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Marine and terrestrial foods as a source of brain-selective nutrients for early modern humans in the southwestern Cape, South Africa

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ABSTRACT

Many attempts have been made to define and reconstruct the most plausible ecological and dietary niche of the earliest members of the human species. While earlier models emphasise big-game hunting in terrestrial, largely savannah environments, more recent scenarios consider the role of marine and aquatic foods as a source of polyunsaturated fatty acids (PUFA) and other brain-selective nutrients. Along the coast of southern Africa, there appears to be an association between the emergence of anatomically modern humans and accumulation of some of the earliest shell middens during the Middle Stone Age (200–40 ka). Fragmentary fossil remains classified as those of anatomically modern humans, along with marine food residues and numerous material cultural indicators of increased social and behavioural complexity have been recovered from coastal sites.

In this paper, new information on the nutrient content of marine and terrestrial foods available to early modern humans in the southwestern Cape is presented and compared with existing data on the nutritional value of some wild plant and animal foods in Africa. The results suggest that coastal foraging, particularly the collection of abundant and predictable marine molluscs, would have allowed early modern humans to exploit some of the richest and most accessible sources of protein, micronutrients and longer-chain omega-6 and omega-3 fatty acids. Reliable and accessible sources of omega-3 eicosapentaenoic and docosahexaenoic acid are considerably more restricted in terrestrial foods.

1. Introduction

Nutrition plays a central role in hypotheses concerning human evolution, including those which attempt to account for the emergence of large-brained, anatomically modern *Homo sapiens* in Africa ~200 ka. Encephalization, that is, the significant increase in brain size relative to overall body size that characterises the human species, depends on the availability of food resources rich in energy as well as trace elements and fatty acids collectively referred to as brain-selective nutrients (Broadhurst et al., 2002; Leonard et al., 2007; Kuipers et al., 2010). Macronutrients, including protein, fat and carbohydrates, are oxidised by the human body to provide energy (Table 1); protein also provides a number of indispensable amino acids for protein synthesis. Trace elements or micronutrients, including iron, copper, zinc, iodine and selenium, are required in relatively small amounts throughout life and in larger quantities at critical times in the growth and reproductive cycle, notably pregnancy, lactation, gestation, the first two years of childhood and, sometimes, adolescence (Table 1). Two classes or families of polyunsaturated fatty acids (PUFAs), namely omega-6 and omega-3, are essential components of the human diet, as they cannot be synthesised by the human body (Hornstra, 2000; Broadhurst et al., 2002). Longer-chain PUFAs including arachidonic and docosahexaenoic acid (AA and DHA) can be obtained directly from dietary sources, or must be synthesised from shorter-chain omega-6 and omega-3 precursors, namely linoleic and α-linolenic acid (LA and ALA), respectively (Bakewell et al., 2006). During gestation, PUFAs are selectively transferred from the maternal circulation system to the foetus in utero via the placenta; neonates obtain them from their mothers' breast milk during lactation (Al et al., 2000; Duta-Roy, 2000; Haggarty, 2002, 2004). Thus, pregnant and lactating women have especially high requirements for eicosapentaenoic acid (EPA)

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Table 1
Nutritional requirements of MSA hunter-gatherers. We follow Ben-Dor et al. (2011) and Leonard et al. (2007) in using weights of 58 and 49 kg 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 0.8 g/kg body weight/day; the requirements of pregnant and lactating women and children have been adjusted proportionally. 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 $700 + 7W \times 1.8$.

Gender and age	Protein (g/day)[a]	Energy (kJ/day)[b]	Iron (mg/day)[a]	Copper (mg/day)[a]	Zinc (mg/day)[a]	Selenium (mg/day)[a]	Iodine (μg/day)[a]
Adult male	46	11,190	8	0.9	11	0.55	150
Adult female	39	7890	18	0.9	8	0.55	150
Pregnant female	46	9360	27	1	11	–	220
Lactating female	46	1020	9–10	1.3	12	–	290
Adolescent male	43	11,190	11	0.89	11	–	150
Adolescent female	39	7890	15	0.89	9	–	150
Child 9–13 years	29	7140	8	0.7	8	–	150
Child 4–8 years	16	7140	10	0.44	5	–	90
Child 1–3 years	13	3372	7	0.34	3	–	90
Infant 7–12 months	–	–	11	0.33	3	–	130
Infant 0–6 months	–	–	0.27	0.20	2	–	11

Gender and age	EPA&DHA (g/day)[c]	DHA (g/day)[d]
Adult male	0.65	
Adult female	0.65	
Pregnant female	0.65	0.30
Lactating female	0.65	0.20
Adolescent male	0.65	
Adolescent female	0.65	
Child 9–13 years	0.65	
Child 4–8 years	0.65	
Child 1–3 years	0.65	

[a] Dwyer, 2008.
[b] World Heath Organization, 1979.
[c] Kris-Etherton et al., 2000.
[d] Kris-Etherton et al., 2009.

and DHA. Maternal deficiency during the most critical times for foetal and neonatal brain development, namely the final trimester of pregnancy and first eighteen months of life, may result in incomplete neurogenesis and irreversible damage (Makrides et al., 1994; Innis, 2000).

There are currently two sets of hypotheses regarding the diets and subsistence strategies likely to have supported the earliest members of our species: those that emphasise the selective consumption of fat-rich portions of terrestrial animals (Speth, 2010), and others that regard the contribution of marine resources as highly advantageous or even essential (Broadhurst et al., 2002; Parkington, 2003; Cunnane et al., 2007; Crawford, 2010; Erlandson, 2010; Cunnane and Crawford, 2014). Debates surrounding the importance of marine resources are part of the wider narrative concerning the evolution of anatomically and cognitively modern *H. sapiens* in southern Africa during the Middle Stone Age (MSA). Excavations at half a dozen coastal sites in this region yielded evidence for the systematic exploitation of shellfish and other marine resources by at least 130 ka. Human fossils classified as anatomically modern, as well as material culture remains often associated with innovative or complex technology and behaviour have been retrieved from these same localities (Parkington, 2003, 2010; Klein et al., 2004; Marean et al., 2007; Avery et al., 2008; Steele and Klein, 2008; Brown et al., 2009; Jerardino and Marean, 2010; Marean, 2010; Watts, 2010). In an earlier paper (Kyriacou et al., 2014), we provide a preliminary assessment of the nutrient content of marine and terrestrial foods with respect to two important nutrients, protein and iron, and suggest a framework for assessing the utility of marine and terrestrial resources. This paper presents new, quantitative information on the macronutrient, micronutrient and PUFA content of an expanded range of marine and terrestrial resources available to early modern humans living along the Atlantic southwest coast and in the adjacent interior, and allows for a better assessment of their nutritional value.

2. Materials and methods

Nutrient determinations were carried out on tissue samples from marine and terrestrial foods known or presumed to have been eaten by Middle Stone Age (MSA) hunter-gatherers in the southwestern Cape, South Africa. Shellfish were hand-collected from the rocky shore around Soetwater in Kommetjie, and Elands Bay beach. Fish were purchased from sellers on the docks at local harbours. Samples from 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, and were derived from animals that died from natural causes or accidents or had to be put down. Roadkills and the carcasses of culled terrestrial animals were provided by participating South African National Parks, private nature reserves and the Zoology Department of the University of Cape Town. Additional samples from frequently hunted game animals were donated by hunters or purchased from local butchers.

Approximately 10 g of tissue (wet weight) were macerated, sonicated and homogenised, and stored at −20 °C. The protein content of samples was determined using Markwell et al.'s (1978) modification of the Lowry procedure. A small-scale adaptation of the Folch extraction was used to isolate the lipid content of samples; the total lipid content was then estimated by means of the Vanillin reaction (Cheng et al., 2011). The energy or kilojoule content of marine and terrestrial foods was calculated from their protein, fat and carbohydrate content. As there is no simple assay for measuring glycogen in meat, the glycaemic starch content of muscle and liver is set at 3 g/100 g, following current estimates. Samples of homogenised tissue (0.5–1 g) were reduced to “wet ash” by oxidation with nitric and perchloric acid in preparation for micronutrient analyses. The iron and zinc content was determined by means of small-scale adaptations of Asan and colleagues' (2008) dimethylformamide method and Benamor and colleagues' (2000)