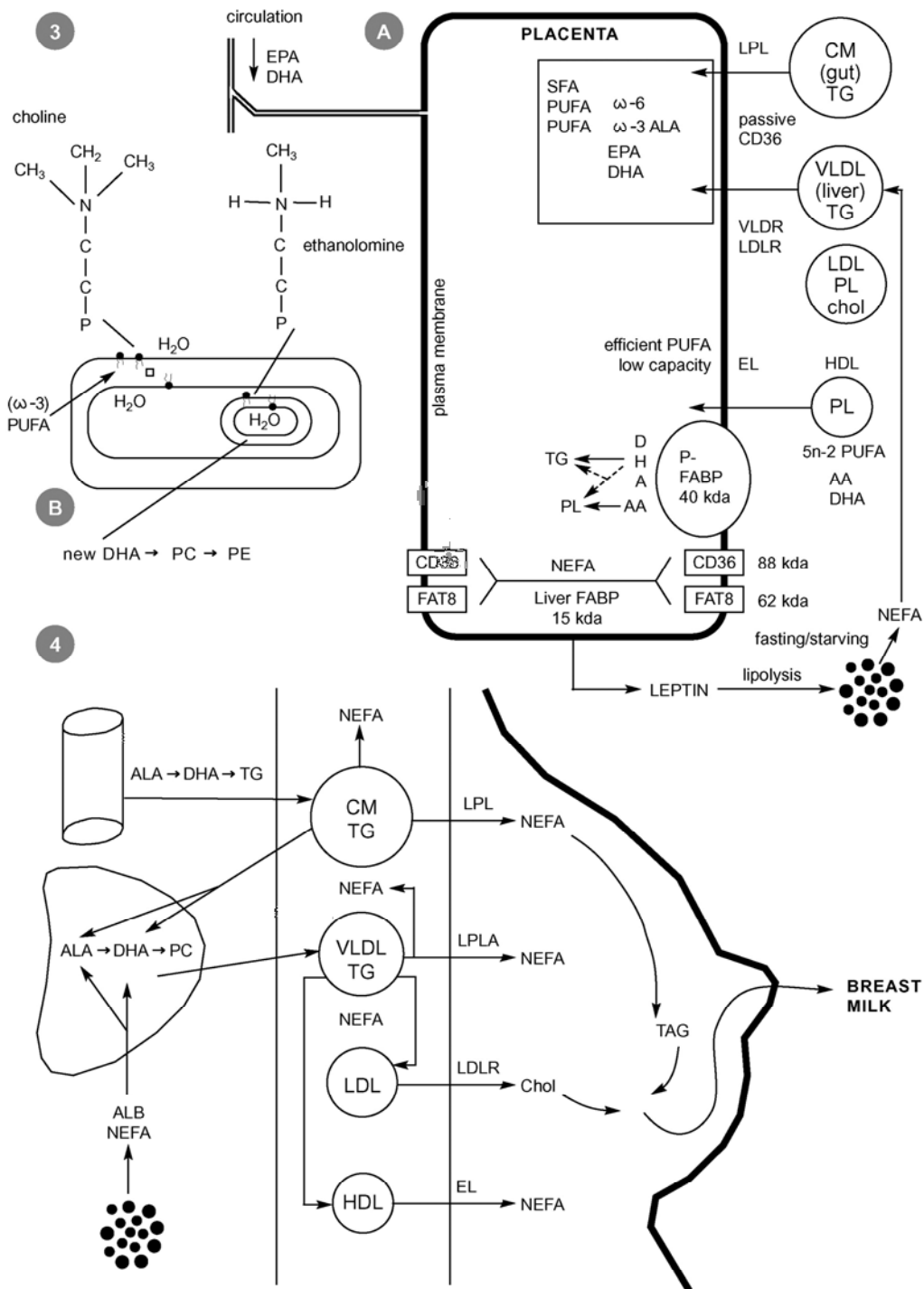


Figure 3.3 Fatty acids in the placenta (A) and maternal circulation system during pregnancy (B) (Pawlosky *et al.* 2003; Haggarty 2002, 2004; Duta-Roy 2000). Illustrations by Neil Rusch.

Figure 3.4 Fatty acids and the production of breast milk during pregnancy and lactation (Pawlosky *et al.* 2003; Haggarty 2002, 2004; Duta-Roy 2000). Illustration by Neil Rusch.

### 3.3 RECONSTRUCTING PREHISTORIC DIETS

Our reconstructions of prehistoric diets are based on several sources of information. While none of these sources provides a complete or definitive picture of prehistoric diet and subsistence, when taken together, they allow us to speculate with some confidence on the likely composition of diets consumed by Middle Stone Age hunter-gatherers. The archaeological record provides, at best, a partial reconstruction of Middle Stone Age subsistence strategies and economic activities based on the interpretation of patterning in the composition of faunal remains (Bird 1997). The exploitation of marine resources by Middle Stone Age hunter-gatherers is firmly attested by the presence of their inorganic residues in numerous securely dated archaeological deposits. Their absence from archaeological contexts predating the Middle Stone Age does not rule out their occasional consumption during this time (Parkington 2003). Intertidal shellfish, particularly large limpets and black mussels, are the most significant component of faunal assemblages from Middle Stone Age coastal sites. In previous years, marine molluscs were primarily regarded as a source of protein. Current models highlight the potential of these and other marine resources as a source of essential fatty acids. The remains of seals and, perhaps, penguins and cormorants, most likely represent carcasses or portions of carcasses obtained from incidental wash-ups.

The remains of terrestrial fauna in archaeological deposits accumulated as a result of the activities of humans as hunters and/or scavengers, or of animals, necessitating a thorough understanding and examination of taphonomic processes (Marean *et al.* 2000). As has been previously mentioned, the hunting proficiency of Middle Stone Age people remains contested among archaeologists, although most agree that they were involved in active hunting at least to some degree. In his alternative to the marine hypothesis, Speth (2010) suggests that certain portions of terrestrial animals, notably the brain and bone marrow, would have been excellent sources of fat, and that they were targeted for this reason rather than to provide protein.

Prehistoric hunter-gatherers' exploitation of plant foods, their most likely source of energy-rich carbohydrates, is considerably more difficult to reconstruct as a result of their perishability. A fairly good record for the exploitation of plant resources, notably the corms

or rootstocks of the *Iridacea* family, exists for the Later Stone Age in the eastern and southwestern Cape. In the western Cape, floral remains in the form of corm bases and tuber casings have been recovered from several archaeological contexts in the Olifants River Valley and Verlorenvlei regions. These are primarily cave sites with Later Stone Age occupations post-dating 2000BP, namely De Hangen, Elands Bay Cave and Andriesgrond. The remains from these sites are from iridaceous genera such as *Watsonia*, *Chasmanthe*, *Moraea*, *Gladiolus*, *Homeria* and *Babiana*, which are assumed to have been an important dietary component of the sites' prehistoric inhabitants (Liegme 1987; Parkington 1977; Parkington and Poggenpoel 1971).

The written accounts of European travellers exploring the Olifants River Valley region during the second half of the seventeenth century provide some additional insight into the subsistence strategies and dietary habits of indigenous people during the final stages of the Stone Age. Van der Stel remarked that the local people referred to as Soaqua subsisted primarily on the bulbs of flowers called "uyenjies", as well as tortoises, caterpillars and locusts (Parkington 1977). Several European observers noted that bulbs were usually consumed just after flowering (Barrow, Sparrman and Thunberg cited in Parkington 1977). It is at this time that corms reach their maximum size and possibly, nutritional value, in order to supply the plant with sufficient food for the next sprouting (Liegme 1987). The flowering seasons of iridaceous plants are staggered throughout spring and summer. Thus, the presence of remains from particular genera at archaeological sites serves as a useful indicator of seasonality (Liegme 1987; Parkington 1976, 2001). Some, notably the larger *Watsonia* and *Chasmanthe*, do not shed their leaves during the dry season, and thus remain visible for longer than those which do shed their leaves. Thus, a seasonal round focusing on smaller genera visible only during flowering and larger ones visible for the greater part of the growth cycle would have been optimal (Parkington 1977).

Archaeological evidence for the exploitation of iridaceous plants by Later Stone Age hunter-gatherers in the eastern Cape derives primarily from two cave sites, namely Scott's Cave and Melkhoutboom Cave, where dry conditions favoured the preservation of floral remains. At the latter site, plant-rich bedding layers yielded the remains of numerous Iridaceae and Cyperaceae; *Watsonia* was the best represented genus, followed by the smaller *Moraea*. Some

relatively coarse patterns in mid- to late-Holocene collection strategies can be inferred. Exploitation appears to have been geared towards geophytes with a wide geographical and seasonal range. The collection of plants which have their own nutrient storage systems in effect nullifies the need for artificial food storage technologies among hunter-gatherers. Seasonal patterns in resource exploitation, site occupation and migration would have been dictated by rainfall patterns, growth cycles and fluctuations in the availability and palatability of corms. These plants are likely to have been dietary staples for Later-Stone Age hunter-gatherers occupying the Cape Folded Belt during spring and summer. During seasons in which these staple plant foods were unavailable, they may have been replaced by other abundant and predictable resources, namely intertidal shellfish. Burning during autumn and winter would have stimulated the growth of iridaceous plants (Deacon 1976).

The economic activities and subsistence strategies of modern hunter-gathers help elucidate those of prehistoric people. Ethnographic studies conducted among the indigenous inhabitants of Australia and the Torres Strait Islands are a fruitful source of information on coastal foraging and the role of marine resources in the diet. Among the Meriam Torres Strait Islanders, for instance, fish, marine turtles, and to a lesser extent, intertidal molluscs are the main sources of protein, providing 600 calories per person, per day. Furthermore, certain types of marine foraging are preferentially performed by different members of the population. Women are frequently involved in shellfish and turtle collecting and beach fishing. Children under the age of fifteen actively participate in beach fishing and shellfish collecting, often preparing and consuming the shellfish they have collected themselves (Bliege Bird and Bird 2002; Bird and Bliege Bird 2000). Meehan's (1972) research among the Anbarra of Australia highlights women and children's participation in marine foraging, provides insight into their shellfish collection strategies and methods of consumption and disposal, and defines the role of shellfish in their diet and subsistence economy. Similar patterns have been inferred for Middle Stone Age people.

Entomophagy, the practice of consuming insects, has been documented in diverse regions of Africa, Asia, Australia and South and Central America (DeFoliart 1999). Edible insects remain a significant dietary component among non-western people exposed to varying degrees of urbanisation. A wide variety of insects is used as food by people living in Africa.

More than 60 species of insects are reportedly eaten by people living in the Democratic Republic of Congo and Zambia, while more than 30 species are eaten in South Africa and Zimbabwe. Caterpillars, winged termites, beetle grubs and grasshoppers are the most commonly exploited (Banjo *et al.* 2006; DeFoliart 1999). They serve as an inexpensive and important source of protein during food shortages, at times of seasonal abundance and availability, and as a regular part of the normal diet (Banjo *et al.* 2006; DeFoliart 1999). In some African countries, notably Zimbabwe, they are usually collected by women (DeFoliart 1999). Insects probably had a similar role in prehistoric diets and subsistence patterns.

Extensive ethnographic research undertaken among modern hunter-gatherers in eastern and southern Africa has transformed archaeologists' and anthropologists' perceptions of hunting and gathering, particularly with regard to the relative contribution of each to the diet.

Richard Lee's (1968, 1979) seminal work among the !Kung of the Kalahari highlighted the importance of gathered plants foods in everyday subsistence. In contrast to game animals, which are unpredictable and sparsely distributed on the landscape, edible plants are plentiful and predictable, and thus constitute the primary component of diets in this region. Meat acquired through the hunt is assigned a higher social value, but provides less than half (around 40%) of the daily caloric intake. Although hunting remains a prestigious activity undertaken by males, it is less energetically rewarding than gathering undertaken by females (Lee 1968, 1979). Ethnographic research among the Hadza of East Africa further suggests that big-game hunting plays a more prominent role in competitive male displays than it does in daily subsistence and family provisioning. O'Connell *et al.* (2002) report that Hadza men successfully acquire large carcasses through hunting or scavenging only once every 30 hunter – days, with a daily failure rate of almost 97%. Middle Stone Age hunter-gatherers would have had similar success rates. Furthermore, the distribution of meat following a successful hunt is not controlled by the hunter responsible for the kill and he and his family do not receive more or larger shares of either his kill or animals brought down by other hunters (O'Connell *et al.* 2002; Hawkes *et al.* 2001). Plant foods are therefore also an important part of Hadza diets. It should be noted, however, that not all of the plant resources exploited by modern hunter-gatherers would have been available to their prehistoric counterparts in the southwestern Cape. San living in certain parts of the Kalahari, for instance, have access to large quantities of mongongo nuts, which are an

excellent source of protein and fat, whilst the Hadza harvest a wide range of edible fruits and nuts (Speth 2010).

Several researchers have used observations of modern hunter-gatherers to reconstruct the nutrient content of prehistoric diets. Eaton *et al.* (1997) for instance, used syntheses of major ethnographic works to construct a model describing the so-called “central tendency” of Palaeolithic diets. They suggest that prehistoric diets were relatively high (>30%) in protein, with animal and plant foods accounting for 35% and 65%, respectively, of dietary resources by weight. They propose a daily protein intake of between 2.5 and 3.5g/kg body weight for Stone Age people; this figure is considerably higher than that currently recommended by nutritionists. Palaeolithic or Stone Age diets are also characterised as being high in non-cereal plant foods and low in fat (20-25% of energy consumed), with a fairly equal distribution of omega-6 and omega-3 polyunsaturated fatty acids (Jenike 2001; Eaton *et al.* 1997). There are, however, several shortcomings in the high protein, high carbohydrate and low fat model, as it does not reflect the great diversity characteristic of hunter-gatherer populations in different regions. Ethnographic research conducted among the Efe and !Kung in southern Africa suggests that protein accounts for a considerably lower proportion of daily energy (13% and 16%, respectively) than expounded by the central tendency model (Jenicke 2001). Other populations in the subtropics, notably the Ache and the Hiwi, and in circumpolar regions, consume even greater proportions of protein than suggested by Eaton and colleagues. Arctic populations dependent on cold-adapted animals for part of the year derive considerably more energy from fat (between 35% and 47%) than those hunting lean African ungulates. The central tendency model furthermore does not account for the consumption in large quantities of seasonal resources when these are available, or seasonal fluctuations in the fat content of regularly hunted animals (Jenicke 2001).

The results of an extensive survey of modern hunter-gatherers compiled by Cordain and colleagues (2000) are consistent with diets high in animal protein of marine and/or terrestrial origin. Of the 229 societies surveyed, 73% derive more than half of their energetic requirements from animal foods, while only 14% acquired more than half from plant foods. Twenty percent of these hunter-gatherers are classified as highly or even exclusively dependent on the proceeds of hunting and/or fishing. Overall, animal foods account for

between 19% and 50% of the total energetic requirement of the societies included in the survey (Cordain *et al.* 2000).

Ongoing excessive consumption of lean meat has been said to produce protein toxicity, also termed “rabbit starvation”, a condition documented among early European explorers forced to survive exclusively on very lean protein (Ben-Dor *et al.* 2011; Speth 2010; Mann 2000). In order to avoid a negative energy balance, hunter-gatherers consuming high protein diets would have had to increase their intake of either fat or carbohydrate-rich plants. The effective exploitation of plant foods is constrained by a number of physiological and technical factors, including the presence of indigestible fibres and toxins, seasonal availability of edible species, and time-consuming and laborious nature of plant food collecting. The consumption of animal fat is therefore obligatory (Ben-Dor *et al.* 2011). A number of strategies could be employed by hunter-gatherers to maximise their fat intake. These include the preferential hunting of larger species with more fat or of species with seasonal fat stores, or the selective butchery and consumption of fat-rich portions of the carcass (Speth 2010; Cordain *et al.* 2000; Mann 2000). In this context, Middle Stone Age hunter-gatherers’ preoccupation with prime-age eland appears deliberate and optimal (Speth 2010) rather than indicative of a lack of hunting proficiency.

Kuipers *et al.* (2010) tested multiple dietary scenarios in different environmental settings including the savannah, the land-water ecotone and a combination of both, in order to estimate the range of nutrient intakes of early modern humans. All of the diets tested, including a selective terrestrial diet from which aquatic foods were excluded, a non-selective aquatic diet from which meat from terrestrial fauna was excluded, and selective and non-selective diets incorporating both aquatic and terrestrial resources, provided sufficient long-chain polyunsaturated fatty acids, notably EPA and DHA. The range of dietary options available to prehistoric people was limited by the physiological ceiling on protein intake, which should not exceed 35% of energy due to the high costs of protein metabolism. Selective consumption of fat-rich organs in terrestrial animals, including brains, bone marrow and adipose tissue, would have increased the fat and long-chain polyunsaturated fatty acid content of the diet. Kuipers *et al.* (2010) conclude that while encephalisation was not hampered by a lack of preformed DHA in savannah or aquatic environments, edible

plants and fish occurring in the land-water ecotone would have been abundant, easily collected source of micronutrients, vitamins and omega-3 fatty acids.

### 3.4 NUTRITIONAL REQUIREMENTS OF PREHISTORIC HUNTER-GATHERERS

Recommended Daily Intakes (RDI's) and Recommended Dietary Allowances (RDA's) cited by nutritionists have been formulated for modern populations, based on the mean stature and body weight of modern, mostly American or European individuals. Needless to say, these are not universally applicable, and are not good standards for prehistoric hunter-gatherers. Reconstructing the stature and especially, the mean body weight, of Middle Stone Age people is challenging, as skeletal remains are partial and poorly preserved. Pfeiffer and Sealy's (2006) investigation of body size patterns among Holocene hunter-gatherers living in the southern and western Cape, based on measurements of maximum femoral lengths and femoral head diameters on dated adult skeletons, shows that these people had the small body size and short stature characteristic of historical Khoesan populations (Eiden *et al.* 2012; Pfeiffer and Harrington 2011; Pfeiffer and Sealy 2006). Anthropometric studies of modern hunter-gatherers indicate that mean stature and body weight varies considerably across different regions (Jenike 2001). Figures recorded for three populations in Africa, namely the G/wi and Dobe !Kung in southern Africa and Hadza in Tanzania are quite low. Mean body weights for these communities range between 49 and 55kg for males and 41 and 50kg for females.

I have followed Ben-Dor *et al.* (2011) and Leonard *et al.* (2007) in using weights of 58 and 49kg for Middle Stone Age males and females, respectively, based on inferences from the African fossil record. Protein requirements for adult males and females are based on 0.8g/kg body weight/day; the requirements of pregnant and lactating women and children have been adjusted proportionally (Table 3.1). The daily energy requirement for adult males is based on the formula  $900 + 10W \times 1.8$ , where  $W$  = body weight and a multiplication factor of 1.8 is used for highly active individuals. The requirement for females is based on the formula  $700 + 7W \times 1.8$  (Dwyer 2011). Kilocalories have been converted into kilojoules following the formula  $1\text{kcal} = 4.2\text{kJ}$ . Daily energy requirements for pregnant and lactating women are increased by 350kcal/day and 550kcal/day, respectively (Bulletin of the World Health Organization 1979). Those for children have been adapted from the Bulletin of the

World Health Organization (1979). Requirements for selected micronutrients (Dwyer 2008) and essential fatty acids are summarised in Tables 3.2 and 3.3. These are not affected by weight differences between modern and prehistoric people.

Table 3.1 Recommended Daily Intakes for protein and energy for Middle Stone Age people.

Gender and Age	Protein (g/day)	Total energy (kJ/day)
Adult male	46	11 190
Adult female	39	7 890
Pregnant female	46	9360
Lactating female	46	1020
Adolescent male	43	11 190
Adolescent female	39	7890
Child 9-13 years	29	7140
Child 4-8 years	16	7140
Child 1-3 years	13	3372

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Table 3.2 Recommended Daily Intakes for selected micronutrients.

Gender and Age	Iron (mg/day)	Copper (mg/day)	Zinc (mg/day)	Selenium (mg/day)	Iodine ( $\mu$ g/day)
Adult male	8	0.9	11	0.55	150
Adult female	18	0.9	8	0.55	150
Pregnant female	27	1	11		220
Lactating female	9-10	1.3	12		290
Adolescent male	11	0.89	11		150
Adolescent female	15	0.89	9		150
Child 9-13 years	8	0.7	8		150
Child 4-8 years	10	0.44	5		90
Child 1-3 years	7	0.34	3		90
Infant 7-12 months	11	0.33	3		130
Infant 0-6 months	0.27	0.20	2		11

Table 3.3 Recommended Daily Intakes for polyunsaturated fatty acids.

Gender and Age	LA(g/day) <sup>1</sup>	ALA (g/day) <sup>1</sup>	EPA&DHA (g/day) <sup>2</sup>	DHA(g/day) <sup>3</sup>
Adult male	17	1.6	0.65	
Adult female	12	1.1	0.65	
Pregnant female	13	1.4	0.65	0.30
Lactating female	13	1.3	0.65	0.20
Adolescent male	16	1.6	0.65	
Adolescent female	11	1.1	0.65	
Child 9-13 years	10-12	1-1.2	0.65	
Child 4-8 years	10	0.9	0.65	
Child 1-3 years	7	0.7	0.65	
	Omega-6	Omega-3		
Infant 7-12 months	4.6	0.5		
Infant 0-6 months	4.4	0.5		

<sup>1</sup>Dwyer 2008

<sup>2</sup>Kris-Etherton *et al.* 2000

<sup>3</sup>Kris-Etherton *et al.* 2009

### 3.5 SUMMARY

In this chapter, the physiological role of nutrients and implications of deficiencies have been discussed and described. Archaeologists' continued preoccupation with the role of nutrition in human evolution has been highlighted, and changing trends in the scenarios they construct to account for the development of modern *H. sapiens* have been reviewed. Modern humans' requirements for a number of essential macronutrients, micronutrients and fatty acids have been presented, and several stages in the human lifecycle, notably pregnancy, lactation, gestation, infancy, and sometimes childhood and adolescence, where our demand for particular nutrients may be increased, have been identified. The endogenous synthesis and storage of EPA and DHA were discussed and it was indicated that women under oestrogenic influence could synthesise significant DHA but requirements

during pregnancy and lactation might not be met. Reconstructions of prehistoric, particularly Middle Stone Age, diets on the basis of archaeological, ethnographic and other evidence have been presented and critically examined, and some of the marine and terrestrial resources likely to have been exploited by Middle Stone Age hunter-gatherers have been mentioned. The nutritional requirements of modern humans have been adjusted to suit their Middle Stone Age counterparts. In the following two chapters, the results of shellfish and nutrient analyses will be presented, and the implications of these findings for Middle Stone Age diets, particularly the role of marine resources, will be examined.

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## CHAPTER FOUR

### SHELLFISH COLLECTING STRATEGIES ALONG THE ATLANTIC WEST COAST

#### 4.1 INTRODUCTION

The substantial body of work dealing with Middle Stone Age people's economic and subsistence strategies in relation to the shoreline and coastal resources was discussed and reviewed in Chapter Two. In this chapter, information on the shellfish assemblages from a recently re-excavated MSA site, Hoedjiespunt (HDP)1, and several previously excavated LSA shell middens are presented in order to shed new light on current debates regarding MSA and Later Stone Age coastal foraging. HDP1 (Figure 4.1) is one of several sites in the western Cape with a record of shellfish exploitation dating to around the Last Interglacial (120 ka). Material from the 2011 field season at this site is combined with that from the previous excavation, and is compared to the well-documented shellfish assemblage from Ysterfontein. The latter site, located 70km north of Cape Town, is the only shell-bearing Middle Stone Age site in the region to have been systematically excavated (Steele and Klein 2008). Archaeological deposits contained within this deeply stratified rock shelter were exposed in the 1980s in the course of construction activities aimed at widening the access road to the adjacent boat harbour, and were excavated over several field seasons (Steele and Klein 2008; Klein *et al.* 2004).

The prehistoric dune cordon near the mouth of the Verlorenvlei (Figure 4.2) is one of the best studied regions in Later Stone Age South African archaeology. Dunefield Midden (DFM), excavated by John Parkington and his colleagues from the University of Cape Town, provides an almost unique window into the shellfish collecting strategies of prehistoric people who visited the site during the Late Holocene (Parkington *et al.* 2009, 2013, 2014; Tonner 2005). More than 2000kg of shellfish residue accumulated in the course of several short episodes of occupation was recovered, identified and analysed. The lack of stratigraphy at this site lent itself to horizontal rather than vertical excavation, allowing for the recovery of material from a wide surface area (Tonner 2005). The finely resolved temporal and spatial framework at Dunefield Midden allows for a novel interpretation of changes in mollusc species frequency and limpet sizes (Parkington *et al.* 2009, 2013). The site

of Elands Bay Cave, with its deep depositional history spanning more than 10 000 years of the Holocene, provides a different and yet complementary perspective on the LSA prehistory of the region. Stratified, anthropogenic deposits dating to 13600-300BP reflect episodes of fairly regular occupation in the form of relatively short visits to the cave by LSA people, interspersed with shorter and longer periods of disuse (Parkington *et al.* 2014).

Numerous other shell middens in the Elands/Lambert's Bay region document important developments and changes in the settlement and subsistence strategies of LSA people living along the southwestern Cape. Some of the largest "megamiddens" on the subcontinent accumulated between 3000-2000 BP in this area (Jerardino 2012, 2010). Other shell middens in the vicinity, for example, Connie's Limpet Bar and Borrow Pit Midden, serve as a record of LSA people's adaptive strategies during the terminal Pleistocene, a time during which contact with Europeans disrupted prehistoric lifeways (Jerardino *et al.* 2009a and b). In this chapter, previously unpublished information on the shellfish assemblages from three Later Stone Age shell middens at Lynch Point near Saldanha Bay (Figure 4.1), and a "DFM-like" occurrence excavated by John Parkington and colleagues in 1996, is presented.

The shellfish assemblages from four LSA sites excavated by the Archaeology Contracts Office (ACO) in Brandsebaai, Namaqualand, and one MSA site in the same vicinity examined by John Parkington, are also examined. With the exception of research conducted at Spoegrivier Cave by Webley (1992, 2007), and more recently, at several other coastal sites in Namaqualand investigated by Dewar (2008) and Orton *et al.* (2005), relatively little is known about LSA hunter-gatherers in this region. Shellfish remains from the LSA sites at Brandsebaai (BSB) will serve as a useful regional and temporal comparison to observations from the well-researched Verlorenvlei area. Changes in the relative abundance of different shellfish species, notably mussels and limpets, are often attributed to changes in coastal morphology (Steele and Klein 2008), and may also reflect separate episodes or palimpsests of occupation (Orton *et al.* 2005). Parkington and colleagues (2014) interpret mussel – and limpet-dominated assemblages as evidence of different shellfish gathering strategies. Differences in mean shellfish size, especially between specimens from MSA and LSA sites, are attributed to various environmental factors which have an affect on their growth and productivity, or to human predation (Steele and Klein 2008). Observations of shellfish

species frequencies and, more importantly, mean sizes, from the Namaqualand middens will be a useful addition to current debates about MSA people's foraging abilities and population sizes.



Figure 4.1 Map showing the location of Middle Stone Age (Sea Harvest and Hoedjiespunt) and Later Stone Age (Lynch Point) shell middens near Saldanha Bay on the southwestern Cape coast. Illustration by Neil Rusch.

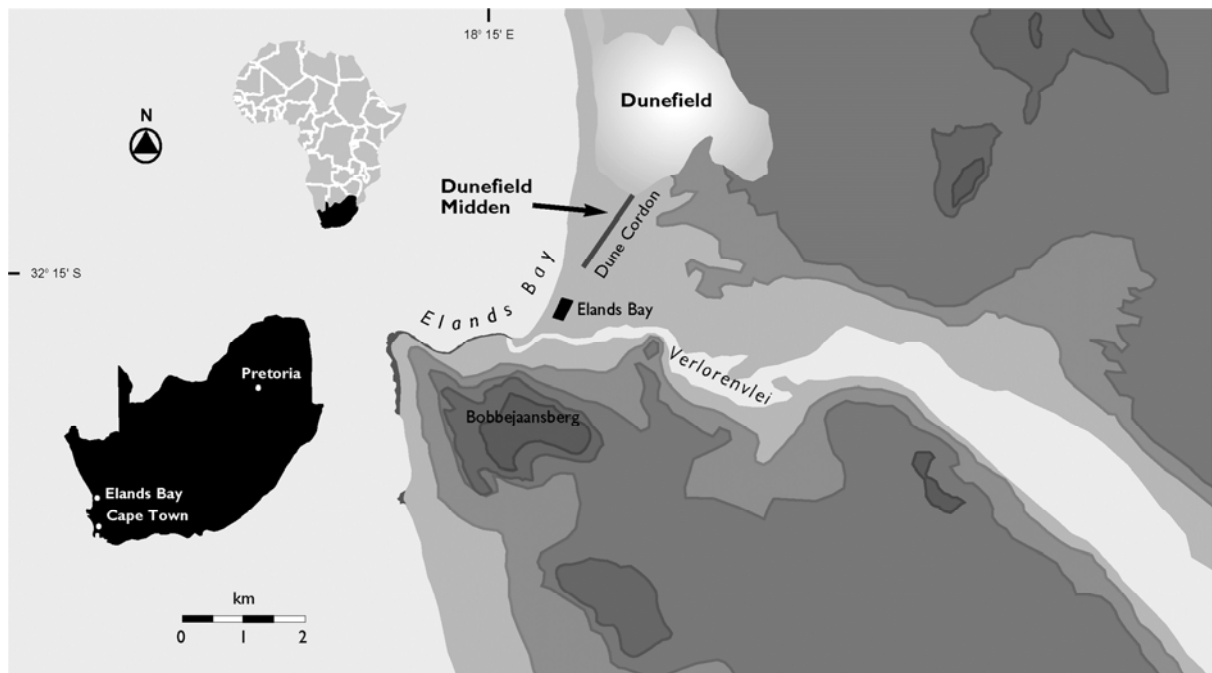


Figure 4.2 Map showing the location of the prehistoric dune cordon, Elands Bay and the Verlorenvlei in the southwestern Cape. Illustration by Neil Rusch.

#### 4.2 FIELD AND LABORATORY METHODS

Some discussion of the fieldwork procedures and analytical techniques used during the excavation of the abovementioned sites, and quantification and analysis of the shellfish remains is necessary. The site of Hoedjiespunt 1 was re-excavated in 2011 by a joint team from the Universities of Cape Town and Tübingen, in part to augment lithic and faunal assemblages derived from an earlier investigation by Parkington in the 1990s. The excavation proceeded in 18m<sup>2</sup> units, according to Parkington's original grid. In each quadrat, the deposits were removed in 2-3cm "abtrage" or spits following the natural slope of the sediments and geological layers. Some of the sediments were highly compacted and difficult to remove without damaging artefactual and faunal remains. Individual finds >2cm were piece plotted in the field using a Leica Total Station and EDM programme. Buckets of sediment were wet-screened with seawater and put through 5mm and 2mm mesh sieves in order to increase the recovery of archaeological material (Will *et al.* 2013). The material was then sorted into lithic and non-lithic components. Further sorting, identification and analysis of the lithic and shellfish assemblages were conducted at the Universities of Tübingen and Cape Town, respectively.

The Later Stone Age material included in this analysis derives from sites which were excavated several years or even decades ago but remain unpublished. Shellfish remains from Lynch Point and Brandsebaai were recovered in the course of rescue excavations aimed at minimising damage to archaeological deposits caused by construction in the case of the former, and mining in the case of the latter. Dunefield Midden 11 was excavated by John Parkington and his colleagues in an attempt to emulate the large-scale horizontal excavation carried out at the original Dunefield Midden site. Standard excavation techniques were employed during all of these excavations. Deposits were removed using brushes and trowels, in accordance with their stratigraphy. The sediments were screened and artefactual and faunal remains retained for sorting and identification. Counts and measurements of shellfish were recorded on shellfish analysis forms, and subsequently collated for analysis.

Shellfish remains are identified to generic or specific level where possible, and MNI's are determined for the different taxa. The Minimum Number of Individuals (MNI) represented within a sample is one of the most common and informative measures of relative abundance employed in the analysis of faunal remains, including molluscs. For bivalves, left and right hinges are counted separately and the higher number is used for the MNI. For limpets, whelks and turban shells, the apices are counted (Jerardino 1997). To determine the mean size of limpets, the total length of unbroken specimens is measured. Specimens <20mm are considered as subadults, and are excluded. Measurements of the mean size of black mussel hinges are derived from the prismatic band located along the border of the shell opposite the anterior retractor scar (Kilburn and Rippey 1982). The width of the prismatic band is proportional to the total length of the shell and thus serves as a useful proxy for size in incomplete and broken specimens (Buchanan 1985). Specimens with a prismatic band width <4.5mm are juveniles, and are excluded from measures of size and relative abundance (Jerardino 1997). The statistical significance of size differences in limpets and mussels within and between sites is determined using the Mann-Whitney U test. This non-parametric test measures the difference between two medians in samples where data are not normally distributed. Statistical analyses were conducted using a programme known as Graphpad Prism. Box and whisker plots depicting and comparing mean limpet and mussel sizes were generated using Statistica. The presence and relative abundance of certain

elements in a shellfish assemblage that cannot be counted to determine their MNI can only be measured in terms of weight. This applies to fragile or friable species such as the large abalone, *Haliotis midae*, which are usually only preserved in archaeological deposits as uncountable fragments. It also applies to barnacles. While alive, a single one of these organisms consists of a number of “flowers” which are introduced into sites in a number of ways. Waterworn shells and pebbles, that is, small particles of worn and polished shell and stone carried into sites as part of the byssus contents of mussels, are sometimes retained in the 1.5mm sieved fraction (Jerardino 1997).

### 4.3 RESULTS OF SHELLFISH ANALYSIS

#### 4.3.1 Hoedjiespunt (HDP) 1 and 3

Hoedjiespunt 1, located at the southern edge of the Hoedjiespunt Peninsula near the harbour town of Saldanha Bay, has long been recognised as one of the earliest MSA shell middens on the southwestern Cape coast. This site is actually one of several archaeological and palaeontological assemblages forming part of a large fossil dune formation resting on a wave-cut platform approximately 6m above the current sea level (Grine and Klein 1993; Stynder 1997). Excavations conducted between 1994 and 1996 by Parkington and colleagues yielded relatively small samples of faunal and lithic remains. Surface material was collected at the adjacent locality of Hoedjiespunt 3. Hoedjiespunt 1 was re-excavated in 2011 by a joint team from the Universities of Cape Town and Tübingen, in response to intense scholarly interest in MSA coastal adaptations, and large-scale excavations at similarly dated sites such as Ysterfontein and Pinnacle Point. The renewed excavations were conducted to assess the extent of the archaeological horizons, refine the chronology of the occupation, and augment existing collections of artefactual and faunal remains.

A stratigraphic framework based on and consistent with that set up during the earlier investigation of the site was employed, and an area of 18 square meters was excavated to the depth of 1.5m. HDP1 was comprised of distinct archaeological horizons, which were found to be in primary context. Stratified layers of occupational debris were preserved beneath a thick calcrete carapace or modern surface layer designated as HUMUS (Figures 4.3 and 4.4). A firmly cemented shell midden (SHEM) consisting of mussels and limpets and

some artefactual remains lay at the base of two meters of calcrete carapace capping the Hoedjiespunt hill. This was underlain by a layer of nodular sand (NOSA), overlying a fauna- and artefact-rich deposit of dark loamy sediment (DAMA). A layer of fine, shelly sand (SHES) demarcated the end of the archaeological and beginning of the palaeontological horizons (Will *et al.* 2013; Stynder 1997). Uranium series dates place the occupation of the archaeological site to before 74ka, most likely between 110-120ka. The faunal and artefactual remains are also consistent with occupation during the last interglacial, or marine isotope stage 5e (Stynder 1997).

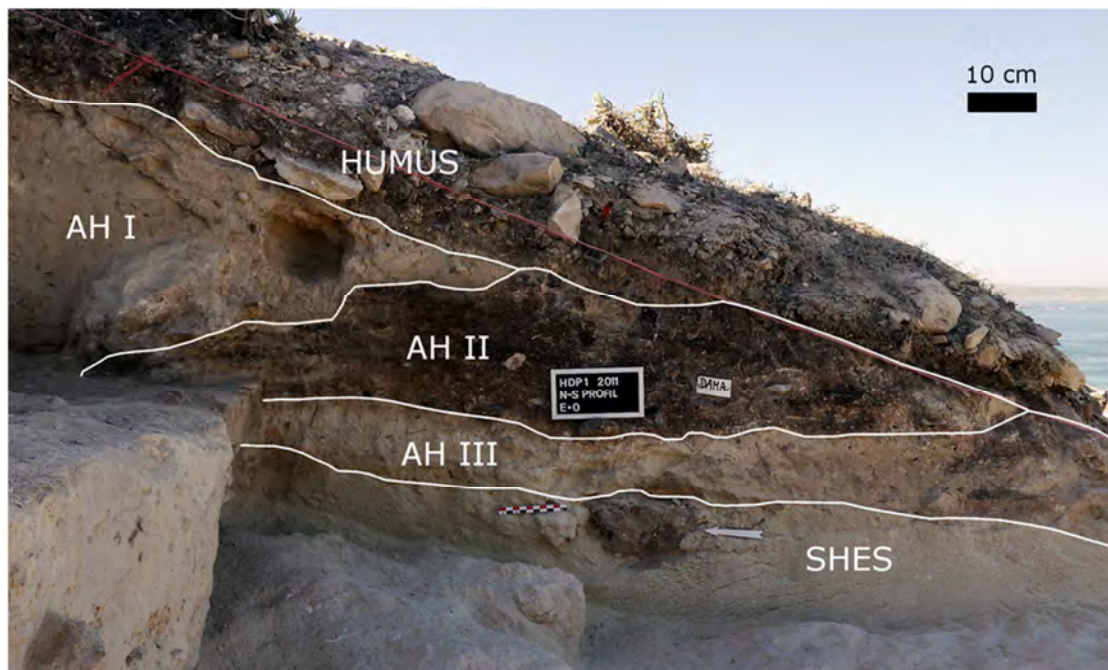


Figure 4.3 Photograph of the stratigraphic section at Hoedjiespunt 1, taken by N. Conard.

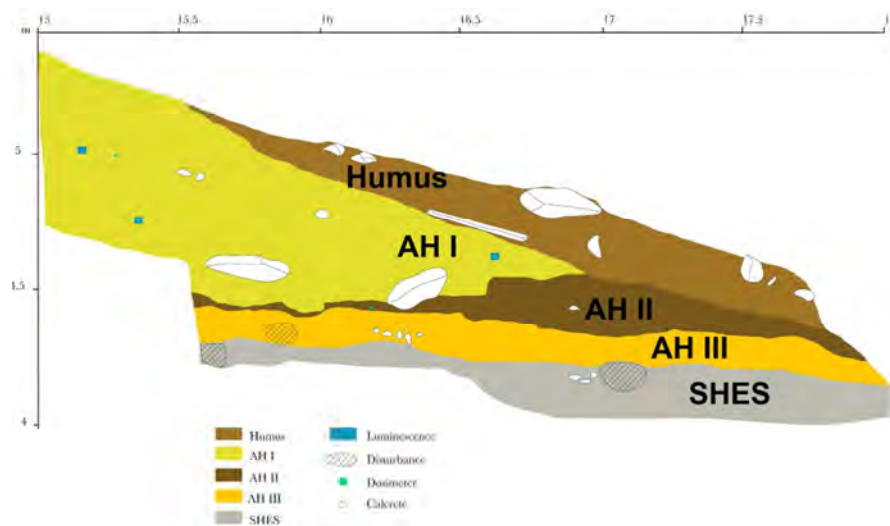


Figure 4.4 Drawing of the stratigraphic section at Hoedjiespunt 1, from Will *et al.* 2013.

Analysis of the enlarged lithic and shellfish assemblages from HDP1 represents a significant contribution to the MSA archaeological record of this region. Manual Will analysed lithic material previously considered as adiagnostic (Stynder 1997), pooling the samples from 1994-1996 and 2011. Shellfish remains from the different field seasons have also been pooled, augmenting the sample considerably.

The shellfish assemblage from HDP1 (Table 4.1 in Appendix A) is dominated by the large mid-tidal limpet, *Cymbula granatina* and, to a lesser extent, the black mussel, *Choromytilus meridionalis*. These two species account for 61.2% and 24.3% of the recovered shellfish remains, respectively. *Scutellastra argenvillei*, a large limpet which inhabits the lower intertidal, and the smaller *Scutellastra granularis*, which favours the upper reaches of the shore, are present in much smaller proportions of 4.8% and 3.3%, respectively. Other limpets, bivalves and whelks are a very minor component of the assemblage. The HDP1 material is similar to, and different from, the assemblage from Ysterfontein (Avery *et al.* 2008). Black mussels outnumber granite limpets at the latter site; the relative abundance of granular and Argenville's limpets is similar.

Mean and median sizes for the three predominant limpet species recovered from HPD1 are presented in Figure 4.5 below, alongside those for shells derived from a surface collection done by Parkington and colleagues at HDP3. This archaeological site is located a few kilometres away from, and is roughly contemporary with, HDP1 (Mathews *et al.* 2005). C.

*granatina* from HDP1 ( $n=72$ ) and HDP3( $n=32$ ) are relatively large, with mean sizes of 69.6mm and 68.3mm, respectively. Very few measurable specimens of the other limpet species were recovered from HDP1; the surface collection at HDP3 yielded more complete and measurable shells. Mean sizes of 47.1mm and 46.6mm were recorded for *S. granularis* from HDP1 ( $n=4$ ) and HDP3 ( $n=67$ ). Large mean sizes of 80.3mm ( $n=11$ ) and 78.8mm ( $n=14$ ) were obtained for *S. argenvillei* from these two assemblages. Mean sizes for all three limpet species are similar to those reported for Ysterfontein (YFT). Granite limpets from eight of the excavated units from Ysterfontein site range between 64.9mm and 73.1mm; granular and Argenville's limpets from groups 1-7 and 8-13 ranged between 41.1mm – 46.2mm and 79.1mm-77.9mm, respectively (Avery *et al.* 2008). As has been previously stated, measures of the prismatic band width of *C. meridionalis* serve as a proxy for overall size. Left hinges from HDP1 ( $n=125$ ) are small (Figure 4.6), and have a mean prismatic band width of 7.3mm; right hinges from the larger samples from HDP3 ( $n=566$ ) yielded a mean of 7.0mm (Figure 4.5). Mean prismatic band widths  $>7.4$ mm and  $<8$ mm were recorded for specimens from YFT (Avery *et al.* 2008).

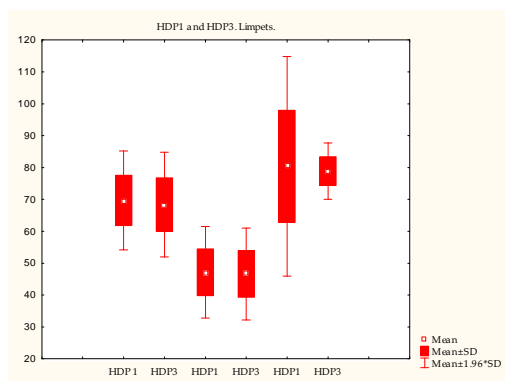


Figure 4.5 Mean total length of *C. granatina*, *S. granularis* and *S. argenvillei* (mm) from HDP1 and HDP3.

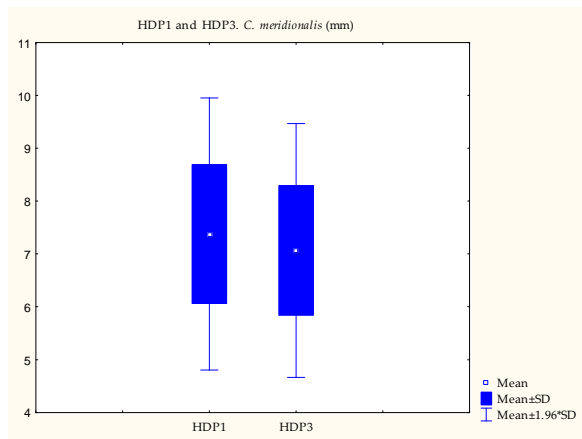


Figure 4.6 Mean prismatic band width of *C. meridionalis* (mm) from HDP1 and HDP3.

#### 4.3.2 Lynch Point (LP), Mykonos

The Lynch Point, Mykonos sites include several shell middens located along the eastern shore of the Langebaan lagoon almost directly opposite the entrance to Saldanha Bay. Excavations at these sites were conducted in 1988 as a joint venture between the ACO and Club Mykonos, Langebaan, in an attempt to minimise damage caused by the construction of the club's new harbour and housing facilities. Shellfish remains from three of these sites, LP18, 19 and 20, are discussed in this thesis. Three other sites, designated LP14, 15 and 16, were partially or wholly destroyed by earthmoving equipment prior to the beginning of systematic excavations. At LP16, located near the rocky spur north of Leeutjiesklip, ephemeral scatters of shell and bone as well as several square meters of *in situ* deposit beneath a layer of sterile sand in the centre of a hill were preserved. Shellfish and other faunal remains on the surface were collected and the *in situ* deposits systematically removed before the hill was completely destroyed (Parkington 1988 unpublished report).

LP18 represents a scatter of shell and bone rapidly accumulated in a series of uneven rocky platforms above the high water mark (Parkington 1988 unpublished report). A four meter long trench was dug at right angles to the shoreline and shellfish remains, fish and mammal bones and some ceramic sherds were recovered from the shallow archaeological deposits. LP19 was comprised of more extensive and deeper shell midden deposits which, like those at LP18, were focused on a series of granite platforms. Ten one meter test holes were dug down to the granite bedrock, yielding the remains of shellfish, fish, and sheep. The sheep bones, as well as some ceramics, derive from the basal layers of the deposit (Parkington 1988

unpublished report). LP20 was similar in structure and contents to its two counterparts. The excavation of this site, which proceeded parallel to the shore, revealed the existence of an emerged shoreline presumed to be the remnants of a previous high sea level at around 4000-5000BP. Among the excavated remains were shellfish residues, the remains of small bovids, domestic fauna including sheep or goats, bones from dune molerats, snakes and tortoises, some fragments of ostrich eggshell and a single ceramic sherd (Parkington 1988 unpublished report).

All of the Lynch Point middens (Table 4.2) are dominated by the three limpet species most abundant on west coast rocky shores, namely *C. granatina*, *S. granularis* and *S. argenvillei*. Some variation in the relative proportions of these species is apparent in the three different sites. Two other large limpet species, *S. cochlear* and *C. oculus*, are also present in significant quantities and varying proportions in all three sites. Limpet species from the upper-, mid- and lower-intertidal are represented. Whelks of the genus *Burnupena*, which inhabit the upper reaches of the shore, are fairly abundant in all of the Lynch Point middens. This is not unexpected in sites where the remains of sheep and pottery have been found. The balanced representation of species from the upper and lower intertidal at Lynch Point indicates broad exploitation strategies. The presence of several low-shore species including *S. argenvillei* and *S. cochlear*, as well as the large abalone *Haliotis* sp., suggest that the lower intertidal zone was easily accessible during low tides in the sheltered conditions of Saldanha Bay. Black mussels are not a major component of the Lynch Point middens and white mussels, *D. serra*, are completely absent. Barnacles, which were recovered from all of the Lynch Point middens, account for only a small percentage of the recovered remains, by weight.

The smallest of the three sites excavated in 1988, LP18, has been dated to 2680BP. The shellfish assemblage is characterised by slightly higher proportions of the small limpet, *S. granularis*, than its larger counterparts, *C. granatina* and *S. argenvillei*. The former accounts for 22.3% of the countable shells recovered, while the latter constitute 15.5% and 15.9% of the assemblage, respectively. The large, slow-growing *S. cochlear*, commonly found in the lower intertidal, is only slightly less numerous, at 11.3%. Whelks (*Burnupena* sp.) are present in similar proportions to *S. granularis*, and constitute 22.6% of the identified shellfish remains.

Black mussels make a negligible contribution (2.9%) to the assemblage. Barnacles were recovered exclusively from I7, and make up 1% of the assemblage, by weight.

Calibrated dates of 580BP, 1300BP and 2370BP were obtained for shell samples from the top, middle and bottom of LP19, respectively. In this assemblage, *C. granatina* and *S. granularis* are present in similar proportions of 22.8% and 23.5%, respectively. Proportions of the large, low-shore species *S. argenvillei* and *S. cochlear* are slightly lower (9.5% and 7.5%) than at LP18. Whelks are less numerous in the assemblage from LP 19(16%), while black mussels are more numerous(7.4%). Barnacles account for 1.2% of the total assemblage by weight. The largest of the LP sites, LP20, is also the oldest, dating to between 1990 and 4250BP. This shellfish assemblage is characterised by an abundance of the small granular limpet, *S. granularis*. This species accounts for 25.1% of the identified shellfish remains. *C. granatina*, is present in slightly lower proportions (20.7%) while *S. argenvillei*, accounts for 16.3% of the assemblage. Whelks constitute 13.4% of the identified remains while black mussels make up only 3.9%.

The mean and median sizes of *C. granatina*, *S. granularis* and *S. argenvillei* recovered from the Lynch Point middens (Figures 4.7-4.9) is fairly consistent across the three sites, and are considerably smaller than specimens from Middle Stone Age sites in the region. Median sizes of 57.7mm, 57.4mm and 55.5mm were obtained for granite limpets from LP 18 ( $n=15$ ), LP19 ( $n=282$ ) and LP20 ( $n=286$ ), respectively. Granular limpets ranged between 33.3mm ( $n=45$ ) at LP18, and 36.6mm at LP19 ( $n=503$ ) and LP20 ( $n=584$ ). Median sizes of 72.2mm ( $n=41$ ), 74.4mm ( $n=165$ ) and 69.9 ( $n=272$ ) were obtained for Argenville's limpets. Mean prismatic bandwidths (Figure 4.9) of 7.5mm ( $n=24$ ), 7.1mm ( $n=359$ ) and 6.2mm ( $n=181$ ) were obtained for black mussel hinges from the LP middens (Figure 4.10); these sizes are within range of those reported for LSA sites along the southwestern Cape coast.

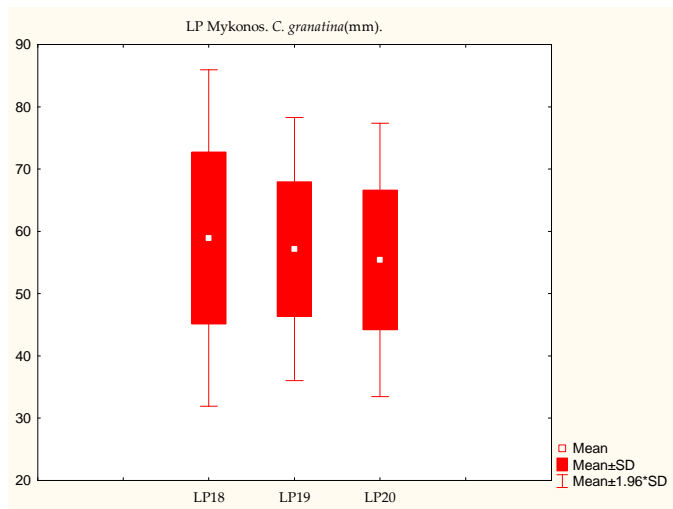


Figure 4.7 Mean total length of *C. granatina* (mm) from the Lynch Point, Mykonos sites.

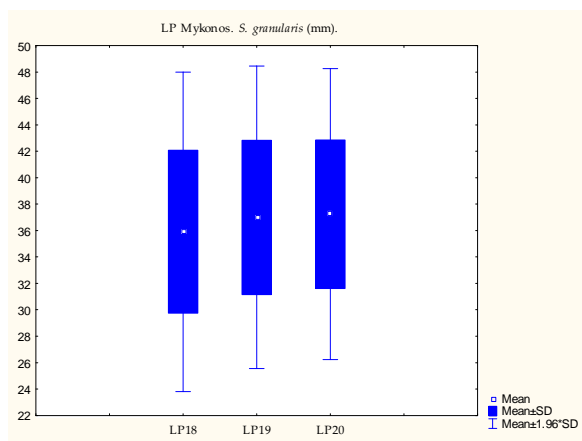


Figure 4.8 Mean total length of *S. granularis* (mm) from the Lynch Point, Mykonos sites.

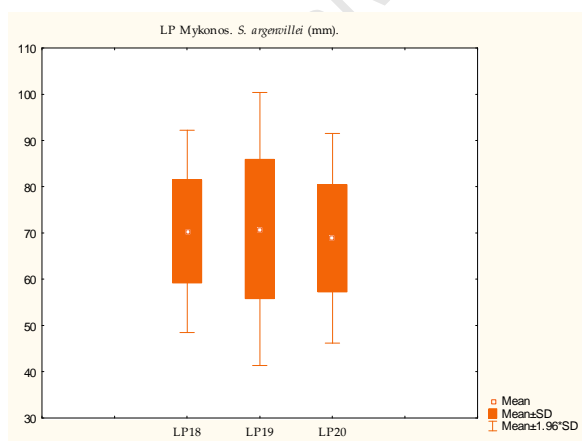


Figure 4.9 Mean total length of *S. argenvillei* (mm) from the Lynch Point, Mykonos sites.

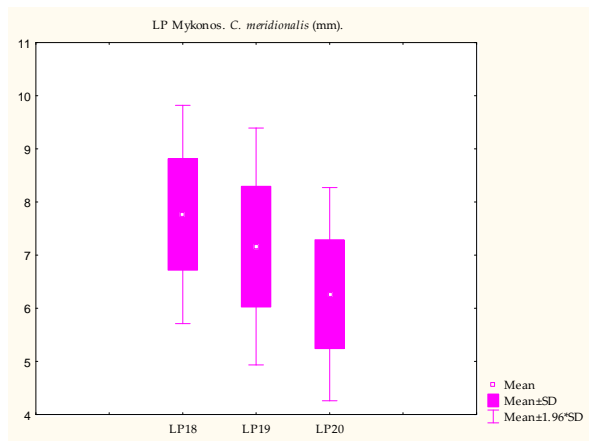


Figure 4.10 Mean prismatic bandwidth of *C. meridionalis* (mm) from Lynch Point, Mykonos.

#### 4.3.3 Dunefield Midden (DFM) 11

Dunefield midden is a large area located several kilometers from the mouth of the Verlorenvlei on the western Cape coast along which numerous discontinuous scatters of archaeological material including shellfish residues, other faunal remains and artefacts have been preserved in a series of deflation hollows along the remnants of a dune cordon. The best-known site in this region, Dunefield Midden 1, consists of material accumulated over the course of several short episodes of occupation during the Late Holocene. It is distinct from similarly dated archaeological contexts in the southwestern Cape in that it represents a substantial horizontal excavation of 850 square meters of Later Stone Age deposit.

Parkington *et al.* (2009) conducted excavations at the site during the mid-1990s with a view to mapping and understanding the spatial and behavioural relationships between activity areas like hearths and associated faunal remains and artefacts. Another site in the vicinity, located approximately 1km away from DFM1 and designated as Dunefield Midden 11, was excavated by Parkington and colleagues in 1996. Like DFM1, DFM11 consisted primarily of ashy shell deposits originating from numerous dumping episodes. In contrast to the former site, hearths were not prominent at DFM11. A total of 28 squares were excavated, yielding a large sample of shellfish remains.

The shellfish assemblage from DFM11 (Table 4.3) is dominated by *C. granatina*, with slightly lower contributions by the smaller *S. granularis*. There is considerable variation in the relative abundance of these two species in the different squares. The former species accounts for between 43.1% and 68.9% of the identified remains per square; frequencies of

between 50% and 60% are the most common. *S. granularis* accounts for between 9.2% and 31.4% of the identified and counted remains; frequencies greater than 20% are unusual. In most, but not all of the squares, greater percentages of *C. granatina* are accompanied by lower ones of *S. granularis* and vice versa. The large low-shore limpet *S. argenvillei* is not present in significant numbers in this assemblage, and accounts for less than 1% of the identified remains in the majority of excavated squares. Another large species, *S. barbara*, is slightly better represented. This is in line with a collection strategy focused on large species from the mid-intertidal.

Black mussels, or *C. meridionalis*, are fairly abundant in the assemblage from DFM11, accounting for between 7.69% and 37% of the identified and counted shells; proportions greater than 20% are unusual. For the most part, squares with a greater contribution from *C. meridionalis* will have lower percentages of the small, upper-shore dwelling *S. granularis*. Whelks and winkles are poorly represented. Very small molluscs, including *Crepidula* and *Helcion*, make up a very small proportion of the shellfish assemblage, and account for less than 1% of countable shells in the majority of squares. These appear to be somewhat better represented (>1%) in squares where *C. granatina* are significantly more abundant than *S. granularis*.

Mean and median sizes of *C. granatina* range between 55.2mm and 49.9mm, and 56.4mm and 49.7mm, respectively (Figures 4.11-15). A mean size of 51.2mm is reported by Tonner (2005) for DFM1. Maximum sizes >80mm are rare, and are recorded in only four of the excavated squares at DFM11, CYR69, CYR84, CYR89 and CYR96. The smaller *S. granularis* ranges more narrowly in terms of size (Figures 4.16-20), with means of between 37.6mm and 34.9mm, and medians of 37.4mm and 34mm. Granular limpets from DFM1 are similar (37.1mm) in size (Tonner 2005). Maximum sizes >49mm are rare. Most of the excavated squares yielded only several, and in some cases only two, measurable *S. argenvillei*, making an analysis of size differences between squares difficult (Figures 4.21-25). Mean and median sizes tended to be between 60mm and 70mm; the mean for this species at DFM1 is right between these two figures (65.9mm). Specimens from DFM 1 and DFM11 are smaller than those recovered from Middle Stone Age contexts. Prismatic bandwidths for *C. meridionalis* (Figures 4.26-30) yielded means of between 6.1mm and 7.7mm, and medians of

between 5.7mm and 7.8mm. A single specimen from the surface of CYR96 with a bandwidth of 9.7mm has been excluded. The mean size of black mussel hinges from DFM1 (8.8mm) is slightly larger (Tonner 2005).

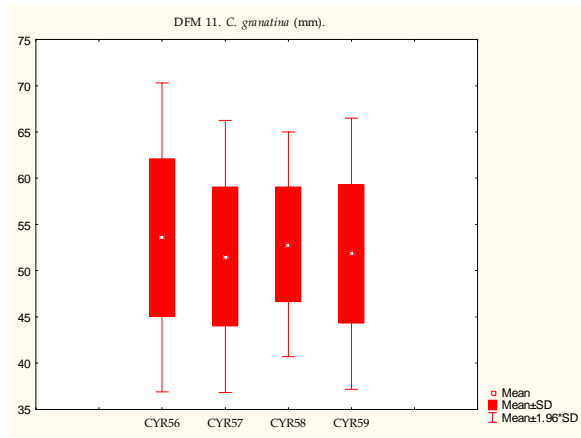


Figure 4.11 Mean total length of *C. granatina* (mm) from CYR56 ( $n=27$ ), CYR57 ( $n=35$ ), CYR58 ( $n=48$ ) and CYR59 ( $n=65$ ).

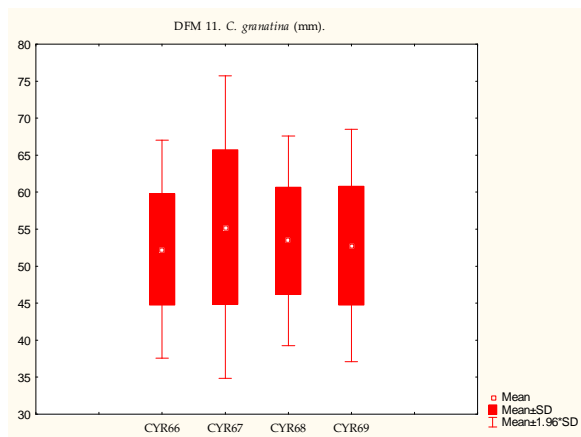


Figure 4.12 Mean total length of *C. granatina* (mm) from CYR66 ( $n=33$ ), CYR67 ( $n=73$ ), CYR68 ( $n=101$ ) and CYR69 ( $n=145$ ).

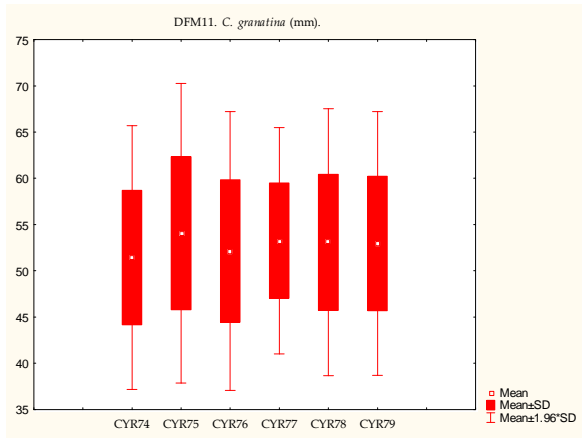


Figure 4.13 Mean total length of *C. granatina* (mm) from CYR74 ( $n=29$ ), CYR75 ( $n=49$ ), CYR76 ( $n=167$ ), CYR77 ( $n=125$ ), CYR78 ( $n=139$ ) and CYR79 ( $n=87$ ).

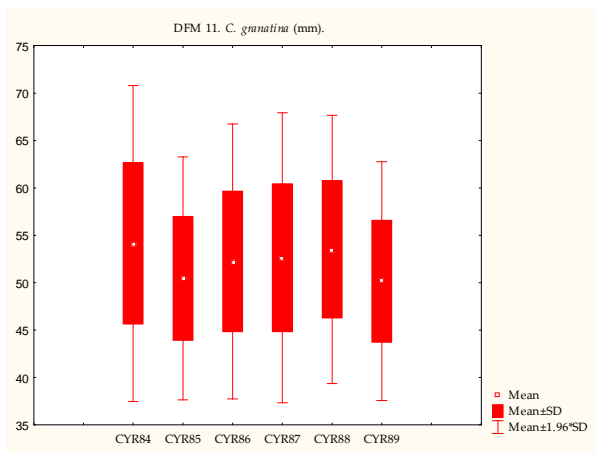


Figure 4.14 Mean total length of *C. granatina* (mm) from CYR84 ( $n=103$ ), CYR85 ( $n=139$ ), CYR86 ( $n=118$ ), CYR87 ( $n=153$ ), CYR88 ( $n=336$ ) and CYR89 ( $n=416$ ).

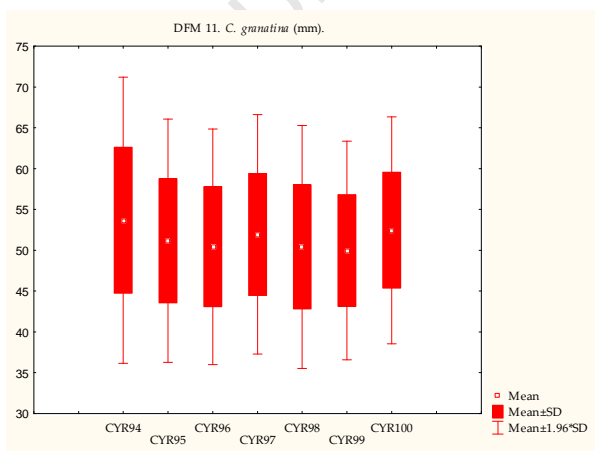


Figure 4.15 Mean total length of *C. granatina* from CYR 94 ( $n=72$ ), CYR95 ( $n=84$ ), CYR96 ( $n=75$ ), CYR97 ( $n=83$ ), CYR98 ( $n=130$ ), CYR99 ( $n=143$ ) and CYR100 ( $n=40$ ).

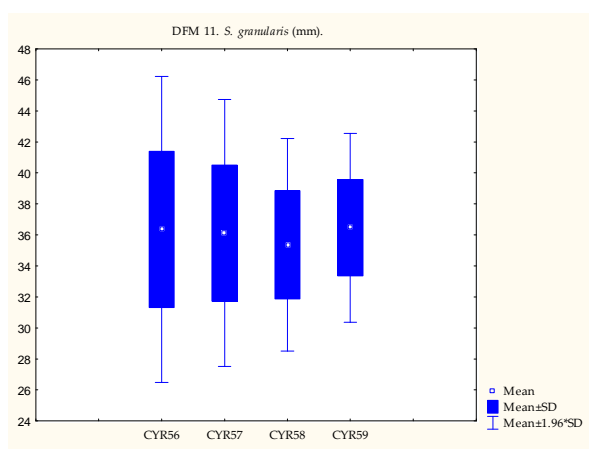


Figure 4.16 Mean total length of *S. granularis* (mm) from CYR56 ( $n=51$ ), CYR57 ( $n=53$ ), CYR58 ( $n=51$ ) and CYR59 ( $n=51$ ).

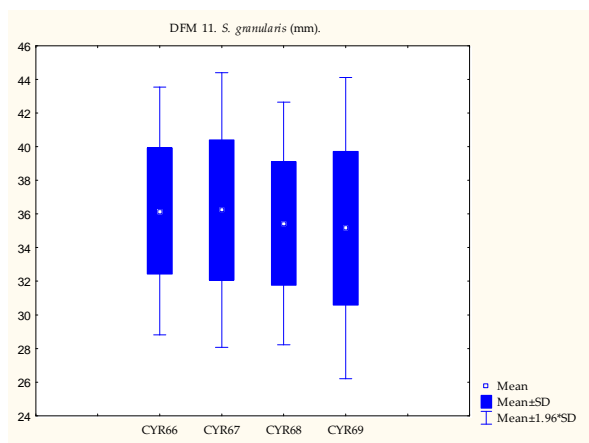


Figure 4.17 Mean total length of *S. granularis* (mm) from CYR66 ( $n=34$ ), CYR67 ( $n=37$ ), CYR68 ( $n=54$ ) and CYR69 ( $n=79$ ).

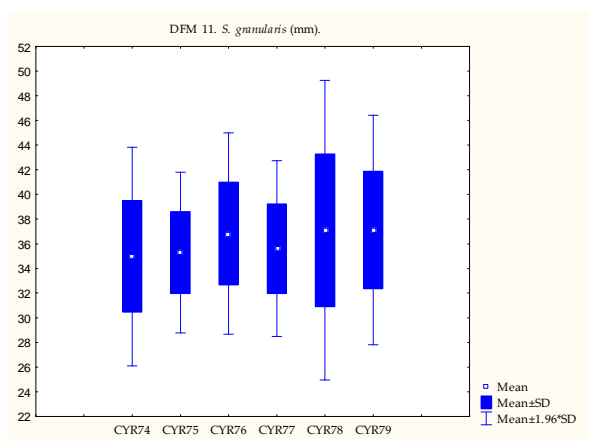


Figure 4.18 Mean total length of *S. granularis* (mm) from CYR74 ( $n=25$ ), CYR75 ( $n=44$ ), CYR76 ( $n=94$ ), CYR77 ( $n=47$ ), CYR78 ( $n=44$ ) and CYR79 ( $n=45$ ).

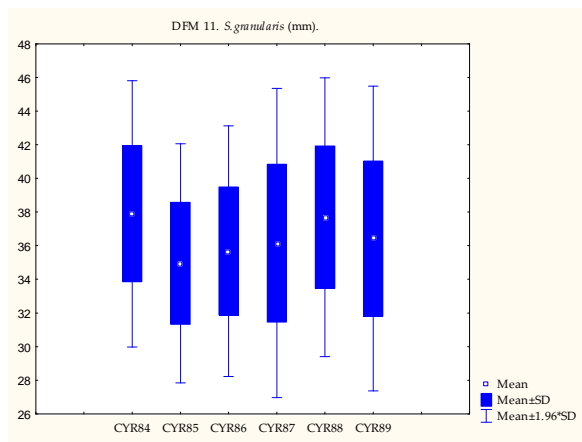


Figure 4.19 Mean total length of *S. granularis* (mm) from CYR84 ( $n=46$ ), CYR85 ( $n=60$ ), CYR86 ( $n=69$ ), CYR87 ( $n=102$ ), CYR88 ( $n=64$ ) and CYR89 ( $n=110$ ).

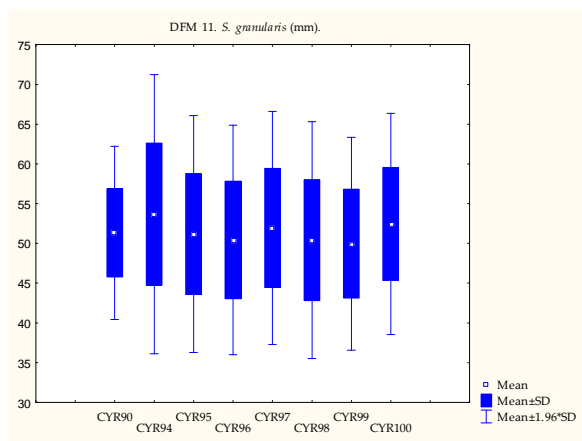


Figure 4.20 Mean total length of *S. granularis* (mm) from CYR90 ( $n=39$ ), CYR94 ( $n=24$ ), CYR95 ( $n=26$ ), CYR96 ( $n=21$ ), CYR97 ( $n=42$ ), CYR98 ( $n=44$ ), CYR99 ( $n=40$ ) and CYR100 ( $n=38$ ).

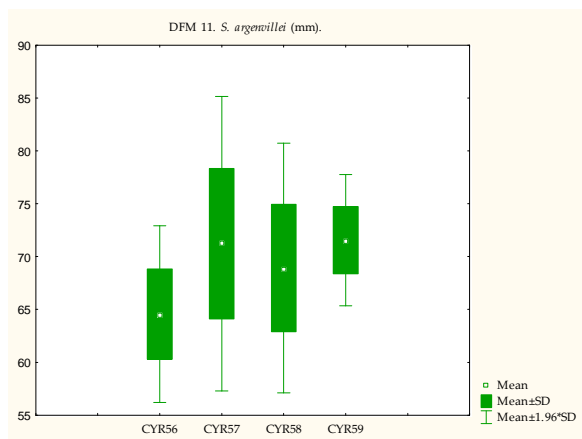


Figure 4.21 Mean total length of *S. argenvillei* (mm) from CYR56 ( $n=3$ ), CYR57 ( $n=3$ ), CYR58 ( $n=3$ ) and CYR59 ( $n=4$ ).

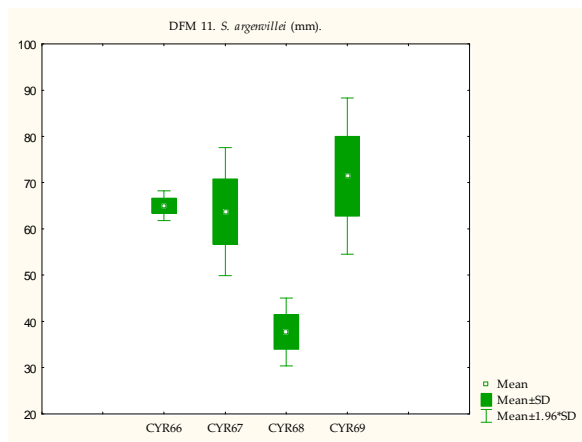


Figure 4.22 Mean total length of *S. argenvillei* (mm) from CYR66 ( $n=2$ ), CYR67 ( $n=2$ ), CYR58 ( $n=2$ ) and CYR69 ( $n=4$ ).

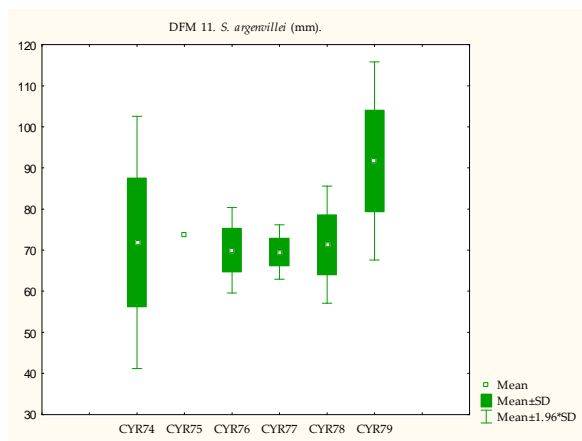


Figure 4.23 Mean total length of *S. argenvillei* (mm) from CYR74 ( $n=2$ ), CYR75 ( $n=1$ ), CYR76 ( $n=2$ ), CYR77 ( $n=2$ ), CYR78 ( $n=4$ ) and CYR79 ( $n=3$ ).

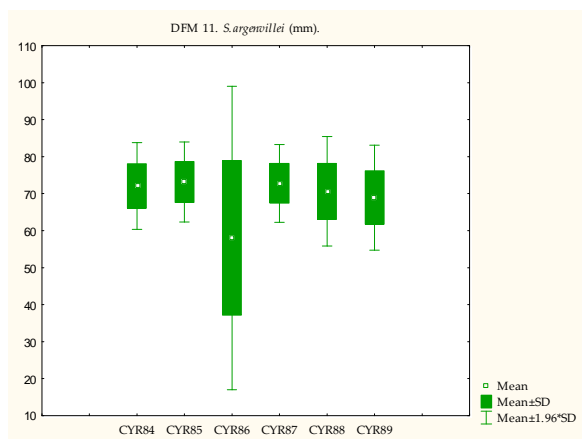


Figure 4.24 Mean total length of *S. argenvillei* (mm) from CYR84 ( $n=7$ ), CYR85 ( $n=5$ ), CYR86 ( $n=7$ ), CYR87 ( $n=18$ ), CYR88 ( $n=11$ ) and CYR89 ( $n=7$ ).

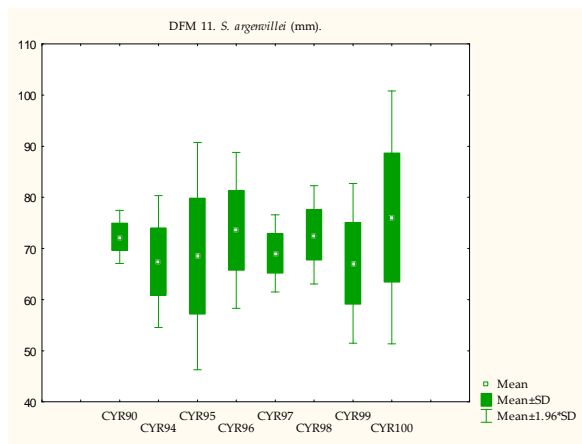


Figure 4.25 Mean total length of *S. argenvillei* (mm) from CYR90 ( $n=5$ ), CYR94 ( $n=10$ ), CYR95 ( $n=12$ ), CYR96 ( $n=2$ ), CYR97 ( $n=7$ ), CYR98 ( $n=11$ ), CYR99 ( $n=2$ ) and CYR100 ( $n=2$ ).

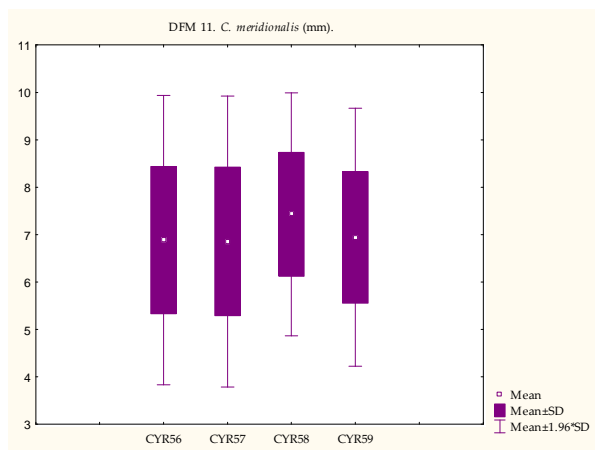


Figure 4.26 Mean prismatic bandwidths of *C. meridionalis* (mm) from CYR56 ( $n=103$ ), CYR57 ( $n=100$ ), CYR58 ( $n=42$ ) and CYR59 ( $n=58$ ).

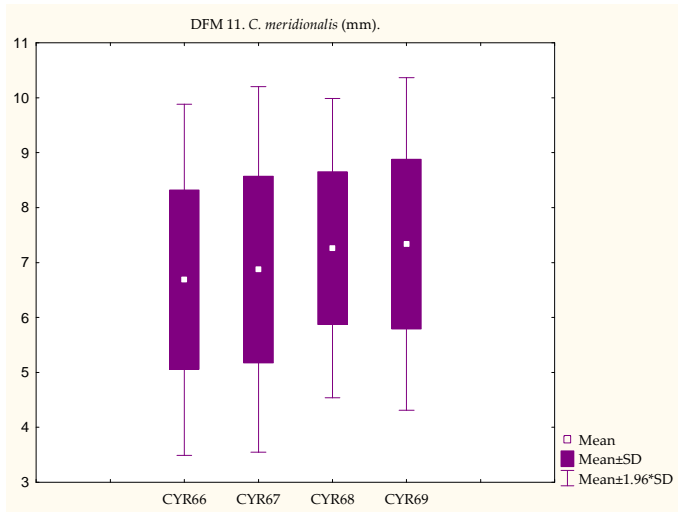


Figure 4.27 Mean prismatic bandwidth of *C. meridionalis* (mm) from DFM11, CYR66 ( $n=143$ ), CYR67 ( $n=115$ ), CYR68 ( $n=54$ ) and CYR69 ( $n=86$ ).

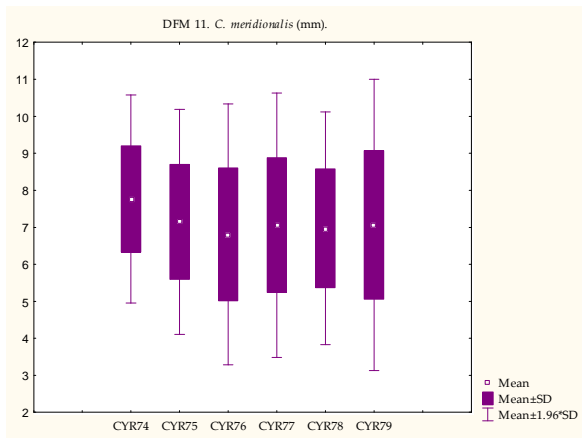


Figure 4.28 Mean prismatic bandwidth of *C. meridionalis* (mm) from CYR74 ( $n=112$ ), CYR75 ( $n=132$ ), CYR76 ( $n=294$ ), CYR77 ( $n=90$ ), CYR78 ( $n=75$ ) and CYR79 ( $n=94$ ).

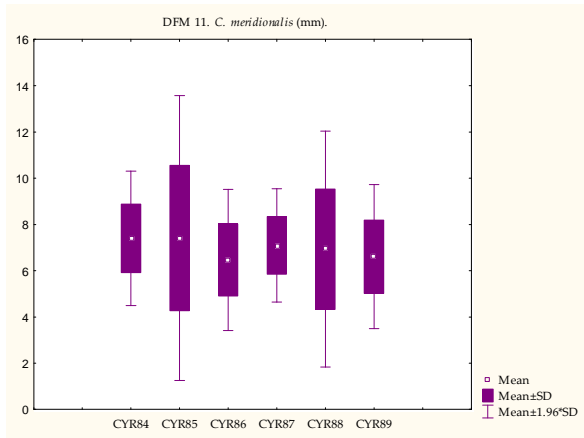


Figure 4.29 Mean prismatic band width of *C. meridionalis* (mm) from CYR84 ( $n=132$ ), CYR85 ( $n=302$ ), CYR86 ( $n=101$ ), CYR87 ( $n=97$ ), CYR88 ( $n=352$ ) and CYR89 ( $n=244$ ).

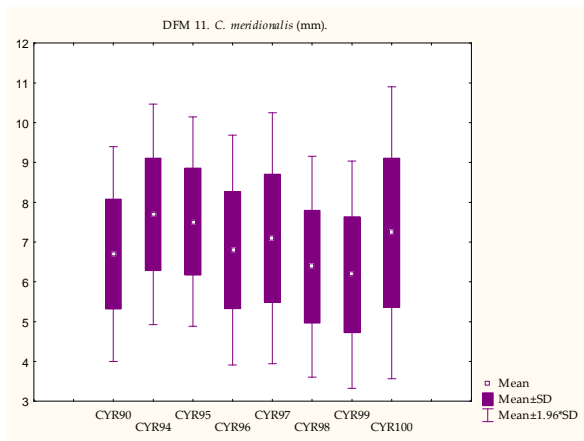


Figure 4.30 Mean prismatic bandwidth of *C. meridionalis* (mm) from CYR90 ( $n=77$ ), CYR95 ( $n=55$ ), CYR95 ( $n=52$ ), CYR96 ( $n=41$ ), CYR97 ( $n=48$ ), CYR98 ( $n=105$ ), CYR99 ( $n=100$ ) and CYR100 ( $n=51$ ).

#### 4.3.4 Brandsebaai (BSB)

The excavation of six archaeological sites at Brandsebaai on the Namaqualand coast was commissioned by a division of De Beers in order to mitigate the possible destruction of archaeological deposits as a result of their near-shore diamond mining operations (Halkett *et al.* 1993). Five of these sites accumulated during the Later Stone Age. Radiocarbon dates indicate that this region was inhabited by prehistoric people from the mid-Holocene (4000BP) to just before historic times (Halkett *et al.* 1993). The excavation of these sites and preservation of additional archaeological contexts in the region is of great importance, given their location in one of the least documented parts of the country (Orton *et al.* 2005). One

notable exception is Spoegrivier Cave. Excavations at this site in 1987 and 1994 produced some of the earliest dated sheep remains in southern Africa. The recovery of sheep bones in stratigraphic units below the oldest ceramic-bearing layers at this site suggests that sheep might have been introduced into the region via the west coast by 2100BP (Webley 2007).

Shellfish remains from four of the five Later Stone Age sites at Brandsebaai (BSB), BSB2, BSB3, BSB4 and BSB6 (Tables 4.4, 4.5, 4.6 and 4.8 in Appendix A) are of interest as a regional comparison with more or less contemporary sites in the well-documented Verlorenvlei region. Brandsebaai 5 (Table 4.7 in Appendix A) represents a collection of archaeological material including large numbers of ostrich eggshell fragments, stone tools, and a partly mineralised faunal assemblage discovered by Parkington and Poggenpoel during the initial survey of the Brandsebaai sites. This is likely to have been a Middle Stone Age open site which accumulated between 120 and 50ka. The lithic assemblage, which is largely adiaagnostic, includes quartzite flakes with prepared platforms characteristic of the MSA. The presence of intertidal shellfish suggests a date around the time of the last Interglacial at 120ka (Halkett *et al.* 1993).

A small patch of shell midden removed from the lower slopes of the seaward side of the coastal bluff designated as Brandsebaai 2 represents two or more layers of occupation dating from the mid-Holocene to 400BP. Shellfish residues from the two youngest layers of the sequence, SSC and LLBS, which also yielded the remains of ceramics, are dominated by the large limpet *C. granatina*. This species accounts for 66.6% and 64.8% of the total identified remains in these two layers, respectively. The smaller *S. granularis* is present in much smaller proportions of 26.2% and 30.5%. Proportions of the two limpet species are more even in the underlying stratigraphic units. In the assemblage as a whole, *C. granatina* is the best represented species (47.7%), followed by *S. granularis* (33.3%). *S. argenvillei* is not well represented at BSB2, and constitutes only 3.3% of the assemblage. The contribution of black mussels is negligible. Contrary to patterns identified at other sites with stratigraphic layers pre- and post-dating 2000 BP, whelks are less numerous in the younger, ceramic-bearing layers of BSB2, where they account for >3% of the identified remains, than in three of the older stratigraphic units predating 2000BP, where they are present in proportions >20%. Whelks make up 14% of the assemblage as a whole.

Brandsebaai 3 is a partially preserved lens of archaeological material buried beneath 20cm of red Aeolian sand. A single date on *C. meridionalis* recovered from the main occupation layer 26cm below the surface, with a marine correction, indicates that the site was inhabited during the Late Holocene, around 2500BP. No faunal remains from domesticated species were found, and ceramics were confined to the surface layers and slope-wash. This indicates that while the youngest portion of the deposit may postdate the introduction of herding, the majority of the sequence accumulated before this (Halkett *et al.* 1993). The shellfish residues from this site consist of slightly larger proportions of *C. granatina* than *S. granularis*, which account for 37% and 28.6% of the identified shellfish remains, respectively. The large *S. argenvillei* is well-represented. It accounts for more than 50% of the identified specimens in one of the main eponymous occupation layers (ARG), and for just over 10% of the assemblage as a whole. Black mussels are also considerably more abundant at this site than at BSB2, and account for 6.2% of the countable shells. Whelks are also a significant component of this site, and are present in slightly larger proportions (17.4%) than at BSB2.

An exploratory excavation of a small sand dune which had been partially destroyed by bulldozers revealed several lenses of thick shell, faunal remains and hearth deposits, the presence of which indicated the survival of an intact archaeological horizon. A four square meter trench was dug into the face of the dune, where sixteen individual stratigraphic units of *in situ* material were identified and removed. The most extensive of these, the so-called DODGE complex (BDO, GDO and WDO) was comprised of a series of hearths and associated food refuse heaps, and most likely represents the main occupation at the site, designated as Brandsebaai 4. A single radiocarbon date on *C. meridionalis* shell places it at around 1900 BP (Halkett *et al.* 1993).

The shellfish assemblage from BSB4 is dominated by the small limpet *S. granularis*, which accounts for between 47% and 70.5% of the identified shellfish remains in the archaeological sequence and 62% of the assemblage as a whole. The larger *C. granatina* is present in proportions of between 17.9% 43.4%, and makes up 30.3% of the identified and counted shellfish remains. The other large limpet *S. argenvillei* is not abundant at this site, accounting for only 2.2% of the shellfish assemblage. *C. meridionalis* is even less well-represented, at 1.6%. Whelks, too, are underrepresented at BSB4, and account for >3% of the

assemblage, in contrast to the assemblages from BSB2 and BSB3, where they are fairly abundant.

The proportions of mussels and limpets in the shellfish assemblage collected from the surface of the MSA site, Brandsebaai 5, is similar to MSA sites in the southwestern Cape. Black mussels are the most numerous component, accounting for >60% of the identified and counted remains. *C. granatina* is the most abundant limpet species (23%), followed by *S. argenvillei* (6.8%) and *S. granularis* (3.2%).

Brandsebaai 6, located just inside the coastal dune system southeast of Geustyn se Gat, is the only site in the immediate vicinity of the nearshore diamond mining area that had not been subject to disturbance or destruction. The digging of a trench across the central portion of the site revealed a shallow sequence of well-defined shell lenses and hearths buried beneath a layer of dune sand. At this site, spatial patterning in archaeological remains and associated activities has been preserved intact. For instance, discrete piles of large limpet shells may represent individual gathering events or meals. A corrected radiocarbon date of ~1700BP derived from *C. granatina* shell and the recovery of several potsherds indicates that at least part of the site accumulated after the introduction of ceramics (Halkett *et al.* 1993). *S. granularis* is the most abundant limpet species in the shellfish assemblage from BSB6, and accounts for 45.1% of the total identified shellfish remains. The larger *C. granatina* and *S. argenvillei* account for 29.6% and 11.9% of the assemblage, respectively. Proportions of *S. granularis* and *S. argenvillei* vary widely in individual stratigraphic units. Whelks are present in similar proportions in the assemblage from BSB6 as in those from the other Brandsebaai middens that yielded the remains of ceramics. Very few countable black mussel hinges were recovered.

Limpets recovered from the LSA sites at Brandsebaai are relatively large (Figures 4.31-33). Mean and median total lengths >66mm were obtained for *C. granatina* from BSB2 ( $n=453$ ) and 4 ( $n=788$ ); specimens from BSB3 ( $n=263$ ) are even larger (71.2mm); those from the youngest site, BSB6 ( $n=298$ ) are the smallest (61.1mm). Three specimens from the surface collection at BSB5 range between 71.4mm and 61.1mm, with a mean of 67.9mm. The smaller *S. granularis* ranges between 38mm and 41mm in total length in the LSA sites, approximately 3mm larger than granular limpets from sites further south. Slightly larger

means and medians were recorded for BSB2 ( $n=307$ ) and BSB3 ( $n=226$ ), and slightly smaller ones for BSB4 ( $n=1473$ ) and BSB6 ( $n=891$ ). A single specimen measuring 48.6mm was recovered from the surface at BSB5. Mean and median sizes for *S. argenvillei* from three of the Brandsebaai middens, BSB2 ( $n=91$ ), BSB3 ( $n=202$ ) and BSB6 ( $n=329$ ), ranged between 75mm and 77.7mm, and 76.9mm and 78.1mm, respectively, 7mm larger than those reported for the Lynch Point sites. Specimens from BSB4 ( $n=100$ ) were somewhat smaller, with a mean of 67mm and a median of 74.1mm. Brandsebaai 4 is dominated by *S. granularis* and to a lesser extent *C. granatina*, with the lowest contribution by *S. argenvillei* (2.17%) in all of the Later Stone Age shell middens.

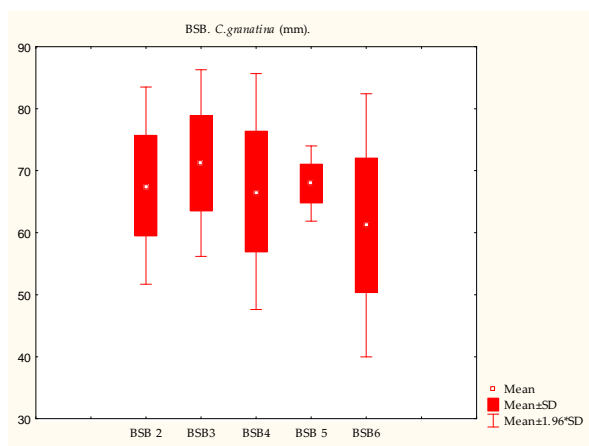


Figure 4.31 Mean total length of *C. granatina* (mm) from BSB2-6.

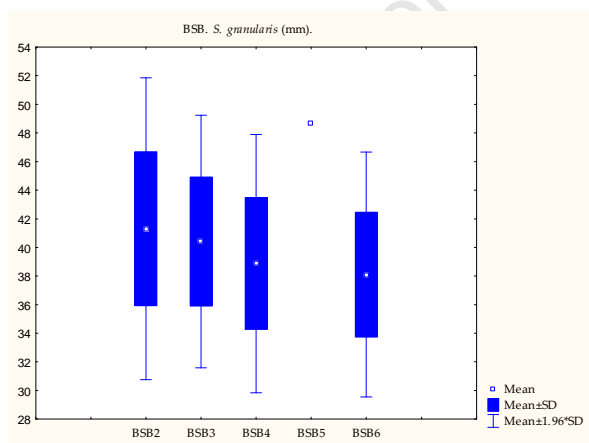


Figure 4.32 Mean total length of *S. granularis* (mm) from BSB2-6.

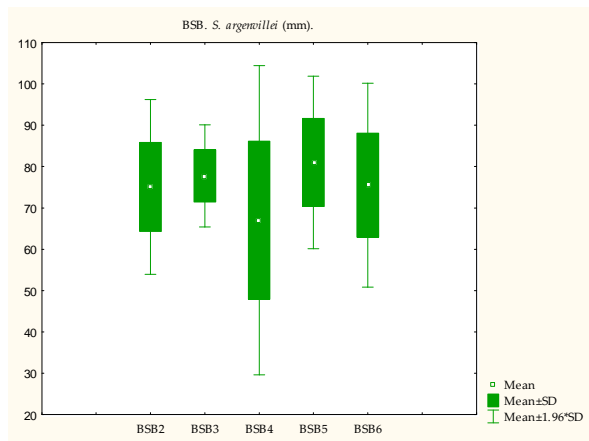


Figure 4.33 Mean total length of *S. argenvillei* (mm) from BSB2-6.

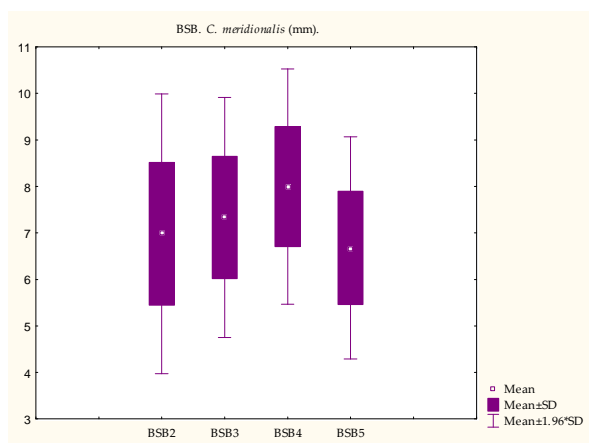


Figure 4.34 Mean prismatic bandwidths (mm) for *C. meridionalis* from Brandsebaai 2-5.

#### 4.4 DISCUSSION: MIDDLE AND LATER STONE AGE SHELLFISH GATHERING STRATEGIES AND THEIR IMPLICATIONS FOR DIET AND NUTRITION AMONG PREHISTORIC HUNTER-GATHERERS

There are two main, quantifiable differences in the shellfish assemblages from Middle and Later Stone Age coastal sites, both of which have important dietary and nutritional implications. The first relates to the presence and relative abundance of particular taxa among the marine faunal remains. The second concerns the average size of mussels and limpets being collected and discarded by prehistoric people. Marine faunal assemblages from MSA sites are characterised as less diverse than Later Stone Age ones: they contain fewer molluscan taxa and, with few exceptions, lack certain categories of remains, notably fish and crayfish (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004). Granite limpets

and black mussels are better represented than granular limpets, even though the latter would have been even more accessible to MSA coastal foragers, and large, mature individuals were available for collection. These patterns have been interpreted by some researchers as evidence for Middle Stone Age peoples' lack of foraging proficiency, and as indicative of less intensive exploitation by smaller populations (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004). However, a number of alternative explanations grounded in optimal foraging theory and ethnography recognise the effect of factors including methods of collecting, field processing and transport distances on prehistoric foraging strategies and the material traces of these activities in the archaeological record (Dusseldorp and Langejans 2013; Ugan 2005).

While environmental conditions and coastal morphology determine the molluscan fauna available for human collection and consumption (Steele and Klein 2008), proportions of the different species represented in an assemblage also reflect prehistoric foragers' economic and dietary choices and preferences. Black mussels and large granite limpets are the most significant component of MSA shell middens on the Atlantic west coast. The ratio of mussels to limpets varies within and between sites and sequences dating to the Middle as well as the Later Stone Ages. Granite limpets outnumber black mussels in the enlarged assemblage from HDP1, whereas black mussels are more abundant than granite limpets in the assemblages from Brandsebaai 5 and Ysterfontein (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004). Limpets are better represented than black mussels in the majority of excavated squares at the Later Stone Age sites of DFM11, and are considerably more abundant in the assemblages from the Lynch Point and Brandsebaai middens.

Variation in the ratios of black mussels and limpets is evident in the substantial horizontal sequences from DFM and DFM11. Such variation within and between sites and assemblages is frequently ascribed to changes in coastal morphology, and the reorganisation of coastal foraging activities in response to these environmental changes (Dusseldorp and Langejans 2013; Jerardino 2012; Steele and Klein 2008). For instance, an increase in the abundance of black or brown mussels in the assemblages from sites along the southwestern and southern Cape coasts, respectively, is regarded as an indication of receding coastlines. Black and brown mussels inhabit dense colonies in the mid-intertidal and sub-tidal and,

unlike limpets which must be collected individually, can be easily mass collected, especially at low tide. The exploitation of these rocky shore bivalves is a highly productive economic activity yielding significant caloric returns, and is likely to be regarded as a worthwhile investment of time, energy and effort even when the shoreline is located ~10km away from archaeological sites (Dusseldorp and Langejans 2013; Jerardino 2012). Mussels are also easier to transport than limpets, as they are stuck together in clumps by “secreted fibres or byssus” (Dusseldorp and Langejans 2013: 113), are less perishable than limpets, as edible soft tissue is enclosed between the two hinges or valves (Jerardino and Marean 2010), and can be mass processed relatively quickly and easily (Dusseldorp and Langejans 2013).

Parkington and colleagues (2014) differentiate between coastal foraging strategies based on the harvesting of live black mussels inhabiting the intertidal, and the collection of individuals uprooted from subtidal beds by storm surges and deposited onto nearby beaches. They refer to the latter activity as “strandloping, a flexible foraging strategy in which large adult mussels, seabirds, and occasionally even marine mammals washed up on the shore can be procured. Strandloping and live collection are not mutually exclusive, but would have been pursued interchangeably by Later Stone Age hunter-gatherers. These two activities have distinct archaeological signatures in the Late Holocene deposits from Elands Bay Cave and Dunefield midden. Strandloping introduces barnacles living on large mussels in subtidal beds into archaeological deposits. When live mussels are collected, small particles of polished shell and stone, as well as small molluscs caught up in mussel byssus are incorporated into archaeological sites. When recorded, the weight of water-worn shell and stone, “incidentals” (Jerardino 1997) and barnacles, expressed as a proportion of the total weight of *C. meridionalis*, therefore serves as a useful indication of whether black mussels were harvested while alive or collected when dead. Adult mussels living in subtidal beds are also larger than those collected from the intertidal. At Elands Bay Cave and Dunefield midden, stratigraphic units with larger proportions of barnacle relative to water-worn shell and stone also yielded mussels with large prismatic bandwidths (Parkington et al. 2014). Proportions of waterworn pebble and shells exceed those of barnacle in all of the excavated squares at the adjacent and contemporary site of Dunefield midden 11 (Table 4.8 in Appendix A). This may indicate a preference for the collection of live animals rather than scavenging for wash-ups.

The large proportions of granite limpets and black mussels in shellfish assemblages from sites in the southwestern Cape, especially to those dating to the Middle Stone Age, are consistent with subsistence strategies focused on the collection of highly abundant, visible and accessible species (Avery *et al.* 2008; Steele and Klein 2008). Mature individuals are also quite large, with relatively substantial yields of edible soft tissue. Patterns in the relative proportions of the three predominant limpet species occurring on the Atlantic coast are also informative. Ratios of the large *C. granatina* and *S. argenvillei* to the much smaller *S. granularis* are fairly consistent in the Middle Stone Age assemblages from HDP1, BSB5 and Ysterfontein: *C. granatina* outnumbers *S. argenvillei*, which in turn is more abundant than *S. granularis*. The prehistoric accumulators of these remains preferentially targeted large granite limpets inhabiting the mid-intertidal zone, which is visible and accessible throughout the tidal cycle. Granular limpets inhabit the upper reaches of the shore, while Argenville's limpets occur in the lower inter-tidal and can only be collected at low tide. The ratio of *S. argenvillei* to *S. granularis* thus reflects a choice between two extremes: the collection of large limpets accessible only at certain times of the day and month, or exploitation of smaller molluscs available at all times.

Ratios of granite, granular and Argenville's limpets are more variable at Later Stone Age than Middle Stone Age sites. The assemblage from Dunefield Midden 11 is characterised by high ratios of *C. granatina* to *S. granularis*, which is similar to the pattern observed at the original Dunefield Midden site (Tonner 2005). Variation in the relative frequencies of these two species does not appear to be correlated with changes in their mean size. There is relatively little variation in the mean size of *S. granularis* at DFM11, and the expectation that smaller sizes will be characteristic in squares with higher frequencies of this limpet has not been met. *S. granularis* is generally more numerous than *S. argenvillei*. The Lynch Point assemblages are not as heavily dominated by *C. granatina* and *S. granularis* as Dunefield Midden 11, and ratios of small granular limpet to larger granite and Argenville's limpets are more even. Large abelones (*Haliotis spadicea* and *midiae*) occurring in the lower-intertidal are also well-represented at the Lynch Point sites. At Brandsebaai 2 and 3, ratios of *C. granatina* to *S. granularis* favour the larger, mid-tidal species. In the assemblages from the two middens postdating 2000BP, namely Brandsebaai 4 and 6, the smaller granular limpet accounts for >60% and the larger >40% of the two species combined. Thus, while they are

considered too small to be of any commercial value (Bosman *et al.* 1990), granular limpets were exploited in significant numbers by the Later Stone Age inhabitants of Late Holocene sites. Marked differences in the ratios of *Argenville's* to granular limpets are also apparent in the shellfish assemblages from the Later Stone Age sites at Brandsebaai. While the larger, less accessible species is not as well represented as the smaller, more accessible one in two of the four Holocene occurrences (BSB2 and BSB4), *S. argenvillei* accounts for >20% of the two species combined in the other two (BSB3 and BSB6).

Greater variation in the relative frequencies of the three main limpet species potentially available to Later Stone Age hunter-gatherers on the southwestern Cape coast demonstrates that their collection strategies were broader and more flexible than those of their Middle Stone Age predecessors. Jerardino and colleagues (2009) have labelled the coastal foraging behaviour of the Late Holocene inhabitants of the Verlorenvlei region as flexible and opportunistic. A wide range of resources available in the immediate vicinity was exploited. This includes several very small molluscs such as winkles and whelks, which are very poorly represented in older, Middle Stone Age sites. Their presence in Later Stone Age assemblages is often regarded as indicative of economic intensification and population pressure. Interestingly, whelks are considerably less abundant at BSB4 and 6, two sites postdating 2000BP, than at Brandsebaai 3, which has been dated to 2500BP. These small molluscs are present in large proportions at Brandsebaai 2, which dates from the mid-Holocene to 400BP. It is possible that Later Stone Age people in Namaqualand did not face the same economic and demographic pressures as their counterparts at Elands Bay, Lambert's Bay and the surrounding regions.

Furthermore, while flexibility is implicit in some patterns in the shellfish remains from Lynch Point and Brandsebaai, others are more consistent with planning and deliberation. *S. argenvillei* makes up a significant proportion (10%) of the identified and counted shellfish in two of the Brandsebaai middens, BSB2 and 6. At both sites, these large limpets are particularly abundant in specific stratigraphic layers, suggesting individual gathering events (Halkett *et al.* 1993). As *S. argenvillei* inhabits the lower intertidal zone on the Atlantic west coast, and would only have been accessible at certain times of the day and lunar cycle, its collection by prehistoric foragers would have to be scheduled to coincide with spring low

tides. The focused collection of *S. argenvillei* at times during which this species is accessible appears to have been an important component of Later Stone Age people's coastal foraging strategies at Brandsebaai and Lynch Point.

A number of researchers have argued that Middle Stone Age peoples' shellfishing behaviour, particularly their preoccupation with large, highly visible and easily accessible granite limpets and black mussels, is less efficient than that of Later Stone Age people, who exploited a wider range of species and size classes (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004; Halkett *et al.* 2003). This statement can be contested by demonstrating that Middle Stone Age collecting strategies are, in fact, efficient in so far as obtaining caloric returns for energy invested is concerned, and that the broader strategies employed by Later Stone Age people were not necessarily advantageous from a nutritional or dietary point of view.

Middle Stone Age coastal foraging strategies show some important commonalities with those of contemporary collectors. Shellfish collecting as practised by modern people in diverse regions of Australia and southern Africa are highly selective. Among the Anbarra of Australia, bivalves constitute 98%, by weight, of the thirteen species regularly exploited (Meehan 1982). On almost 50% of the collecting days observed and documented by Meehan (1982), only a single species was taken. When collecting on flat reefs, Meriam women target specific clams and conch shells (Bird *et al.* 2004; Bliege Bird *et al.* 2002). Black and brown mussels are the most frequently and intensively harvested molluscs in the coastal regions of southern Africa (Bigalke 1973). Collections by the Anbarra, Meriam and Nguni are often scheduled to coincide with the maximal exposure of the littoral zone during spring low tides (Bird *et al.* 2004; Meehan 1982; Bigalke 1973).

*C. meridionalis* and *C. granatina* are highly abundant along the southwestern Cape coast. Both are fairly large and have relatively high meat yields representing good caloric returns. Argenville's limpets are larger and have higher meat yields, but are less accessible than other limpets and black mussels. Granular limpets and, especially, winkles and whelks, are considerably smaller than granite limpets and black mussels and have lower edible yields. Thus, despite their abundance and accessibility, these small species have poorer caloric and nutritional returns than the larger species. Larger numbers would have to be collected and

processed to meet peoples' nutrient requirements. Winkles and whelks would take longer to process and prepare than limpets and bivalves. Like the large alikreukel *T. sarmaticus* (Dusseldorp and Langejans 2013) they would have to be cooked before the edible soft tissue could be easily extracted from the shell. Unlike *T. sarmaticus*, which has a high meat yield, the processing of large number of winkles and whelks would have minimal returns. Thus, the addition of these and other small molluscs to the diet of Later Stone Age hunter-gatherers more likely reflect economic intensification in the face of population and other pressures than an improvement in coastal foraging strategies.

The second major difference between shellfish remains from Middle and Later Stone Age sites is that specimens from Middle Stone Age assemblages are significantly larger. A number of environmental factors influence the maximum size and growth rates of limpets. These include water turbidity, population density, coastal geomorphology and topography and exposure to wave action, among others (Steele and Klein 2008; Bustamante and Branch 1996 a and b; 1997). Human predation may also affect the size and structure of shellfish populations (Bosman *et al.* 1990), especially in the case of slow-growing limpets. Unlike mussels, which are harvested in patches, limpets are collected individually, allowing for greater selectivity by collectors (Parkington *et al.* 2013). Modern collectors preferentially target larger individuals; small ones are frequently discarded (Parkington *et al.* 2013; Bliege Bird 1997; Meehan 1982; Bigalke 1973). The regular exploitation of large, mature individuals will drive the mean size of animals down. Differences in mean limpet sizes between the Middle and Later Stone Age, and at certain times during the Late Holocene, are often interpreted as evidence of more or less intensive exploitation (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004; Halkett *et al.* 2003).

Large mean sizes have been recorded for *C. granatina*, *S. granularis* and *S. argenvillei* from the MSA sites of Hoedjiepunt 1 and 3 (Figure 4.35-37). No statistically significant differences ( $p>0.05$ ) are apparent between specimens from these two closely adjacent and most likely contemporary sites (Tables 4.9-11 in Appendix A). A few measurable *C. granatina* and *S. argenvillei* collected from the surface at the MSA site of Brandsebaai 5 are similar in size to those from the Hoedjiepunt sites; a single granular limpet from the latter locality is considerably larger. Large means documented for limpets from the MSA sites of

Ysterfontein 1 (Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004; Halkett *et al.* 2003) are also similar. Granite and granular limpets from Hoedjiespunt 1 and 3 are significantly larger than those from the three Late Holocene sites at Lynch Point, Mykonos. Statistically significant differences are also apparent between *C. granatina* and *S. granularis* from the Hoedjiespunt sites and the squares at Dunefield Midden 11 yielding the largest and smallest means for the two species. Argenville's limpets from the two Middle Stone Age sites are also significantly larger than those from LP18, 19 and 20, and the square at Dunefield Midden yielding the most measurable specimens for this species.

There are no statistically significant size differences between granite limpets from the Later Stone Age sites of Brandsebaai 2 and 3 and the Middle Stone Age assemblages from Hoedjiespunt. Specimens from Brandsebaai 4 and 6, which accumulated exclusively after 2000BP, namely Brandsebaai 4 and 6, are significantly smaller. Granular limpets from all of the Later Stone Age assemblages from Brandsebaai are significantly smaller than those from Hoedjiespunt 3. This species is a much more significant component of the Brandsebaai sites than the Hoedjiespunt ones. Smaller sizes may be attributed to more intensive exploitation or environmental factors. Argenville's limpets from Brandsebaai 2,3 and 6 are not significantly different from those collected at Hoedjiespunt 3; only those from Brandsebaai 4 are significantly smaller.

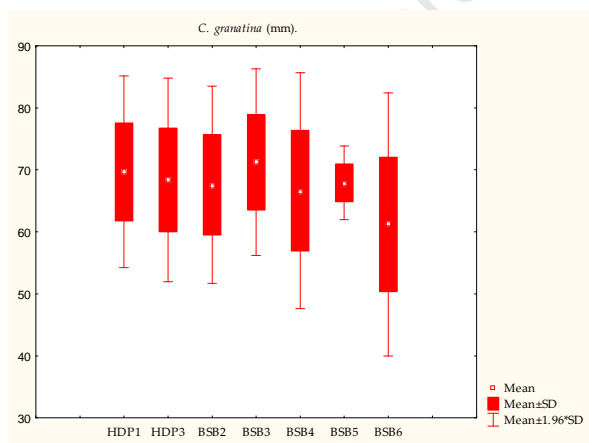


Figure 4.35 Mean total lengths for *C. granatina* from Hoedjiespunt 1 and 3 and the Middle (BSB5) and Later Stone Age sites at Brandsebaai.

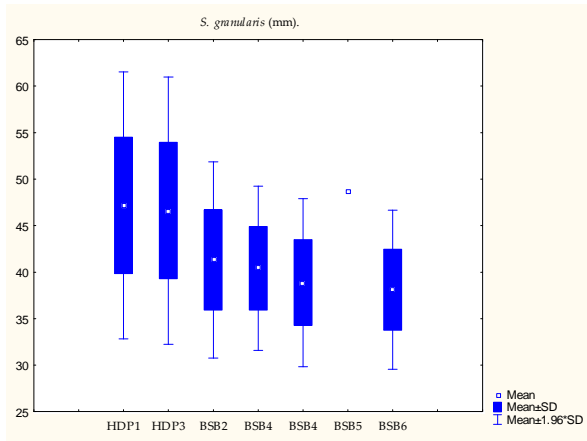


Figure 4.36 Mean total lengths for *S. granulatis* from Hoedjiespunt 1 and 3 and the Middle (BSB5) and Later Stone Age sites at Brandsebaai.

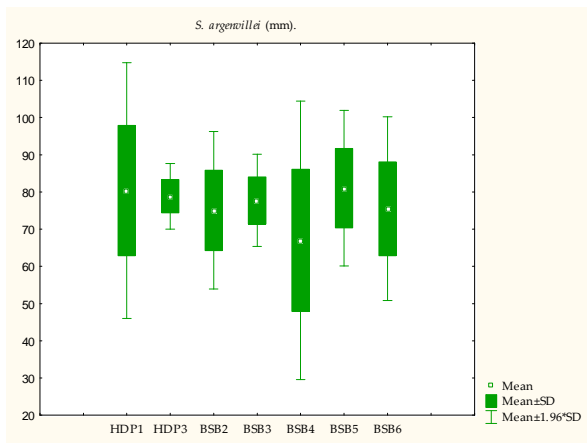


Figure 4.37 Mean total lengths of *S. argenvillei* from Hoedjiespunt 1 and 3 and the Middle (BSB5) and Later Stone Age sites at Brandsebaai.

There is statistically significant variation in the size of all three limpets at Brandsebaai. Larger and smaller means for *C. granatina* have been recorded for Brandsebaai 3 and 6, respectively. Differences in the size of granular limpets from all four of these Later Stone Age sites are statistically significant. *S. argenvillei* from Brandsebaai 4 are significantly smaller than those from the other three sites. These size differences are not clearly correlated with the relative abundance of the different species within individual sites. If this were the case, it would strengthen the argument for intensive exploitation as a driver for decreasing size.

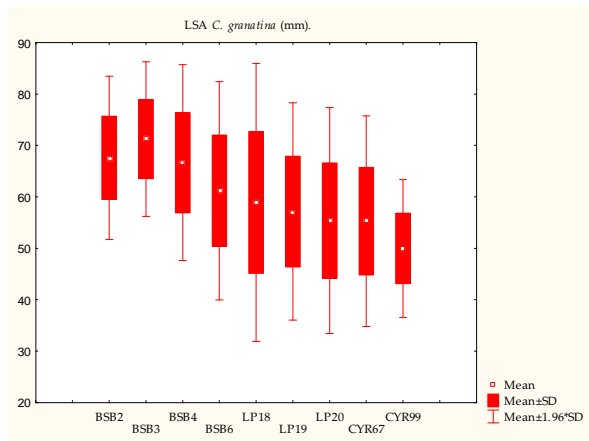


Figure 4.38 Mean total lengths for *C. granatina* from the Later Stone Age sites of Brandsebaai and Lynch Point, and from selected squares at Dunefield Midden 11.

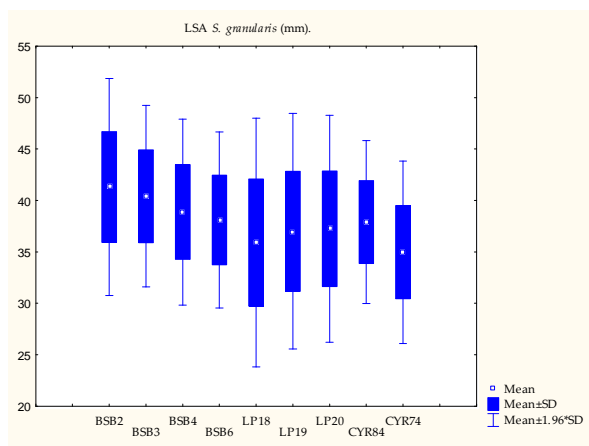


Figure 4.39 Mean total lengths of *S. granularis* from the Later Stone Age sites of Brandsebaai (BSB2,3,4 and 6) and Lynch Point, and selected squares of Dunefield Midden 11.

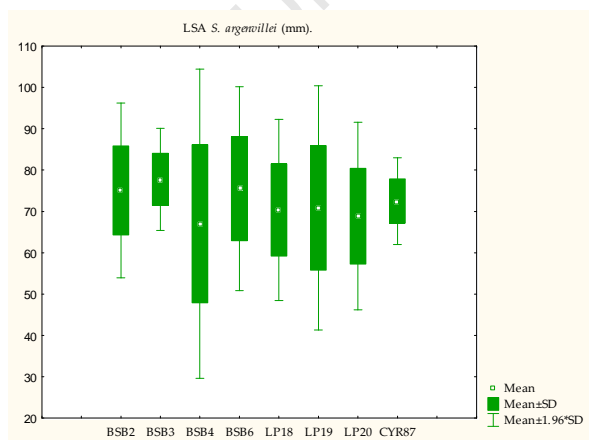


Figure 4.40 Mean total lengths of *S. argenvillei* from the Later Stone Age sites of Brandsebaai (BSB2,3,4 and 6) and Lynch Point, and a single square of Dunefield Midden 11.

Granite limpets from Brandsebaai 2, 3 and 4 are significantly larger than those from all of the Lynch Point sites as well as specimens from two squares at DFM11 yielding the largest and smallest means for this species (Figure 4.38). Specimens from Brandsebaai 6 are similar to those from LP18 and different from the other two sites and from Dunefield Midden 11. There are no statistically significant size differences in *C. granatina* from the three Lynch Point, Mykonos sites, or between granite limpets from these sites and those from CYR67 at Dunefield Midden 11. Specimens from CYR99, the square with the smallest mean size for *C. granatina*, are significantly smaller than those from CYR67 at the same site, and from all three Lynch Point sites.

Granular limpets (Figure 4.39) from Brandsebaai 2 and 3 are significantly larger than those from the three Lynch Point sites and two squares from Dunefield Midden 11; specimens from Brandsebaai 4 and 6 are similar to those from CYR84, a square from Dunefield Midden 11 with the largest recorded mean for granular limpets. *S. granularis* from Lynch Point 18 ( $n=45$ ) are significantly smaller than those from Lynch Point 19 ( $n=503$ ) and Lynch Point 20 ( $n=584$ ). This may be a result of differences in sample size. LP 18, the smallest of the Lynch Point sites, has the most even ratio of granite to granular limpets. *S. argenvillei* from Brandsebaai 2,3 and 6 are significantly larger than those from LP18,19 and 20, and CYR87, a square from Dunefield Midden 11 yielding the most measurable specimens of this species (Figure 4.40). Argenville's limpets from Lynch Point 19 are significantly larger than those from Lynch Point 20. The latter site has a higher ratio of *S. argenvillei* to *S. granularis* than the latter site.

Overlap in the mean size of *C. meridionalis*(Figure 4.41)from Middle and Later Stone Age shellfish assemblages has been documented at several sites along the southwestern Cape coast (Steele and Klein 2008). Black mussels from the Middle Stone Age sites of Hoedjiespunt 1 and 3 and Brandsebaai 5, and Late Holocene middens from Brandsebaai, Lynch Point and Dunefield midden 11 differ in size across time and space. Variation in the median size of black mussel hinges from two Middle Stone Age sites at Hoedjiespunt is statistically significant at the 0.05 level. *C. meridionalis* from these two sites also differ significantly from those collected at Brandsebaai. Mussel hinges from Brandsebaai 2,3 and

4 are all significantly different from one another; this also applies to specimens from the Later Stone Age sites at Lynch Point.

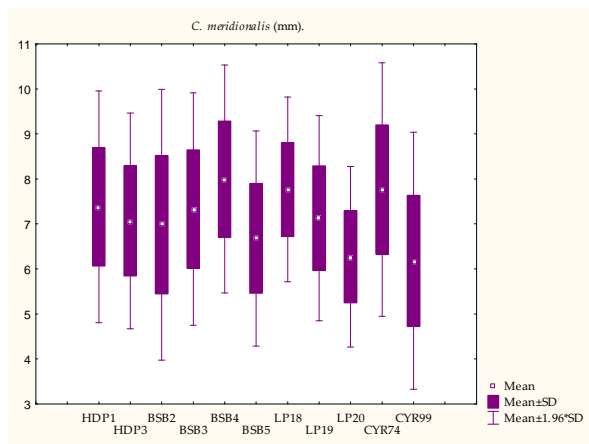


Figure 4.41 Mean prismatic bandwidths (mm) of *C. meridionalis* from Hoedjiespunt, Brandsebaai, Lynch Point and Dunefield midden 11.

Contrary to patterns observed in granite, granular and Argenville's limpets, where specimens from Middle Stone Age sites are always larger, black mussel hinges from Middle Stone Age assemblages are sometimes smaller than those from Later Stone Age sites. The largest prismatic bandwidths recorded in this study (>7.8mm) are from specimens from Brandsebaai 4 and a single square at Dunefield Midden 11. Medians >7mm have also been recorded for hinges from Hoedjiespunt1, Brandsebaai 3 and Lynch Point 18 and 19. Prismatic bandwidths <7mm were obtained for specimens from Hoedjiespunt 3, Brandsebaai 2 and 5 and Lynch Point 20. Medians <6mm have been recorded for specimens from three squares at Dunefield Midden 11, CYR86, 98 and 99. Specimens from CYR99 produced the smallest recorded mean of 5.7mm. The difference in size between these mussel hinges and those from the square with the largest median is statistically significant (Table 4.12 in Appendix A).

As has been previously stated, the relationship between large mussels and barnacles, and smaller animals and water-worn shell and stone, is not as apparent at Dunefield Midden 11 as at Dunefield Midden 1 and Elands Bay Cave. Some of the excavated squares with percentages of barnacle >0.1% also yielded black mussels with prismatic bandwidths >6.5mm. Two of the squares with high percentages of barnacle and large black mussels have low proportions (0.6 and 0.13%) of water worn shell and pebbles. However, the

squares with the highest recorded percentages (>0.25%) of barnacle yielded specimens with prismatic bandwidths <6.5mm. The largest mean prismatic bandwidth (7.7mm) obtained for black mussel hinges Dunefield Midden 11 is 1mm smaller than the mean for Dunefield Midden 1, a difference which translates to about 10mm in total length (Tonner 2005). The larger specimens from Dunefield Midden 11 could represent mussels obtained as wash-ups, as has been inferred for Dunefield Midden 1 and Elands Bay Cave (Parkington et al. 2014; Tonner 2005).

The observation that variation in the size of black mussels from Middle and Later Stone Age sites does not follow, and in some instances seems to contradict, patterns evident in limpets has been explained in a number of ways. Because *C. meridionalis* inhabit the intertidal and subtidal zones, and grow faster and re-colonize more quickly and easily than slow-growing limpets, they are regarded as less vulnerable to the effects of human predation (Jerardino et al. 2009; Steele and Klein 2008). Environmental factors have also been invoked in explanations for patterned size differences between black mussels and limpets. With the exception of *S. cochlear*, which occurs in large numbers along rocky coastlines in the southern Cape, most limpet species grow larger in bays which provide shelter from strong wave action. *C. meridionalis*, on the other hand, are more productive and reach larger sizes on exposed shores (Jerardino et al. 2009; Bustamante and Branch 1996a and b). Jerardino and colleagues (2009) propose that ecological conditions gave rise to differences in mussel and limpet sizes at Elands Bay Cave and Connie's Limpet Bar, two Late Holocene sites in the Verlorenvlei region. Black mussels were larger at the former cave site, situated close to an exposed shoreline, and smaller at the latter, located near a sheltered bay. However, this explanation cannot account for all of the statistically significant variation in the size of mussel hinges from adjacent sites in diverse regions including Saldanha Bay, the Verlorenvlei and Namaqualand. Nor does it explain statistically significant variation within large horizontal sequences at Dunefield Midden 1 and 11.

The size of black mussels and limpets available to and exploited by Middle and Later Stone Age hunter-gatherers on the southwestern Cape coast has important dietary and nutritional ramifications. There is a direct proportional relationship between the size of a limpet or mussel shell and the amount of edible soft tissue it contains (Bosman et al. 1990; Rebelo in

Buchanan 1986). Thus, a decrease in the mean total lengths of limpets and prismatic bandwidths of black mussels recovered from archaeological assemblages represents a corresponding reduction in the edible yield of each individual mollusc. Large granite limpets (>80mm) and black mussels (>90mm) collected in 2010 and 2011 from Elands Bay beach yield around 25 grams of edible soft tissue. The mean size of granite limpets measured along the unexploited rocky shore at Elands Bay are larger (>70mm) than those recovered from archaeological deposits dating to the Middle and Later Stone Age (Figure 4.42). *C. granatina* from the Hoedjiespunt sites and three of the four Brandsebaai middens (BSB2, 3 and 4) are relatively large (70mm), and would yield approximately 16 grams of edible tissue (Rebello in Buchanan 1986). Smaller specimens (<60mm) derived from the Lynch Point sites and Dunefield Midden 11 would provide half as much edible tissue.

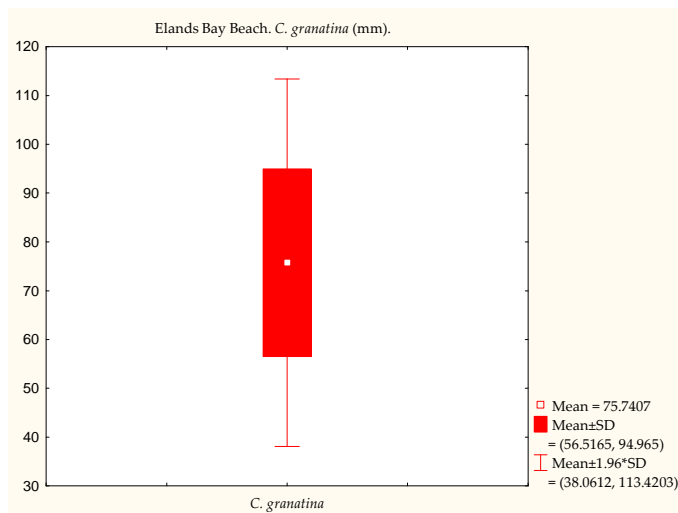


Figure 4.42 Mean total lengths of *C. granatina* from Elands Bay Beach.

#### 4.5 SUMMARY

The analysis and quantification of an enlarged sample of shellfish residues from the Middle Stone Age site of Hoedjiespunt 1, and collation of previously collected material from Lynch Point, Dunefield Midden 11 and Brandsebaai has considerably augmented archaeological observations on marine foraging along the Atlantic west coast. Patterns in the relative abundance of molluscan taxa, and the mean size of limpets and black mussels, which have been documented at other Middle and Later Stone Age sites in the vicinity, are strongly supported by analysis of material from these four localities. Specifically, the large mid-tidal

limpet, *C. granatina* and black mussel, *C. meridionalis*, constitute the best represented species in the majority of these shell middens, irrespective of their location and chronology (Parkington et al. 2014). Granite limpets and black mussels are large, with relatively high meat yields, abundant, visible and accessible. Limpets are more abundant than mussels in the majority of Middle and Later Stone Age assemblages investigated. The occurrence of middens comprised predominantly or even exclusively of limpets is a well-known phenomenon, especially in Namaqualand (Orton *et al.* 2005). Small granular limpets and whelks are a significant component of the Later Stone Age assemblages from Lynch Point and Brandsebaai; both of these localities yielded the remains of sheep and/or ceramics. The collection of large limpets and, at Lynch Point, abalones occurring in the lower intertidal and accessible only at certain times of the day or month, is also evident in the Later Stone Age assemblages from Lynch Point and Brandsebaai.

*C. granatina*, *S. granularis* and *S. argenvillei* recovered from the Middle Stone Age sites of Hoedjiespunt 1 and 3 are significantly larger than those from Late Holocene sites in the Saldanha Bay and Verlorenvlei region. However, with some exceptions, usually the two middens which post-date 2000BP, limpets from the Later Stone Age sites at Brandsebaai resemble those from Middle Stone Age contexts more closely than specimens from the Later Stone Age sites of Dunefield Midden 11 and Lynch Point. This is likely to reflect differences in the intensity or frequency of marine foraging and in population sizes between groups of hunter-gatherers living in the Namaqualand and the Verlorenvlei region during the Late Holocene. Middle Stone Age hunter-gatherers, and Later Stone Age people living in less densely populated regions, appear to have had access to larger limpets with correspondingly higher meat yields than the Late Holocene inhabitants of the Verlorenvlei and its surroundings. The reduction in mean limpet size evident in the archaeological record, and decrease in the meat yield of each individual collected, would have necessitated the collection of larger number of small individuals.

Statistically significant differences in the size of limpets from Later Stone Age sites at Brandsebaai, Lynch Point and Dunefield Midden 11 may also be the result of human impact rather than environmental factors. An environmental explanation is not sufficient to account for statistically significant variation in limpet sizes at closely adjacent and broadly

contemporary sites, or within horizontal sequences at Dunefield Midden and Dunefield Midden 11. As has been previously mentioned, changes in the frequency of water-worn pebbles and stone and barnacles at Dunefield Midden and Elands Bay Cave document shifts in Late Holocene hunter-gatherers' preference for targeting dead and live mussels, respectively. Larger mussels are strongly associated with barnacles, and smaller ones with water-worn shell and pebbles, at Dunefield Midden and Elands Bay Cave (Parkington et al. 2014). These patterns are only partially supported by the data from Dunefield midden 11. Statistically significant variation in the size of black mussel hinges from this site may reflect engagement in two different but not mutually exclusive subsistence strategies, namely strandloping and the collection of live individuals. In the following chapter, the results of nutrient analyses carried out on marine molluscs and a variety of other coastal and terrestrial foods available to prehistoric hunter-gatherers in the southwestern Cape will be presented, and the nutritional content of these foods will be explored.

University of Cape Town

## CHAPTER FIVE

### THE NUTRIENT CONTENT OF MARINE AND TERRESTRIAL ANIMALS AND PLANTS

#### 5.1 INTRODUCTION

In this chapter, new information on the nutritional content of a range of marine and terrestrial foods known or presumed to have been eaten by prehistoric hunter-gatherers is presented. These include marine molluscs such as mussels and limpets; large marine mammals including seals, whales and dolphins; marine fish, crustaceans and freshwater frogs; terrestrial bovids and smaller terrestrial vertebrates; insects including caterpillars, termites and grasshoppers; ostrich eggs, and the edible corms of fruits of indigenous plants. Information on the macronutrient, micronutrient and fatty acid composition of these potential foods provides a quantitative framework against which their relative nutritional value and possible contribution to prehistoric diets can be assessed. Marine and terrestrial subsistence strategies and resources can be compared and contrasted, and possible dietary challenges, constraints or advantages can be identified and discussed. In this way, a number of hypothetical scenarios for the emergence of anatomically modern humans in the southwestern Cape can be evaluated.

#### 5.2 MATERIALS AND METHODS

##### 5.2.1 Collection of samples

My sample collection strategy was informed by the substantial and still growing archaeological record of the Middle and Later Stone Age in the southwestern Cape; ethnographic accounts of modern hunter-gatherers living in coastal regions of Australia and in Africa and observations recorded by Europeans travelling through the Cape Folded Belt in the seventeenth century AD (Parkington 1977). In order to collect a comprehensive range of animals and plants likely to have been eaten by Middle Stone Age hunter-gatherers in the Cape fynbos region, a network of relations was established with South African National Parks (SANParks), other organisations and private individuals.

Edible plants were collected from two main localities, namely Table Mountain Nature Reserve and Bontebok National Park, with permission from the relevant authorities. Visits to the parks began in 2011 and continued into 2013, and were staggered throughout the year so as to capture seasonal variation in plant food availability and perhaps nutritional value. Particular emphasis was placed on large as well as smaller iridaceous species assumed by archaeologists including Curtis Marean, Hilary Deacon and John Parkington, to have been an abundant source of carbohydrates for prehistoric hunter-gatherers. The tough, fibrous casings that surround edible corms have been recovered from several archaeological sites dating to the Later Stone Age. Edible fruits including several indigenous berries as well as sour figs or *Carpobrotus edulis* were collected when available. Other potentially edible portions from indigenous plant species which were collected include the green shoots of members of the *Trachyandra* genus, the soft heads of bracken ferns, stems from *Oxalis pes caprae* and seeds produced by the *Chasmanthe* genus. While every attempt was made to sample as many potentially edible plants as possible during each site visit, the species included in my analysis do not constitute an exhaustive list of all of the plants which could have been eaten by Middle Stone Age hunter-gatherers. Time constraints as well as limited knowledge regarding the vast numbers of flora making up the Cape fynbos biome did not allow for more thorough collection. Seasonal patterns in the nutritional content of certain bulbs are also tentative; large-scale sampling and further research are required in order to refine them.

Several species of marine molluscs recovered from archaeological sites are still abundant on the southwestern Cape coast today. These were collected by hand using a general collector's permit purchased from the Post Office. The collection of insects from non-conservation areas does not require a permit. Marine fish were purchased from sellers on the docks at local harbours. Tissue samples of marine mammals and birds were donated by Marine and Coastal Management (MCM) and the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), respectively. These were derived from animals which had either died from natural causes or accidents, or which had to be put down. Samples from large and small terrestrial fauna including bovids, mammals, reptiles and amphibians were obtained from numerous collaborators. Roadkills and the carcasses of animals that had been culled were provided by SANParks, other nature reserves and the

Zoology Department of the University of Cape Town. Ethical Clearance for the use of this tissue was granted by the latter department. Additional samples from terrestrial bovids were donated by hunters or purchased from local butchers. Wherever possible, several potentially edible tissues including muscle, liver, brain and subcutaneous fat were sampled from a particular specimen.

The necessity of obtaining animal tissues from donor organisations imposed some limitations on my collection strategy. As I did not have control over the availability of samples derived from roadkills, other accidental deaths or culls, or those donated by hunters, I have not been able to sample all of the fauna likely to have been included in Middle Stone Age diets. For instance, while the eland is well-represented in some Middle Stone Age faunal assemblages, I was unable to obtain any samples of this animal from my collaborators. Similarly, the remains of small animals, notably rock hyraxes and angulate tortoises, are abundant in numerous archaeological sites in the southwestern Cape. However, their small size means that they are unlikely to be noticed or encountered by rangers operating in participating nature reserves, with the result that they were not sampled and are not included in my analysis. These challenges notwithstanding, a comprehensive collection of local animals and plants known or assumed to have been eaten by hunter-gatherers populations inhabiting the southwestern Cape during the Middle Stone Age has been assembled. These samples have allowed me to generate new quantitative data on the macronutrient, micronutrient and essential fatty acid components of prehistoric diets.

#### 5.2.2 Processing, preparation and storage of samples

Tissue samples were processed and stored in the Chemical Pathology Department of the University of Cape Town. Where whole carcasses were available, these were crudely dissected and smaller samples of edible tissues taken for processing and analysis. Inedible components of plant and animal samples such as corm casings, mollusc shells and animal skins were removed and discarded. Plant samples were washed with distilled water to remove soil and other inclusions. Portions of edible tissue weighing approximately ten grams were macerated and sonicated to form homogenates. Small plants, molluscs and insects were processed in their entirety and pooled to yield approximately ten grams of material for homogenisation. The macerated and sonicated tissue samples were brought up

to 20ml with distilled water and frozen at -20 degrees celcius. Tissue samples were kept on ice during preliminary processing to prevent enzymatic changes or deterioration, although this is unlikely to have had a significant effect on the results, and would also likely reflect the real life phenomena of foodstuffs that were not consumed immediately. Weights and volumes were recorded to ensure accurate quantification. Funding for laboratory analysis was limited and necessitated in-house assays to be developed and performed by myself. Simple colorimetric or spectrophotometric methods were used to determine the macro- and micronutrient content of samples using appropriate standards purchased from Sigma Chemical Company. Fatty acid profiles were determined by means of an Agilent gas chromatograph acquired during the project.

### 5.3 MACRONUTRIENTS

The mean protein and fat content of a range of marine and terrestrial fauna are presented in Table 5.1. The glycogen content of muscle and liver tissue from marine and terrestrial mammals, marine birds and terrestrial bovids is set at 3g/100g, following current estimates as there is no facile assay for this carbohydrate. The macronutrient content of several species of edible indigenous plants is presented in Table 5.2. Protein content was determined by means of the Markwell modification of the original Lowry procedure. The addition of sodium dodecyl sulphate to the alkali reagent and increasing the amount of copper tartrate reagent simplified the original method. It improves dispersion of membranes and can be applied to protein samples without prior extraction or stabilisation (Markwell *et al.* 1978).

With some exceptions, muscle tissue from marine mammals and birds and terrestrial animals contains between 10 and 20g of protein per 100g. The protein content of liver tissue from these animals is often but not always higher, with values >20g/100g recorded for some marine mammals. Brain tissue is usually lower (<12g/100g) in protein, while blubber contains only negligible amounts (<1g/100g) of this macronutrient. Marine fish and shellfish contain protein in similar, if slightly lower (<14g/100g) amounts to the muscle tissue of marine mammals and birds and terrestrial bovids. The protein content of ostrich egg yolk (11.7g/100g) and albumen (13.1g/100g) is similar; that of terrestrial invertebrates is similar and sometimes higher (9.0-18.6g/100g).

A small-scale adaptation of the Folch extraction was used to extract the lipid component of small samples (0.5-1g) of homogenised plant and animal tissue. Methanol and chloroform are added to the samples in a ratio of 2:1 and the monophasic mixture is spun to separate the supernatant from the pellet of insolubles. After three repetitions, chloroform and water are added to the supernatant pool and spun to separate the supernatant water containing a few remaining insoluble peptides and the chloroform infranatent containing the lipids, which is dried and retained for analysis. The dried infranatent was re-dissolved with chloroform and split into two portions for the determination of total lipid and fatty acid content, respectively. A small-scale adaptation of the Vanillin reaction (Appendix B) was used to determine the total lipid content of plant and animal samples. The reaction of lipids with heated sulphuric acid solution exposed to vanillin and phosphoric acid yields a pink product with maximal absorption at 525nm. This method is useful for crude assays of lipid, primarily triacylglycerol and phospholipid (Cheng 2011).

The fat content of muscle tissue from marine and terrestrial animals is relatively low (<4g/100g). Proportions of fat in wild animals are considerably lower than that of their domesticated counterparts, where high fat content has been actively selected for (Eaton *et al.* 1997). Figures for the fat content of meat from a variety of game animals hunted in Latvia and reported by Strazdina *et al.* (2012) range between 1.3 and 2.8g/100g. These correspond well with my results for eight species of terrestrial bovid (0.8 – 1.8g/100g). In their paper on the chemical composition of rib-cut samples from three South African game species, namely springbok, blesbok and impala, van Zyl and Ferreira (2004) note significant differences in the fat content of meat from male and female animals. The latter have considerably more fat (5.8-9g/100g) than the former (1.8-3.5g/100g). Factors such as seasonality and age also affect the fat content of wild game meat. The fat content of marine fish and shellfish, terrestrial invertebrates, as well as reptiles and amphibians is similar or in some cases higher (>2g/100g) than that found in muscle tissue.

In vertebrate species, liver and brain tissue generally contain more lipid than muscle tissue. My figures for the fat content of muscle, liver and brain tissue, derived from the Vanillin reaction, are slightly lower than those cited by Kuipers *et al.* (2010), but show the same proportional differences. The fat content of adipose tissue from marine and terrestrial

vertebrate fauna is more significantly underestimated. This appears to be an artefact of preliminary processing procedures in which tissue samples are homogenised and combined with distilled water, causing the lipids to separate from the remainder of the homogenate. Therefore, around 25% of water-soluble lipid is recovered from aliquots of homogenised adipose tissue on which the Folch extraction has been performed. Even less is recovered in aliquots from homogenates that have been frozen and thawed. By contrast, full recovery of insoluble lipids is possible in aliquots of unprocessed tallow. In line with these findings, the fat content of adipose tissue in marine and terrestrial vertebrates can be corrected up to the generally accepted figure of 90g/100g or 90%.

The energy content of foods can be determined from their protein, fat and carbohydrate content. Each gram of protein and carbohydrate yields four kilocalories (Kcal); every gram of fat, the most energy dense macronutrient, provides nine kilocalories. Energy content is expressed as kilojoules ( $\text{kJ} = \text{kcal} \times 4.2$ ). Muscle and liver tissue from marine and terrestrial vertebrates usually contains between 300 and 500 kilojoules per 100g. The energy content of brain tissue tends to be somewhat lower ( $<300\text{kJ}$ ). Ostrich egg yolk contains more energy ( $>400\text{kJ}$ ) than albumen ( $<300\text{kJ}$ ). Marine mussels and limpets contain between 200 and 300kJ/100g. The energy content of edible insects ranges between 266 and 481kJ/100g.

Table 5.1 Mean protein, fat and energy content of marine and terrestrial animals (g/100).

Common Name	Species	Tissue	Protein (g/100g) <sup>1</sup>	Fat (g/100g) <sup>2</sup>	Energy (kJ/100g) <sup>3</sup>
Marine and freshwater fauna					
Cape fur seal	<i>A. pusillus</i>	muscle	15.0(n = 3)	3 (n = 3)	415
		liver	24.1(n = 1)	2.7 (n = 3)	557
		brain	7.5(n = 3)	5.6 (n = 1)	338
Common dolphin	<i>D. capensis</i>	muscle	16.0(n = 2)	1.0 (n = 1)	357
		liver	17.9 (n=2)	2.9 (n=2)	461
		brain	11.8 (n = 2)	2.9 (n = 2)	308
		adipose	0.2 (n=1)	-	-
Risso's dolphin	<i>G. griseus</i>	liver	7.1(n = 1)	11.9 (n = 1)	619
		brain	9.3(n = 1)	4.8	337
		adipose	0.1 (n=1)	-	-
Pygmy sperm whale	<i>K. breviceps</i>	muscle	20.1(n = 2)	0.9 (n = 1)	422
		liver	11.8(n = 2)	0.8 (n = 1)	279
		brain	10.8(n = 2)	1.5 (n=1)	238
		adipose	0.6 (n=1)	-	-
Layard's beaked whale	<i>M. layardii</i>	muscle	8.9(n = 1)	0.3 (n=1)	211
		brain	12.7(n = 1)	2.0 (n=1)	289

Common Name	Species	Tissue	Protein (g/100g) <sup>1</sup>	Fat (g/100g) <sup>2</sup>	Energy (kJ/100g) <sup>3</sup>
		adipose	Bd	-	-
Killer whale	<i>O. orca</i>	muscle	15.9(n = 1)	1.4 (n = 1)	370
		liver	17.3(n=1)	2.4 ( n = 1)	432
		brain	6.5 (n=1)	8.9 ( n = 1)	445
		adipose	0.5 (n=1)	-	-
Bottlenose dolphin	<i>T. truncatus</i>	muscle	16.7(n = 2)	1.4 (n = 2)	384
		liver	23.8(n = 2)	3.0 (n = 2)	564
		brain	10.3(n = 2)	5.4 ( n = 1)	377
Hartlaub's gull	<i>C. hartlaubi</i>	muscle	17.6(n = 2)	1.5 (n = 5)	403
		liver	10.3(n = 1)	2.3 ( n = 3)	310
Kelp gull	<i>L. dominicanus</i>	muscle	13.2(n = 2)	1.9 (n = 2)	344
		liver	17.6(n = 3)	2.7 ( n = 3)	444
		adipose	0.6 (n=1)	-	-
Cape gannet	<i>M. capensis</i>	muscle	10.9 (n=1)	1.2 (n = 2)	279
		liver	12.2(n = 1)	3.7 ( n = 3)	395
		brain	10.0(n = 2)	4.4 ( n = 2)	334
		adipose	2.3 (n=1)	-	-
Cape cormorant	<i>P. capensis</i>	muscle	8.3(n = 4)	3.9 (n = 3)	337

Common Name	Species	Tissue	Protein (g/100g) <sup>1</sup>	Fat (g/100g) <sup>2</sup>	Energy (kJ/100g) <sup>3</sup>
		liver	13.7(n = 5)	3.1 ( n = 4)	398
		adipose	Bd <sup>4</sup>	-	-
White-breasted cormorant					
	<i>P. lucidus</i>	muscle	19.4(n = 1)	1.2 (n=1)	422
		liver	16.2(n = 2)	4.5 (n=3)	493
Swift tern	<i>S. bergii</i>	muscle	7.1(n = 1)	1.6 ( n = 1)	230
		liver	6.7(n = 1)	4.8 ( n = 1)	344
African penguin	<i>S. demersus</i>	muscle	15.7(n = 4)	2.9 ( n =4)	424
		liver	14.4(n = 5)	1.5 ( n = 2)	349
		brain	8.2(n = 2)	2.5 ( n = 1)	232
		adipose	Bd	-	-
Longfin tuna	<i>T. alalunga</i>	muscle	11.9 ( n = 1)	1.5 ( n = 1)	307
		liver	10.0 ( n = 1)	1.8 (n=1)	286
Black mussel	<i>C. meridionalis</i>	all	6.8 ( n = 4)	0.9 (n=4)	198
White mussel	<i>D. serra</i>	all	8.8 ( n = 2)	1.0 (n=3)	236
Granite limpet	<i>C. granatina</i>	all	10.5(n = 4)	2.2 ( n = 2)	310
		gonad	10.3(n = 5)	7.5 (n=1)	507
		foot	2.9 (n=4)	0.7 ( n =1)	125

Common Name	Species	Tissue	Protein (g/100g)	Fat (g/100g)	Energy (kJ/100g) <sup>1</sup>
Granular limpet	<i>S. granularis</i>	all	9.0(n = 4)	2.1 (n = 3)	281
		gonad	8.1(n = 1)	4.4 (n=1)	353
		foot	3.1 (n=1)	1.0 (n=1)	249
Rock lobster	<i>J. lalandii</i>	muscle	8.4(n = 1)	0.8 (n = 1)	222
African clawed frog	<i>X. laevis</i>	all	15.1 (n=1)	1.7 (n=1)	368
Terrestrial Fauna					
Red hartebeest	<i>A. caama</i>	muscle	9.5 (n=1)	1.3 (n = 1)	259
		liver	13.8(n = 1)	6.8 ( n = 1)	539
		brain	9.1(n = 1)	4.6 ( n = 1)	327
Springbok	<i>A. marsupialis</i>	muscle	12.0 (n =3)	1.4 (n =3)	305
		liver	10.5(n = 2)	2.9 ( n = 2)	336
		brain	5.9	5.9 ( n = 2)	322
Blue wildebeest	<i>C. taurinus</i>	muscle	9.7 (n=1)	1.3 (n = 1)	262
		liver	-	1.9 (n=1)	-
		brain	7.8 (n=1)	7.7(n = 1)	422
Blesbok	<i>D. pygarus phillipsii</i>	muscle	16.9 (n=1)	1.7 ( n = 1)	398

Common Name	Species	Tissue	Protein (g/100g)	Fat (g/100g)	Energy (kJ/100g) <sup>1</sup>
		liver	12.0(n = 1)	2.0 ( n = 1)	328
		brain	7.8(n = 1)	8.2 ( n = 1)	441
		adipose	3.0(n = 1)	-	-
Gemsbok	<i>O. gazelle</i>	muscle	10.9(n = 1)	1.8 ( n = 1)	301
		brain	9.4 (n=1)	3.3 ( n = 1)	283
Grey rhebok	<i>P. capreolus</i>	liver	12.2(n = 1)	1.7 ( n = 1)	320
		brain	9.5(n = 1)	3.4 ( n =1)	288
Steenbok	<i>R. campestris</i>	muscle	15.4(n = 1)	0.8 (n=1)	339
		liver	22.6(n = 1)	0.7 ( n = 1)	456
		brain	7.5 (n=1)	11.7 (n=1)	568
Cape grysbok	<i>R. melanotis</i>	muscle	9.8 (n=1)	0.9 (n=1)	249
		liver	19.4 (n=1)	2.8 (n=1)	482
Kudu	<i>Tragelaphus sp.</i>	muscle	12.9(n = 1)	1.0 ( n = 1)	305
Cape dune	<i>B. suillus</i>	muscle	11.1(n = 1)	-	-
molerat		liver	16.5(n = 1)	1 ( n = 1)	379
Cape porcupine	<i>H. africae australis</i>				
		muscle	7.4(n = 1)	0.6 ( n =2)	199
		liver	10.0(n = 1)	3.0 ( n = 1)	332

Common Name	Species	Tissue	Protein (g/100g)	Fat (g/100g)	Energy (kJ/100g) <sup>1</sup>
Gray mongoose	<i>G. pulverulenta</i>	muscle	7.8 (n=1)	0.7 (n = 1)	208
Ostrich	<i>S. camelus</i>	egg yolk	11.7 (n = 1)	5.3 (n = 1)	447
		albumen	13.1 (n = 1)	0.2 ( n = 2)	228
Cape cobra	<i>N. nivea</i>	muscle	5.7(n = 1)	1 (n=1)	184
		liver	10.5(n = 1)	2.7 ( n = 1)	329
Puffadder	<i>B. arietans</i>	muscle	8.5 (n = 1)	2.2 (n = 1)	276
		liver	9.2 (n = 1)	1.4 ( n = 1)	258
Harvester termite	<i>M. viator</i>	all	11.3	2.5	335
Emperor moth	<i>I. tyrrhea</i>	larvae	9.0	1.7	266
Large grasshopper	<i>P. hoplohopha</i>	all	17.3	2.4	432
Small grasshopper	<i>B. stolli</i>	all	18.6	3.1	481

<sup>1</sup>CV = 8%

<sup>2</sup>CV = 10%

<sup>3</sup>kJ = Kcal x 4.2

<sup>4</sup>Bd – Below detection

Table 5.2 Mean protein, fat, starch and energy content of plants.

Common name	Species	Season	Edible portion	Protein (g/100g)	Fat (g/100g)	Starch (g/100g) <sup>1</sup>	Energy (kJ/100g)
Slime lilly	<i>Albuca</i> sp.	September	corm	Bd <sup>2</sup>	0.5 (n=4)	Bd	-
Bobejaanetjie	<i>Babiana</i> sp.	September/October	corm	1.5 (n=1)	0.5 (n=3)	10.2 (n=1)	215
Cobra lilly	<i>C. aethiopica</i>	July	corm	4.0 (n=5)	0.8 (n=5)	23.0 (n=4)	483
		September	corm	1.4 (n=5)	0.9 (n=5)	14.1 (n=1)	294
Sword lilly	<i>Gladiolus</i> sp.	October	corm	Bd	0.6 (n=1)	-	-
Blou-uintjie	<i>Moreae tripetala</i>	October	corm	2.9	1.0g	7.7 (n=1)	216
Red root	<i>Wachendorfi</i> sp.	July	corm	4.4	1.1	5.1 (n=1)	201
		February	corm	4.0 (n=2)	0.3 (n=3)	5.1 (n=1)	162
		July	corm	3.1 (n=5)	1.2 (n=5)	9.0 (n=3)	249
Bugle lilly	<i>W. tabularis</i>	October	corm	3.3 (n=4)	1.0 (n=5)	26.9 (n=4)	545
Cape gorse	<i>A. ovatus</i>	December	berry	-	1.2	1.3	-
Cobra lilly	<i>Chasmanthe</i> sp.	September	seeds	2.6	1.4	Bd	-
	<i>C. compressum</i>	October	berry	-	1.0	0.3	-
Sour fig	<i>C. edulis</i>	November	fruit	3.4 (n=7)	1.2 (n=7)	0.3	-
		February	fruit	4.9 (n=1)	1.8 (n=7)	0.2	-
Tick berry	<i>C. monilifera</i>	July	berry	-	0.7	Bd	-
Skilpad bessie	<i>N. spinosa</i>	December	berry	-	1.4	0.7	-

Common name	Species	Season	Edible portion	Protein (g/100g)	Fat (g/100g)	Starch (g/100g)	Energy (kJ/100g)
Blue kuni-bush	<i>R. glauca</i>	October	berry	-	0.4	0.1	-
Wildeblomkool	<i>Trachyandra</i> sp.	September	fruit	4.3	0.3	Bd	1
Sourgrass	<i>O. pes caprae</i>	June	stems	2.2	0.0	0.1	-
Bracken fern	<i>P. aquilium</i>	July	stems	2.8	0.5	0.1	-
Wildeblomkool	<i>T. ciliata</i>	October	shoots	3.9	Bd	0.0	-
Wildeblomkool	<i>T. revoluta</i>	October	shoots	3.2	1.0	0.0	-

<sup>1</sup> CV = 7%

<sup>2</sup>Bd = Below detection

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The edible components of a variety of indigenous plants contain between one and five grams per hundred grams of protein. The fat content of the underground storage organs, berries, other fruits and green stems and shoots included in this analysis are also low (<2g/100g). Carbohydrates are organic nutrients which occur as simple sugars or monosaccharides, disaccharides and oligosaccharides. Larger polymers occur in starch or glycogen. Sample preparation involves the separation of the soluble (mono- to oligosaccharides) from the insoluble fraction by dissolving the former in 80% ethanol (Appendix B). Free sugars are not a significant component of most of the plants tested, with the exception of a few seasonally abundant fruits. They are not reported in this thesis. Determining the carbohydrate content of plant tissues is difficult and problematic.

An adaptation of Kanehira *et al.*'s (2009) method (Appendix B) was applied to determine the starch content of indigenous edible plants collected from Table Mountain Nature Reserve and Bontebok National Park. Corn starch was used as a standard for calculating the starch concentration in homogenised tissue samples from a variety of corms, berries, fruits, stems and shoots. The reaction between iodine and amylase produces a blue colour when read at 600nm. This method was found to underestimate the starch content of my samples, as well as others starches tested against the corn starch standard. This is most likely the result of changes in the conformation of starch molecules rendering them less accessible to the iodine in the reaction, thus rendering the assay less efficient. It is also noted that amylopectin does not react well with iodine. After experimentation, a correction factor of 12.8 was found to consistently apply, and was used for my samples.

The starch content of corms from several species of terrestrial plants which produce underground storage organs ranges from five to twenty seven grams per hundred grams. The highest values (>20g/100g) were obtained for two of the larger iridaceous species, namely *Chasmanthe aethiopica* and *Watsonia tabularis*, which also yield the most energy (483 and 545kJ/100g, respectively). These corrected figures are similar to those reported by Huanget *al.* (2009) for edible corms including two species of taro and breadfruit, and by Schoeninger *et al.* (2001) for tubers regularly consumed by Hadza hunter-gatherers in Tanzania. The starch content of *Watsonia* corms appears to vary according to their seasonal growth cycles. The remainder of the plants analysed contain little (<4g/100g) or no insoluble

starch. Long-term sampling and more accurate methods of carbohydrate determination are needed before seasonal variation in the nutritional content of indigenous plants can be fully understood.

#### 5.4 MICRONUTRIENTS

Small samples of homogenised tissue were processed into “wet ash” by oxidation with perchloric and nitric acid in preparation for micronutrient analyses. Iron content was determined by means of the dimethylformamide method adapted from Asan (Asan *et al.* 2003). Copper content was measured by means of Matthew’s (2007) method. A small-scale adaptation of Benamor and colleagues’ (2000) Xylenol Orange (XO) assay was used to determine the zinc content of marine and terrestrial samples. This spectrophotometric assay is based on the principle that zinc, XO and cetylpyridinium Cl (CPC) form a ternary complex at a pH of 5.5 that has a characteristic absorbance at 580nm. A reagent blank without zinc is used to obtain the absorbance of XO-CPC, while a standard curve of zinc serves to determine the concentration of unknowns. An attempt was made to measure selenium in marine and terrestrial animals, but the selenium content of my samples was below detection on the standard curve. No facile assay for iodine could be found. This micronutrient is known to be abundant in marine foodwebs.

The micronutrient content of several potentially edible portions of a range of marine and terrestrial animals is presented in Table 5.3. Muscle and liver tissue from marine mammals and avian fauna contain between 0.9 and 5.2 mg/100g, and 1.0 and 6.1mg/100 of iron, respectively. Liver tissue is often but not always higher in this essential trace element than muscle tissue. Similar, if slightly lower proportions are found in the muscle (0.9-4.9mg/100g) and liver (1.4-4.8mg/100g) tissue of several terrestrial bovids. Similar figures (1.8-2.5mg/100g) are reported by Hoffman *et al.* (2008) for the iron content of lean meat from kudu and impala, and by Falandysz (1994) for muscle and liver tissue from big game animals typically hunted in Poland (24-31mg/kg or 2.4-3.1mg/100g and 40-54mg/kg or 4-5.4mg/100g, respectively. Brain tissue and blubber tend to contain less (<1mg/100g) iron than muscle and liver tissue.

In marine mammalian and avian fauna, muscle tissue contains between 0.7 and 7.6mg/100g of another essential trace element, copper. Figures obtained for muscle tissue from terrestrial bovids are lower and narrower in range (1 – 1.7mg/100g). Considerably lower figures (<1.0mg/100g) are reported for the muscle tissue of big game species including the kudu, impala and red deer by Hoffman *et al.* (2008) and Falandysz *et al.* (2005), respectively. The copper content of liver tissue from marine and terrestrial fauna is considerably higher (3.6-13.3mg/100g). Muscle and liver tissue from marine mammals and birds contains 0.9 – 3.7mg/100g and 1.0 – 6.8mg/100g of zinc, respectively. In terrestrial bovids, muscle tissue contains between 2.3-2.7mg/100g of this micronutrient; these figures are similar to those reported by Hoffman *et al.* (2008) for kudu and impala (1.1-2.8mg/100g), and by Falandysz (1994) for wild boar, roe deer and stag (32-37mg/kg or 3.2-3.7mg/100g). Liver tissue contains similar amounts (1.7-1.9mg/100g) to muscle tissue.

From the scanty information available on the nutritional value of seafood, it would appear that the micronutrient content of marine fish and shellfish is highly variable. According to Dietary Reference Intakes published by the NAS in 2004, the iron content of miscellaneous wild caught fish and molluscs ranges between 0.18 and 13.98mg/100g raw edible tissue. Shellfish are reportedly among the best sources of copper and zinc, with concentrations ranging from 0.05 – 1.89mg/100g and 0.36 – 16.62mg/100g. This variability is evident in my data for intertidal shellfish. Black mussels contain relatively little iron (<1mg/100g); white mussels contain somewhat more (1.8mg/100g). The iron content of two limpet species common along the western Cape coast, namely *C. granatina* and *S. granularis*, is higher than expected for these invertebrate animals (3.4 – 5.3mg/100g), and is comparable to proportions found in the muscle and liver tissue of terrestrial mammals, birds and terrestrial ungulates. Muscle tissue from the west coast rock lobster contains iron in similar amounts to fish. Limpets are considerably higher in copper (<10mg/100g) than black and white mussels (0.6mg/100g and 2.2mg/100g, respectively) and muscle tissue from crayfish (0.5mg/100g) and fish (1.9mg/100g). Mussels and limpets are both richer in zinc (>6.0mg/100g) than terrestrial fauna.

Terrestrial invertebrates such as grasshoppers, termites and caterpillars are also purported to be a good source of some micronutrients (DeFoliart 1999). Banjo and colleagues (2006)

analyzed the nutrient content of fourteen edible insects frequently consumed in Nigeria. Most contained between 0.35 and 2.3mg/100g of iron; unusually high concentrations (>25mg/100g) were found in winged termite queens. Ajai *et al.* (2013) determined the micronutrient content of edible locusts, crickets, grasshoppers and termites with respect to iron ( $390 \pm 31.61$  mg/kg); copper ( $85.5 \pm 3.4$ mg/kg) and zinc ( $208.11 \pm 63.9$ mg/kg); locusts were found to be highest and iron and most other trace elements. Caterpillar larvae and two species of grasshopper collected in the Bidouw Valley during the spring of 2012 contain 1.4-2.0mg/100g of iron, and 2.6 – 4.3mg/100g of zinc. Larvae of the emperor moth or *Imbrasia tyhrrea* contain 1.1mg/100g of copper; two species of grasshopper contain considerably more (>6mg/100g) of this trace element.

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Table 5.3 Mean iron, copper and zinc content of marine and terrestrial animals (mg/100g).

Common name	Species	Tissue	Iron (mg/100g) <sup>1</sup>	Copper (mg/100g) <sup>2</sup>	Zinc (mg/100g) <sup>3</sup>
Marine Fauna					
Cape fur seal	<i>A. pussilus</i>	muscle	2.0 (n=2)	1.4 (n=1)	1.5 (n=1)
		liver	3.8 (n=2)	5.9 (n=2)	6.8 (n=2)
		brain	0.9 (n=3)	0.5 (n=1)	Bd <sup>4</sup>
Common dolphin	<i>D. capensis</i>	muscle	1.5 (n=3)	0.7 (n=1)	1.0 (n=2)
		liver	3.7 (n=3)	5.5 (n=1)	2.4 (n=3)
		brain	0.6 (n=3)	3.6 (n=1)	Bd
		fat	0.5 (n=1)	3.7 (n=1)	Bd
Risso's dolphin	<i>G. griseus</i>	muscle	2.3 (n=1)	7.6 (n=1)	1.5 (n=1)
		liver	3.5 (n=1)	8.5 (n=1)	1.2 (n=1)
		brain	0.7 (n=1)	0.5 (n=1)	0.7 (n=1)
Pygmy sperm whale	<i>K. breviceps</i>	muscle	1.6 (n=2)	1.8 (n=3)	1.0(n=2)
		liver	2.7 (n=2)	5.9 (n=2)	2.3 (n=1)
		brain	0.6 (n=2)	1.4 (n=2)	0.1 (n=1)
		fat	0.4 (n=2)	1.4 (n=1)	Bd
Layard's beaked whale	<i>M. layardi</i>	muscle	3.8 (n=1)	1.5 (n=1)	3.7 (n=1)
		brain	1.1 (n=1)	3.0 (n=1)	0.2 (n=1)

Common name	Species	Tissue	Iron (mg/100g) <sup>1</sup>	Copper (mg/100g) <sup>2</sup>	Zinc (mg/100g) <sup>3</sup>
Killer whale	<i>O. orca</i>	adipose	0.4 (n=1)	0.3 (n=1)	Bd
		muscle	1 (n=1)	0.7 (n=1)	0.3 (n=1)
		liver	3.5 (n=1)	5.7 (n=1)	0.9 (n=1)
		brain	0.9(n=1)	0.7 (n=1)	0.5 (n=1)
Bottlenose dolphin	<i>T. truncatus</i>	adipose	0.6 (n=1)	4.8 (n=1)	Bd
		muscle	0.9 (n=1)	3.7 (n=1)	3.3 (n=1)
		liver	1.9 (n=1)	7.2 (n=1)	1.4 (n=2)
		brain	0.5 (n=1)	3.0 (n=2)	Bd
Hartlaub's gull	<i>C. haurtlaubi</i>	fat	0.7 (n=1)	2.3 (n=1)	Bd
		muscle	5.2 (n=3)	2.7 (n=4)	1.6 (n=2)
		adipose	6.1 (n=4)	10.1 (n=3)	4.0 (n=5)
Kelp gull	<i>L. dominicanus</i>	muscle	2.1 (n=2)	1.3 (n=2)	1.7 (n=3)
		liver	6.1 (n=4)	13.3 (n=1)	1.0 (n=1)
		adipose	1.8 (n=1)	1.4 (=1)	Bd
Cape gannet	<i>M. capensis</i>	muscle	2.0 (n=3)	1.4 (n=3)	1.3 (n=2)
		liver	2.4 (n=2)	3.6 (n=1)	1.5 (n=2)
		brain	0.9 (n=2)	0.3 (n=2)	0.4 (n=2)
		adipose	1.0 (n=1)	5.0 (n=2)	Bd

Common name	Species	Tissue	Iron (mg/100g) <sup>1</sup>	Copper (mg/100g) <sup>2</sup>	Zinc (mg/100g) <sup>3</sup>
Cape cormorant	<i>P. capensis</i>	muscle	1.3 (n=6)	5.6 (n=3)	0.9 (n=4)
		liver	2.7 (n=4)	10.5 (n=3)	2.8 (n=4)
		brain	0.8 (n=1)	Bd	Bd
		adipose	1.1 (n=1)	1.8 (n=1)	Bd
White-breasted cormorant	<i>P. lucidas</i>	muscle	1.2 (n=2)	0.8 (n=1)	0.7 (n=1)
		liver	4.1 (n=2)	3.9 (n=1)	4.0 (n=1)
Swift tern	<i>S. bergii</i>	muscle	1.2 (n=1)	0.6 (n=1)	1.6 (n=1)
		liver	1.0 (n=1)	7.0 (n=1)	4.2 (n=1)
African penguin	<i>S. demersus</i>	muscle	1.9 (n=4)	4.4 (n=2)	1 (n=1)
		liver	2.8 (n=5)	9.8 (n=3)	2.4 (n=4)
		brain	0.6 (n=2)	1.8 (n=2)	0.4 (n=1)
		adipose	1.2 (n=1)	Bd	Bd
Longfin tuna	<i>T. alalunga</i>	muscle	3.2 (n=1)	0.6 (n=1)	0.3 (n=1)
		liver	1.1 (n=1)	1.9 (n=1)	3.9 (n=1)
Black mussel	<i>C. meridionalis</i>	all	0.8 (n=5)	0.6 (n=5)	3.5 (n=3)
White mussel	<i>D. serra</i>	all	1.8 (n=2)	2.2 (n=4)	1.6 (n=4)
Granite limpet	<i>C. granatina</i>	all	3.4 (n=5)	10.5 (n=2)	4.6 (n=3)
		gonad	2.2 (n=3)	11.7 (n=4)	21.1 (n=2)

Common name	Species	Tissue	Iron (mg/100g) <sup>1</sup>	Copper (mg/100g) <sup>2</sup>	Zinc (mg/100g) <sup>3</sup>
		foot	2.1 (n=4)	7.7 (n=2)	15.8 (n=2)
	<i>C. oculus</i>	all	2.4 (n=1)	4.4 (n=1)	3.9 (n=1)
Argenville's limpet	<i>S. argenvillei</i>	all	7.3 (n=1)	6.7 (n=1)	3.1 (n=2)
Granular limpet	<i>S. granularis</i>	all	5.3 (n=2)	14.6 (n=3)	5.0 (n=2)
West coast rock lobster	<i>J. lallandii</i>	muscle cephalothorax	2.1 (n=1) 3.4 (n=1)	0.5 (n=1) 2.6 (n=1)	0.3 (n=1) 6.3 (n=1)
Terrestrial fauna					
Red hartebeest	<i>A. caama</i>	liver	0.6 (n=1)	10.4 (n=1)	0.2 (n=1)
		brain	0.8 (n=1)	1.0 (n=1)	0.2 (n=1)
Springbok	<i>A. marsupialis</i>	muscle	0.9 (n=3)	1.4 (n=1)	2.3 (n=1)
		liver	2.6 (n=2)	4.4 (n=1)	1.2 (n=1)
		brain	1.2 (n=1)	1.2 (n=1)	0.6 (n=1)
Blue wildebeest	<i>C. taurinus</i>	muscle	0.9 (n=1)	1.0 (n=1)	0.2 (n=1)
		liver	2.0 (n=1)	5.8 (n=1)	1.7 (n=1)
Blesbok	<i>D. pygrrarus</i>	muscle	3.1 (n=1)	1.7 (n=1)	2.0 (n=1)
	<i>phillipsii</i>	liver	3.0 (n=1)	6.9 (n=1)	1.4 (n=1)
		brain	0.5 (n=1)	0.3 (n=1)	1.3 (n=1)
		adipose	0.6 (n=1)	3.3 (n=1)	Bd

Common name	Species	Tissue	Iron (mg/100g)	Copper (mg/100g)	Zinc (mg/100g)
Gemsbok	<i>O. gazelle</i>	muscle	4.1 (n=1)	1.4 (n=1)	2.7 (n=1)
		brain	0.5 (n=1)	0.3 (n=1)	0.3 (n=1)
Grey rhebok	<i>P. capreolus</i>	muscle	2.8 (n=1)	1.2 (n=1)	2.8 (n=1)
		liver	4.8 (n=1)	5.7 (n=1)	1.9 (n=1)
		brain	1.2 (n=1)	0.8 (n=1)	0.6 (n=1)
Steenbok	<i>R. campestris</i>	muscle	2.5 (n=1)	1.4 (n=1)	1.5 (n=1)
		liver	1.4 (n=1)	6.7 (n=1)	1.4 (n=1)
		brain	0.7 (n=1)	1.6 (n=1)	0.5 (n=1)
Cape grysbok	<i>R. melanotis</i>	muscle	4.6 (n=1)	1.1 (n=1)	1.2 (n=1)
		liver	2.5 (n=1)	1.5 (n=1)	1.4 (n=1)
Cape dune molerat	<i>B. suillus</i>	muscle	0.7 (n=1)	Bd	1.9 (n=1)
		liver	1.2 (n=1)	3.5 (n=1)	5.0 (n=1)
Cape porcupine	<i>H.</i>	muscle	2.5 (n=1)	4.7 (n=1)	1.9 (n=1)
	<i>Africae australis</i>	liver	1.1 (n=1)	5.0 (n=1)	2.4 (n=2)
Gray mongoose	<i>G. pulverulenta</i>	muscle	1.0 (n=1)	6.6 (n=1)	0.2 (n=1)
Ostrich	<i>S. camelus</i>	egg albumen	0.3 (n=1)	Bd	Bd
		egg yolk	1.4 (n=1)	2.8 (n=1)	1.0 (n=1)
Cape cobra	<i>N. nivea</i>	muscle	0.8 (n=1)	6.8 (n=1)	0.3 (n=1)

Common name	Species	Tissue	Iron (mg/100g)	Copper (mg/100g)	Zinc (mg/100g)
		liver	6.2 (n=1)	11.6 (n=1)	0.5
Puffadder	<i>B. arietans</i>	muscle	2.5 (n=1)	3.5 (n=1)	2.2 (n=1)
		liver	7.9 (n=1)	1.1 (n=1)	0.7 (n=1)
Mole snake	<i>S. cana</i>	liver	3.7 (n=1)	2.2 (n=1)	1.1 (n=1)
African clawed frog	<i>X. laevis</i>	all	1.2 (n=2)	1.3 (n=2)	1.1 (n=1)
Emperor moth	<i>I. tyrrhea</i>	all	1.4 (n=2)	1.1 (n=2)	3.4 (n=1)
Large locust	<i>Pamphrigidaea</i>	all	2.0 (n=1)	6.3 (n=1)	4.3 (n=1)
	<i>Hoplolopha</i>				
Small locust	<i>B. stolli</i>	all	1.5 (n=1)	6.8 (n=1)	2.6 (n=1)

<sup>1</sup>CV = 1%

<sup>2</sup>CV = 6%

<sup>3</sup>CV = 1%

<sup>4</sup>Below detection

## 5.5 ESSENTIAL FATTY ACIDS

The fatty acid methyl ester (FAME) analysis was adapted from the method described by Ichihara and colleagues (2010), and was performed on pooled lipid samples from individual marine and terrestrial animals and plants to provide estimates of the contents. Lipid samples that had been dried under nitrogen were reconstituted in n-hexane and injected into the GC for analysis. GC analysis was performed on an Agilent 7820A gas chromatograph (Agilent Technologies, South Africa, model # 19091J-413E). The GC was fitted with a 30m HP-5 column (Agilent Technologies), ID 0.320mm and film thickness 0.25 $\mu$ m. Hydrogen was used as the carrier gas at a flow rate of 30mL/min. The injector and flame ionization temperatures were set at 260°C and 300°C respectively. The column oven temperature was programmed as follows: 120°C held for 5min, then ramped to 240°C at a rate of 4°C/min. Split injection of 2 $\mu$ L was used with a split ratio of 15:1. Identification of FAMES was done by comparing retention times to those of the relevant, specific known standards (Sigma-Aldrich, Kempton Park South Africa).

The fatty acid content of edible animals and plants with respect to some of the most important fatty acids, including linoleic and arachidonic acid (omega-6), and  $\alpha$ -linolenic, eicosapentaenoic and docosahexaenoic acid (omega-3), is presented in Table 5.4. Oleic acid is the predominant fatty acid in iridaceous plants collected from Table Mountain Nature Reserve and Bontebok National Park, and is present in amounts ranging from 0.2-0.7g/100g. Most also contain small quantities of palmitic and stearic acid. These fatty acids were also identified in most of the edible fruits tested. No fatty acids could be detected in three species of berries and two edible shoots. Only three of the plants tested, namely sour figs or *Carpobrotus edulis*, and the corms of two iridaceous species, *Watsonia pyramidata* and *Watsonia tabularis*, contain linoleic acid (LA), the precursor of the longer-chain arachidonic acid (AA).  $\alpha$ -Linolenic acid, the precursor of the omega-3 LCPUFAs, could be identified in only one of the samples, *W. tabularis*. Some seasonal variation in the fatty acid content of edible corms seems apparent and warrants further investigation.

The edible tissues of marine and terrestrial vertebrate fauna, as well as marine and terrestrial invertebrates, contain palmitic, stearic and oleic acid in varying amounts. Linoleic acid is present in the muscle and liver tissues of marine birds (0.4-1.5g/100g), terrestrial bovids,

reptiles, amphibians and insects (0.1 – 1.9g/100g), in large quantities (3.8g/100g) in ostrich egg yolk, and some marine molluscs in very small amounts (<0.1g/100g). This fatty acid was not detected in the edible tissues of marine mammals. Liver, brain and in some cases muscle tissue from marine mammals and birds contain arachidonic acid, as well as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). The shorter-chain precursor of the latter two fatty acids,  $\alpha$ -linolenic acid, was not detected in these samples.

With regard to marine molluscs, the edible soft tissue of black and white mussels contains 1 omega-6 and omega-3 polyunsaturated fatty acids. In black mussels, DHA is present in larger amounts (1.2g/100g) than EPA (0.5g/100g) and AA (0.2g/100g). Granite and granular limpets contain AA (0.1g/100g) and EPA (0.1g and 0.5g/100g, respectively); DHA is probably present in small amounts but was undetected in my samples. Fish liver yielded the highest value (2.9g/100g) for DHA. Arachidonic, eicosapentaenoic and docosahexaenoic acid are present in the liver and brain tissues of terrestrial bovids; proportions of omega-6 fatty acid are larger than those of the omega-3 polyunsaturates. Some ALA is also present in the muscle and liver tissues of these terrestrial animals. Ostrich egg yolk contains both the shorter-chain precursors and longer-chain derivatives of the omega-6 and omega-3 classes. While AA, EPA and DHA were undetected in four species of terrestrial invertebrates, these all contain ALA, sometimes in significant amounts (0.8-2.5g/100g).

Table 5.4 Fatty acid content of marine and terrestrial animals and plants (g/100g).

Common name	Species	Tissue	LA	ALA	AA	EPA	DHA
Marine fauna							
Cape fur seal	<i>A. pusillus</i>	muscle	N	N	N	N	U
		liver	<0.1	U	0.5	1.0	0.5
		brain	U	U	0.1	U	0.1
Common dolphin	<i>D. capensis</i>	muscle	U	U	0.5	<0.1	0.4
		liver	U	U	0.5	0.1	0.5
		brain	U	U	0.6	U	1.3
		adipose	N	U	N	U	U
Risso's dolphin	<i>G. griseus</i>	brain	N	U	0.2	U	0.2
Pygmy sperm whale	<i>K. breviceps</i>	muscle	U	N	U	U	U
		liver	U	U	0.5	U	<0.1
		adipose	U	0.4	0.3	U	U
Layard's beaked whale	<i>M. layardii</i>	adipose	U	U	<0.1	U	U
Killer whale	<i>O. orca</i>	muscle	N	U	<0.1	N	N
		liver	U	U	0.1	U	U
		adipose	U	U	0.1	U	0.3

Common name	Species	Tissue	LA	ALA	AA	EPA	DHA
Bottlenose dolphin	<i>T. truncatus</i>	muscle	U <sup>1</sup>	U	0.1	0.2	0.2
		brain	N <sup>2</sup>	U	0.1	U	0.4
Hartlaub's gull	<i>C. hartlaubi</i>	muscle	1.5	U	0.9	0.1	0.1
		liver	0.4	U	0.5	U	<0.1
Kelp gull	<i>L. dominicanus</i>	muscle	0.8	U	1.1	<0.1	U
		liver	0.6	U	1.3	U	0.4
		adipose	0.4	U	0.1	U	U
Cape gannet	<i>M. capensis</i>	liver	U	N	0.1	U	0.2
		brain	N	N	0.3	U	1.1
		fat	0.1	<0.1	0.7	0.3	0.2
Cape cormorant	<i>P. capensis</i>	muscle	U	U	<0.1	U	U
		liver	U	U	0.1	U	0.2
White-breasted cormorant							
	<i>P. lucidus</i>	liver	U	N	0.1	U	0.1
African penguin	<i>S. demersus</i>	muscle	N	N	N	U	U
		brain	U	U	0.2	U	1.5
Longfin tuna	<i>T. alalunga</i>	muscle	N	N	N	U	N

Common name	Species	Tissue	LA	ALA	AA	EPA	DHA
		liver	U	U	0.1	0.5	2.9
Black mussel	<i>C. meridionalis</i>	all	<0.1	U	0.2	0.5	1.2
White mussel	<i>D. serra</i>	all	U	U	U	1.0	0.5
Granite limpet	<i>C. granatina</i>	all	U	N	0.1	0.5	U
		gonad	U	U	0.2	0.3	U
	<i>C. oculus</i>	all	U	U	0.3	0.2	N
Granular limpet	<i>S. granularis</i>	all	U	N	0.1	0.1	U
		gonad	<0.1	U	0.3	0.5	U
Rock lobster	<i>J. lalandii</i>	muscle	N	N	U	U	U
Terrestrial Fauna							
Red hartebeest	<i>A. caama</i>	muscle	0.3	U	0.1	U	U
		liver	0.1	U	0.1	0.1	U
		brain	U	U	0.4	U	0.4
Springbok	<i>A. marsupialis</i>	muscle	0.8	0.1	0.7	0.1	U
		liver	2.2	0.4	1.2	0.4	0.1
		brain	U	N	U	U	U

Common name	Species	Tissue	LA	ALA	AA	EPA	DHA
Blue wildebeest	<i>C. taurinus</i>	muscle	0.1	U	U	U	U
		liver	0.8	U	1.2	<0.1	U
Blesbok	<i>D. Pygarrus phillipsii</i>	brain	U	U	0.2	U	<0.1
		adipose	U	U	U	U	U
Gemsbok	<i>O. gazelle</i>	brain	U	1.0	1.0	U	0.5
Grey rhebok	<i>P. capreolus</i>	muscle	1.1	U	1.6	U	U
		liver	0.2	U	0.1	U	U
		brain	U	0.1	0.4	<0.1	0.5
Steenbok	<i>R. campestris</i>	muscle	N	N	N	N	N
		liver	1.6	U	0.6	U	U
		brain	U	N	0.2	N	U
Cape grysbok	<i>R. melanotis</i>	muscle	U	U	U	U	U
		liver	0.8	0.2	1.0	0.4	<0.1
Kudu	<i>Tragelaphus sp.</i>	muscle	U	U	U	U	U
Cape dune molerat	<i>B. suillus</i>	liver	0.2	U	0.2	U	U
Cape porcupine	<i>H. africae australis</i>	muscle	1.1	U	0.3	U	U
		liver	1.9	0.3	1.4	U	0.1

Common name	Species	Tissue	LA	ALA	AA	EPA	DHA
Molesnake	<i>P. cana</i>	muscle	0.5	U	0.3	U	U
		liver	1.1	<0.1	1.6	U	0.6
Cape cobra	<i>N. nivea</i>	liver	0.4	U	0.4	U	0.1
Gray mongoose	<i>G. pulverulenta</i>	muscle	U	N	N	N	N
Ostrich	<i>S. camelus</i>	egg yolk	3.8	0.6	1.3	0.3	0.5
African clawed frog	<i>X. laevis</i>	all	0.4	<0.1	0.3	0.3	0.1
Harvester termite	<i>M. viator</i>	all	0.4	U	U	N	U
Emperor moth	<i>I. tyrrhea</i>	larvae	0.7	2.5	U	N	U
Large grasshopper	<i>P. hoplohopa</i>	all	0.4	0.8	U	U	U
Small grasshopper	<i>B. stolli</i>	all	0.2	0.2	U	U	U
Plants							
Sour fig	<i>C. edulis</i>	fruit	0.2	N	N	N	N
	<i>W. pyramidata</i>	corm	0.3	N	N	N	N
Bugle lilly	<i>W. tabularis</i>	corm	0.2	N	0.2	N	N

<sup>1</sup>U = undetectable on standard curve

<sup>2</sup>N = not present

## 5.6 DISCUSSION

On the basis of the results of these analyses, some generalisations about the nutrient content of marine and terrestrial animals and plants likely to have been eaten by Middle Stone Age people can be made. Protein is fairly abundant in marine (Figure 5.1) and terrestrial (Figure 5.2) fauna. Muscle (~7.5-15g/100g) and liver (~10-15g/100g) tissue from marine and terrestrial vertebrates are especially rich in this macronutrient. Ostrich egg yolk (11.7g/100g) and albumen (13.1g/100g) are also good sources of protein. So are small freshwater frogs (15.1g/100g) and terrestrial invertebrates such as caterpillars (9g/100g), grasshoppers (~17-19g/100g) and termites (11.3g/100g). Marine invertebrates are somewhat lower (<11g/100g) in protein; edible plants contain much smaller amounts (<5g/100g). Brain (~2-8g/100g) and adipose tissue from marine mammals and birds and terrestrial bovids are the best sources of total fat or lipids (Figures 5.3 and 5.4), followed by ostrich egg yolk (5.3g/100g). Muscle tissue from marine and terrestrial vertebrates is relatively low (<2g/100g) in fat; liver tissue is somewhat higher (>2g/100g). Marine shellfish, notably limpets, and terrestrial invertebrates contain slightly more fat (>2g/100g) than vertebrate muscle tissue (<2g/100g). Plants contain very little (<1g/100g) fat. Edible corms from iridaceous plants represent the only significant source of starch (~5-25g/100g) available to prehistoric hunter-gatherers.

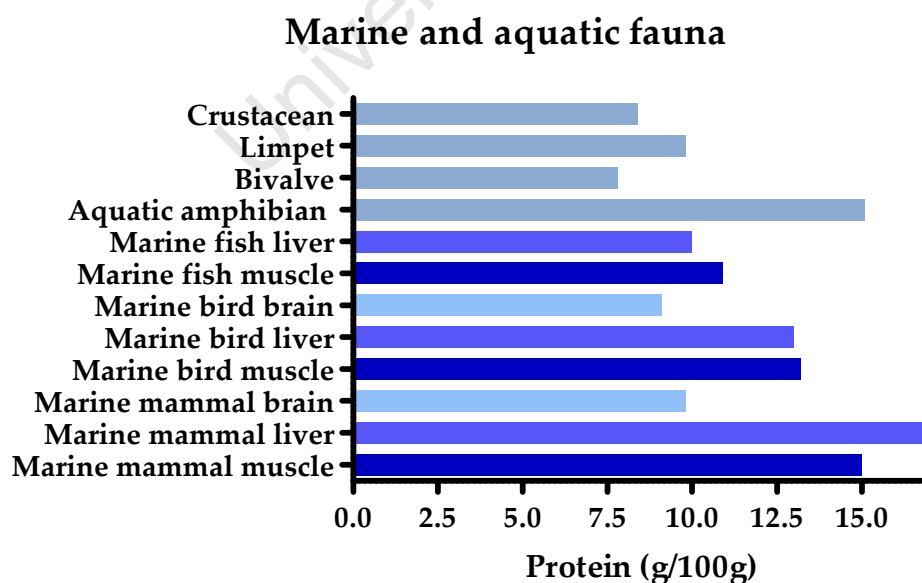


Figure 5.1 Protein content of marine and freshwater fauna.

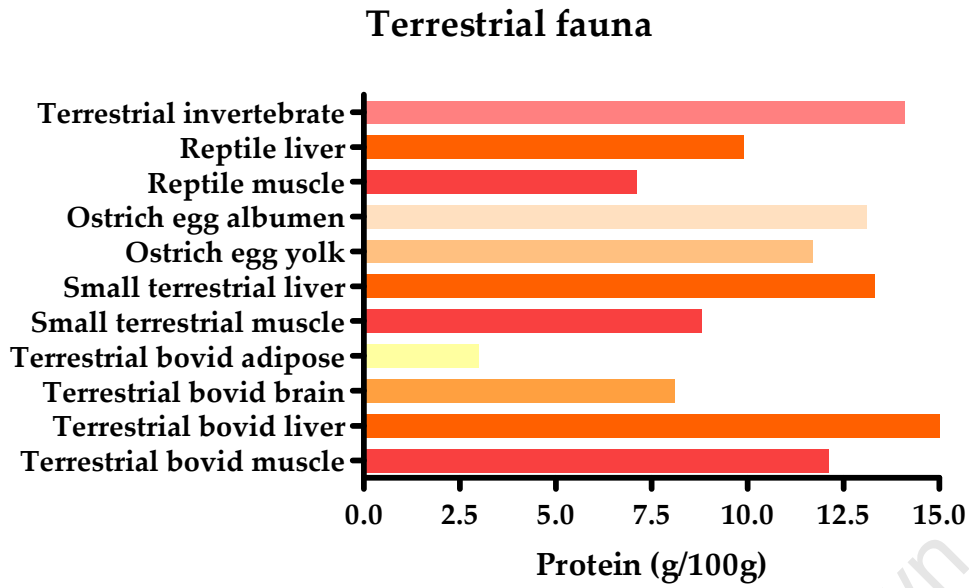


Figure 5.2 Protein content of terrestrial fauna.

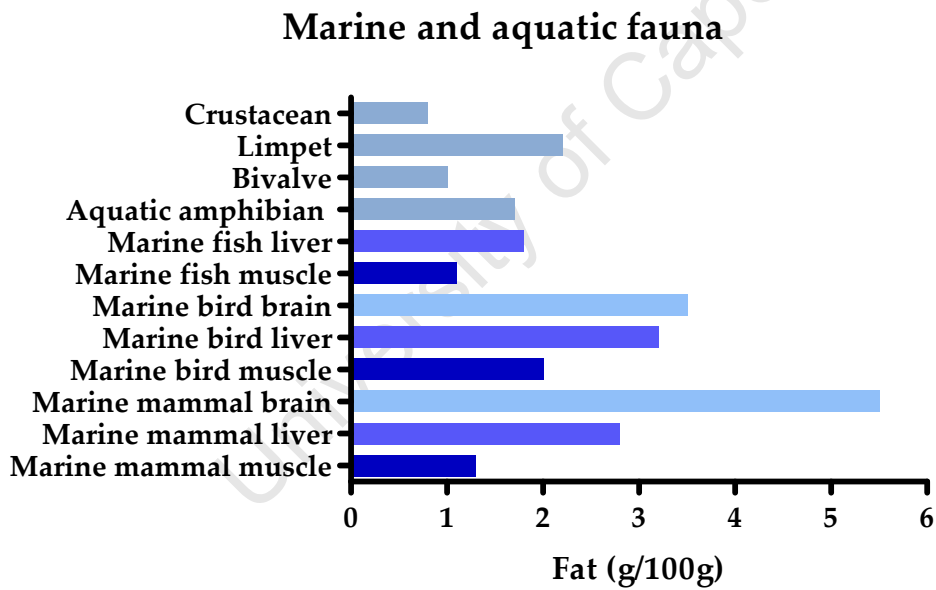


Figure 5.3 Fat content of marine and freshwater fauna.

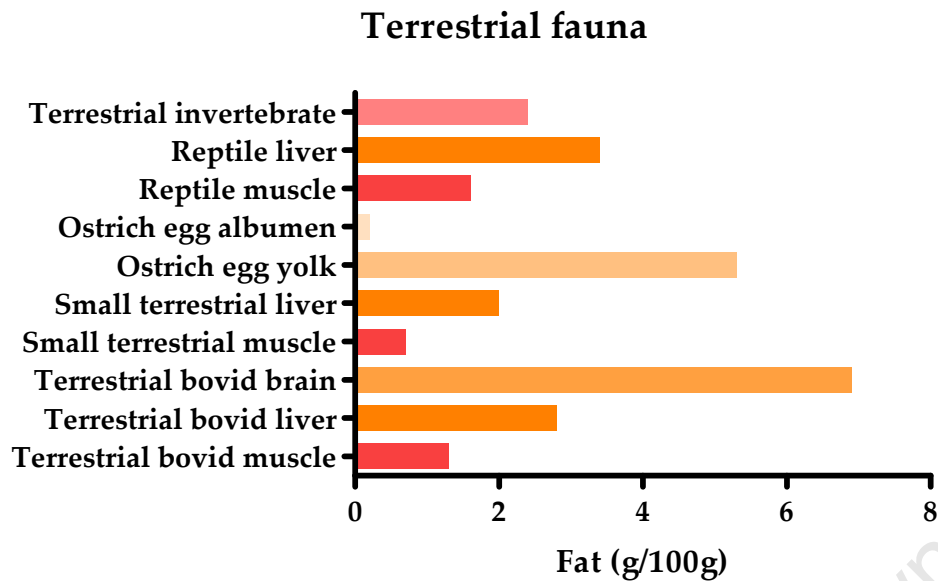


Figure 5.4 Fat content of terrestrial fauna.

Essential micronutrients (Figures 5.5-10) are also fairly abundant in marine and terrestrial foodwebs. Limpets represent one of the best source of iron (>4mg/100g) among a range of marine resources. The lower iron content of white and, especially, black mussels (<2mg/100g) may be due to their higher water content. Limpets also contain large amounts of copper (>8mg/100g) and zinc (>4mg/100g). Muscle and liver from marine mammals, fish and seabirds contain ~1.5-3.5mg/100g of iron, ~1-8mg/100g of copper (Figure 5.6.8) and ~1-4mg/100g of zinc (Figure 5.6.10). Variation within particular taxa may reflect differences in their diets, or could be an artefact of small sample sizes and the variable condition of tissue samples submitted for analysis. Essential micronutrients are fairly abundant in terrestrial foods, too (Figures 5.6.7, 5.6.9 and 5.6.11). Muscle and liver tissue from terrestrial bovids, smaller mammals and reptiles contain ~1.5-6mg/100g of iron and copper and ~1-4mg/100g of zinc. Terrestrial invertebrates are a good source of copper (>4mg/100g), zinc (>3mg/100g) and, to a lesser extent, iron (>1mg/100g).

### Marine and aquatic fauna

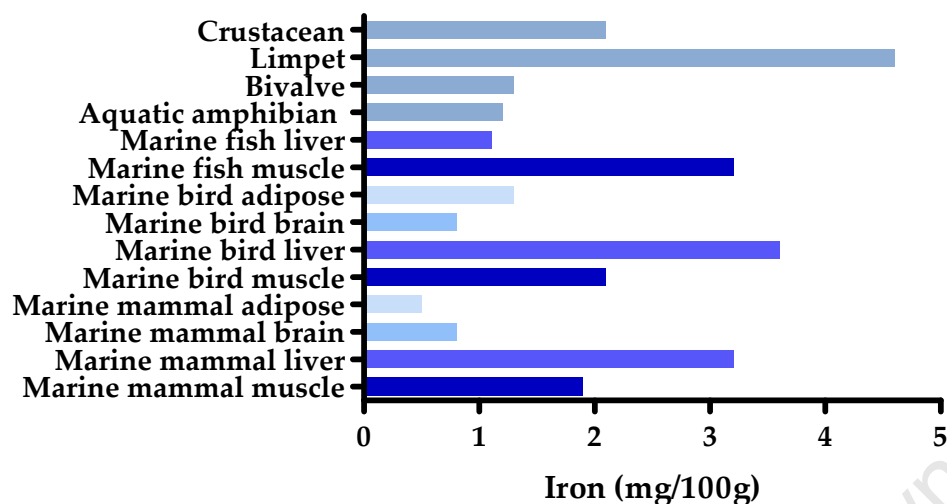


Figure 5.5 Iron content of marine and freshwater fauna.

### Terrestrial fauna

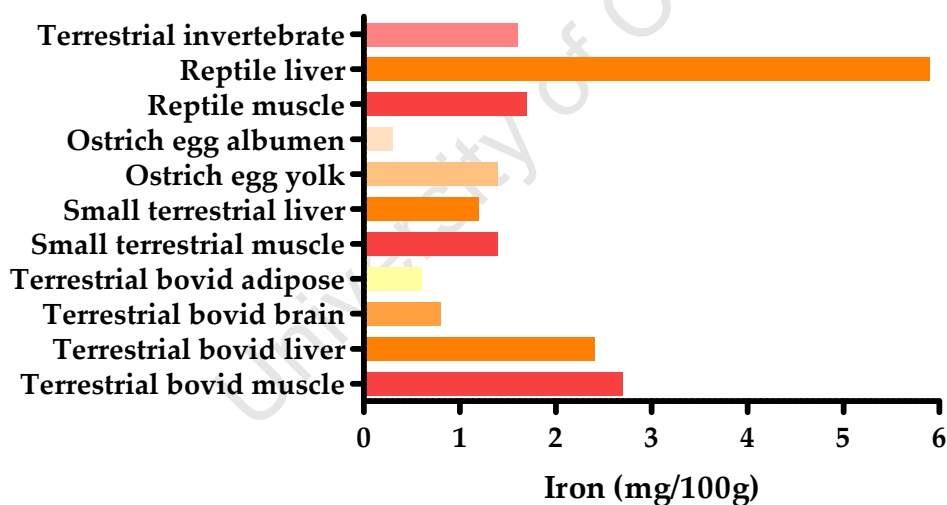


Figure 5.6 Iron content of terrestrial fauna.

### Marine and aquatic fauna

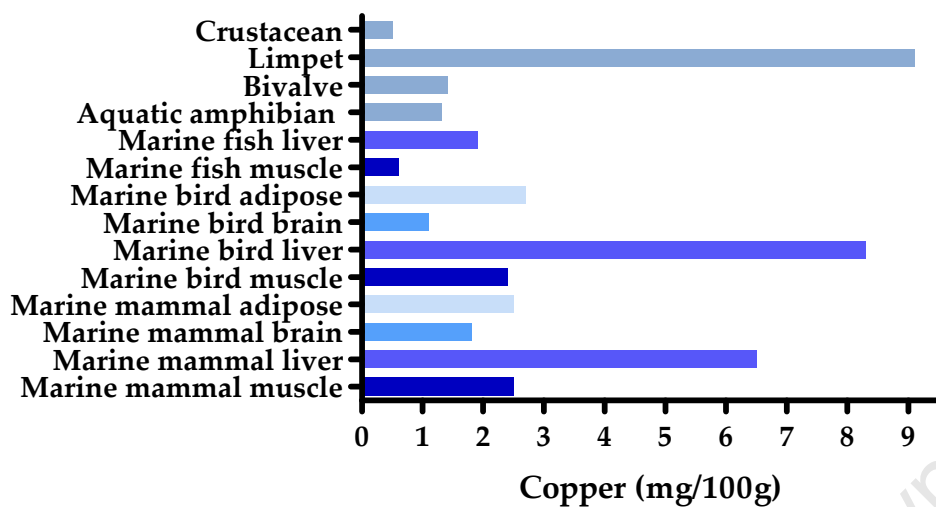


Figure 5.7 Copper content of marine and freshwater fauna.

### Terrestrial fauna

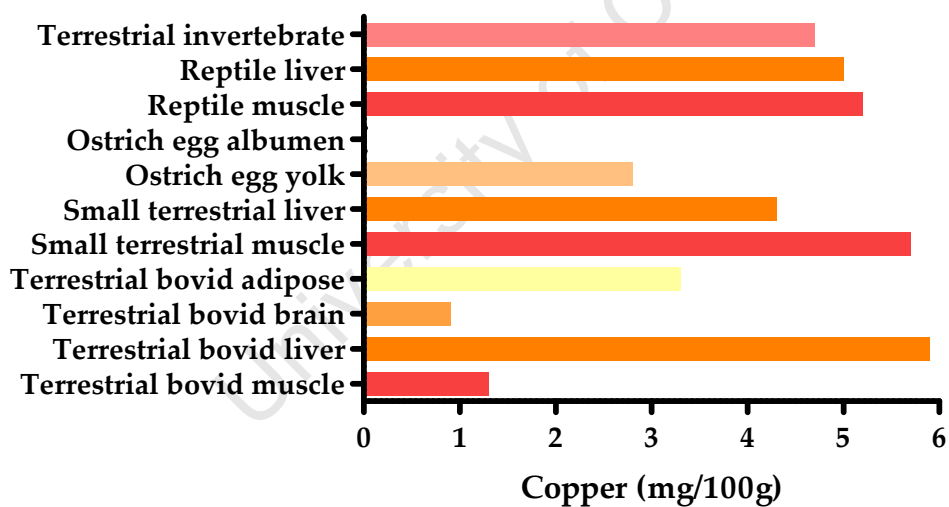


Figure 5.8 Copper content of terrestrial fauna.

### Marine and aquatic fauna

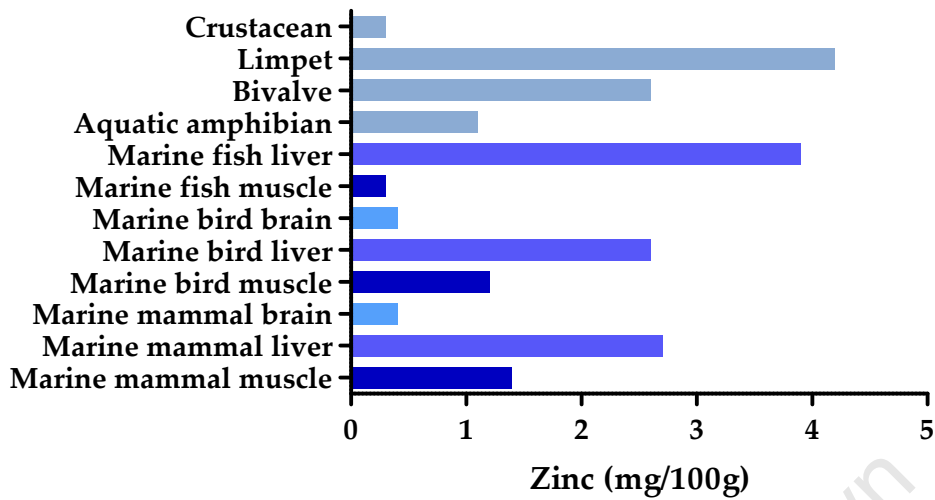


Figure 5.9 Zinc content of marine and freshwater fauna.

### Terrestrial fauna

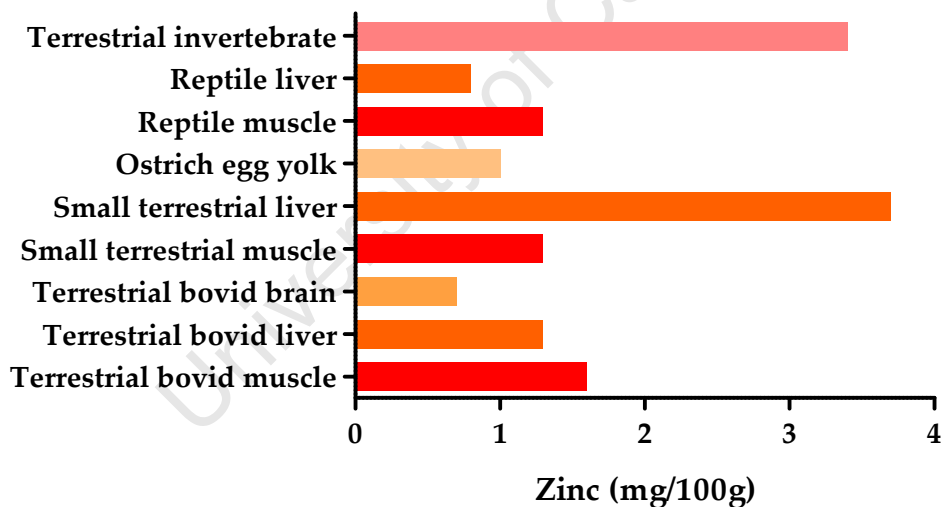


Figure 5.10 Zinc content of terrestrial fauna.

Linoleic acid is more abundant in terrestrial than marine resources (Figures 5.6.11-12). As all of the plants tested contain little (0.2-0.3g/100g) of this essential fatty acid, terrestrial fauna would have been the best source of linoleic acid among prehistoric hunter-gatherers. Ostrich egg yolk is particularly abundant (>3g/100g) in this omega-6 fatty acid. Muscle and liver tissue from terrestrial vertebrates contain ~1g/100g of linoleic acid. It can also be found

in some of the tissues of marine avifauna (~0.5-1g/100g), and in the African clawed frog (>1g/100g).  $\alpha$  - Linolenic acid, the shorter-chain precursor of the omega-3 family, is less well represented in the terrestrial foods than linoleic acid. The edible components of terrestrial vertebrates contain small amounts (<0.5g/100g) of  $\alpha$ -linolenic acid (Figure 5.13). Invertebrate insects are the best source of this fatty acid (>1g/100g) in the terrestrial food chain, followed by ostrich egg yolk (>0.5g/100g). Ostrich egg yolk contains more omega-6 linoleic than omega-3  $\alpha$ -linolenic acid; insects contain larger amounts of the omega-3 precursor.  $\alpha$ -linolenic acid is also present in the edible components of marine mammals and birds (~0.5-2g/100g).

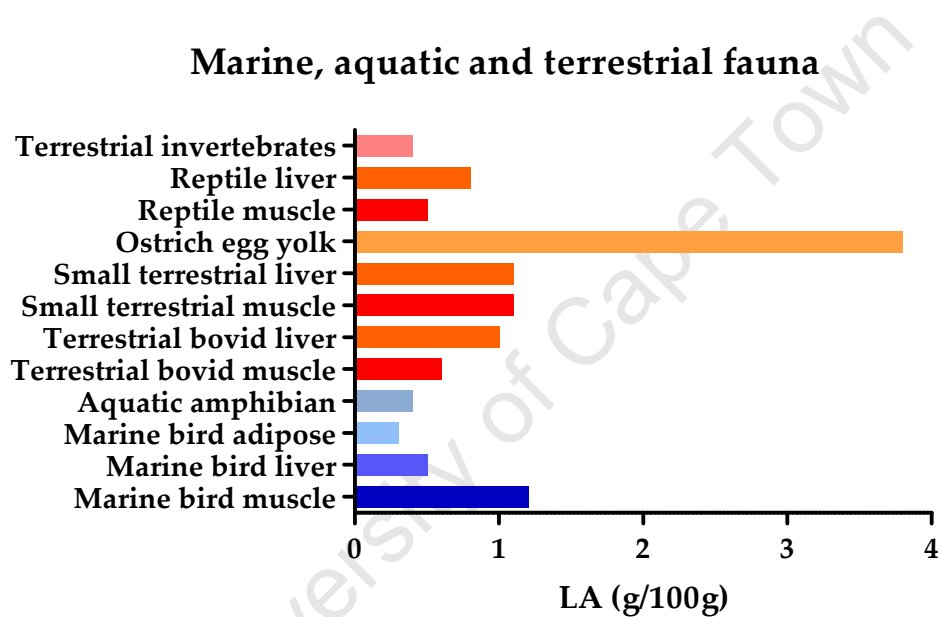


Figure 5.11 Linoleic acid (LA) content of marine, freshwater and terrestrial fauna.

## Marine, aquatic and terrestrial fauna

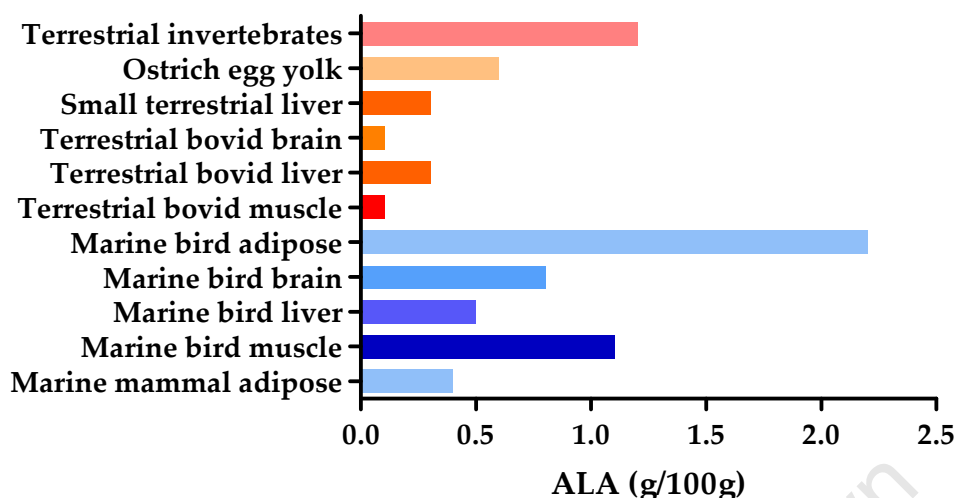


Figure 5.12  $\alpha$ -linolenic acid (ALA) content of marine, freshwater and terrestrial fauna.

Arachidonic acid, the most unsaturated fatty acid in the omega-6 class, is fairly abundant in marine and terrestrial fauna (Figure 5.13 and 14). It is present in all of the edible components of marine mammals and birds, and terrestrial vertebrates (<0.5 – 1g/100g), and in smaller amounts in freshwater amphibians and marine invertebrates (<0.5g/100g).

Ostrich egg yolk is the best source of arachidonic acid (>1g/100g). It was not detected in terrestrial invertebrates. Eicosapentaenoic acid is more abundant in marine than in terrestrial resources (Figure 5.15). The edible soft tissue of bivalve molluscs represents the best source of this omega-3 fatty acid (0.8g/100g), followed by liver tissue from marine fish and mammals (>0.5g/100g). EPA is also present in the muscle tissue of marine mammals and birds, freshwater amphibians and limpets (~0.1-0.2g/100g). In terrestrial resources, it appears to be restricted to ostrich egg yolk and liver tissue from terrestrial bovids, which together constitute the best terrestrial sources of this long-chain fatty acid (>0.2g/100g), and to a lesser extent in bovid muscle tissue (<0.2g/100g). Docosahexaenoic acid is also unevenly distributed in marine and terrestrial resources (Figure 5.16 and 17). Fish liver (~3g/100g), followed by brain tissue from marine avifauna and bivalve molluscs (>1g/100g), are the best sources of this long-chain omega-3 fatty acid in the marine foodchain. It is present in smaller amounts (<1g/100g) in all of the edible components of marine vertebrate fauna, and also in freshwater amphibians. In terrestrial resources, DHA is present in the

brain tissue of terrestrial bovids and ostrich egg yolk (~0.5g/100g), and to a lesser extent in liver tissue from terrestrial vertebrate fauna (~0.2-0.4g/100g).

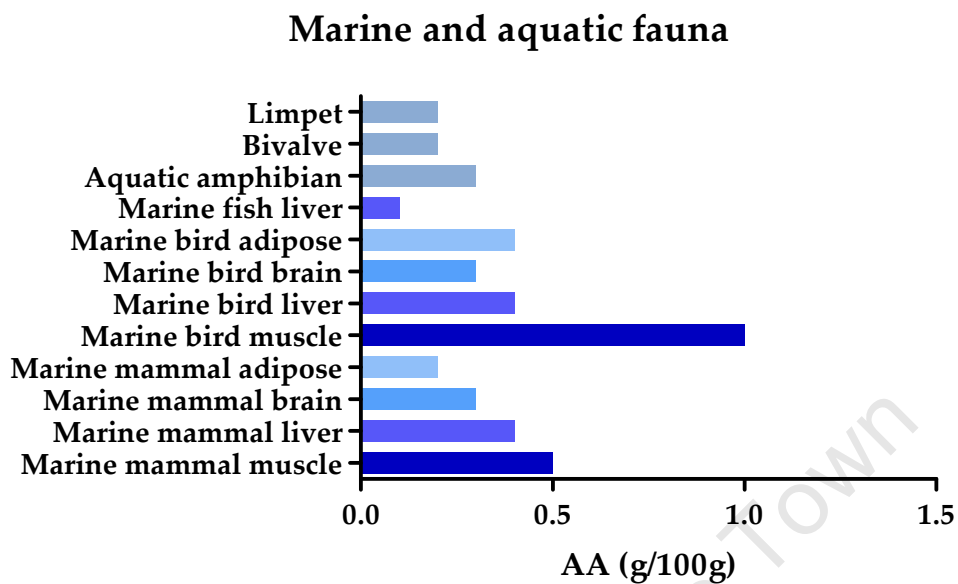


Figure 5.13 Arachidonic acid (AA) content of marine and freshwater fauna.

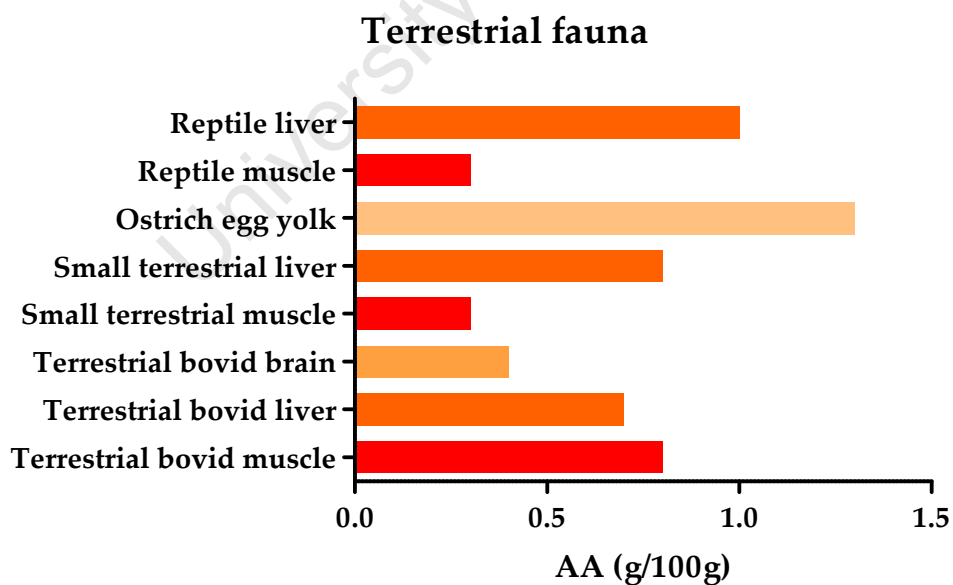


Figure 5.14 Arachidonic acid (AA) content of terrestrial fauna.

### Marine, aquatic and terrestrial fauna

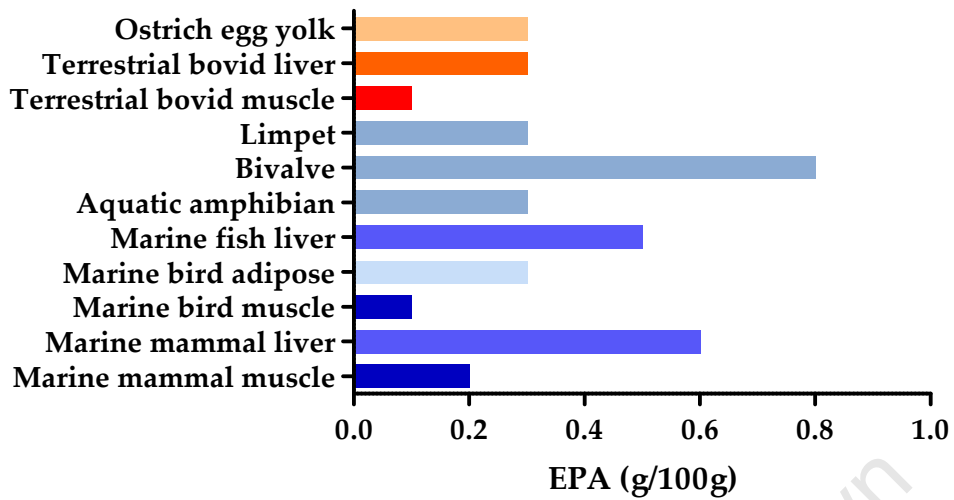


Figure 5.15 Eicosapentaenoic acid (EPA) content of marine, freshwater and terrestrial fauna.

### Marine and aquatic fauna

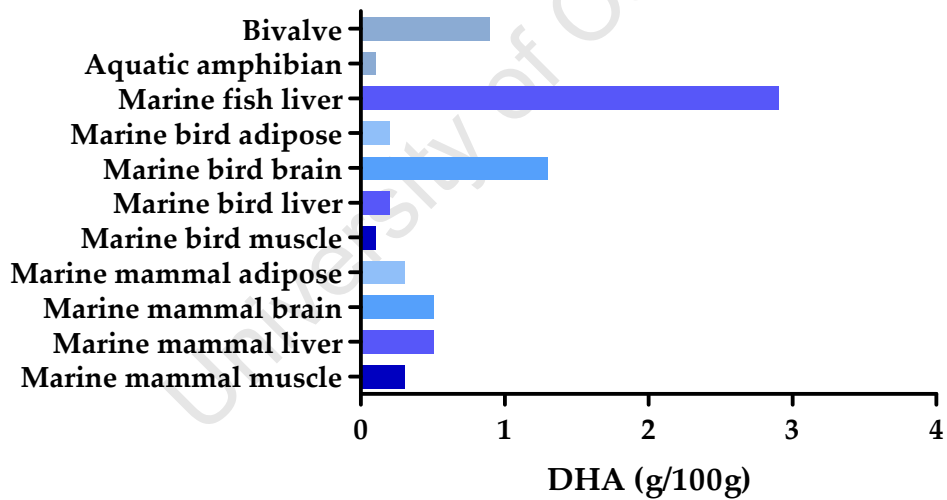


Figure 5.16 Docosahexaenoic acid (DHA) content of marine and freshwater fauna.

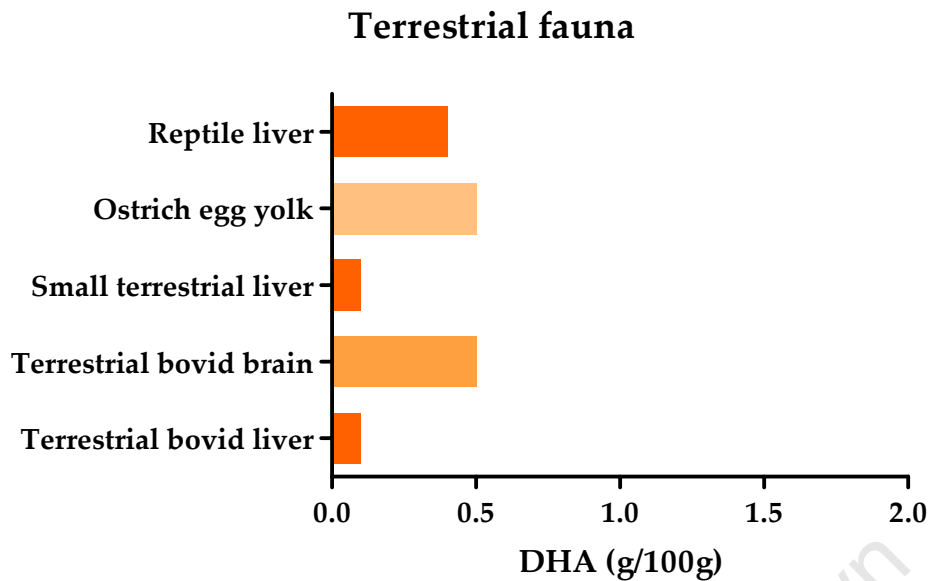


Figure 5.17 Docosahexaenoic acid (DHA) content of terrestrial fauna.

#### 5.7 SUMMARY

There is some overlap in the content of marine and terrestrial foods with respect to one essential macronutrient, namely protein, and three essential trace elements, namely iron, copper and zinc. With few exceptions, these nutrients are fairly abundant in the edible components of marine and terrestrial animals. Two other energy-providing macronutrients, namely fat and carbohydrates, are less evenly distributed, and are abundant in selected resources or edible portions. Lipid or fat is highest in the liver, brains and especially, adipose tissue of vertebrate animals, while starch is present in significant amounts only in the edible corms produced by iridaceous plants. Omega-6 fatty acids, including linoleic and arachidonic acid, are fairly abundant in a variety of terrestrial animals, and are also found in small amounts in plants. Omega-3 fatty acids, including  $\alpha$ -linolenic acid, eicosapentaenoic and docosahexaenoic acid, are present in a more circumscribed range of potential foods. The abundance and distribution of essential nutrients in marine and terrestrial resources likely to have been exploited by Middle Stone Age hunter-gatherers would have a number of nutritional implications for populations of early modern humans living in the southwestern Cape. These are discussed and explored in the following chapter, in which several scenarios for prehistoric settlement and subsistence are evaluated.

## CHAPTER SIX

### DISCUSSION

#### 6.1 THE “NUTRITIONAL LANDSCAPE” OF THE SOUTHWESTERN CAPE: A FRAMEWORK FOR ANALYSIS

The “nutritional landscape” consists of a series of subsistence opportunities and nutrient packages available to Middle and Later Stone Age hunter-gatherers in a particular region. It is an analytical construct in terms of which the distribution of marine and terrestrial resources, and of nutrients within these resources, can be better understood. The natural environment determines and constrains the types of food resources available for exploitation. In the southwestern Cape, a highly productive littoral environment is juxtaposed against a relatively poor terrestrial one (Dusseldorp and Langejans 2013; Parkington 2003).

Extensive kelp forests along the Atlantic west coast support large communities of intertidal shellfish including filter-feeding mussels and grazing limpets. This region, influenced by intertidal upwelling of the cold Benguela current, has the greatest biomass ( $\text{g}/\text{m}^2$ ) of marine invertebrates on the subcontinent (Bustamante and Branch 1996a and b). Filter-feeders are the predominant taxa on exposed shores, with a maximum recorded biomass of  $3300\text{g}/\text{m}^2$ . Greater water turnover and a corresponding increase in food in the form of kelp derived detritus, the main source of organic carbon and nitrogen for filter-feeding molluscs, may account for the high productivity of filter-feeders on rocky exposed shores. The greatest concentration of biomass occurs between the mid and lower shore (Bustamante and Branch 1996a and b; 1997). Grazers are more productive at coastal sites offering some shelter from wave action. At these sites, biomass is concentrated on the low shore. The large granite limpet *C. granatina* occurs in dense stands that can reach an average biomass of almost  $190\text{g}/\text{m}^2$  in the mid-to-low intertidal region. Populations of *S. argenvillei*, which form a conspicuous band in the low intertidal, can achieve an even greater biomass of almost  $347\text{g}/\text{m}^2$  on semi-exposed shorelines (Bustamante and Branch 1997; 1996a).

The southwestern Cape falls within the Cape Floral Region, in which 9000 plant species can be found within a  $90\,000\text{km}^2$  area (Marean 2010). The winter rainfall Cape fynbos biome

contains the greatest concentration of geophyte species in the world. More than 500 individual species have been identified (Sorban, Cowling and du Preez 2005). However, when not subjected to controlled fire regimes to encourage growth, they can be fairly unproductive relative to intertidal resources (Dusseldorp and Langejans 2013), and the carrying capacity of the Cape Floral region is actually quite low. Furthermore, edible plants indigenous to the Cape fynbos biome have strictly seasonal patterns of growth; they would be available for collection and consumption only during certain parts of the year. The southwestern Cape is further characterized by a relatively low diversity of large mammals, and is dominated by small-bodied browsers (Marean 2010; Klein 1983).

The nutritional landscape also has an overtly social dimension. Subsistence strategies and food distribution patterns are socially mediated components of all human economies. The division of economic activities according to gender is ubiquitous among modern hunter-gatherers (Bliege Bird 2008), and can be cautiously extrapolated to their prehistoric counterparts. In the ethnographic literature, women are often identified with activities such as shellfish and plant collecting, which are characterised as subsistence strategies with little variance in energetic returns and virtually no risk of failure. Participation in these low-risk, high reward activities allows them to provide for their own needs, as well as those of their immediate family and dependents, within the physiological and behavioural constraints imposed by pregnancy, lactation and childcare (Bliege Bird 2008; Bliege Bird *et al.* 2001). Men, on the other hand, are frequently associated with big-game hunting, a risky economic activity with high but unpredictable rewards. Meat sharing within and sometimes even between groups of hunter-gatherers serves as a means of correcting the unequal returns of individual hunters (Speth 2010; Bliege Bird *et al.* 2001, 2002; Hawkes *et al.* 1991, 2001).

Food sharing is another common feature of modern hunter-gatherer communities. Resources collected from different localities are returned to a “central place” for distribution, sometimes processing and preparation, and consumption. This central place is situated at the intersection of several profitable or productive resource patches; its location is likely to change according to the relative productivity of these (Dusseldorp and Langejans 2013). The involvement of men and women in different subsistence strategies, and the patterns according to which hunted and collected resources are re-distributed within a group,

determine which foods and, by extension, nutrients, particular people are likely to have had access to. Contemporary hunter-gatherers in sub-Saharan Africa live in fairly fluid groups or bands ranging in size from about sixteen to thirty five people of mixed gender and age (Hawkes *et al.* 2001; Lee 1968, 1979). Although it is not possible to accurately reconstruct the average group size of Middle Stone Age hunter-gatherers, twenty five people seems to be a reasonable estimate for a hypothetical group.

Nutritional requirements and Recommended Daily Intakes are based on the physiological needs of individuals. Like their modern counterparts, prehistoric people would have had general and more specific nutritional demands. Water, and energy in the form of protein, fat and/or carbohydrates, would be needed on a daily basis for short-term survival.

Unaware of these and their other nutrient requirements, Middle and Later Stone Age hunter-gatherers would have been driven by hunger to satisfy them. The human brain requires a constant supply of these energy-providing macronutrients, in addition to specific micronutrients and essential fatty acids. Iron, iodine, and long-chain omega-3 fatty acids are required by all people, but are needed in especially large amounts by pregnant and lactating women, children under the age of two years, and fast-growing adolescents.

Using new information on the nutrient, and especially fatty acid content of marine and terrestrial resources likely to have been exploited by Middle Stone Age people, and combining this with existing knowledge of people's nutritional requirements, and patterns in the ethnographic and archaeological records, it is possible to critically assess and discuss some possible scenarios for Middle Stone Age settlement and subsistence. These include occasional visits to the coast, permanent residence at the coast, the complete avoidance of the coast and marine and aquatic resources, and the integration of coastal and inland regions and resources. The archaeological record of the Middle and Later Stone Age provides some means of discriminating between these scenarios. Nutritional constraints associated with particular settlement and subsistence strategies may have had important implications for the emergence of anatomically modern humans in the southwestern Cape.

## 6.2 EVALUATING COMPETING STRATEGIES AND IDENTIFYING CONSTRAINTS

### 6.2.1 Why visit the coast?












The coast is likely to have been attractive to Middle Stone Age hunter-gatherers, and would have afforded them subsistence opportunities unavailable in the adjacent interior. Large communities of intertidal shellfish form dense clusters or patches which are unevenly distributed along the linear shoreline (Parkington 2003; Bustamante and Branch 1996a and b, 1997; Bosman *et al.* 1990). These marine molluscs are sessile, abundant, predictable and can be collected in large numbers with relatively little effort or technology and no risk of failure (Parkington 2003, 2010). The majority of shellfish species recovered from Middle Stone Age sites, notably granite and granular limpets and black mussels, inhabit parts of the intertidal which remain visible throughout the tidal cycle. Others, such as Argenville's limpets, and large adult black mussels, are visible and accessible to coastal foragers only during spring low tides. The deliberate scheduling of shellfish collecting to coincide with these low tides is a common occurrence among modern coastal foragers, and has been inferred for their prehistoric counterparts. White mussels, which burrow beneath the sand on long, exposed beaches, are more difficult to locate and to extract. They are not a regular component of Middle Stone Age shellfish assemblages (Dusseldorp and Langejans 2013; Jerardino and Marean 2010). With the exception of filter-feeding bivalves, which often become toxic during the summer months as a result of seasonal phytoplankton blooms (Woodborne *et al.* 1995; Parkington 1976, 2001), marine molluscs would have been available to prehistoric foragers throughout the year. Seasonal changes in the nutrient content of particular species (Dusseldorp and Langejans 2013) require further investigation.

Intertidal shellfish are "small nutrient packages" with a relatively low flesh yield relative to their total weight. Simple field processing would increase the total number of shellfish collected by reducing their weight and associated transport costs (Dusseldorp and Langejans 2013; Ugan 2005). An increase in the field processing or shucking of the large alikreukel, *T. sarmaticus*, which is well-represented in Middle and Later Stone Age sites in the southern Cape, is indicated by the abundance of opercula relative to apices of this species in the Howiesons Poort levels of Blombos Cave. The Howiesons Poort layers at this site accumulated during a time characterised by falling sea levels, which would have increased

the distance between the cave and the shore (Dusseldorp and Langejans 2013; Thackeray 1989). The potential for mass collection (Ugan 2005) further enhances the productivity and utility of intertidal shellfish. The edible soft tissue of mussels and limpets is likely to have been consumed in its entirety by prehistoric people. This non-selective consumption would ensure that the full nutrient content or value was available to the human body. The foot process of limpets is tough, and appears to be less nutritious than the gonad. Cooking may have improved the palatability and digestibility of limpets. It would also make it easier to remove the edible soft tissue of *T. sarmaticus* from the shell (Dusseldorp and Langejans 2013). However, the affect of cooking on the nutrient content of shellfish has not been determined.

The results of this study indicate that mussels and limpets are good sources of many essential nutrients. A large granite limpet with an edible yield of 25g would provide 2.6 grams of protein, around half a gram of fat, and about 78 kilojoules (Figure 6.1). A single specimen would also provide approximately one milligram of iron and zinc, and one hundred milligrams of eicosapentaenoic acid (Figures 6.1 and 6.2). Black mussels appear to be lower in macronutrients and iron, possibly because of their higher water content, and higher in omega-3 polyunsaturated fatty acids. A single black mussel with an edible yield of 25g would yield 300 milligrams of docosahexaenoic acid, which is the full recommended daily requirement of a pregnant woman.

Nevertheless, large numbers of marine molluscs would be needed to meet many of the nutritional requirements of individuals and, especially, groups of prehistoric people. For instance, a dozen large granite limpets would be needed to meet the daily zinc requirement of an adolescent boy; twenty individuals would be required to provide sufficient iron for an adult woman of reproductive age; a pregnant woman would require ten more; and more than a hundred limpets would be needed to provide adequate energy for an active adult man. Considerably larger numbers of the much smaller granular limpet, or of calorie and iron poorer black mussels, would be required. In comparison, small quantities of limpets and black mussels would provide sufficient EPA and DHA to meet the requirements of a hypothetical group of hunter-gatherers which includes pregnant and lactating women.

	Species	Tissue	Edible yield	Protein (g)	Fat (g)	kJ	Iron (mg)	Copper (mg)	Zinc (mg)
	Granite limpet	total	25g	2.6	0.6	78	0.9	2.6	1.2
	Granular limpet	total	12g	1	0.3	34	0.6	1.8	0.6
	Black mussel	total	25g	1.5	0.2	50	0.2	0.2	0.9
	White mussel	total	20g	1.8	0.3	47	0.4	0.4	0.3
	Adult Cape fur seal	muscle	18.5kg	2775	555	69930	370	259	278
		liver	4.5kg	1085	121	23379	171	265.5	306
		brain	265g	20	15	928	2.4	1.4	Bd
		adipose	18kg	162000	612 3600	-	-	-	
		<b>total</b>	<b>41kg</b>	<b>1105</b>	<b>162691</b>	<b>62117837</b>	<b>543.4</b>	<b>526</b>	<b>584</b>
	African penguin	muscle	400g	63	11.6	1699	7.6	18	4
		liver	24g	3.5	0.3	82	0.7	2.3	0.6
		brain	8g	0.6	0.3	21	<0.1	0.1	<0.1
		adipose	60g	Bd	56.2*	2124	0.7	Bd	Bd
		<b>total</b>	<b>492g</b>	<b>67.1</b>	<b>68.4</b>	<b>3926</b>	<b>9</b>	<b>20.4</b>	<b>4.6</b>
	Longfin tuna	muscle	1.1kg	131	16.5	2825	35.2	6.6	3.3
		liver	70g	7	1.4	171	0.8	2.4	0.8
		<b>total</b>	<b>1.8kg</b>	<b>138</b>	<b>17.9</b>	<b>2996</b>	<b>36</b>	<b>9</b>	<b>4.1</b>
	African clawed frog	total	13.3g	2.0	0.2	41	0.2	0.2	0.1
	Eland	muscle	230kg	27830	2990	580616	6210	2990	4173
		liver	14kg	2100	392	50148	366	828	184
		brain	980g	79.4	67.6	3889	7.8	7.7	5.7
		adipose	35kg	1050	315000	1190700	210	1155	Bd
		<b>total</b>	<b>280kg</b>	<b>31059.4</b>	<b>3153450</b>	<b>1825353</b>	<b>6793.8</b>	<b>4980.7</b>	<b>4362.7</b>
	Large locust	total	3.5g	0.6	0.1	14	0.1	0.2	0.5
	Emperor moth	larvae	10g	0.9	0.2	23	0.1	0.1	0.3









	Species	Tissue	Edible yield	Protein (g)	Fat (g)	kJ	Iron (mg)	Copper (mg)	Zinc (mg)
	Hartebeest	muscle	50kg	6050	650	151410	1350	650	907
		liver	3kg	450	84	13003	72	177	40
		brain	210g	17.0	14.5	834	1.7	1.6	1.2
		adipose	7.5kg	225	6750	258930	45	248	Bd
		<b>total</b>	<b>60.7kg</b>	<b>6742</b>	<b>7498.5</b>	<b>424177</b>	<b>1468.7</b>	<b>1076.6</b>	<b>948.2</b>
	Blesbok	muscle	20kg	2420	260	60564	540	260	363
		liver	1.7kg	255	47.6	6940	41	100.5	22
		brain	85g	6.9	5.7	331	0.7	0.7	0.5
		adipose	3kg	90	2700	103572	18	99	Bd
		<b>total</b>	<b>25.6kg</b>	<b>2772</b>	<b>3013</b>	<b>171407</b>	<b>599.7</b>	<b>460.2</b>	<b>285.5</b>
	Steenbok/grysbok	muscle	3.3kg	399	43	9992	89	43	60
		liver	200g	30	5.6	817	4.8	12	2.6
		brain	17g	1.4	1.2	69	0.1	0.1	0.1
		adipose	500g	15	450	17262	3	16.5	Bd
		<b>total</b>	<b>4.2kg</b>	<b>445</b>	<b>500</b>	<b>28149</b>	<b>96.9</b>	<b>71.6</b>	<b>62.7</b>
	Cape cobra	muscle	193g	11	2.0	1218	1.5	13	0.6
		liver	11.6g	1.2	0.3	38	0.7	1.3	0.1
		<b>total</b>	<b>204.6g</b>	<b>12.2</b>	<b>2.3</b>	<b>1256</b>	<b>2.2</b>	<b>14.3</b>	<b>0.7</b>
	Dune mole rat	muscle	250g	27.8	<0.1	593	1.8	Bd	4.8
		liver	15g	1.8	<0.1	38	0.2	0.5	0.8
		<b>total</b>	<b>265g</b>	<b>29.6</b>	<b>&lt;0.1</b>	<b>631</b>	<b>2.0</b>	<b>0.5</b>	<b>5.6</b>
	Ostrich egg	yolk	260g	30.4	13.8	1033	3.6	7.3	2.6
		albumen	518g	67.9	1	1179	1.6	Bd	Bd
		<b>total</b>	<b>778</b>	<b>98.3</b>	<b>14.8</b>	<b>2212</b>	<b>5.2</b>	<b>7.3</b>	<b>2.6</b>
	Bugle lily	corm	60g	2.1	0.6	340	-	-	-

Figure 6.1 Edible yield, macronutrient content, energy content and micronutrient content of selected marine and terrestrial animals and plants.

Illustrations by Neil Rusch.



Species	Tissue	Edible yield	LA(g)	ALA(g)	AA(g)	EPA(g)	DHA(g)
Granite limpet	total	25g	U	N	<0.1	0.1	U
Granular limpet	total	12g	U	N	<0.1	<0.1	U
Black mussel	total	25g	<0.1	U	0.1	0.1	0.3
White mussel	total	20g	U	U	U	0.2	0.1
Adult Cape fur seal	liver	4.5kg	<0.1	U	22.5	45	22.5g
	brain	265g	U	U	0.3	U	0.3g
	<b>total</b>	<b>4.77kg</b>	-	-	<b>22.8</b>	<b>45</b>	<b>22.8</b>
African penguin	brain	8g	U	U	<0.1	U	0.1
Longfin tuna	liver	70g	U	U	<0.1	0.4	2.1
African clawed frog	total	13.3g	0.1	<0.1	0.1	0.1	<0.1
Eland	muscle	230kg	13 80	230	1840	U/N	U/N
	liver	14kg	140	42	98	14	14
	brain	980g	U	1.0	3.9	U/N/<0.1	4.9
	<b>total</b>	<b>245kg</b>	<b>1520</b>	<b>273</b>	<b>1942</b>	<b>14</b>	<b>19</b>
Hartebeest	muscle	50kg	300	50	400	U/N	U/N
	liver	3kg	30	9	21	3	3
	brain	210g	U	0.2	0.8	U/N/<0.1	1.1
	<b>total</b>	<b>53.21kg</b>	<b>330</b>	<b>59.2</b>	<b>421.8</b>	<b>3</b>	<b>4.1</b>
Blesbok	muscle	20kg	120	20	160	U/N	U/N
	liver	1.7	17	5.1	12	1.7	1.7
	brain	85g	U	0.1	0.3	U/N/<0.1	0.4
	<b>total</b>	<b>22.55kg</b>	<b>137</b>	<b>25.2</b>	<b>172.3</b>	<b>1.7</b>	<b>2.1</b>



Species	Tissue	Edible yield	LA(g)	ALA(g)	AA(g)	EPA(g)	DHA(g)
Steenbok/grysbok	muscle	3.3kg	19.8	3.3	26.4	U/N	U/N
	liver	200g	2	0.6	1.4	0.2	0.2
	brain	17g	U	<0.1	0.1	U/N/<0.1	0.1
	<b>total</b>	<b>3.67kg</b>	<b>21.8</b>	<b>3.9</b>	<b>27.9</b>	<b>0.2</b>	<b>0.3</b>
Cape cobra	liver	11.6g	<0.1	U	<0.1	U	<0.1
Ostrich egg	yolk	260g	9.9	1.6	3.4	0.8	1.3
Emperor moth	larvae	10g	0.1	0.3	U	N	U
Bugle lilly	corm	60g	0.1	-	0.1	-	-

Figure 6.2 Fatty acid content of selected marine and terrestrial animals and plants. Illustrations by Neil Rusch.

Among contemporary coastal foragers, women spend a large proportion of their time engaged in shellfish collecting (Bird *et al.* 2004; Bliege Bird *et al.* 2002; Meehan 1982). Children often participate in this activity, although their exploitation patterns and preferences differ somewhat from those of adults (Bliege Bird and Bird 2002; Meehan 1982). Post-menopausal, pregnant and lactating women also take part (Meehan 1982; Bigalke 1973). The proceeds of daily collections are returned to camps and shared within the immediate families of the collectors (Bird *et al.* 2004; Bliege Bird *et al.* 2002). Prehistoric women living in proximity to the coast and engaged in shellfish collecting would have enjoyed guaranteed access to one of the richest sources of eicosapentaenoic and docosahexaenoic acid, and would have been able to provision themselves and their dependent offspring with an adequate supply of these and other brain-specific nutrients, with no assistance from males. Visits to the coast by groups of Middle Stone Age hunter-gatherers and the consumption of large numbers of marine molluscs may have allowed people to build up reserves of essential acids to be drawn on in times of critical need, notably during pregnancy and lactation. However, the accumulation of reserves within the adipose tissue is predicated on the consumption of surplus energy.

While intertidal shellfish are the most abundant and best represented marine faunal remains at Middle Stone Age sites, other marine animals were sometimes available to and exploited by early modern humans. Cape fur seals (*A. pusillus*) inhabit the islands and coasts of southern Africa. The recovery of their remains from archaeological deposits dating to the Middle Stone Age attests to their presence in this region for thousands of years. When they are not at sea, these large marine mammals haul out on small offshore islets and rocky promontories which remain partially dry at high tide. Males and females haul out for the summer birthing season; the majority of pups are born between late November and early December (Smithers 1983). Cape fur seals occasionally wash up onto beaches, where they would be accessible to human foragers. They could also have been hunted from onshore rookeries at particular locations (Marean 2010). The majority of Cape fur seal remains recovered from Middle Stone Age assemblages represent either adults or, to a lesser extent, juveniles older than one year. These were most likely derived from wash-ups (Dusseldorp and Langejans 2013; Parkington 2003, 2010). The remains of large cetaceans, which are also

represented by whale barnacles, recovered from Middle Stone Age sites definitely derive from infrequent strandings (Dusseldorp and Langejans 2013).

Portions of adipose tissue scavenged from marine mammals with a lot of blubber would have substantial caloric returns (~3470kJ/100g). Muscle tissue from seals and cetaceans would also yield large quantities of protein, iron and zinc. However, the nutritional value of partially decomposed carcasses is likely to have been lower than that of fresh kills. This is suggested by the relatively low fat content of liver and brain tissue from washed-up seals, dolphins and whales donated to this project as compared to samples from freshly killed animals. Furthermore, it is likely that only certain edible components would be scavenged from washed-up carcasses, and that their full nutritional value would not be recovered. The tissues richest in omega-3 fatty acids, notably the liver and brain, are unlikely to have been processed, extracted and consumed.

The littoral zone also supports large and diverse fish and seabird populations. However, the remains of marine fish and avifauna are not well-represented in Middle Stone Age faunal assemblages (Dusseldorp and Langejans 2013; Avery *et al.* 2008; Steele and Klein 2008; Klein *et al.* 2004; Halkett *et al.* 2003; Parkington 2003). The relative scarcity of fish and flying birds is regarded by some researchers as an indication that their inhabitants lacked the technical know-how needed to exploit them (Avery *et al.* 2009; Klein *et al.* 2004). Dusseldorp and Langejans (2013) postulate that, within the context of the Middle Stone Age, the acquisition of these resources would have been too costly in light of their low energetic returns in relation to other, more accessible and productive resources. This is borne out by the results of nutrient analyses carried out on tissue samples from several species of marine birds and fish.

Marine birds found in Middle Stone Age deposits are also likely to represent the remains of individuals scavenged from occasional wash-ups (Avery *et al.* 2008; Klein *et al.* 2004). Some species, particularly penguins, may have been actively pursued and clubbed. An African penguin with around 500g of edible tissue would have a caloric yield of around 4000 kJ. A single bird would therefore provide enough protein to meet the daily requirement of one adult or two children, and sufficient iron for an adult male or a child. The tiny brain would yield only 100mg of docosahexaenoic acid, one third of the daily requirement of a pregnant

woman. A single longfin tuna with an edible yield of 1.8kg (specimen purchased from Kalk Bay harbour) would provide sufficient protein for three adult males or females, and enough iron for four males or one pregnant female. With the exception of the liver, which is rich in iron and zinc, and is the best source of preformed omega-3 polyunsaturated fatty acids in marine and terrestrial food chains, these fish are lower in protein, micronutrients and essential fatty acids than intertidal shellfish. Although not specifically mentioned by Dusseldorp and Langejans (2013) west coast rock lobster or *Jassus lalandii* may also fit into this category. The durable mandibles of this crustacean are absent from Middle Stone Age assemblages in comparison with Later Stone Age ones. Explanations for this include the influence of taphonomic factors on the preservation of faunal remains, the inaccessibility of crustaceans inhabiting the subtidal, and an inability to recognise rock lobsters as potential food resources (Avery *et al.* 2008; Klein *et al.* 2004; Parkington 2003). In common with marine fish, west coast rock lobster are considerably lower in essential macronutrients, micronutrients and fatty acids than more accessible marine and terrestrial invertebrates.

A number of energy- and mineral-rich terrestrial resources would have been available to Middle Stone Age hunter-gatherers within a short radius of the highly productive shore, and would have compensated for the relatively low caloric yield of intertidal shellfish. Some of these would have been relatively easy to collect. Edible plants resemble marine molluscs in a number of interesting ways: they are sessile, predictable, generally collected by women and re-distributed within individual families or households (Hawkes *et al.* 2001; Draper 1975; Lee 1968, 1979). The edible corms of particular iridaceous genera, namely *Watsonia* and *Chasmanthe*, are likely to have been favoured by prehistoric people on account of their size and geographical distribution. *Watsonias* grow in fairly dense stands which can be located and identified when the plant is not flowering by its characteristic flat leaves. They produce an edible corm of up to sixty grams (Thompson *et al.* 2011). Other potentially edible species, including *Moraea* and *Gladiolus*, not only produce corms that are considerably smaller, but are much more widely distributed across the landscape. A large *Watsonia* corm would provide 340 kilojoules, that is, four times the amount of energy derived from a large granite limpet, and more than six times the amount from a large black mussel. Whereas most of the energy in marine molluscs derives from protein, starch is the most abundant macronutrient in edible plants. The consumption of carbohydrate-rich

edible plants would offset the high-protein, low-fat content of the remainder of the diet, and would also provide small amounts of omega-6 linoleic acid not found in limpets or mussels. The corms of iridaceous plants, seasonal fruits and green stems and shoots also contain some protein, but this would have been of lower quality than animal protein.

Grinding, pounding, and especially cooking, increases the digestibility and improves the dietary quality of edible geophytes, including corms (Dusseldorp and Langejans 2013; Carmody *et al.* 2011; Wrangham *et al.* 1999). Cooking destroys husks, skins and other potential barriers to digestion; bursts cells, making them more accessible to digestion and absorption; modifies the structure of protein and starch molecules, making them more accessible to digestive enzymes; and denatures toxins or compounds that may impede digestion (Wrangham *et al.* 1999). However, extensive food processing represents a considerable investment of time and energy, which would have offset the increase in caloric returns (Dusseldorp and Langejans 2013).

Along with small terrestrial vertebrates including tortoises, dune molerats and hyraxes, ostrich eggs appear to have been an important dietary component for the Middle Stone Age inhabitants of the southwestern Cape. Large quantities of ostrich eggshell have been recovered from sites including Hoedjiespunt, Sea Harvest, Ysterfontein and Diepkloof Rock Shelter (Steele and Klein 2013; Avery *et al.* 2009). Ostriches lay their eggs in unconcealed sandy hollows which would also have been relatively easy to locate. Ostrich eggs are frequently collected and consumed by men and women among the Kalahari Kung (Lee 1979). The results of this study indicate that they are an excellent source of energy, micronutrients and essential fatty acids. The edible contents of a single egg (778g– specimen from Jakkalsfontein Nature Reserve) would provide 2212 kilojoules, almost the same amount as a large fish with twice the edible tissue. It contains sufficient protein for two adult males, almost fifteen grams of fat, and just over 5 milligrams of iron. The yolk (260g) contains enough  $\alpha$ -linolenic acid (1.6g) to meet the daily requirement of an adult male, and sufficient docosahexaenoic acid (1.3g) for four pregnant or six lactating women.

The collection and consumption of edible insects, including caterpillar larvae, grasshoppers and termites, is not evident in the archaeological record, but is well-documented among contemporary hunter-gatherers. Like marine molluscs and plants, these terrestrial

invertebrates could have been mass collected, maximising their nutritional returns (Dusseldorp and Langejans 2013; Ugan 2005). They are high in protein (~14g/100g), iron (~1.6g/100g) and zinc (~3.4mg/100g). The larvae of the zigzag emperor moth or *Imbrasia tyrraea* is also a good source of omega-3  $\alpha$ -linolenic acid (2.5g/100g). Five larvae weighing approximately 10g (specimens from the Bidouw Valley) would satisfy the recommended daily requirement of an adult male. The small aquatic African clawed frog (*Xenopus leavis*) contains fairly large amounts of long-chain omega-6 arachidonic (0.3g/100g) and omega-3 eicosapentaenoic and docosahexaenoic acid (0.4g/100g). These would have been available in freshwater streams. Seven individuals with an edible yield of around 13.3g would provide sufficient omega-3 LCPUFAs for an adult male. The remains of six families of frogs have been recovered from the Middle Stone Age site of Klasies River Mouth, which indicates the presence of these amphibians in the region during the Late Pleistocene (van Dijk 2006). They may have been exploited by the site's prehistoric inhabitants. Prehistoric people in the southwestern Cape are likely to have visited the coast in order to exploit abundant and accessible marine resources, notably molluscs, as well as easily collected terrestrial foods available in close proximity to the shore.

#### 6.2.2 Why not stay permanently at the coast?

As has been previously illustrated, Middle Stone Age hunter-gatherers living along the highly productive Atlantic west coast would have had access to abundant marine resources, particularly intertidal mussels and limpets. These represent one of the most readily available and easily exploited sources of eicosapentaenoic and docosahexaenoic acid, as well as other brain-specific nutrients. Furthermore, a variety of additional energy sources in the form of edible plants and terrestrial animals would also have been available in the immediate vicinity. So then why not simply remain at the coast all year round?

Length of stay and/or group size would have been constrained by the carrying capacity of shellfish populations. While the carrying capacity of the intertidal zone in the southwestern Cape is considerable, prolonged and intensive predation has a measurable detrimental affect on the size and structure of targeted communities (Parkington *et al.* 2013; Bosman *et al.* 1990). Slow-growing limpet species including *C. granatina* and *S. argenvillei* are more vulnerable to overexploitation than rapidly recolonising black mussels. A partially denuded patch from

which all large, mature individuals have been removed takes more than a year to recolonise (Bosman *et al.* 1990). Smaller, immature individuals have less edible tissue and lower nutritional returns than larger ones. Thus, when no large adult specimens are available, greater numbers of small, immature ones are needed, and population densities continue to decline. Contemporary collectors show some awareness of this, in preferentially exploiting large adults and allowing smaller ones to grow (Meehan 1982; Bigalke 1973).

Very large quantities of molluscs would therefore be needed to support a hypothetical group of 25 hunter-gatherers. More than 2500 large granite limpets would be required to meet the group's daily energy requirement and almost twenty thousand would be needed to provide them with adequate energy for one week. This renders year-round coastal residence, accompanied by the continued and heavy reliance on shellfish as a source of food, unlikely. Furthermore, intensive and ongoing exploitation of limpets by Middle Stone Age hunter-gatherers is not consistent with the archaeological record. *C. granatina* from the recently re-excavated site of Hoedjiespunt 1, as well as Hoedjiespunt 3 and Ysterfontein are all large (69mm). This indicates that mature specimens >60mm (Bosman *et al.* 1990) were available and exploited by Middle Stone Age coastal foragers. The comparatively large mean size of some terrestrial species, including the angulate tortoise, in faunal assemblages from Ysterfontein and other more or less contemporary sites further reflects less intensive predation by Middle Stone Age people (Avery *et al.* 2008). Based on the low energy content of marine molluscs, and large numbers required to sustain groups of prehistoric people, as well as information on the detrimental affect of over-exploitation and patterns in the archaeological record, it does not appear that early modern humans lived at particular coastal sites all year round.

### 6.2.3 Was it possible to live inland, with no contribution from marine resources?

Given the productivity of the littoral zone, and of marine resources, it seems unlikely that the coast, and coastal foods, would have been ignored by prehistoric people who had access to or lived in proximity to them. Nevertheless, archaeological evidence indicates that Middle Stone Age people inhabited a range of environments, engaged in multiple economic and subsistence strategies, and ate different diets (Henshilwood and Marean 2003; McBrearty and Brooks 2000). New quantitative information on the nutrient content of

terrestrial resources available to early modern people in the southwestern Cape indicates that early modern people would have been able to survive on diets without a marine component. However, the interior offers fewer subsistence opportunities and resources, and particularly sources of eicosapentaenoic and docosahexaenoic acid.

Terrestrial bovids are likely to have been an important source of protein and especially energy, for prehistoric people in the interior. In contrast to abundant marine resources, large prey animals are widely and discontinuously distributed across the landscape in the southwestern Cape (Marean 2010; Parkington 2003). Furthermore, unlike sessile molluscs and plant foods, they are mobile, unpredictable and difficult to catch (Parkington 2003, 2010; Lee 1968, 1979) and pose a risk of injury to the hunters. Unless they can be ambushed from natural or artificially constructed blinds, the hunting of terrestrial game requires many hours of planning, tracking and active pursuit, all without the guarantee of a successful outcome. Among contemporary hunter-gatherers, hunting is engaged in almost exclusively by males. This physically demanding activity yields considerable energetic rewards, particularly in the case of large prey, but the risk of failure is high. Success rates reported for modern hunters in sub-Saharan Africa are relatively low, with an average of one large animal per month extrapolated for the Hadza (Hawkes *et al.* 2001), and one animal in four hunter-days for the Dobe Kung (Lee 1968, 1979). Kung and Hadza hunters are equipped with specialised toolkits comprised of large spears, bows and poisoned arrows (Hawkes *et al.* 2001; Lee 1968, 1979). Middle Stone Age people were probably limited to spears constructed of stone points hafted onto wooden handles (Lombard 2005); their success rates may have been even lower. The meat from a large kill is shared widely within the group as a whole. This serves as an effective mechanism for reducing risk, as access to the proceeds of a hunt is not predicated on individual success, and all families or households receive a similar share (Hawkes *et al.* 2001; Lee 1968, 1979).

Large vertebrate taxa have the highest caloric returns, and are therefore the most highly ranked prey animals taken by modern hunter-gatherers (Dusseldorp and Langejans 2013; Dusseldorp 2010; Speth 2010; Ugan 2005). The carcass of a single male eland (*Taurotragus oryx*), with a maximum live weight of 700kg (Smithers 1983), and an estimated edible yield of 280kg (Lee 1979), would provide >31 000 grams of protein and almost 2 000 000 kilojoules.

It would also yield >6000mg of iron, and >4000mg of copper and zinc. The successful capture of just one eland per month would provide the entire monthly protein, iron, copper and zinc requirement for a hypothetical group of twenty five people, and about a third of their monthly energy requirement. However, meat from a large kill would have to be consumed within a few days to preclude rotting, unless it could be smoked to prevent spoilage or sterilised with heat. The prevalence of large docile eland in the faunal assemblages from some Middle Stone Age sites, notably Klasies River Mouth and Die Kelders (Klein and Cruz-Urbe 1996, 2000) may indicate the deliberate selection of high-ranking species amenable to driving (Dusseldorp 2010). A hartebeest (*Alceplephus buselaphus*) weighing 150kg (Smithers 1983) with an estimated edible yield of around 50kg, would yield >6000 grams of protein, >1000mg of iron and >900mg of zinc; that is, sufficient protein and selected micronutrients for a group of twenty five hunter gatherers for one week. A 70kg (Smithers 1983) blesbok (*Damaliscus dorcas phillipsi*) with an edible yield of approximately 25kg would provide sufficient protein (2772g), energy (171407kJ), iron (600mg) and zinc (285mg) to meet the daily requirement of a group of twenty five hunter-gatherers of mixed gender and age.

It should be noted that MNI's do not always provide an accurate measure of the relative abundance of different taxa in the faunal assemblages from archaeological sites. Excavation techniques may be biased towards the recovery of larger species or skeletal elements, which skews reconstructions of prehistoric subsistence strategies and diets. Furthermore, the presence of remains from particular species does not necessarily indicate that they were obtained by means of hunting rather than scavenging, or that whole carcasses were acquired by or available to Middle Stone Age hunter-gatherers. In the case of scavenging, only some edible components of a carcass remain available for consumption; these are often the least nutritious and/or accessible portions. Patterns in the faunal remains from some Middle Stone Age sites, notably Die Kelders, suggest that MSA hunters were capable of exploiting a range of terrestrial ungulates including some large, highly ranked species, and that they enjoyed early access to highly nutritious portions of kills (Marean *et al.* 2000; Milo 1998).

Smaller terrestrial animals are often easier to capture than larger ones, but have proportionally lower caloric and other nutritional returns (Dusseldorp and Langejans 2013;

Dusseldorp 2010). Small and very small bovids can be obtained by snaring or trapping, which reduces the effort involved in their acquisition. A single steenbok (*Raphicerus campestris*) or grysbok (*Raphicerus melanotis*) weighing around 10kg (Smithers 1983) and with an estimated edible yield of just over 4kg provides 445 grams of protein, <30 000 kilojoules, 97mg of iron and 63mg of zinc; considerably less energy and trace elements than larger bovids. Small terrestrial vertebrates including hyraxes, snakes, dune molerats and tortoises present in the archaeological assemblages from several Middle Stone Age sites in the southwestern Cape (Steele and Klein 2013; Avery *et al.* 2008; Klein *et al.* 2004; Parkington 2003) can be considered “gathered” rather than “hunted” resources, and would be collected by both men and women in the course of their other economic activities. A Cape cobra (*Naja nivea*) with an edible yield of around 200g (specimen from Tokai) would provide 12.2 grams of protein, 2.3 grams of fat, just over 1200 kilojoules and small amounts of iron (2.2mg) and zinc (0.7mg). A dune molerat (*Bathyergus suillus*) with a similar edible yield would provide 30 grams of protein, 631 kilojoules, 2mg of iron and 5.6 mg of zinc.

In contrast to marine and terrestrial invertebrates, eggs and edible plants, which have already been discussed, terrestrial vertebrates are comprised of a number of edible tissues or portions. Essential nutrients are often unevenly distributed within these different edible components; this has potentially important implications for prehistoric people. Lean muscle tissue accounts for a substantial proportion (approximately one third of the live weight) of edible tissue in terrestrial animals (Lee 1979). While the muscle tissue of terrestrial bovids represents a good source of protein, it is low in insoluble fat or triacylglycerol (<2g/100g). Cooking may have improved the palatability of meat from terrestrial ungulates, which is very bland when consumed raw (Speth 2010). Carmody *et al.* (2011) contend that cooking also increases the caloric returns of meat. Cooking produces several types of changes in the weight of cooked relative to raw foods, depending on the kind of food and cooking method that is employed; these changes have a measurable affect on the macro- and micronutrient content of foods (Murphy *et al.* 1975). Cooking procedures available to Middle Stone Age people would have been restricted to roasting directly over a fire or over hot coals, as they did not manufacture ceramic vessels in which water could be boiled. Nevertheless, the retention of specific macro- and micronutrients in cooked foods warrants further investigation.

The livers and, to a greater extent, brains of terrestrial bovids contain more fat than lean muscle tissue. These findings are consistent with those of previous researchers (Kuipers *et al.* 2010; Speth 2010; Broadhurst *et al.* 2002; Cordain *et al.* 2000; Eaton *et al.* 1997). Liver tissue is also higher in protein, iron and copper than muscle tissue. Adipose tissue, which consists of stored triacylglycerol, with small amounts of protein and trace elements, represents the best source of dietary lipid. Essential fatty acids, particularly eicosapentaenoic and docosahexaenoic acid, are the most unevenly distributed nutrients in terrestrial resources. Muscle tissue from terrestrial vertebrates included in this study contains variable amounts (0.1 – 1.1g/100g) of linoleic and arachidonic acid. Omega-3 fatty acids are present in a narrower range of terrestrial foods. Small but measurable amounts (0.1g/100g) of  $\alpha$ -linolenic acid were detected in a single sample of muscle tissue from a springbok (*Antidorcas marsupialis*). Liver tissue from terrestrial bovids, other mammals and reptiles, and ostrich egg yolk, also contain some (0.1-0.6g/100g)  $\alpha$ -linolenic acid, but always in smaller amounts than linoleic acid (0.1-3.8g/100g). Measurable amounts of eicosapentaenoic and docosahexaenoic acid (0.1-0.5g/100g) are found almost exclusively in liver and brain tissue of terrestrial mammalian fauna.

The relatively high fat and omega-3 fatty acid content of liver, brain and bone marrow in terrestrial species prompted Kuipers and colleagues (2010) and Speth (2010) to suggest that the selective consumption of these fat-rich organs would have been an important dietary strategy for early modern humans eating exclusively terrestrial diets without a marine or aquatic component. However, these organs are small in relation to other potentially edible components of a carcass (weights of livers and brains in Figures 6.1 and 6.2 are adapted from Kuipers *et al.* 2010), notably muscle and adipose tissue, and are also less accessible, requiring more time and effort to extract. Furthermore, the fatty acid rich livers and brains of large terrestrial animals are among the portions most likely to be consumed by hunters immediately after a successful kill (Hawkes *et al.* 2001; Lee 1968, 1979), making them even less accessible to women and children, who have some of the highest requirements for brain-specific nutrients. Some alternative sources of eicosapentaenoic and docosahexaenoic fatty acid have been identified in the course of this study. These include ostrich eggs and small aquatic frogs than would have been available to prehistoric hunter-gatherers living at the

coast as well as inland. They may have been particularly important for women and children in the interior, who did not have access to marine resources.

In the absence of dietary sources containing longer-chain omega-3 fatty acids, it may have been possible to synthesise eicosapentaenoic (C20) and docosahexaenoic acid (C22) from their shorter-chain precursor,  $\alpha$ -linolenic acid (C18). Some researchers contend that rates of biosynthesis are very low, and that this would be insufficient for the high demands of pregnant and lactating women, infants and young children. *In vivo* studies cited by Plourde and colleagues (2007) indicate that approximately 5% of  $\alpha$ -linolenic acid is converted into eicosapentaenoic acid, and that <0.5% is converted into docosahexaenoic acid. However, the results of some other studies (Burdge and Calder 2005; Giltay *et al.* 2004 a and b; Pawlosky *et al.* 2003; Burdge and Wootton 2002) suggest that women of reproductive age are able to upregulate the elongation and desaturation of  $\alpha$ -linolenic into longer-chain omega-3 fatty acids. Biosynthesis of eicosapentaenoic acid, and further elongation and desaturation into docosahexaenoic acid is dependent on the availability of sufficient  $\alpha$ -linolenic acid in terrestrial resources. Fatty acid analyses conducted on an admittedly small sample of edible plants likely to have been collected by prehistoric people in the southwestern Cape show that these do not contain detectable amounts of the omega-3 precursor, and would not have been providers of  $\alpha$ -linolenic acid for elongation and desaturation. The fatty acid content of edible terrestrial plants indigenous to the southwestern Cape requires further investigation through the analysis of larger numbers of unpooled samples.

Muscle and liver tissue from the terrestrial vertebrates included in this study contain less  $\alpha$ -linolenic acid than the shorter-chain omega-6 precursor, linoleic acid. As the elongation and desaturation of both fatty acid families takes place along the same molecular pathway, the consumption of dietary resources with higher ratios of linoleic to  $\alpha$ -linolenic acid would lead to the preferential synthesis of arachidonic acid. Consumption of the majority of edible components in terrestrial animals available to prehistoric hunter-gatherers in the southwestern Cape is unlikely to have led to *de novo* synthesis of eicosapentaenoic and docosahexaenoic acid. Some of the terrestrial invertebrates that may have been eaten by Middle and Later Stone Age people, notably caterpillar larvae and large grasshoppers, contain larger amounts of  $\alpha$ -linolenic (2.5g and 0.8g, respectively) than linoleic (0.7 and 0.4g)

acid. These edible insects may have served as important sources of  $\alpha$ -linolenic acid as a precursor for eicosapentaenoic and docosahexaenoic acid for women and children living inland. Thus, in spite of having limited access to a narrow range of foods containing preformed eicosapentaenoic and docosahexaenoic acid, populations of early modern humans could have survived on diets comprised exclusively of terrestrial resources.

#### 6.2.4 Why and how would prehistoric hunter-gatherers integrate marine and terrestrial resources in their diets?

Like some of their Later Stone Age counterparts and contemporary hunter-gatherers, Middle Stone Age people in the southwestern Cape could have integrated marine and terrestrial strategies and resources. They could respond to changes in the relative productivity of particular environments or resource patches by redirecting their economic activities towards marine or terrestrial foods (Dusseldorp and Langejans 2013). This re-orientation of subsistence strategies and resources could take the form of seasonal movement between coastal and inland regions. Among modern foraging people, circular mobility between different habitats or regions optimises the exploitation of key resources by avoiding or reducing depletion associated with prolonged or intensive collection and predation (Whallon 2006; Lieberman *et al.* 1993). Patterns of seasonal mobility between the southwestern Cape coast and Cape Folded Mountain Belt have been reconstructed for the Later Holocene inhabitants of the region on the basis of archaeological evidence and inference (Parkington 1972, 1976, 2001). For instance, age distributions for hyraxes and seals in the faunal assemblages from the inland and coastal sites of De Hangen and Elands Bay Cave, respectively, suggest winter residence at the coast followed by movement into the interior in spring and summer (Parkington 1972, 1976, 2001; Woodborne *et al.* 1995; Fletemeyer 1974). Unusually well preserved plant remains recovered from the site of Melkhoutboom Cave in the eastern Cape are also consistent with spring and summer residence in the mountains (Deacon 1976, Fletemeyer 1974).

The southwestern Cape coast is characterised by strong seasonal variation in the availability, palatability and macronutrient content of terrestrial plants and, to a lesser extent, animals (Marean 2010; Parkington 2003, 2010). This would have rendered seasonal movement between the coast and adjacent hinterland likely, as well as advantageous. Most

iridaceous and fruit-bearing plants in this winter-rainfall region flower during spring and early summer; edible corms and fruits are at their most abundant, nutritious and palatable shortly thereafter (Marean 1986, 2010; Parkington 1976, 2001). Samples of *Watsonia tabularis* corms collected during November had the highest corrected starch content (27g/100g) of the plants tested in this study. However, seasonal changes in the carbohydrate content of these and other geophytes require further investigation and quantification through the use of more accurate methods. The abundance of edible plants in summer would be followed by a dearth of plant foods during winter (Marean 2010; 1986; Parkington 1972, 1976, 2001). Furthermore, the old withered corms of some iridaceous species are believed to become highly unpalatable or even toxic at this time (Marean 1986). Other terrestrial resources are also available on a seasonal basis. Edible insects including caterpillar larvae and locusts are abundant during spring. Snakes and tortoises are also more active, and therefore more visible to potential hunters and collectors during the warmer seasons (Avery *et al.* 2008; Klein *et al.* 2004; Parkington 1976, 2001). The condition and, by extension, nutritional value, of large marine and terrestrial animals also changes during different seasons. Terrestrial mammals are in poor condition during the dry season (Dusseldorp and Langejans 2013; Marean 1986) which, in the southwestern Cape, occurs during late summer or early autumn.

The abundance and availability of nutritious plant and animal foods during the summer may have attracted Middle Stone Age hunter-gatherers into, and enabled them to survive in, the interior. Regular movement away from the coast would have prevented the overexploitation of marine resources, especially sessile and predictable mussels and limpets, and may have allowed people to build up reserves of energy. Prehistoric people may have moved back to the coastal plain in winter, during which the terrestrial environment is depleted of animal and, especially, plant resources (Marean 1986, 2010; Parkington 2001, 2003). Intertidal molluscs would serve as an abundant and readily available source of energy, primarily derived from protein, as well as essential micronutrients and fatty acids.

Visits to the coast would have allowed groups of early modern people to integrate marine resources rich in eicosapentaenoic and docosahexaenoic acid into their diet. This would have been particularly beneficial for young children and, especially, women of reproductive age, who would have limited access to sources of preformed EPA and DHA in terrestrial

environments. The consumption of sufficient omega-3 fatty acid rich marine resources while at the coast may have contributed to the build-up of reserves for mobilisation during times of critical need, notably pregnancy and lactation. Alternatively, marine resources may have been transported from the coast to the interior. Shellfish residues have been recovered from Middle Stone Age sites such as Diepkloof Rock Shelter and Sibudu, which were located more than 10km from the nearest rocky shore. *C. meridionalis* shells wrapped in leaves have also been found at the Later Stone Age site of De Hangen, located in the Cape Folded Mountains (Parkington 2001). Bivalves are more suitable for long-distance transportation than limpets, as the edible soft tissue is encased between the two valves and remains fresher for longer (Dusseldorp and Langejans 2013). The soft tissue could also have been removed from the shells and dried, concentrating the protein content of the meat by eliminating moisture, and increasing the amount of edible tissue that could be carried.

### 6.3 SUMMARY

Early modern humans living in the southwestern Cape would be confronted with a number of challenges, limitations and constraints in meeting their general and more specific nutrient requirements. Prehistoric people living at the coast and subsisting primarily on intertidal shellfish may have struggled to obtain sufficient energy. Marine molluscs contain moderate amounts of protein but are relatively low in fat (<2.5g/100g); much of this is omega-3 fatty acid. These small nutrient packages have lower caloric yields than larger marine and terrestrial animals. The large numbers of marine molluscs needed to support groups of highly active Middle Stone Age hunter-gatherers may have been an impediment to year-round coastal residence. Intensive and ongoing exploitation of marine resources during the Middle Stone Age is not indicated in the archaeological record.

The consumption of other marine or terrestrial resources rich in either carbohydrates or fat would compensate for the low calorie content of shellfish, and offset the high protein content of diets with a significant contribution from marine molluscs. Some of these foods would be relatively easy to collect, accessible and available in the immediate vicinity of the coastal plain. Edible plants are a seasonal feature of the nutritional landscape in the southwestern Cape; their abundance, edibility, palatability and macronutrient content fluctuates according to the seasons in this winter rainfall region. The starchy corms of

iridaceous plants represent one of the few sources of carbohydrates available to prehistoric people at the coast and inland. Ostrich eggs are a relatively good source of fat, and appear to have been consumed by Middle Stone Age people living at Hoedjiespunt, Sea Harvest and Ysterfontein along the southwestern Cape coast. Muscle tissue and, especially, blubber from Cape fur seals would provide large amounts of energy. However, these appear to have been opportunistically scavenged rather than systematically exploited by the Middle Stone Age inhabitants of sites along the southern and southwestern Cape coast. Intertidal shellfish are one of the best and most abundant and accessible sources of eicosapentaenoic and docosahexaenoic acid. These would have been readily available to Middle Stone Age people, particularly women and children, living in proximity to the shore. The third trimester of pregnancy and first two years of life are the most critical times for neurological development. Thus, obtaining sufficient eicosapentaenoic and, especially, docosahexaenoic acid, during pregnancy, lactation, infancy and early childhood is absolutely crucial.

The edible components of terrestrial animals available adjacent to the shore as well as further inland, including large and small mammals, reptiles and invertebrates, are good sources of protein, micronutrients and omega-6 fatty acids. Early modern people living year-round in the interior and subsisting exclusively on terrestrial resources acquired through hunting and/or scavenging, regular gathering and opportunistic collecting, would have been able to obtain adequate energy for general nutrition, as well as sufficient iron, copper and zinc. However, sources of omega-3 polyunsaturated fatty acids are more limited in terrestrial than marine environments. Foods containing eicosapentaenoic and docosahexaenoic acid would have been in short supply. These fatty acids are not present in measurable amounts in muscle tissue from terrestrial animals; they are restricted to some of the smallest and least accessible edible components in vertebrate taxa, namely the liver and brains.

Women and young children, in particular, would have had very limited access to the portions of terrestrial animals richest in omega-3 fatty acids. Some alternative and more accessible sources of eicosapentaenoic and docosahexaenoic acid are available in terrestrial environments, including ostrich eggs and small aquatic frogs. The large quantities of ostrich eggshell recovered from Middle Stone Age sites in the southwestern Cape, and

presence of frog remains in the faunal assemblage from Klasies River Mouth, suggests that early modern humans had access to and probably exploited them. In the absence of readily available sources of preformed EPA and DHA, it may have been possible for prehistoric people to synthesise these fatty acids from the ALA in some terrestrial foods. Plants do not appear to contain measurable amounts of  $\alpha$ -linolenic acid, and the edible components of most terrestrial animals contains greater proportions of linoleic than  $\alpha$ -linolenic acid. Some terrestrial invertebrates, notably caterpillar larvae and locusts, are exceptions, and contain higher ratios of ALA to LA. They may have served as an important substrate for the synthesis of EPA and DHA in populations of early modern humans living away from the coast and pursuing exclusively terrestrial subsistence strategies.

Middle Stone Age people living in the southwestern Cape would have been able to survive in coastal and inland regions, eating diets comprised of marine and/or terrestrial resources. The integration of marine and terrestrial foods would have enabled early modern humans to overcome some of the nutritional challenges and constraints inherent in coastal and terrestrial environments, strategies and resources. Prehistoric people living in the coast would have already had the distinct nutritional advantage of being able to combine terrestrial resources high in energy-providing macronutrients with marine foods high in micronutrients and longer-chain omega-3 fatty acids. Middle Stone Age hunter-gatherers in the interior would not have had access to marine resources. People in both regions would have to adapt to seasonal patterns in the abundant and availability of terrestrial animals and plants. Seasonal mobility between the coast and adjacent hinterland seems a likely response to these discontinuities; this hypothesis requires further testing.

## CHAPTER SEVEN

### CONCLUSIONS

In this thesis, new information on the nutrient content of marine and terrestrial resources available to prehistoric hunter-gatherers in the southwestern Cape has been presented and integrated into the existing body of research concerning the ecological niche, subsistence strategies and settlement and mobility patterns of Middle and Later Stone Age people in this region. Some of the earliest evidence for the systematic use of marine foods derives from Middle Stone Age sites located along the Atlantic and Indian coasts of southern Africa (Marean 2010; Marean *et al.* 2007; Parkington 2003, 2010). Human fossil and material cultural remains consistent with the development of anatomically modern forms and new and innovative behaviours, respectively, are often recovered from the same, or similar, localities (Jerardino and Marean 2010; Marean 2010; Parkington 2003). The southwestern Cape coast and adjacent hinterland is a key research area in which the emergence of modern *Homo sapiens* during the Middle Stone Age can be investigated.

Encephalising humans would have had a number of general and specific nutritional requirements (Cunnane *et al.* 1993). Water and energy-providing macronutrients, namely protein, fat and carbohydrates, would be required on a daily basis throughout life to ensure short-term survival. Other nutrients, including iodine, iron, and especially preformed omega-3 fatty acids (eicosapentaenoic and docosahexaenoic fatty acid), are essential for the growth, maintenance and optimal function of the large and complex human brain. Endogenously synthesised EPA and DHA requires  $\alpha$ -linolenic acid, and preferably relatively low amounts of linoleic acid to be successful. It is still not established whether this biosynthesis could by itself provide adequate EPA and DHA in times of high demand when stores are depleted. The dietary resources and subsistence strategies that could have supported prehistoric populations in the process of becoming modern have been modelled and reconstructed by various researchers over the last twenty years (Kuipers *et al.* 2010; Speth 2010; Broadhurst *et al.* 2002; Cordain *et al.* 2000; Eaton *et al.* 1997). These fit into two broad categories: scenarios in which some dietary contribution from marine and aquatic resources is regarded as essential or highly advantageous (Broadhurst *et al.* 2002; Cordain *et*

*al.* 2000; Cunnane and Crawford 2014; Cunnane *et al.* 1993, 2007), and those which emphasise the selective consumption of fat-rich tissues from terrestrial animals (Speth 2010).

In order to compare and assess marine and terrestrial strategies and resources available to prehistoric hunter-gatherers, and identify possible nutritional challenges and constraints inherent in them, the nutrient content of potentially edible animals and plants indigenous to the region was measured. A number of generalisations about the nutritional value of marine and terrestrial resources, and the distribution of nutrients within the different edible components of these resources can now be made. Protein is the only macronutrient that is fairly abundant (~10-20g/100g) and evenly distributed in most of the edible tissues of marine and terrestrial vertebrate and invertebrate fauna. Obtaining sufficient protein for energy and amino acid synthesis is unlikely to have been a challenge in marine or terrestrial environments. Lipid or fat is very unevenly distributed in the different edible portions of marine and terrestrial vertebrates: muscle tissue contains relatively little (<3g/100g) of this macronutrient; liver (>2.5g/100g) and brain (~5-10g/100g) tissue contains more; and adipose tissue is comprised almost exclusively (90%) of stored triacylglycerol. The fat content of marine and terrestrial invertebrates ranges between 1 and 3g/100g. Seasonally available geophytes produced by iridaceous plant species represent the only significant source of carbohydrates in the form of starch (~5-25g/100g) available to prehistoric hunter-gatherers in the southwestern Cape.

Intertidal shellfish are rich in essential micronutrients including iron (~1-3mg/100g), copper (~2-10mg/100g) and zinc (~2-5mg/100g). Similar amounts of these trace elements are found in the muscle and liver tissues of marine and terrestrial vertebrate animals, as well as edible insects including termites, caterpillar larvae and locusts. Adequate supplies of iron and zinc, which perform vital nutritional functions in pregnancy in females and spermatogenesis in males, respectively, are not limited in marine or terrestrial environments and resources. The most important omega-6 and omega-3 fatty acids for neurological structure and function, namely arachidonic, eicosapentaenoic and docosahexaenoic acid, and their shorter-chain precursors linoleic and  $\alpha$ -linolenic acid, are unevenly distributed in the different edible components of vertebrate animals, and in marine and terrestrial foodwebs. Very few of the potentially edible plants included in this analysis contain detectable amounts of

linoleic and arachidonic acid. The corms of the bugle lilly or *Watsonia tabularis* and fruits of the sour fig or *Carpobrotus edulis* both contain 0.2g of linoleic acid; the former also contain 0.2g/100g of arachidonic acid. None of the plant samples tested contain measureable quantities of omega-3 fatty acids.

Linoleic and arachidonic acid are present in the muscle and liver tissues of marine and especially terrestrial vertebrate fauna in greater proportions than  $\alpha$ -linolenic, eicosapentaenoic and docosahexaenoic acid. Some terrestrial invertebrates, notably the larvae of the zigzag emperor moth or *Imbrasia tyrrhea* and the large grasshopper *Pamphigidaea hoplohopa*, contain fairly large amounts (2.5 and 0.7g/100g, respectively) of  $\alpha$ -linolenic relative to linoleic acid (0.7 and 0.4g/100g, respectively). In terrestrial vertebrate fauna, eicosapentaenoic and docosahexaenoic acid (0.1-0.5g) are restricted to the liver and brain. Ostrich egg yolk also contains omega-3  $\alpha$ -linolenic, eicosapentaenoic and docosahexaenoic acid (0.3-0.6g/100g), but in smaller amounts than omega-6 fatty acids. Eicosapentaenoic and docosahexaenoic acid are particularly abundant in fish liver (3.4g/100g), the soft tissue of intertidal mussels (~1.5g/100g) and limpets (0.1-0.5g/100g) and edible components of marine mammals and birds (0.1-1.5g/100g).

This new and original information on the nutrient content of marine and terrestrial animals and plants indigenous to the southwestern Cape serves as a point of departure for the evaluation of scenarios concerning the subsistence strategies and settlement and mobility patterns of the Middle Stone Age inhabitants of this region. It also provides a quantitative framework for testing broader hypotheses concerning the most likely or advantageous ecological and dietary niche for evolving hominins in southern Africa and beyond, and for comparison with patterns in the archaeological record. As hypothesised in the Introduction to this thesis, coastal foraging with an emphasis on shellfish collecting would have provided emerging modern humans with adequate protein and essential micronutrients, and more than enough preformed eicosapentaenoic and docosahexaenoic fatty acid to meet the requirements of even pregnant and lactating women. Additional energy could be obtained from a number of terrestrial resources in the immediate vicinity. Ostrich eggs, reptiles and small bovids and other mammals are likely alternatives; their remains have been recovered from several Middle Stone Age sites in the southwestern Cape. Permanent

residence at the coast by groups of Middle Stone Age hunter-gatherers would be constrained by the large numbers of marine molluscs necessary to obtain sufficient energy. Prolonged and intensive exploitation of littoral resources is not indicated by the large mean size of limpets in Middle Stone Age shellfish assemblages, including the enlarged sample from Hoedjiespunt 1; the relatively low density of shellfish residues in archaeological deposits predating the Holocene; and the absence or scarcity of the remains of other marine fauna including fish, flying birds and yearling seals.

Small populations of Middle Stone Age hunter-gatherers would have been able to survive inland, on diets comprised exclusively of terrestrial resources. Movement along rivers would have afforded an intermediate supply of omega-3 fatty acids through frogs, insects and possibly fish, allowing inland excursions at times made favourable by rains. The edible components of terrestrial animals, especially large grazing ungulates, contain large quantities of energy, principally in the form of protein from lean muscle and fat from adipose tissue, as well as essential micronutrients and omega-6 fatty acids. Plants provide energy in the form of carbohydrates, and small amounts of linoleic and arachidonic acid. Sources of omega-3 fatty acids, particularly eicosapentaenoic and docosahexaenoic acid, are considerably more restricted. These polyunsaturates are found exclusively in some of the small and inaccessible portions, namely the liver and brains, of terrestrial animals. Alternatively, it may have been possible to synthesise longer-chain omega-3 fatty acids from  $\alpha$ -linolenic acid obtained from terrestrial food resources. Based on the results of this study, it appears that plants are not a potential substrate for *de novo* synthesis of EPA and DHA. Furthermore, most terrestrial foods contain linoleic acid in much higher proportions than  $\alpha$ -linolenic acid. As the elongation and desaturation of omega-6 and omega-3 precursors occurs along the same pathway, resulting in competition between the two families, the consumption of foods rich in linoleic acid is likely to lead to the synthesis of the longer-chain omega-6 fatty acid, arachidonic acid, rather than of omega-3 eicosapentaenoic and docosahexaenoic acid. Two of the terrestrial invertebrates included in this study, namely caterpillars and grasshoppers, appear to be exceptions, and contain the shorter-chain omega-3 precursor in larger quantities than linoleic acid. These edible insects may have been of considerable dietary importance as an alternative terrestrial source of omega-3 fatty acids. Seasonal mobility between the coast and surrounding hinterland would integrate marine

foods, particularly molluscs, high in omega-3 fatty acids and energy dense terrestrial resources into the diets of prehistoric people, effectively meeting their general and more specific nutrient requirements. Furthermore, regular movement between the coast and adjacent Cape Folded Belt would mitigate the extreme seasonality of terrestrial plants and some animals in the southwestern Cape, and prevent overexploitation of calorically-poor intertidal shellfish.

In conclusion, the littoral environment would have presented prehistoric foragers with a number of reliable and predictable subsistence opportunities and abundant, easily collected nutrient packages. Marine foods, including and sometimes especially simple molluscs, are relatively high in protein and high in iron, copper, zinc and eicosapentaenoic and docosahexaenoic fatty acid. Human beings have to acquire the latter two fatty acids, particular during pregnancy, lactation and the first two years of life. Coastal diets high in preformed EPA and DHA would have been particularly beneficial for women and children. Intertidal mussels and limpets are among the best sources of these fatty acids, and would have been readily accessible to the members of prehistoric populations who required them the most. The results of this study strongly support the assertion that women at the coast would have been able to meet their requirement for brain-specific nutrients including iron and omega-3 fatty acids through their own subsistence efforts, and would not have been dependent on male provisioning. This would confer a survival advantage during neurological development.

In contrast, exclusively terrestrial diets with no contribution from marine foods are low in preformed eicosapentaenoic and docosahexaenoic acid. These omega-3 polyunsaturates are confined to specific edible tissues in terrestrial vertebrates, notably the liver and brain. The selective consumption of these and other fat-rich portions of terrestrial fauna as a strategy for obtaining sufficient EPA and DHA is problematic in a number of respects. Although based on the analysis of a single lipid sample, adipose tissue from terrestrial ungulates does not seem to contain long-chain omega-3 fatty acids. This is consistent with findings reported by Broadhurst and colleagues in 2002. Fat-rich organs such as liver and brains would not be available to prehistoric people engaged in opportunistic scavenging and require considerable time and effort to extract from fresh kills. Furthermore, women and

children are unlikely to have enjoyed the same early access to them as male hunters. They may have relied on alternative sources of preformed EPA and DHA. Egg yolk and small aquatic frogs are two possibilities. It may have been possible for prehistoric people to extend  $\alpha$ -linolenic to eicosapentaenoic and docosahexaenoic acid, provided the foods consumed contained adequate  $\alpha$ -linolenic acid for *de novo* synthesis. None of the indigenous plants tested contain traceable amounts of ALA, and the edible tissues of most of the terrestrial animals predominate in saturated fatty acids, monounsaturated fatty acids and linoleic acid. However, two terrestrial invertebrates not visible in the archaeological record are high in ALA, and may have served as an important source of this fatty acid. Mobility between coastal and inland regions would have allowed Middle Stone Age hunter-gatherers to integrate marine resources rich in brain-specific nutrients into their diets.

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**APPENDIX A**

**SHELLFISH SPECIES ABUNDANCES AND RESULTS OF STATISTICAL ANALYSES**

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Table 4.1 Shellfish species abundances for HDP1.

Layer	SHEM/NOSA		NOSA		UDAMA		SHEM/DAMA	
Species	MNI	%	MNI	%	MNI	%	MNI	%
<i>Scutellastra argenvillei</i>	4	3.54	7	3.2	1	2.6	3	42.8
<i>Scutellastra granularis</i>	3	2.65	5	2.3	0	0.0	1	14.3
<i>Scutellastra tabularis</i>	1	0.88	0	0.0	0	0.0	0	0.0
<i>Cymbula granatina</i>	48	42.48	139	62.6	17	43.6	3	42.8
<i>Cymbula miniata</i>	0	0.00	0	0.0	0	0.0	0	0.0
Unidentified limpet	0	0	2	0.9	0	0.0	0	0.0
<i>Aulacomya ater</i>	1	0.88	1	0.5	0	0.0	0	0.0
<i>Choromytilus meridionalis</i>	49	43.36	57	25.7	18	46.2	0	0.0
<i>Donax serra</i>	1	0.88	1	0.5	0	0.0	0	0.0
<i>Perna perna</i>	1	0.88	1	0.5	1	2.6	0	0.0
Unidentified bivalve	0	0.00	1	0.5	0	0.0	0	0.0
Whelk	4	3.54	4	1.8	1	2.6	0	0.0
<i>Crepidula porcellana</i>	0	0.00	1	0.5	0	0.0	0	0.0
Terrestrial snail	0	0.00	2	0.9	1	2.6	0	0.0
Unidentified	1	0.88	0	0.0	0	0.0	0	0.0
TOTAL	113	100	222	100	39	100	137	100

Layer	DAMA		NOSA 2		SHES	
Species	MNI	%	MNI	%	MNI	%
<i>Scutellastra argenvillei</i>	6	4.6	20	7.3	0	0.0
<i>Scutellastra granularis</i>	5	3.9	14	5.11	0	0.0
<i>Scutellastra tabularis</i>	0	0.0	0	0.0	0	0.0
<i>Cymbula granatina</i>	82	65.4	226	82.5	1	50.0
<i>Cymbula miniata</i>	0	0.0	1	0.7	0	0.0
Unidentified limpet	2	1.5	0	0.0	0	0.0
<i>Aulacomya ater</i>	2	1.5	3	1.1	0	0.0
<i>Choromytilus meridionalis</i>	32	24.6	50	18.6	0	0.0
<i>Donax serra</i>	1	0.8	0	0.0	0	0.0
<i>Perna perna</i>	1	0.8	0	0.0	0	0.0
Unidentified bivalve	0	0.0	4	1.5	0	0.0
Whelk	1	0.8		5	1.7	0
<i>Crepidula porcellana</i>	0	0.0	2	0.7	0	0.0
Terrestrial snail	2	1.5	3	2.2	1	50.0
Unidentified	0	0.0	0	0.0	0	0.0
TOTAL	137	100	328	100	2	100

Layer	ALL	
Species	MNI	%
<i>Scutellastra argenvillei</i>	41	4.8
<i>Scutellastra granularis</i>	28	3.3
<i>Scutellastra tabularis</i>	1	0.1
<i>Cymbula granatina</i>	521	61.2
<i>Cymbula miniata</i>	1	0.1
Unidentified limpet	4	0.5
<i>Aulacomya ater</i>	7	0.8
<i>Choromytilus meridionalis</i>	207	24.3
<i>Donax serra</i>	3	0.4
<i>Perna perna</i>	4	0.5
Unidentified bivalve	5	0.6
Whelk	15	1.8
<i>Crepidula porcellana</i>	3	0.4
Terrestrial snail	9	1.1
Unidentified	1	0.1
TOTAL	851	100

Table 4.2 Shellfish species abundances for LP18,19 and 20.

Site	LP18		LP19		LP20	
Species	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	164	15.95	470	9.58	1019	16.32
<i>S. barbara</i>	21	2.04	124	2.53	165	2.64
<i>S. cochlear</i>	117	11.38	372	7.58	582	9.32
<i>S. granularis</i>	230	22.37	1154	23.52	1571	25.16
<i>C. granatina</i>	160	15.56	1123	22.89	1295	20.74
<i>C. miniata</i>	2	0.19	1	0.02	11	0.18
<i>C. oculus</i>	22	2.14	216	4.40	159	2.55
<i>A. ater</i>	0	0.00	4	0.08	1	0.02
<i>C. meridionalis</i>	30	2.92	366	7.46	245	3.92
<i>Argobuccinum</i> sp.	4	0.39	20	0.41	39	0.62
<i>Burnupena</i> sp.	233	22.67	788	16.06	837	13.4
<i>Oxystele</i> sp.	2	0.19	176	3.59	53	0.85
<i>Haliotis</i> sp.	10	0.97	18	0.37	36	0.58
<i>Amblycheps</i> sp.	1	0.19	0	0.00	0	0.00
<i>Bullia</i> sp.	0	0.00	0	0.00	2	0.03
<i>C. porcellana</i>	31	3.02	60	1.22	223	3.57
<i>Deutella</i> sp.	1	0.10	3	0.06	0	0.00
<i>Pentunculus</i> sp.	0	0.00	2	0.04	1	0.02
<i>Scutella</i> sp.	0	0.00	7	0.14	3	0.05
<i>Turitella</i> sp.	0	0.00	3	0.06	0	0.00
TOTAL	1028		4907		6244	

Table 4.3 Shellfish species abundances for DFM11.

Square	CYR56		CYR57		CYR58		CYR59		CYR66		CYR67		CYR68		CYR69	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	5	0.7	5	0.6	5	0.8	15	3.3	6	0.9	4	0.6	4	0.5	17	1.7
<i>S. barbara</i>	11	1.6	7	0.7	17	2.6	10	2.2	6	0.9	2	0.3	12	1.5	19	1.9
<i>S. cochlea r</i>	1	0.1	0	0.0	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0
<i>S. granularis</i>	146	21.9	203	26.2	140	21.1	143	31.4	102	16.4	97	14.8	164	19.9	171	17.4
<i>C. granatina</i>	351	52.7	398	51.4	440	67.4	211	46.4	268	43.2	369	56.5	569	68.9	661	67.2
<i>C. miniata</i>	1	0.1	1	0.1	0	0.0	2	0.4	0	0.0	2	0.3	0	0.0	0	0.0
Limpet sp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	4	0.4
<i>A ater</i>	0	0.0	0	0.0	2	0.3	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1
<i>C. meridionalis</i>	137	20.5	144	18.6	51	7.7	64	14.1	231	37.2	160	24.5	61	7.4	95	9.6
<i>D. serra</i>	3	0.4	2	0.2	2	0.3	1	0.2	1	0.2	2	0.3	0	0.0	6	0.6
<i>V. corrugata</i>	0	0.0	0	0.0	0	0.0	0	0.0	3	0.5	1	0.2	3	0.4	1	0.1
<i>Argobuccinum</i>	0	0.00	0	0.0	0	0.0	0	0.0	1	0.2	0	0.00	0	0.0	0	0.0
Whelk	8	1.2	7	0.9	6	0.9	3	0.7	3	0.5	10	1.5	6	0.7	4	0.4
<i>Oxystele</i> sp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>Crepidula</i> sp.	0	0.0	3	0.3	0	0.0	5	1.1	0	0.0	0	0.0	2	0.2	0	0.0
<i>Helcion</i> sp.	3	0.4	4	0.52	0	0.0	0	0.0	0	0.0	6	0.9	4	0.5	4	0.4
<i>Fissurella</i> sp.	0	0.0	0	0.00	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
TOTAL	666		773		663	455			621		653		825		983	

Square	CYR74		CYR75		CYR76		CYR77		CYR78		CYR79		CYR84		CYR85	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	11	2.1	6	1.0	4	0.3	4	0.5	11	1.7	12	1.54	15	2.0	9	0.7
<i>S. barbara</i>	29	5.5	14	2.4	21	1.7	13	1.5	3	0.5	20	2.57	19	2.6	22	1.8
<i>S. cochlear</i>	2	0.4	0	0.0	0	0.0	0	0.0	0	0.5	1	0.13	1	0.1	2	0.2
<i>S. granularis</i>	69	13.1	92	15.6	197	15.9	128	15.4	91	14.5	99	12.71	90	12.2	132	10.9
<i>C. granatina</i>	253	47.9	294	49.8	633	51.3	527	63.4	429	68.2	493	63.29	420	57.1	685	56.7
<i>C. miniata</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.13	0	0.0	3	0.2
Limpet sp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.00	0	0.0	0	0.0
<i>A ater</i>	2	0.4	1	0.2	1	0.1	3	0.4	0	0.0	1	0.13	4	0.5	1	0.1
<i>C. meridionalis</i>	146	27.6	164	27.8	346	28.0	127	15.3	88	13.9	136	17.46	160	21.8	329	27.2
<i>D. serra</i>	3	0.6	2	0.3	4	0.3	4	0.5	5	0.8	4	0.51	6	0.8	4	0.3
<i>V. corrugata</i>	1	0.2	2	0.3	5	0.4	0	0.0	1	0.2	0	0.00	0	0.0	0	0.0
<i>Argobuccinum</i>	1	0.2	2	0.3	0	0.0	0	0.0	0	0.0	0	0.00	0	0.0	2	0.2
Whelk	5	0.9	5	0.8	2	0.2	11	1.3	1	0.2	5	0.64	6	0.8	4	0.3
<i>Oxystele</i> sp.	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0	0	0.00	0	0.0	1	0.1
<i>Crepidula</i> sp.	3	0.6	1	0.2	0	0.0	2	0.2	0	0.0	0	0.00	3	0.4	5	0.4
<i>Helcion</i>	3	0.6	5	0.8	21	1.7	11	1.3	0	0.0	6	0.77	11	1.5	9	0.7
<i>Fissurella</i> sp.	0	0.0	1	0.2	0	0.0	1	0.1	0	0.0	1	0.13	0	0.0	0	0.0
TOTAL	528		590		1234		831		629		779		735		1208	

Square	CYR86		CYR87		CYR88		CYR89		CYR90		CYR94		CYR95		CYR96 SURFACE	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	10	1.1	24	2.1	14	0.8	14	0.8	10	1.5	20	4.6	16	3.3	2	3.4
<i>S. barbara</i>	19	2.0	24	2.1	36	1.9	28	1.5	9	1.4	9	2.1	11	2.2	4	6.9
<i>S. cochlear</i>	1	0.1	0	0.0	1	0.1	1	0.1	1	0.1	1	0.2	0	0.0	1	1.7
<i>S. granularis</i>	137	14.6	228	19.8	165	9.1	210	11.1	108	16.5	52	11.9	64	13.1	8	13.8
<i>C. granatina</i>	618	65.9	737	63.9	1105	61.1	1274	67.6	397	60.5	256	58.8	295	60.2	36	62.1
<i>C. miniata</i>	0	0.0	0	0.0	1	0.1	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0
Limpet sp.	0	0.0	2	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>A ater</i>	1	0.1	5	0.4	6	0.3	4	0.2	0	0.0	4	0.9	3	0.6	0	0.0
<i>C. meridionalis</i>	126	13.4	106	9.2	426	23.5	312	16.5	119	18.1	79	18.2	97	19.8	7	12.1
<i>D. serra</i>	5	0.5	2	0.2	6	0.3	5	0.3	0	0.0	2	0.5	4	0.8	0	0.0
<i>V. corrugata</i>	1	0.1	2	0.2	0	0.0	1	0.1	2	0.3	1	0.2	0	0.0	0	0.0
<i>Argobuccinum</i>	0	0.0	0	0.0	0	0.0	3	0.1	0	0.0	1	0.2	0	0.0	0	0.0
Whelk	7	0.7	5	0.4	6	0.3	15	0.8	6	0.9	9	0.3	0	0.0	0	0.0
<i>Oxytele</i> sp.	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>Crepidula</i> sp.	1	0.1	15	1.3	0	0.0	3	0.2	0	0.0	1	0.2	0	0.0	0	0.0
<i>Helcion</i>	10	1.1	0	0.0	38	2.1	15	0.8	3	0.5	0	0.0	0	0.0	0	0.0
<i>Fissurella</i> sp.	0	0.00	0	0.0	5	0.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
TOTAL	938				1809		1885		656		435		490		58	

Square	CYR96		CYR97		CYR98		CYR99		CYR100	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	3	0.6	10	1.9	32	4.4	6	0.8	6	1.7
<i>S. barbara</i>	4	0.8	21	4.1	12	1.7	8	1.1	3	0.8
<i>S. cochlear</i>	1	0.2	1	0.2	0	0.0	0	0.0	0	0.0
<i>S. granularis</i>	55	11.6	72	14.1	89	12.4	90	12.2	86	23.9
<i>C. granatina</i>	328	69.3	341	66.9	420	58.3	465	63.2	187	52.1
<i>C. miniata</i>	0	0.0	0	0.0	1	0.1	1	0.1	0	0.0
Limpet sp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>A ater</i>	6	1.3	0	0.0	1	0.1	1	0.1	0	0.0
<i>C. meridionalis</i>	67	14.2	53	10.4	146	20.3	145	19.7	65	18.1
<i>D. serra</i>	2	0.4	1	0.2	3	0.4	2	0.3	2	0.5
<i>V. corrugata</i>	1	0.2	0	0.0	0	0.0	0	0.0	1	0.3
<i>Argobuccinum</i>	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0
Whelk	2	0.4	1	0.2	6	0.8	6	0.8	0	0.0
<i>Oxystele</i> sp.	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0
<i>Crepidula</i> sp.	0	0.0	1	0.2	1	0.1	1	0.1	1	0.3
<i>Helcion</i>	3	0.6	7	1.4	9	1.2	11	1.5	8	2.2
<i>Fissurella</i> sp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
TOTAL	473		509		720		736		359	

Table 4.4 Shellfish species abundances from BSB2

Stratigraphic unit	SSC		LLSB		BSBL		BRL		BBRL		DLP		ALL	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	34	4.3	14	1.1	94	3.9	1	2.7	27	7.1	12	2.3	182	3.3
<i>S. barbara</i>	5	0.6	5	0.4	9	0.4	0	0.0	0	0.0	0	0.0	19	0.3
<i>S. granularis</i>	208	26.2	407	30.7	837	35.5	14	37.8	55	14.4	222	42.1	1743	32.1
<i>C. granatina</i>	530	66.7	860	64.9	884	37.5	17	45.9	192	50.4	155	29.4	2638	48.6
<i>C. miniata</i>	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.0
<i>C. meridionalis</i>	1	0.1	1	0.1	19	0.8	1	2.7	6	1.6	7	1.3	35	0.6
Whelk	16	2.0	39	2.9	485	21.0	1	2.7	101	26.5	124	23.5	766	14.1
<i>Crepidula</i>	0	0.0	0	0.0	22	0.9	3	35.1	0	0.0	6	1.1	31	0.6
<i>Oxysetele</i> sp.	0	0.0	0	0.0	6	0.2	0	0.0	0	0.0	1	0.2	7	0.1
TOTAL	795		1326		2356		37		381		527		5422	

Table 4.5 Shellfish species abundances for BSB3

Stratigraphic unit	SURF		TERMITE		CB		HSL		ARG		LARG		BEE		LBEE	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	7	6.3	0	0.0	17	5.5	46	8.7	93	52.2	68	8.5	35	7.6	24	8.5
<i>S. barbara</i>	0	0	0	0.0	0	0.0	2	0.4	1	0.6	3	0.4	0	0.0	1	0.4
<i>S. cochlear</i>	1	0.9	0	0.0	1	0.3	3	0.6	3	1.7	6	0.8	0	0.0	0	0.0
<i>S. granularis</i>	16	14.3	3	42.9	84	27.3	144	27.1	22	12.4	242	30.4	135	29.3	104	37.0
<i>C. granatina</i>	61	54.5	2	28.6	112	36.4	187	35.2	40	22.5	292	36.6	178	38.7	93	33.1
<i>C. miniata</i>	0	0.0	0	0.0	0	0.0	0	0.0	2	0.4	0	0.0	0	0.0	0	0.0
<i>C. meridionalis</i>	3	2.7	0	0.0	6	1.9	18	3.4	10	5.6	117	14.7	54	11.7	28	10.0
Whelk	24	21.4	2	28.6	88	28.6	129	24.3	9	5.1	69	8.7	58	12.6	31	11.0
TOTAL	112	100	7	100	308	100	531	100	178	100	797	100	460	100	281	100

Stratigraphic unit	THL		CIT		SBTL		LIM2		BL2		ALL	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	161	12.5	13	5.9	31	6.4	22	6.6	10	7.4	551	9.9
<i>S. barbara</i>	6	0.5	0	0.0	3	0.6	0	0.0	0	0.0	27	0.5
<i>S. cochlear</i>	4	0.3	0	0.0	3	0.6	0	0.0	0	0.0	23	0.4
<i>S. granularis</i>	353	27.5	80	36.5	187	38.4	102	30.6	46	33.8	1596	28.6
<i>C. granatina</i>	647	50.4	75	34.2	150	30.8	118	35.4	33	24.3	2067	37.0
<i>C. miniata</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	0.0
<i>C. meridionalis</i>	46	3.6	21	9.6	19	3.9	15	4.5	7	5.1	345	6.2
Whelk	66	5.1	29	13.2	93	19.1	75	22.5	40	29.4	971	17.4
<i>Crepidula</i> sp.	0	0.0	1	0.5	1	0.2					2	0.0
TOTAL	1283	100	219	100	487	100	333	100	136	100	5582	100

Table 4.6 Shellfish species abundances for BSB4.

Stratigraphic unit	WAL		BAL		CHE		WCH		BCH		DOD		GDO		WDO	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	2	2.4	3	3.2	7	0.7	6	2.9	0	0.0	7	4.6	28	5.3	22	3.2
<i>S. barbara</i>	0	0.0	1	1.1	6	0.6	3	1.5	0	0.0	0	0.0	5	0.9	8	1.2
<i>S. cochlear</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>S. granularis</i>	53	64.6	67	70.5	599	58.0	103	50.2	17	50.0	77	51.0	311	58.6	377	54.6
<i>C. granatina</i>	27	32.9	24	25.3	402	38.9	89	43.4	16	47.1	49	32.5	135	25.4	255	36.9
<i>C. miniata</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.7	1	0.2	0	0.0
<i>C. meridionalis</i>	0	0.0	0	0.0	14	1.4	1	0.5	0	0.0	6	4.0	35	6.6	16	2.3
Whelk	0	0.0	0	0.0	3	0.3	3	1.5	1	2.9	8	5.3	5	0.9	12	1.7
<i>Crepidula</i>	0	0.0	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0	4	0.8	0	0.0
<i>Oxysetele</i> sp.	0	0.0	0	0.0	1	0.1	0	0.0	0	0.0	3	2.0	7	1.3	0	0.0
<i>P. cpmpressa</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1
TOTAL	82	100	95	100	1033	100	205	100	34	100	151	100	531	100	691	100

Stratigraphic unit	BDO		ROBD		GES		WES		BES		SES		FIA		TRU	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	21	1.6	7	1.2	4	2.2	24	2.3	10	2.1	2	0.7	1	0.8	4	12.5
<i>S. barbara</i>	4	0.3	5	0.8	0	0.0	20	2.0	1	0.2	1	0.3	0	0.0	0	0.0
<i>S. cochlear</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>S. granularis</i>	852	63.5	394	66.6	97	52.7	661	64.6	353	73.8	207	68.5	91	74.0	15	47.0
<i>C. granatina</i>	419	31.2	142	24	33	17.9	278	27.1	101	21.1	88	29.1	30	25.0	8	25.0
<i>C. miniata</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>C. meridionalis</i>	15	1.1	4	0.7	0	0.0	9	0.9	5	1.0	1	0.3	0	0.0	4	12.5
Whelk	30	2.2	40	6.8	50	27.2	32	3.1	8	1.7	3	1.0	0	0.0	0	0.0
<i>Crepidula</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>Oxysetele</i> sp.	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.8	0	0.0
<i>P. cympressa</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
TOTAL	1341	100	592	100	184	100	1024	100	478	100	302	100	123	100	32	100

Stratigraphic unit	ALL	
Species	MNI	%
<i>S. argenvillei</i>	150	2.2
<i>S. barbara</i>	55	0.8
<i>S. cochlear</i>	0	0.0
<i>S. granularis</i>	4280	62.0
<i>C. granatina</i>	2095	30.3
<i>C. miniata</i>	2	0.0
<i>C. meridionalis</i>	108	1.6
Whelk	195	2.8
<i>Crepidula</i>	5	0.1
<i>Oxysetele</i> sp.	12	0.2
<i>P. compressa</i>	1	0.0
TOTAL	6903	100

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Table 4.7 Shellfish species abundances for BSB5.

BSB5		
Species	MNI	%
<i>S. argenvillei</i>	28	6.8
<i>S. cochlear</i>	1	0.2
<i>S. granularis</i>	13	3.2
<i>C. granatina</i>	95	23.1
<i>C. miniata</i>	1	0.2
<i>A. ater</i>	5	1.2
<i>C. meridionalis</i>	261	63.5
<i>Crepidula</i>	3	0.7
<i>Helcion</i> sp.	2	0.5
<i>P. compressa</i>	1	0.2
<i>Fissurella</i> sp.	1	0.2
TOTAL	411	100

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Table 4.7 Shellfish species abundances for BSB6.

Stratigraphic unit	SURF		SS1		ALP		BET		CHA		DEL		ECH		FOX	
Species	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	88	5.8	53	11.6	22	7.3	1	1.5	10	45.5	20	25.0	77	67.0	4	8.9
<i>S. barbara</i>	1	0.1	1	0.2	1	0.3	0	0.0	0	0.0	0	0.0	0	0.0	2	4.4
<i>S. cochlear</i>	2	0.1	6	1.3	7	2.3	1	1.5	0	0.0	5	6.3	6	5.2	0	0.0
<i>S. granularis</i>	648	43.0	210	46.2	135	44.8	54	78.3	10	45.5	6	7.5	9	7.8	29	64.4
<i>C. granatina</i>	419	27.7	88	19.3	86	28.6	13	18.8	2	9.1	23	28.8	11	9.6	9	20.0
<i>C. miniata</i>	0	0.0	0	0	0	0.0	0	0.0	0	0	0	0.0	0	0.0	1	2.2
<i>C. meridionalis</i>	2	0.1	0	0	0	0.0	0	0.0	0	0	0	0.0	0	0.0	0	0.0
Whelk	352	23.3	96	21.1	49	16.3	0	0.0	0	0	23	28.8	12	10.4	0	0.0
<i>Crepidula</i>	0	0	0	0.0	0	0.0	0	0.0	0	0	3	3.8	0	0.0	0	0.0
<i>Oxysetele</i> sp.	0	0	0	0.0	1	0.3	0	0.0	0	0	0	0.0	0	0.0	0	0.0
<i>C. algoensis</i>	0	0.0	1	0.2	0	0.0	0	0.0	0	0	0	0.0	0	0.0	0	0.0
TOTAL	1512	100	455	100	301	100	69	100	22	100	80	100	115	100	45	100

Stratigraphic unit	GOLF		PIL		PBO		ALL	
Species	MNI	%	MNI	%	MNI	%	MNI	%
<i>S. argenvillei</i>	44	8.3	148	34.7	25	4.3	492	11.9
<i>S. barbara</i>	3	0.6	5	1.2	1	0.2	14	0.3
<i>S. cochlear</i>	3	0.6	12	2.8	5	0.9	47	1.1
<i>S. granularis</i>	273	51.2	141	33.1	349	60.1	1864	45.1
<i>C. granatina</i>	204	38.3	114	26.8	199	34.3	1168	28.2
<i>C. miniata</i>	0	0.0	0	0.0	0	0.0	0	0.0
<i>C. meridionalis</i>	0	0.0	0	0.0	0	0.0	2	0.0
Whelk	6	1.1	6	1.4	2	0.3	546	13.2
<i>Crepidula</i>	0	0.0	0	0.0	0	0.0	0.0	0.0
<i>Oxysetele</i> sp.	0	0.0	0	0.0	0	0.0	0.0	0.0
<i>C. algoensis</i>	0	0.0	0	0.0	0	0.0	0.0	0.0
TOTAL	533	100	426	100	581	100	4131	100

Table 4.8 Barnacles and water-worn shell and pebbles as a percentage of the total weight of *C. meridionalis* at DFM11.

Square	% barnacle	% wwsp
CYR56	0.06	0.46
CYR57	0.06	2.03
CYR58	0.02	0.37
CYR59	0.13	2.67
CYR66	0.08	1.39
CYR67	0.08	1.26
CYR68	0.16	0.60
CYR69	0.18	1.10
CYR74	0.08	0.60
CYR75	0.11	0.13
CYR76	0.00	0.41
CYR77	0.05	1.53
CYR78	0.24	0.00
CYR79	0.18	1.2
CYR84	0.00	0.00
CYR85	0.00	0.20
CYR86	0.06	0.91
CYR87	0.16	1.18
CYR88	0.14	0.96
CYR89	0.56	1.22
CYR90	0.00	2.46
CYR94	0.00	0.94
CYR95	0.05	0.20
CYR96	0.31	3.37
CYR97	0.19	1.48
CYR98	0.31	2.16
CYR99	0.27	1.98
CYR100	0.25	4.44

Table 4.9 Results of Mann-Whitney U tests carried out on *C. granatina* from Middle and Later Stone Age sites in the southwestern and Northern Cape.

Site A	Median(mm)	Site B	Median (mm)	p level
HDP1	70.5	HDP3	69.3	0.26
HDP1	70.5	BSB2	68.6	0.06
HDP1	70.5	BSB3	71.6	0.18
HDP1	70.5	BSB4	68.0	0.02
HDP1	70.5	BSB5	66.1	0.00
HDP1	70.5	BSB6	61.5	0.65
HDP1	70.5	LP18	57.7	0.01
HDP1	70.5	LP19	57.4	0.00
HDP1	70.5	LP20	55.5	0.00
HDP1	70.5	CYR67	56.4	0.00
HDP1	70.5	CYR99	49.9	0.00
HDP3	69.3	BSB2	68.6	0.99
HDP3	69.3	BSB3	71.6	0.02
HDP3	69.3	BSB4	68.0	0.70
HDP3	69.3	BSB5	66.1	0.97
HDP3	69.3	BSB6	61.5	0.01
HDP3	69.3	LP18	57.7	0.02
HDP3	69.3	LP19	57.4	0.00
HDP3	69.3	LP20	55.5	0.00
HDP3	69.3	CYR67	56.4	0.00
HDP3	69.3	CYR99	49.9	0.00
BSB2	68.6	BSB3	71.6	0.00
BSB2	68.6	BSB4	68.0	0.28
BSB2	68.6	BSB5	66.1	0.81
BSB2	68.6	BSB6	61.5	0.0
BSB2	68.6	LP18	57.7	0.01
BSB2	68.6	LP19	57.4	0.00

Site A	Median(mm)	Site B	Median (mm)	p level
BSB2	68.6	LP20	55.5	0.00
BSB2	68.6	CYR67	56.4	0.00
BSB2	68.6	CYR99	49.9	0.00
BSB3	71.6	BSB4	68.0	0.00
BSB3	71.6	BSB5	66.1	0.26
BSB3	71.6	BSB6	61.5	0.00
BSB3	71.6	LP18	57.7	0.01
BSB3	71.6	LP19	57.4	0.00
BSB3	71.6	LP20	55.5	0.00
BSB3	71.6	CYR67	56.4	0.00
BSB3	71.6	CYR99	49.9	0.00
BSB4	68.0	BSB5	66.1	0.98
BSB4	68.0	BSB6	61.5	0.00
BSB4	68.0	LP18	57.7	0.02
BSB4	68.0	LP19	57.4	0.00
BSB4	68.0	LP20	55.5	0.00
BSB4	68.0	CYR67	56.4	0.00
BSB4	68.0	CYR99	49.9	0.00
BSB5	66.1	BSB6	61.5	0.19
BSB5	66.1	LP18	57.7	0.19
BSB5	66.1	LP19	57.4	0.05
BSB5	66.1	LP20	55.5	0.02
BSB5	66.1	CYR67	56.4	0.01
BSB5	66.1	CYR99	49.9	0.01
BSB6	61.5	LP18	57.7	0.41
BSB6	61.5	LP19	57.4	0.00
BSB6	61.5	LP20	55.5	0.00
BSB6	61.5	CYR67	56.4	0.00
BSB6	61.5	CYR99	49.9	0.00

Site A	Median(mm)	Site B	Median (mm)	p level
LP 18	57.7	LP19	57.5	0.75
LP18	57.7	LP20	55.5	0.43
LP18	57.7	CYR67	56.4	0.53
LSP18	57.7	CYR99	49.9	0.14
LP19	57.5	LP20	55.5	0.09
LP19	57.5	CYR67	56.4	0.28
LP19	57.5	CYR99	49.9	0.00
LP20	55.5	CYR67	56.4	0.89
LP20	55.5	CYR99	49.9	0.00
CYR67	56.4	CYR99	49.9	0.00

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Table 4.10 Results of Mann-Whitney U tests carried out on *S. granularis* from Middle and Later Stone Age sites in the southwestern and Northern Cape.

Site A	Median(mm)	Site B	Median (mm)	p level
HDP1	49.3	HDP3	47.3	0.89
HDP	49.3	BSB2	41.0	0.08
HDP1	49.3	BSB3	39.9	0.06
HDP1	49.3	BSB4	38.7	0.03
HDP1	49.3	BSB6	38.0	0.02
HDP1	49.3	LP18	33.8	0.02
HDP1	49.3	LP19	36.6	0.01
HDP1	49.3	LP20	36.6	0.01
HDP1	49.3	CYR84	36.8	0.02
HDP1	49.3	CYR74	35.7	0.02
HDP3	47.3	BSB2	41.0	0.00
HDP3	47.3	BSB3	39.9	0.00
HDP3	47.3	BSB4	38.7	0.00
HDP3	47.3	BSB6	38.0	0.02
HDP3	47.3	LP18	33.8	0.00
HDP3	47.3	LP19	36.6	0.00
HDP3	47.3	LP20	36.6	0.00
HDP3	47.3	CYR84	36.8	0.00
HDP3	47.3	CYR74	35.7	0.00
BSB2	41.0	BSB3	39.9	0.03
BSB2	41.0	BSB4	38.7	0.00
BSB2	41.0	BSB6	38.0	0.00
BSB2	41.0	LP18	33.8	0.00
BSB2	41.0	LP19	36.6	0.00

Site A	Median(mm)	Site B	Median (mm)	p level
BSB2	41.0	LP20	36.6	0.00
BSB2	41.0	CYR84	36.8	0.00
BSB2	41.0	CYR74	35.7	0.00
BSB3	39.9	BSB4	38.7	0.00
BSB3	39.9	BSB6	38.0	0.00
BSB3	39.9	LP18	33.8	0.00
BSB3	39.9	LP19	36.6	0.00
BSB3	39.9	LP20	36.6	0.00
BSB3	39.9	CYR84	36.8	0.01
BSB3	39.9	CYR74	35.7	0.00
BSB4	38.7	BSB6	38.0	0.00
BSB4	38.7	LP18	33.8	0.00
BSB4	38.7	LP19	36.6	0.00
BSB4	38.7	LP20	36.6	0.00
BSB4	38.7	CYR84	36.8	0.12
BSB4	38.7	CYR74	35.7	0.00
BSB6	38.0	LP18	33.8	0.00
BSB6	38.0	LP19	36.6	0.01
BSB6	38.0	LP20	36.6	0.01
BSB6	38.0	CYR84	36.8	0.65
BSB6	38.0	CYR74	35.7	0.01
LP18	33.8	LP19	36.6	0.03
LP18	33.8	LP20	36.6	0.03
LP18	33.8	CYR84	36.8	0.01
LP18	33.8	CYR74	35.7	0.97
LP19	36.6	LP20	36.6	0.49
LP19	36.6	CYR84	36.8	0.23
LP19	36.6	CYR74	35.7	0.10
LP20	36.6	CYR84	36.8	0.37
LP20	36.6	CYR74	35.7	0.07

Site A	Median(mm)	Site B	Median (mm)	p level
CYR84	36.8	CYR74	35.7	0.03

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Table 4.11 Results of Mann-Whitney U tests carried out on *S. argenvillei* from Middle and Later Stone Age sites in the southwestern and Northern Cape.

Site A	Median(mm)	Site B	Median (mm)	p level
HDP1	86.0	HDP3	80.1	0.20
HDP1	86.0	BSB2	76.9	0.04
HDP1	86.0	BSB3	77.4	0.06
HDP1	86.0	BSB4	74.1	0.01
HDP1	86.0	BSB5	80.9	0.76
HDP1	86.0	BSB6	78.1	0.76
HDP1	86.0	LP18	72.2	0.01
HDP1	86.0	LP19	74.4	0.00
HDP1	86.0	LP20	69.9	0.00
HDP1	86.0	CYR87	72.8	0.01
HDP3	80.1	BSB2	76.9	0.20
HDP3	80.1	BSB3	77.4	0.47
HDP3	80.1	BSB4	74.1	0.02
HDP3	80.1	BSB5	80.9	0.70
HDP3	80.1	BSB6	78.1	0.55
HDP3	80.1	LP18	72.2	0.01
HDP3	80.1	LP19	74.4	0.03
HDP3	80.1	LP20	69.9	0.00
HDP3	80.1	CYR87	72.8	0.00
BSB2	76.9	BSB3	77.4	0.15
BSB2	76.9	BSB4	74.1	0.01
BSB2	76.9	BSB5	80.9	0.55
BSB2	76.9	BSB6	78.1	0.17
BSB2	76.9	LP18	72.2	0.01
BSB2	76.9	LP19	74.4	0.03

Site A	Median(mm)	Site B	Median (mm)	p level
BSB2	76.9	LP20	69.9	0.00
BSB2	76.9	CYR87	72.8	0.01
BSB3	77.4	BSB4	74.1	0.00
BSB3	77.4	BSB5	80.9	0.70
BSB3	77.4	BSB6	78.1	0.94
BSB3	77.4	LP18	72.2	0.00
BSB3	77.4	LP19	74.4	0.00
BSB3	77.4	LP20	69.9	0.00
BSB3	77.4	CYR87	72.8	0.00
BSB4	74.1	BSB5	80.9	0.28
BSB4	74.1	BSB6	78.1	0.00
BSB4	74.1	LP18	72.2	0.71
BSB4	74.1	LP19	74.4	0.41
BSB4	74.1	LP20	69.9	0.03
BSB4	74.1	CYR87	72.8	0.61
BSB5	80.9	BSB6	78.1	0.60
BSB5	80.9	LP18	72.2	0.16
BSB5	80.9	LP19	74.4	0.28
BSB5	80.9	LP20	69.9	0.12
BSB5	80.9	CYR87	72.8	0.23
BSB6	78.1	LP18	72.2	0.00
BSB6	78.1	LP19	74.4	0.00
BSB6	78.1	LP20	69.9	0.00
BSB6	78.1	CYR87	72.8	0.00
LP18	72.2	LP19	74.4	0.25
LP18	72.2	LP20	69.9	0.54
LP18	72.2	CYR87	72.8	0.62
LP19	74.4	LP20	69.9	0.00
LP19	74.4	CYR87	72.8	0.4

Site A	Median(mm)	Site B	Median (mm)	p level
LP20	69.9	CYR87	72.8	0.15

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Table 4.12 Results of Mann-Whitney U tests carried out on *C. meridionalis* from Middle and Later Stone Age sites in the southwestern and Northern Cape.

Site A	Median(mm)	Site B	Median (mm)	p level
HDP1	7.4	HDP3	7.1	0.02
HDP1	7.4	BSB2	6.8	0.02
HDP1	7.4	BSB3	7.3	0.65
HDP1	7.4	BSB4	7.9	0.65
HDP1	7.4	BSB5	6.4	0.00
HDP1	7.4	LP18	7.4	0.20
HDP1	7.4	LP19	7.1	0.06
HDP1	7.4	LP20	6.1	0.00
HDP1	7.4	CYR74	7.8	0.04
HDP1	7.4	CYR99	5.7	0.00
HDP3	7.1	BSB2	6.8	0.34
HDP3	7.1	BSB3	7.3	0.00
HDP3	7.1	BSB4	7.9	0.00
HDP3	7.1	BSB5	6.4	0.00
HDP3	7.1	LP18	7.4	0.01
HDP3	7.1	LP19	7.1	0.62
HDP3	7.1	LP20	6.1	0.00
HDP3	7.1	CYR74	7.8	0.00
HDP3	7.1	CYR99	5.7	0.00
BSB2	6.8	BSB3	7.3	0.02
BSB2	6.8	BSB4	7.9	0.00
BSB2	6.8	BSB5	6.4	0.07
BSB2	6.8	LP18	7.4	0.01
BSB2	6.8	LP19	7.1	0.27
BSB2	6.8	LP20	6.1	0.00
BSB2	6.8	CYR74	7.8	0.00
BSB2	6.8	CYR99	5.7	0.00

Site A	Median(mm)	Site B	Median (mm)	p level
BSB3	7.3	BSB4	7.9	0.00
BSB3	7.3	BSB5	6.4	0.00
BSB3	7.3	LP18	7.4	0.12
BSB3	7.3	LP19	7.1	0.02
BSB3	7.3	LP20	6.1	0.00
BSB3	7.3	CYR74	7.8	0.00
BSB3	7.3	CYR99	5.7	0.00
BSB4	7.9	BSB5	6.4	0.00
BSB4	7.9	LP18	7.4	0.29
BSB4	7.9	LP19	7.1	0.00
BSB4	7.9	LP20	6.1	0.00
BSB4	7.9	CYR74	7.8	0.20
BSB4	7.9	CYR99	5.7	0.00
BSB5	6.4	LP18	7.4	0.00
BSB5	6.4	LP19	7.1	0.00
BSB5	6.4	LP20	6.1	0.00
BSB5	6.4	CYR74	7.8	0.00
BSB5	6.4	CYR99	5.7	0.00
LP18	7.4	LP19	7.1	0.01
LP18	7.4	LP20	6.1	0.00
LP18	7.4	CYR74	7.8	0.88
LP18	7.4	CYR99	5.7	0.00
LP19	7.1	LP20	6.1	0.00
LP19	7.1	CYR74	7.8	0.00
LP19	7.1	CYR99	5.7	0.00
LP20	6.1	CYR74	7.8	0.00
LP20	6.1	CYR99	5.7	0.04
CYR74	7.8	CYR99	5.7	0.00

**APPENDIX B**  
**METHODS USED FOR NUTRIENT ANALYSES**

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## SPECTROPHOTOMETRIC ASSAY OF TOTAL LIPID BY VANILLIN REACTION

### INTRODUCTION

Although lipid can be assayed gravimetrically by performing a lipid extraction from a sample and then drying and weighing it, this process is tedious and likely to be inaccurate owing to losses and retention of water. Another approach to assessing the lipid content of a biologic sample would be to assay each component of the lipid profile separately and summing the components. A spectrophotometric method that was popular about 50 years ago to determine the total lipid has been resurrected in a form that is useful for crude assays of lipid, chiefly triacylglycerol and phospholipid.

Vanillin is 4-methoxy-3-hydroxy-benzaldehyde,  $C_8H_8O_3$  with a molecular mass of 152.15da, soluble to 1g/100ml in water. The reaction of the lipid with heated sulphuric acid solution exposed to vanillin and phosphoric acid yields a pink product with maximal absorption at 525nm. A carbon to carbon double bond probably reacts with sulphuric acid to produce a carbonium ion that is stable for several hours, and the vanillin forms a phosphate ester with phosphoric acid making a more reactive carbonyl group. The carbonium and carbonyl groups react to form the colour compound. Colour yield depends on the UFA: oleic acid has a more intense colour than linoleic acid which has a more intense colour than cholesterol. There may be steric hindrance with 2 or more double bonds. Saturated fats and glycerol do not react. Note that about 30% of plasma fatty acids are saturated. Flax oil behaves very differently. It may be argued that the standards used should be adapted to the materials analysed, but for convenience, **sunflower oil** can be used.

### STANDARD MACRO METHOD

Serum or plasma can be used for the macro assay. The analysis should be done on the same day but the sample can be frozen at -20C for several days.

### MATERIALS

Sulphuric acid (concentrated)

**Vanillin-Phosphoric acid reagent.** 0.1g vanillin in 16ml of distilled water to which is added 34ml of concentrated phosphoric acid.

Olive oil or sunflower oil as a standard, gravimetrically 240mg/mL of chloroform. Can be made in a 10x stock solution. Store in dark and at -20C

## PROCEDURE

Prepare the standard curve by drying in heat-tolerant glass test tubes, 0, 12, 24, 48, 96, 148, 240µg of lipid in the standard solution. Let the samples dry. React as for plasma samples.

To 20µL of plasma add 500µL of conc sulphuric acid. Stopper the tube and incubate at 100C for 10min in a water bath. Add 300µL of vanillin reagent. React in the dark for 60min. Read absorbance at 520nm.

Use the standard curve to derive the lipid in the unknown samples.

## MICROTITRE PLATE METHOD

A careful adaptation was done for microtitre plate analysis. For the micro assay the work is done on a lipid extract after which the sample is dissolved in Folch monophasic mixture (chloroform:methanol 2:1), transferred and dried.

The reaction proceeds by exposure to concentrated sulphuric acid whereafter vanillin and phosphoric acid are introduced. The correlation coefficient ( $r^2$ ) with gravimetric lipid is 0.81. Note that the microtitre plates are susceptible to damage from organic solvents and strong acids. Chloroform:methanol 2:1 is less damaging than chloroform alone. The Costar polystyrene microtitre plate is usable but probably also the more organic solvent-resistant plates (Greiner). It seems better to use the microtitre plate only once.

**Sample Preparation.** A small scale adaptation for the Folch extraction is useful. The sample (homogenised foodstuff) should be fairly liquid in a water suspension. Starting with 0.8mL of liquid homogenate containing the fat to be extracted, add 2.0mL methanol and vortex. Now add 1.0mL chloroform and vortex the monophasic. Spin at 2000rpm (but <3000G-force to avoid breaking glass tubes) for 10min. The pellet of insolubles is left behind as the supernatant fluid (SNF1) is decanted to a 15mL graduated tube with a cap. To the pellet add 1mL methanol and 0.5mL chloroform and vortex. Spin the tube again and decant the SNF(2) to the tube for SNF. Repeat the wash of the pellet once more and decant SNF3 to the SNF. Now add 2mL chloroform and mix, then add 2mL water and mix. Spin at 2000rpm for

10min. The infranatent chloroform (4mL) contains the lipid extract which can be collected after removing the supernatent water and few insoluble peptides. The 4mL of chloroform is dried - can be done at 40C under nitrogen jet but for chromatography should be dried at ambient or cooler temperatures.

**Standard solution.** Sunflower oil in chloroform:methanol (2:1), at 1mg per ml; conveniently, about 50mg of oil is dissolved in Folch solvent and then brought to 5.0 mL, yielding 1 $\mu$ g/ $\mu$ L.

**Vanillin reagent.** 0.2mg/mL of 17% phosphoric acid (concentrated phosphoric acid is 68% or 85%, requiring 1/4 or 1/5 for the solution). The vanillin takes a while to dissolve.

**Procedure.** Set up a standard curve of 0-120 $\mu$ g in wells, beginning with about 3 $\mu$ g. Transfer the unknowns into the wells as well in Folch solvent, preferably in volumes of <100 $\mu$ L. Dry the solvent off at 90C for 15-30min. Preheat the heating block before the analysis is commenced. After the drying, chill the plate on ice.

Add 100 $\mu$ L of concentrated sulphuric acid and heat at 90C for 20min. Chill on ice. Read the baseline absorbance at 540nm. The lipid turns increasingly yellow. Higher amounts than 120 $\mu$ g leave the well opaque owing to the amount of chloroform.

Now add 50 $\mu$ L of vanillin reagent at room temperature and react for 20min. The lipid turns cerise in moments and readings can be done at 10min to at least 40min without loss of linearity. Read absorbance at 540nm. Derive the difference in absorbance for regression analysis which is a linear function up to about 100 $\mu$ g.

The linear regression is with absorbance of close to 0 going to about 2.0 and having a linear regression of  $r^2 > 0.98$ .

## CARBHOHYDRATE METHODOLOGY

### OVERVIEW

The **definition** of carbohydrates is that they are organic nutrients with the general formula of  $C_nH_{2n}O_{nc}$ , found in plants and animals and utilised in simple or polymerised forms for energy; additionally carbohydrates form covalent compounds with lipids (glycolipids), and with proteins (glycoproteins ). In the nutritional sense, the bulk of carbohydrates are not in covalent linkage with other classes of molecules. The carbohydrates are alcohol-substituted alkanes with a carbonyl functional moiety (aldehyde) and can polymerise. The commonly

encountered building blocks of carbohydrates are 6-carbon molecules or hexoses such as glucose, fructose and galactose; or 5-carbon molecules such as arabinose and xylose which are encountered in plants. The monosaccharides glucose, fructose, galactose have sweet tastes, as do sucrose and maltose, the disaccharides and the term sugars are best restricted to these few species. Fructans are oligo- or polysaccharides in which fructose predominates over glucose ( found in chicory, and cool season grasses). The starch content of maize kernels is high (~75% of mass) and of the legume seeds is about 60% but in contrast to most other starches, a significant portion is classified as **resistant**. This is resistant to conventional amylases but in the colon bacteria can ferment these to short chain fatty acids. The potato contains about 20% starch in its wet weight.

The **nomenclature** can be simplified into simple sugars, comprised of monosaccharides (pentoses and hexoses) and disaccharides (sucrose is glucose + fructose, lactose is glucose + galactose), oligosaccharides of polymers of between 3 and 20, and polysaccharides of polymers >20. Homopolysaccharides contain only one species, e.g. glucose in starch, cellulose, or glycogen but linkage can be 1,4 or 1,6. Starch from plant sources is a blend of two classes of polysaccharides: **amylose** is a linear chain of 1,4 linkages which coils into cylindrical structures, with molecular masses of about 250 kd. Amylose constitutes about 10-30% of starch and **amylopectin** comprises about 90-70%. This component is branched from a 1,4 chain at 1,6 linkages and has molecular masses of 50 000 to 500 000 kda. The 1,4 links are branched at about 25 saccharide sequences Cellulose is an indigestible polysaccharide to mammals, whereas starch is digestible; first by amylase and then the oligosaccharides and remaining maltose are digested by glucosidase. Glycogen is an animal storage form of glucose. Dietary starch originates from plants but technically can include similar polymers from animals in which there are  $\alpha$ -linked 1,4 and 1,6 glucose molecules susceptible to amylases after heat has gelatinised them into digestible form in acid milieu. Heteropolysaccharides contain more than one species of saccharide: pectin, hemicellulose, and gums.

The **physical properties** can be summarised simply that polar molecules will dissolve in polar solvents (water) up to a certain chain length but very large chains form insoluble granular forms that can be solubilised by heat and are subject to hydrolysis under acidic conditions. Monosaccharides, disaccharides and oligosaccharides dissolve in water or 80% ethanol and this preparatory step that will exclude polysaccharides, dietary fibre, proteins; and lipid as well but retaining phenolics, amino acids and other small polar molecules. Note that high water content of samples means that the final concentration of alcohol may be affected and the lower alcohol concentration allows more solubilisation of polysaccharides. Polysaccharides (starch) can be solubilised (gelatinised) by heating them in suspension in water at 65C, especially in alkaline or acidic conditions but the latter can hydrolyse linked saccharides. Gelatinisation by disruption of all hydrogen bonds can also be achieved by heating the sample in water alkalised with NaOH or KOH to 130C (autoclave) but

neutralisation with acetic acid may introduce a high salt matrix that can interfere with subsequent chemical assays.

**Preparation** of carbohydrates for analysis. The samples should be rapidly processed, preferably at very low temperature and desiccated under vacuum conditions. If heating is used for drying the sample, then the temperature is recommended to be 50°C. Dry mass should be used as a starting point, alternatively the sample can be ground to a fine powder after being solidified by liquid nitrogen in a similarly cooled mortar and pestle. Hereafter the material is divided into the soluble fraction (mono- to oligosaccharides) and the insoluble fraction by mixing in water or 80% ethanol, and filtering the suspension, yielding a **filtrate** with mono- to oligosaccharides and a retentate containing polysaccharides along with proteins and other material. The filtrate contains many substances that may interfere with assays, including amino acids, organic acids, pigments, vitamins, minerals. A commonly used clarifying agent is lead acetate which forms insoluble complexes with many interfering complexes and these can be pelleted by centrifugation. Otherwise ion-exchange systems can be used as saccharides are non-charged. Alcohol may be evaporated before further analysis. Exposure to chloroform will remove chlorophyll. The retentate is analysed after dissolving it in strong alkali solution and neutralising the final product. Typically NaOH or KOH is used at 0.4M and neutralisation is with glacial acetic acid.

**Assays** for mono and oligosaccharides vary according to the purpose of the information desired. Physical methods are convenient and inexpensive but rely on relatively pure and simple preparations of saccharides, chemical methods are also convenient and inexpensive whilst requiring more time and skill. The most accurate determination of mono- to oligosaccharides for the amount and type of carbohydrate is HPLC but is expensive. A new development is the use of immunoassays against saccharides with monoclonal antibodies raised through hapten formation. Assays for polysaccharides need to ensure that these large, granular (3-60µm) though heat during processing may change this to linear amylose (500 - 2000 glucose units) and amylopectin (>1 000 000 glucose units). Poorly soluble compounds are dissolved for access of reagents.

**Physical descriptions** can be summarised as mass or density, polarimetric, refractive, infrared absorption. Consider the oligosaccharides first. The **mass** of the extract can be determined after drying, but the mass per volume (density) can be described as well. A given, accurate volume can be weighed but an hygrometer can also be used in larger volumes of sample. **Polarimetry** is possible with asymmetric carbons in the sugar. These rotate the plane of polarised light. The extent  $\alpha$  of rotation is a function of path length(L) and concentration ( c ), as well as temperature and wavelength so that  $\alpha = A.L.c$  where A is the optical activity which is a property of the molecule. The analysis is done at 20°C and with a light wavelength of 589.3nm (D line of Na). A calibration curve can be used. **Refractive index**  $n$  is the ratio of velocities of light in a vacuum ( $v_v$ ) and in the material of interest ( $v_s$ ); Snell's law being that  $\sin i / \sin r = v_2/v_1$  and can be obtained by measuring the angle of

refraction (  $r$  ) of light when it passes through the material relative to the incident angle. Considering light striking the medium at an angle  $i$ , from the perpendicular to the point, there will be an identical angle of reflection but some light will enter the material and travel at the angle  $r$  relative to the perpendicular. **Infrared spectrometry** is feasible because carbohydrates absorb infrared light at wavelengths not absorbed by other compounds. Polysaccharide analysis by density after isolation can be done after precipitation. Starch has a density of  $1500\text{kg/m}^3$

**Chemical descriptions** are standard for mono- and oligosaccharides and several rely on the fact that monosaccharides are reducing substances, so that acid hydrolysis may be required of disaccharides and oligosaccharides ahead of or during the analysis. **Titration** methods such as the Lane-Eynon method utilise a burette to drip the carbohydrate into a flask of boiling copper sulphate and the point at which copper is completely precipitated is indicated by a colour change from an indicator. The reaction is not simply stoichiometric and hence standards have to be used. **Gravimetric** methods such as the Munson and Walker method rely on the oxidation of copper sulphate and alkaline tartrate to produce a precipitate of  $\text{CuO}_2$ . By filtration and dessication, the mass of copper can be related to the mass of carbohydrate by using known standards. **Colorimetric** methods may be done using chemically or enzymatically formed colour products. The anthrone reaction is useful for mono- to oligosaccharides. Under sulphuric acid conditions boiling the anthrone reagent hydrolyses saccharides and brings about a blue-green colour which is read in a spectrophotometer at  $620\text{nm}$ . The phenol-sulphuric acid method requires a clear solution before the addition of phenol and then sulphuric acid and produces a yellow-orange colour read at  $420\text{nm}$ . Both of these methods require standards that are appropriate to the composition of the saccharides as different saccharides respond differently in the reaction. Since the absorbances at  $490\text{nm}$  were similar and the molecular masses of glucose, fructose and galactose are similar, Chow suggested using a standard for sugars assay that combines these 3 and accept a linear response up to  $200\mu\text{g/mL}$

**Acid hydrolysis** of polysaccharides is attractive but is not always appropriate for human nutrition as it cleaves a broader range of polysaccharides, including cellulose. The acid conditions range from  $10\text{mM}$  to  $400\text{mM}$  sulphuric acid at  $95\text{C}$  for 1 hour or longer. Enzymatic digestion of polysaccharides simulates the human gut and yields monosaccharides for analysis. However, enzymatic assays for monosaccharides are specific: a glucose oxidase reaction is linked to a reactive dye to yield a coloured product for analysis. Polysaccharides can be hydrolysed by  $\alpha$ -amylase (at every 3<sup>rd</sup> link in 1,4 series) and oligosaccharides by amyloglucosidase to yield glucose from starch. These enzymes seem to be active at  $55\text{C}$  but may require many hours. Alpha-glucosidase converts the disaccharides maltose and sucrose to their component monosaccharides. Polysaccharide can be analysed by the reaction with iodine in iodide that forms a dark blue insoluble product. An interesting method (Li) reacted starch with iodine whereafter a methanol/phosphoric acid

was used as a mobile phase in a size exclusion column with UV detection at 224nm. This had a detection limit of 0.2ng/mL and was linear from 1ng/mL to 100ng/mL for iodide, with a recovery of >90%.

### **Procedure**

Proceed with all materials and solutions chilled on ice to prevent enzymatic actions leading to significant changes. The most effective strategy is to perform the oligosaccharide solution first and to set this drying whilst the starch preparation takes place, Consider using vacuum drying. Commence with about 500mg macerated material placed in a 15mL plastic tube. The sample is crushed with a glass rod of which the end has been rounded.

**Oligosaccharides** Add 6mL of 80% ethanol to the sample prepared as above, by running the liquid down the mincing rod. Mix vigorously. Insert sonicating probe and do 20 bursts of 1 second at midway setting (12) and place in sonicating waterbath at 50C for 15 min, then at 80C for 15min. Centrifuge at 4000rpm to pellet insolubles and remove supernatant to a 50mL tube if to be dried in the heating block or suitable tube for vacuum drying. Add 3mL of 80% ethanol to the pellet, mix vigorously, incubate in sonicating waterbath for 15min. Spin again. Transfer the supernatant to the previous one. Repeat once more. The pooled supernatants represent the **oligosaccharides**. This solution can be evaporated to near dryness or dryness to be analysed. Redissolve in an exact volume - optimal probably 1mL but certain foodstuffs will need much dilution.

**Starch** is solubilised as follows. The 15mL tube containing the pellet with starch, protein, and lipid receives 6mL of distilled water. Loosen the pellet with a solid stainless steel needle. Sonicate as above to ensure complete resuspension. Place in sonicating waterbath at 50C for 1 hours. Cool and bring to an exact volume for analysis, from 6 to 10mL depending on the amount of starch suspected. Remove a fraction (half) for lipid extraction by Folch Procedure. Centrifuge to pellet the insoluble material before using the supernatant for the starch assay.

### **STARCH ASSAY BY IODINE ADAPTED FROM KANEHIRA**

The reaction of KI with starch requires between 2.5 and 80mmol/L of KI which associates with the otherwise insoluble iodine. This assay appears to detect as little as 2µg of starch. The I<sub>3</sub><sup>-</sup> has a brown-yellow colour but this changes when the molecule enters the cylindrical amylose molecule and does not form with amylopectin. The dark blue colour forms within seconds. Higher amounts give maximal colour at 20 to 30minutes and precipitation of starch becomes a problem. Thus the assay can crudely estimate the amounts of starch between 100 and 500µg at about 1min after reacting and 2 to 100µg at about 15 to 30min. Scanning the wavelengths for absorbance of the colour product shows a low hill with the peak changing little between 540 and 570nm; thus 560nm is selected as preferred wavelength. The absorbance decreases by <6% over 75 minutes. The linearity is good

between 2 and 200 $\mu$ g:  $r^2 > 0.970$ . The full curve on non-linear regression has  $r^2 > 0.99$  when analysed at 5 minutes and remains good at 45min. Effect of high salt (neutralised NaOH or KOH with) and pH still to be established.

### **Starch-iodide reaction materials**

*Starch solution*, 10mg/mL. Clarified corn starch can be used (Maizena). Wet powder with water, add boiling water, stir until solution clear. Stable at room temperature for about 30 days. Dilute for use in lower range of standard curve.

*KI solution* 300mmol/L. KI = 166.0 dalton. Thus 498mg in 10ml. Stable indefinitely.

*Colour developer*. 30% H<sub>2</sub>O<sub>2</sub>:ethanol:distilled water 1:7:1. Stable.

In a microtitre plate, place a standard curve of starch through 0, 1, 2.5, 5, 10, 25, 50, 100, 200, 500 $\mu$ g and bring the volume to 100 $\mu$ L with water. Add 100 $\mu$ L of KI solution, using forcible pipetting to mix the solutions. Shake gently and stand for a few minutes. Take the microtitre plate to the instrument and there add 2x50 $\mu$ L of colour reagent, mixing the solutions with the jet of solution. Read as soon as possible at 560nm, within 5 minutes and later but granule formation soon begins to interfere. Non-linear regression is best for deriving unknown concentrations. Note whether granulation has occurred because this clustering of insoluble starch-iodine will lead to false low readings. Thus the assay is best in the range below 200 $\mu$ g.

## **ASSAY FOR IRON**

### **INTRODUCTION**

<sup>26</sup>Fe has an atomic mass of 55.84 amu and is essential for life as a micronutrient. The adult body contains about 5g of iron, 2/3 of which is in haemoglobin. The daily requirement is 12mg for adults, 15mg for pregnancy (extending into lactation) and 9mg for children; though in puberty the need is 14mg/d. Best absorbed as haem and thus in muscle tissue from animal sources rather than in plants.

Chelated iron is not always accessible to assay in solution and thus ash is used. For ease of preparation wet ash after chemical oxidation is preferred over dry ash produced in a furnace. Note that ferrous ions readily oxidise to ferric ions but are stable under very acidic conditions. Solutions containing ferric ions can form ferric oxide and ferric hydroxide complexes that are insoluble and also require acidic conditions. Hydrogen peroxide is typically used to oxidise all iron to ferric form for assays.

The best assays are atomic mass absorption spectrometry and inductive coupling mass spectrometry but these are neither affordable nor are they readily available.

Spectrophotometric methods vary in their sensitivity towards ferrous and ferric ions, and can have interference from many other metallic ions. Titration methods are too laborious for multiple samples. Some spectrophotometric methods could be adapted as batch assays in microtitre plate assays. In more complex assays, the difference in absorbance that different metallic ions give with colour reagents can be used to deconvolute an absorbance spectrum into its component concentrations of the contributing ions. Other assays may split the assay process to provide assays for more than one metallic ion. In modern analytical systems flow injection analysis (FIA) is preferable but such pump devices are not available in the lipid lab.

The principles of some methods are outlined here. **Asan** describes the use of **dimethylformamide** (MW 73.09), a chelating agent that has a sharp absorption at 310nm when binding ferric ions. This liquid melts at -61C, boils at 153C and has a density of 0.9445g/mL. The assay was found to be linear in the 5-90ng/mL concentration range. The pH was 5.5 and needs no buffers. Only Ni<sup>++</sup> and Mn<sup>++</sup> form complexes amongst a range of metallic ions, but the absorption at 310nm is negligible.

#### WET ASH PREPARATION

Performed in a 16 x100 borosilicate tube. The preparation requires about 20-50mg of material with some differences in ensuring sample volumes are appropriate for the digestion. Serum or plasma 100µL, whole blood 50µL, red cells 50µL, and egg yolk 50µL do not need additional liquid. Other materials like wheat or muscle require about 20mg and about 100µL of 0.1M HCl is added and mixing is done before proceeding. When the volume of the sample is scaled up, the acids should be increased in the same proportion.

Add 400µL of nitric acid and 100µL of perchloric acid to the sample and vortex for 30 seconds. Heat at 185-200C in a fume cupboard for 90min using a heating block with a shield to ensure the whole tube reaches the appropriate temperature. Leave the tubes open to the air and cool the samples.

Add 500µL hydrochloric acid and vortex for 20 seconds. Heat the tube again for 60min at 150C.

#### MATERIALS

Ferric chloride solution. FeCl<sub>3</sub>.6H<sub>2</sub>O. Dilute on the day of use with distilled water or more ).1 molar HCl.

#### ASAN ASSAY

The assay was published for a flow injection system which concentrates iron en route to mixing it with the dimethylformamide solution. An adaptation was made for this assay to be practicable in a microtitre plate reader.

**Samples** should be collected in acid milieu and should be oxidised with hydrogen peroxide. Sample preparation for river, dam or sea water involves adding nitric acid, filtering through 0.45µm filter and oxidising all the ferrous to ferric with H<sub>2</sub>O<sub>2</sub> (10% v/v H<sub>2</sub>O<sub>2</sub>).

**FeCl<sub>3</sub> standard solution.** Stock solution is made accurately aiming at 10mg/mL of Fe (55.8da) as FeCl<sub>3</sub> 6H<sub>2</sub>O MW 270.3da in 0.10mol/L of HCl. This is conveniently done as 550mg in 10ml, providing 11.36mg Fe per mL or diluted to 1/10 provides 1.13mg/ml or 1.13µg/µL.

**Hydrogen peroxide** 30% v/v is used to ensure ferric status by oxidising ferrous ions. Can be added at the time of preparing the sample or at the time of the assay, 10µL per well.

**DMF reagent.** Handle the dimethylformamide in the fume cupboard and avoid contact with eyes. Prepare a 5% solution in distilled water. The 30% hydrogen peroxide can be combined for convenience at 1%

The **microtitre plate** should be compatible with UV readings. The assay is designed to present the test solution and standards in 50µL in a microtitre plate well. The standard curve should be 0, 1, 2, 10, 20, 50, 100µg. Distilled water can be used to make up the volume. Add 250µL of DMF reagent; in two steps (150µL + 100µL) so that there is good mixing. Read the absorbance at 310nm.

The reaction is nearly complete in a minute and stable results apply for at least 2 hours. The standard curve can be analysed by linear regression ( $r^2 > 0.99$ ) for up to 50µg but is better analysed by non-linear regression ( $r^2 > 0.985$ ) if higher values are incorporated in the standard curve.

## SPECTROPHOTOMETRIC ASSAY FOR Cu

### INTRODUCTION

<sup>29</sup>Cu (63.546 dalton) is an essential trace element in living organisms, primarily in the blood and some pigments (haemocyanin in invertebrates). In the human body it is concentrated in the liver and bones. It has antibacterial action at relatively low concentrations and there is concern that industrial contamination of water may pose human toxicity as well. The usual blood concentration ranges between 120-140µg/L and in urine 35-45µg/L.

The assays that are most convenient in the lipid laboratory are spectrophotometric and fluorometric, especially if they can be done in microtitre plates. In most instances, Cu is best assayed in elemental form as dry or wet ash. In many cases other metallic ions may interfere and masking with other reagents is necessary. Whilst assays could be a result of direct chemical reaction and changes in absorption of compounds, some assays require extraction and then a reaction.

### MATHEW'S METHOD

Azure B is related to other reticulocyte staining dyes, brilliant cresyl blue and new methylene blue and can be applied to histology as well. The principle of the method is that Azure B is a redox reagent. The structure is of two benzene rings bridged by a S and a N (double bond) forming an intermediate bridge and amines at the o-positions; on each benzene ring. One amine is monomethylated and the other is dimethylated and has a double bond subject to bleaching to create the leucoform. When Cu reacts with KI in an acidic medium (pH 1 to 1.5), iodine is released quantitatively and this bleaches the violet dye, which has a peak absorbance at 644nm. It is linear between 2 and 12µg/mL, with a molar extinction coefficient of 1.760E5/M/cm. The method was adopted to be done in a microreaction vial and then transferred to a microtitre plate.

There could be significant interference from nitrite and sulphite at 100µg/mL of each but the other metals interfere little up to 10µg/mL for Al, Pt; 25µg/mL for In and for Ni, Co, Ti, Mo, U about 50µg/mL; Hg, Cd, Zn 75µg/mL and M, Ba, Ferric borate 100µg/mL. Acetate, chloride, 100µg/mL.

Wet ash should preferably be neutralised with dilute ammonia before the assay or dry ash could be used.

#### MATERIALS

Azure B. C<sub>15</sub>H<sub>16</sub>ClN<sub>3</sub>S. Green crystalline powder. Dissolve 0.1% in methanol:water. Sigma.

CuSO<sub>4</sub>.5H<sub>2</sub>O. 249.68da. for standard solution.

KI 2g%.

HCl 2M

#### PROCEDURE

The original method used samples of Cu (2-12µg/mL) which were then treated with 1mL 2% KI and 1mL HCl whereafter mixing resulted in the yellow colour of iodine. Now 0.5mL of Azure B reagent was added and the volume brought to 10mL before the absorbance is read at 644nm.

Using 1.5mL reaction vials, set up a standard curve providing 0, 1, 2, 4, 8, 10, 12, 16µg. Bring the volume to 100µL with pure water. Add 100µL of KI solution and 100µL of HCl and mix thoroughly. When yellow, add 50µ of Azure B and mix well. Add 750µL of pure water and mix. Aliquot 250µL into the well (duplicates desirable). Read absorbance at 644nm. Derive unknowns from the standard curve by regression analysis.

### SPECTROPHOTOMETRIC ASSAY FOR ZINC

#### INTRODUCTION

The **element**,  $^{30}\text{Zn}$  65.37da mostly forms colourless salts because of its filled d orbitals which, for other transition metals, allow much complexation and absorbance in the visible wavelengths. Strongly antiseptic by complexing microbial proteins.

The daily **requirement** for an adult appears to be about 10mg/d with an upper limit set at about 40mg/d. More than 100 enzymes need Zn and it also plays a role in insulin synthesis and nucleic acid metabolism. The best animal sources are meats (pork, beef, poultry, fish) with lesser amounts in eggs and dairy. Nuts, legumes and whole grains contain reasonable amounts but fruits and vegetables are generally poor in Zn. In blood about 80% of the Zn is in red cells and carbonic anhydrase, 15% in plasma and almost 3% in leucocytes. About 1/3 of plasma Zn is loosely bound to albumin and the remainder is more tightly bound to  $\alpha$  globulins. The serum levels reported in normal subjects vary by the methodology but range from 400-1400ug/L.

**Deficiency** of Zn impairs DNA synthesis and delays wound healing including the synthesis of collagen. During pregnancy the deficiency may cause serious fetal malformations. Toxicity acutely is with abdominal pain and may lead to anaemia.

Zinc like Cu, Mg, Ni, and Cd, forms a complex with tetrapyrrols to increase the absorbance and stability of porphyrins, Zn being the best. However, to use this in an assay, porphyrin methyl esters need to be prepared and isolated by chloroform extraction and TLC preparation (Doss). This can make for an extremely sensitive assay (Makino)

Methods for determining zinc concentration range from spectrophotometric as the least expensive and most convenient, to atomic absorption spectroscopy, inductively coupled plasma atomic spectrometry.

**Preparation** of samples is important. In some instances the assays are for inorganic zinc and dry or wet ash preparation is required with redissolution in nitric acid. In some instances proteins are precipitated to release Zn into the supernatant (1mL serum + 1ml 20% trichloroacetic acid) but 4M guanidine HCl can also be used to displace this element.

#### XYLENOL ORANGE ASSAY (Benamor)

The principle of this assay is that Zn, XO and cetylpyridinium Cl (CPC, hexadecylpyridinium) form a ternary complex at pH 5.5 that has a characteristic absorbance of 580nm compared with XO alone which peaks at ~450nm and does not absorb above 500nm, and XO-CPC which has a peak at 595nm. A reagent blank without Zn is used to obtain the absorbance of XO-CPC whilst a standard curve of Zn serves to determine the concentration of unknowns. Note that some interference can come from ferric and aluminium ions but these are masked by NaF whilst interference from divalent Ni, Cu and Pb is eliminated by EDTA.  $\text{Ag}^+$ ,  $\text{Cd}^{2+}$ ,  $\text{Hg}^{2+}$ ,  $\text{Co}^{2+}$  do not interfere.

#### MATERIALS

Acetic acid. Glacial Acetic acid is 18 Molar. Dilute to 0.5 Molar

NaOH (40.00 da) 0.5 Molar is 20g/L.

ZnSO<sub>4</sub>·7H<sub>2</sub>O. 287.56da. Standard solution in distilled water 71.80mg in 25mL for 10mmol/L solution. Zn is 653.7mg/L, 653.7ng/μL.

Xylenol Orange. 3,3'-bis[N,N-bis(carboxymethyl)aminomethyl]-o-cresolsulfonephthalein tetrasodium. 760.58 amu. C<sub>31</sub>H<sub>28</sub>N<sub>2</sub>NaO<sub>13</sub>S 1mmol/L (19mg in 25mL distilled water)

Cetylpyridinium Cl Hexadecylpyridinium Cl.H<sub>2</sub>O. 358.0 amu. C<sub>21</sub>H<sub>38</sub>ClN 10mmol/L (89.5mg in 25mL distilled water)

Acetate buffer from 0.5Molar acetic acid and 0,5 Molar NaOH adjusted to pH 5.5.

NaF 41.99 amu 1mmol/L

EDTA 372.42 amu 1mmol/L

## PROCEDURE

**ORIGINAL** Place the sample in a 25mL flask, add 2mL XO, 1mL CPC and buffer (consider 5mL) and then make up to 25mL with pure water. Read absorbance at 580nm of blank and standard curve as well as samples.

**PREPARATION OF WET ASH SAMPLES FOR ANALYSIS.** The assay is sensitive to pH and the wet ash preparation selected uses nitric and perchloric acids which leave behind a lot of acid. To neutralise this most practicably, a procedure was developed as below. Note that ammonium hydroxide is incompatible as it forms the same colour complex with the reagent mix. The use of KOH as an alkali is not good because it forms insoluble salts. NaOH does not form insoluble salts.

The procedure was to use 100μL of wet ash, add 2μL of saturated phenolphthalein solution (10mg/ml in distilled water), and then to add 100μL of 200mg/mL NaOH (2 pellets/mL). The colour of phenolphthalein turns purple. Now add 20μL of glacial acetic acid. The solution turns clear. Whilst phenolphthalein above pH 8.3 has a significant absorption at 580nm, when colourless, there is no absorption over background.

When this procedure is followed, the reaction with Zn is preserved and the absorbance of the blank is lowered. Hence it is important to use a wet ash control that has been through the same procedure as the tissue turned into wet ash. In the assay, it is suggested that the volume of a wet ash blank is used equal to the volume of the wet ash sample, and balanced with acetate buffer.

**ADAPTATION FOR 96 WELL MICROTITRE PLATE.** Standard curve 0 to 1.5 to 5  $\mu\text{g}$  of  $\text{Zn}^{++}$  presented in 100  $\mu\text{L}$  of water or acetate buffer. For wet ash analysis use an equal volume of blank wet ash to determine the Zn in the test wet ash samples most accurately.

Mix reagent as follows: 2 mL acetate buffer + 100  $\mu\text{L}$  CPC + 200  $\mu\text{L}$  XO solution. Mix well. To this can be added the masking solutions.

Add 200  $\mu\text{L}$  of the reagent mix to the above. The purplish colour of the Zn complex forms immediately and then declines at a very slow rate over a few hours. Read absorbances at 580 nm.

ANALYSIS Nonlinear regression.

### ICHIHARA METHOD FOR PREPARING LIPID SAMPLES FOR GAS CHROMATOGRAPHY

**Lipid extract method.** The method is described for about 0.3 mg of lipid. Dissolve the lipid in 0.2 mL of toluene in a 16.5 x 105 mm screw capped tube. In strict order add 1.5 mL of methanol and then 0.3 of the 8% HCl. This makes the final concentration of HCl 1.2%. Vortex and incubate overnight at 45°C (>14 hours) for mild methanolysis or at 100°C for 1 hour for rapid methanolysis. After cooling, extract the FAME by adding 1 mL of hexane and then 1 mL of water. The FAME partition in the supernatant hexane.

### Examiner 1

1. The term “hominid” has been replaced with “hominin” throughout the document.
2. The misspelling of G. Burdige’s name has been corrected throughout the document.
3. In the introduction, I have made it clear that the consumption of marine foods was “special” and important because it represents a significant broadening in the subsistence base of early modern humans.
4. Also in the introduction, I have deleted the word “intelligence” from the sentence at the end of the 2<sup>nd</sup> paragraph, so that SB and HP artefacts are linked with increased technological proficiency but not overall intelligence.
5. I have separated the issues of brain development and maintenance: fatty acids play an important role in brain development and neurogenesis.
6. I have made it more explicit that marine foods played an important role in the diet of modern humans living along the coast of southern Africa.
7. In the literature review, I have deleted the statement about the earliest hominids being scavengers rather than active hunters. I have also deleted the statement about the hunting proficiency of MSA humans. I have not added more recent citations on mtDNA, as this is not pertinent to my thesis as a whole, and is discussed only very briefly in the literature review.
8. At the beginning of chapter three, I have deleted the misleading statement about “the theoretical shift from savannah to coast”, as well as that concerning “women as the passive recipients of male provisioning”.
9. Also in Chapter 3, I have modified my statement about MSA hunters having lower success rates than the Hadza – they were probably similar.
10. I have corrected my statement regarding the contribution of animal foods rather than protein to hunter-gatherer diets.

### Examiner 2

I have made the two most important changes stipulated by this examiner:

1. I have added a hypothesis-driven statement to the introduction.
2. I have shortened the conclusion considerably, so that it is focused on the results of my nutrient analyses. I have not deleted the sections summarising the scenarios entirely, but have condensed them into two shorter paragraphs. I have deleted some repetitious paragraphs at the start of the conclusion, have restated the hypothesis I added to the introduction, and deleted some speculative paragraphs near the end of the conclusion.

I have also made several other changes recommended by this examiner:

3. I added Braun *et al.* 2010 as a reference to the presence of cut-marked fish bones at Koobi Fora.

4. I have added a sentence to chapter four giving the location and dating of HDP3. I have also added a new reference.
5. I have made some minor revisions to the figures and tables.
6. I have made several minor corrections to the text, especially in chapters 3,4 and 5.
7. I have identified and corrected several inconsistencies in the citations and referencing section.
8. I have **not** added a map of southern Cape coastal sites to chapter four, as suggested by this examiner, as these sites are not central to my thesis.
9. I have elected **not** to argue that the consumption of marine resources rich in preformed EPA and DHA would have been essential, as suggested by this examiner: I prefer to offer a balanced view of the debate concerning preformed EPA and DHA vs. biosynthesis of ALA and the upregulation of this process by women (especially since two of my examiners are on opposite sides of this debate).
10. I have **not** elaborated on the dangers of consuming too much liver, as I do not suggest that MSA people were eating a lot of liver as this is a small, relatively inaccessible organ in marine and terrestrial vertebrates.

### Examiner 3

1. On pg 125, I explained that lipid samples were dried under nitrogen.
2. The in-house assays were not validated against other methods. The results of my analyses were compared with published material, and found to be within the range of most reported values.
3. I made most of the minor corrections to the text and tables suggested by this examiner.