

## Human Impact on Precolonial West Coast Marine Environments of South Africa

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WITH VERY EXTENSIVE, DIVERSE, and productive coastlines, it is no surprise that South Africa offers a superb opportunity to understand how marine ecosystems function, and the effects of people on these environments. This prospect is heightened by the realization of the tremendous time depth of human occupation, including the first emergence of modern humans in Africa and, by default, in the world (Erlandson 2001; Marean et al. 2007). This endeavor is multidisciplinary by necessity: marine ecology and archaeology go hand in hand, along with other closely related specialties such as oceanography, geology, and palaeo-environmental studies. While ecological studies can provide an understanding of the ecology of present species, their vulnerability to harvesting, and the way they are influenced by physical factors, archaeology and palaeoenvironmental studies offer a window into the past where such ecological relationships and physical variables can be seen changing through time. The result of this multidisciplinary dialogue not only feeds much needed academic debate but also brings new and important dimensions into marine conservation policies and fisheries management. Because of this, the relevance of archaeol-

ogy to modern society extends beyond its perceived status as a highly specialized and rather esoteric field (Erlandson and Rick, this volume). As demonstrated below, we also propose that this multidisciplinary dialogue benefits the way coastal archaeological sites are studied, by bringing a more exhaustive and systematic approach to answering questions, and by highlighting their main trait as archives of both human and environmental history. Seen in this perspective, the protection, conservation, and management of coastal archaeological sites must be a priority as promoted by the current South African heritage legislation (National Heritage Resources Act, No. 25, 1999).

In this chapter, we explore the relationship that people established with the marine environment on the South African West Coast over several millennia. Such effects have frequently been demonstrated for terrestrial environments worldwide (Redman 1999), but few convincing cases have been made for marine systems. A broad account of the long-term precolonial human settlement of the West Coast of South Africa sets the background for a more focused analysis of selected archaeological sequences in the Lamberts Bay area. An integrated approach

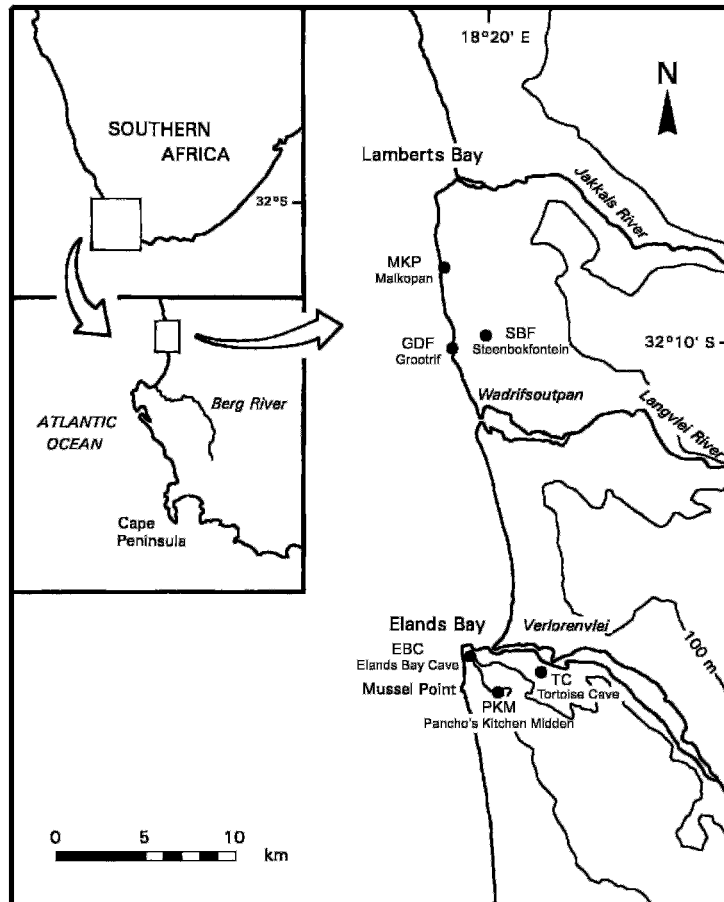


FIGURE 12.1. Map of the study area showing location of sites and places mentioned in the text.

that combines sampling of faunal remains from archaeological sites, current knowledge of the ecology of the species exploited in the past, and detailed palaeoenvironmental reconstructions is employed as a powerful tool for unraveling long-term variability in marine ecosystems and their responses to human intervention. A case is made for human harvesting having been responsible for the local depletion of black mussels and limpets stocks, as reflected by shrinking mean sizes at a time when human population densities were peaking and when reliance on marine resources was greatest. A concurrent decline in rock lobster size for the Lamberts Bay area (Figure 12.1) is interpreted differently, given the likely resilience of this species to subsistence harvesting and its susceptibility to environmental changes. This adds a note of caution in terms of the methodology

employed to answer questions regarding human impacts on marine harvested species: not all changes in populations are necessarily related to the same causes. Consequently, all possible lines of evidence and hypotheses deserve serious and equal attention when tackling these types of questions.

#### PREHISTORIC EXPLOITATION OF MARINE INVERTEBRATES ON THE WEST COAST OF SOUTH AFRICA

Some of the earliest evidence for the exploitation of marine resources in the world is found in South Africa, mostly from deeply stratified sequences along the South Coast dating to between 165,000 and 120,000 years BP (Jacobs et al. 2003a, 2003b; Marean et al. 2007; Thackeray 1988; Vogel 2001). A few Middle Stone

Age (MSA) West Coast sites confirm that subsistence harvesting is very ancient, including reasonably well developed shell middens near the towns of Yzerfontein and Saldanha dated to about 70,000 years ago (Klein et al. 2004; Volman 1978). It is possible that marine resources were collected before this time too, but many of these sites are likely to have been washed out due to a high sea-level stand before the last interglacial period around 127,000 years ago (Klein et al. 2004; Parkington 2003).

The number of marine species present at these early MSA sites is similar to that observed in younger and nearby Later Stone Age (LSA) sites. Only a few species such as rock lobster (*Jasus lalandii*) and fish are either not present in MSA sites or their presence there cannot be attributed to human agency with certainty. The species diversity, however, appears to differ between MSA and LSA sites (Klein et al. 2004). Whether this reflects behavioral or environmental fluctuations is yet to be established, and resolution will require more systematic excavation of MSA sites and analysis of larger shellfish samples. Another pattern emerging from West Coast MSA sites is the significantly larger mean sizes of at least three limpet species when compared to those of LSA sites (Halkett et al. 2003; Parkington 2003; Steele and Klein 2005). No changes in the mean sizes of black mussels (*Choromytilus meridionalis*), however, are observed in previous comparisons of MSA and LSA sites. Less-intense harvesting of limpets during the MSA due to lower human population levels at that time, and greater ecological resilience of black mussels have been invoked to explain these patterns (Klein et al. 2004; Parkington 2003; Steele and Klein 2005).

Although this scenario seems plausible, it is also important to consider other explanations, such as marked differences in the residential permanence of human groups with similar population levels during both MSA and LSA times. In other words, low exploitation pressure on MSA limpets could well have resulted from shorter visits by people to the coast, while relatively longer visits characterized the latter

period. Moreover, there are many factors other than exploitation that influence the size composition of marine invertebrates, including differences or changes in environmental conditions and the intrinsic properties of the species themselves. As shown in this chapter, zonation, exposure to wave action, aquatic productivity, and turbidity can profoundly affect the size composition of limpets and black mussels. It also remains to be explained why black mussel sizes remained relatively constant through time despite the facts that (1) the black mussel is the most abundant species in MSA and LSA sites, and (2) rocky-shore mussels are susceptible to overexploitation as reflected by reductions in their mean sizes caused by modern subsistence harvesting (Lasiak 1992). Data on early shellfish gathering behavior in southern Africa is still preliminary. It needs to be recognized that the number, and at times the size, of available MSA shellfish samples is small when compared to those analyzed from LSA sites (Jerardino 1993, 1997, 2007; Jerardino and Yates 1997; Tonner 2005). Thus, more variables need to be assessed when explaining the observed reductions in limpet sizes between MSA and LSA sites, and more; as well, larger samples of MSA shellfish are also necessary to support any interpretation.

A considerable time gap separates coastal occupation of MSA sites and those of earliest LSA age, probably because most, if not all, former coastal sites dating to this gap were drowned by rising sea levels, and only a few of these may have survived on the Atlantic continental shelf (Miller 1990; van Andel 1989). Given the focused research efforts in the Elands Bay and Lamberts Bay areas for the last 30 years (Figure 12.1), it is not surprising that the earliest LSA radiocarbon-dated evidence for the exploitation of marine invertebrates along the West Coast of South Africa comes from several caves and shelters at these adjacent locations. Shell midden horizons appear for the first time in Elands Bay Cave and Tortoise Cave around 12,000 and 7700 BP (all dates presented in this chapter are uncalibrated), respectively (Parkington 1981;

Robey 1987), and well-developed shell lenses dating to ca. 8400 BP have been excavated from Steenbokfontein Cave (Jerardino and Swanepoel 1999) (Figure 12.1). Bedrock at this latter site is far below these deposits, and further excavations are likely to uncover older shell lenses. Early Holocene evidence for shellfish collection might also be present in Spoegrivier Cave, located about 200 km north of Lamberts Bay, although no radiocarbon dates are yet available for these basal deposits (Webley 2002). Once sea level transgressed to within a few kilometers of these sites during the Early Holocene, a wide range of marine invertebrates (and several vertebrate species) were exploited, including limpets, mussels, whelks, winkles, chitons, and rock lobsters. All of these species would have been collected from rocky shores, although sandy beaches appear to be exploited to a small but significant extent, which was not repeated during subsequent occupations throughout the Late Holocene (A.J., personal observation).

After about 5000 BP, coastal shell middens abound along the West Coast, reflecting a full range of settlement and subsistence choices and new cultural and economic developments (Buchanan 1988; Buchanan et al. 1978; Conard et al. 1999; Jerardino 1996, 2007; Jerardino and Yates 1996, 1997; Parkington et al. 1988; Robertshaw 1978, 1979; Sadr and Smith 1992; Sealy et al. 2004; Smith et al. 1991). With few exceptions, coastal archaeological sites accumulated in close proximity to rocky shores from where much of the marine subsistence was obtained (Jerardino 2003). Although sketchy, differences in the above social and economic variables are apparent among subregions along the West Coast (e.g., Namaqualand, Elands Bay and Lamberts Bay area, Vredenburg Peninsula). These differences seem to have been dictated by environmental variability (rainfall, geomorphology, and availability of resources), changing human population levels, and cultural contact situations. Much work remains to be done in each of these subregions for this emerging and variable picture of coastal har-

vesting along the West Coast of South Africa to have a more solid empirical foundation. Some of these subregions have been sampled and studied more extensively than others, with the Lamberts Bay and Elands Bay area (hereafter referred to as "the study area") offering more numerous and chronologically deeper sequences. This chapter presents a case study from this particular subregion and attempts to ascertain the nature of the interaction between humans and their marine environment during the Late Holocene. Multiple lines of evidence are used to achieve this goal, including data on population levels and dietary mix, palaeoenvironmental reconstructions, the biology and ecology of rocky shore marine invertebrates, current understanding of the effect of modern harvesting on similar species along other South African shorelines, and statistical analyses on metrical observations of body size for four species of marine invertebrates recovered from several archaeological sites.

#### SETTLEMENT AND SUBSISTENCE PATTERNS AT LAMBERTS AND ELANDS BAY

The chronological record of the study area shows that relatively few sites were occupied between 8,000 and 4,500 years ago (Figure 12.2). Between 4,500 and 3,000 years ago, human settlement occurred in cave sites and shelters, with volumes of deposit ranging mostly between 1 and 10 m<sup>3</sup>. Human impact on marine resources was probably negligible at this time. Around 3500 BP, new sites were being occupied for the first time. Rates of deposition started to increase along with the size of floor areas at sites that had been previously occupied. Longer residential permanence is inferred from higher densities of artifacts that, according to ethnographic observations, were manufactured and/or lost or discarded during longer visits to sites (Jerardino 1995a, 1996; Jerardino and Yates 1996). Volumes of deposits range between 10 and 100 m<sup>3</sup> per site around this time. These are the first signs of population increase in the study area. Subsequently, between 3000 and

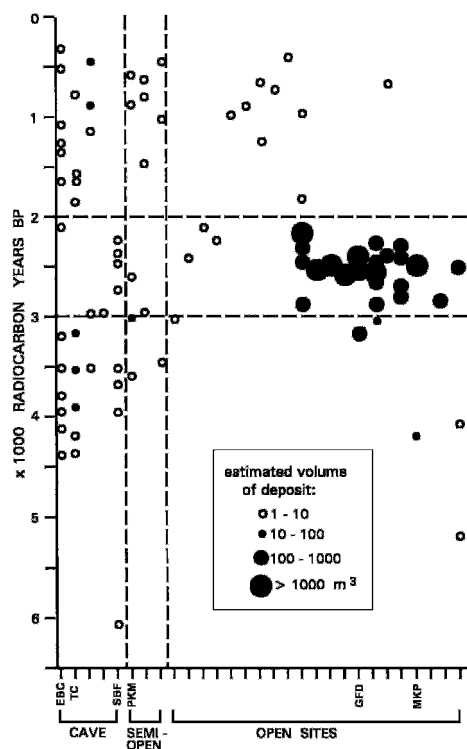


FIGURE 12.2. Intensity of site occupation in the study area (uncalibrated radiocarbon years BP).

2000 BP, settlement focused on very large open shell middens situated immediately behind rocky shorelines (Figures 12.2 and 12.3). Tons of marine shell and low densities of artifacts and terrestrial fauna characterize these enormous shell middens (Jerardino and Yates 1997). The term “megamiddens” was coined for these site types when first observed 30 years ago (Parkington 1976). Volumes of deposit range from a hundred to several thousand cubic meters per site. A range of activities was performed at these sites, including the processing of vast quantities of shellfish, possibly for drying and later consumption, stone knapping, and processing of terrestrial animal foods (Henshilwood et al. 1994; Jerardino and Yates 1997). Dating of caves and shelters has also shown that only two such sites were occupied during the megamidden period, namely Steenbokfontein Cave and Pancho’s Kitchen Midden (Figure 12.1). Either residential permanence continued

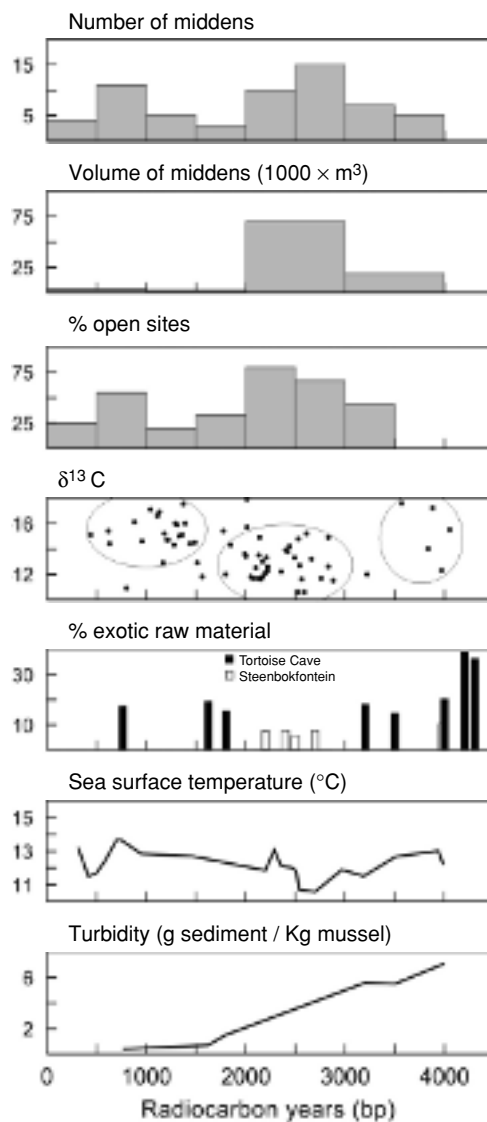


FIGURE 12.3. Summary of settlement, diet, and palaeo-environmental changes in the study area (uncalibrated radiocarbon years BP).

to be as extended as before or even longer periods of habitation were involved (Jerardino 1996, 1998; Jerardino and Yates 1996). After 2000 BP, population densities declined sharply as reflected by the overall lower number of sites and reduced volumes of deposits. Settlement also returned to caves and shelters over the last 2,000 years (Figures 12.2 and 12.3), and short visits seem to have characterized this period (Jerardino 1996, 1998).

Changes in hunter-gatherer mobility can be inferred from fluctuations in the frequency of lithic raw materials from Steenbokfontein and Tortoise caves, both with sequences that extend to the Early Holocene. Although never dominant, exotic raw materials such as silcrete and indurated shale (known locally as "hornfels") were more commonly used between 8,000 and 4,000 years ago with frequencies of 13 to 36 percent (Jerardino 1996; new data) (Figure 12.3). Around 3500 BP, these materials were still used regularly, but in a highly variable fashion, with frequencies of 3 to 21 percent. During the subsequent megamidden period, exotic raw materials were rarely used at Steenbokfontein Cave, comprising 6 to 8 percent of the flaked stone assemblage. Slightly smaller frequencies are recorded from contemporary occupations at Pancho's Kitchen Midden (Jerardino 1998). Exotic raw materials continued to be used infrequently over the last 2,000 years as shown by Tortoise Cave and other sites dating to the last 1,000 years (Jerardino 1996, 2000; Orton 2006). From this, a coherent picture of shifting settlement patterns emerge for the study area. As the land became more populated with groups settling for longer periods around 3,500 years ago, and reaching a maximum between 3,000 to 2,000 years ago, hunter-gatherer mobility became increasingly restricted to the coastal margin. Contact with inland areas and beyond the Oliphant River to the north and Berg River to the south was not only rare during the megamidden period, but also after 2000 BP, when human occupation of the study area waned. Lack of contact between the coast and the interior during the megamidden period is also supported by the dearth of radiocarbon dates from hinterland sites (2 out of 42) falling between 3000 and 2000 BP (Jerardino 1996:87). Hence, the suggestion by Henshilwood et al. (1994) that dried shellfish would have been transported from the coast to the interior for their final consumption during this millennium is not supported by the available evidence.

Concomitant changes in subsistence are also reflected in the archaeological record. Iso-

topic evidence based on carbon isotope measurements on collagen and bone apatite from human skeletons buried along the West Coast shows an increase in marine food intake between 3000 and 2000 BP, the so-called megamidden period (Figure 12.3). Much of the protein and a significant portion of energy-rich foodstuffs were obtained from marine resources during this millennium. In contrast, the last 2,000 years saw a greater contribution of terrestrial proteins and carbohydrates into people's diets (Lee-Thorp et al. 1989; Sealy 1989; Sealy and Van der Merwe 1988). These subsistence trends are closely mirrored by changes in the density of dietary remains that have been preserved in archaeological sites for which we have sufficiently detailed observations. The dietary mix, as reconstructed from density ratios of marine and terrestrial resources from Steenbokfontein Cave and Pancho's Kitchen Midden show an increase in marine foodstuffs during the megamidden period, particularly around 2,600 and 2,500 years ago (Jerardino 1996, 1998; Jerardino and Yates 1996; new data). Thus, both archaeological and isotopic evidence are in agreement, suggesting that hunter-gatherer diet during the megamidden period was more marine than ever before or after. Given the magnitude and nature of these trends in population levels, settlement patterns, and subsistence, it is reasonable to suspect that people would have had their greatest impact on the local marine fauna during the megamidden period.

#### MEASURING HUMAN IMPACT ON MARINE INVERTEBRATES

Marine ecologists working with invertebrate species have several complementary ways of exploring hypotheses related to human impact on rocky shores (Lasiak 1992; Siegfried et al. 1994). These include (1) the quantification of the volumes or mass of harvested resources and their recruitment levels through time; (2) species composition of catches; and (3) comparison of richness, abundance, and size-frequency

distribution of species in areas where human harvesting is prevented, versus areas where harvesting takes place. These observations are evaluated against an understanding of the influence of the physical environment on the collected species, and the biology and community structure of the species under study. Unfortunately, archaeologists have a narrower set of choices when looking for ways to answer similar questions, but species composition of the catches and body-size observations can be retrieved fairly directly from the archaeological record. Proxies can also be established for the physical environment (e.g., degree of exposure of shoreline, water turbidity, and sea surface temperatures). Although archaeologists are able to evaluate their observations through time as marine biologists do, the chronological control allowed by radiocarbon dating does not match that available to researchers working in the present day. Nevertheless, archaeologists have managed over the last 15 years to extricate exciting observations reflecting the ability of people to exert a tangible impact on marine invertebrate species (Jerardino et al. 1992; Spennemann 1986; Swadling 1976).

#### ARCHAEOLOGICAL OBSERVATIONS FROM THE STUDY AREA

Three molluskan species, namely *Choromytilus meridionalis* (the black mussel), *Cymbula granatina* (the granite limpet), and *Scutellastra granularis* (the granular limpet), and one species of crustacean, *J. lalandii* (the West Coast rock lobster), are considered in this chapter. These species belong to three different trophic levels, and some of them have direct ecological links. Black mussels are filter feeders, the limpets are intertidal grazers, and rock lobsters are top predators with a powerful ability to modify the relative abundance of their prey and that of other species associated with them (Castilla et al. 1994). In particular, rock lobsters consume mussels, urchins, and winkles. Elimination or depletion of these groups by rock lobsters has powerful effects on other

elements of the biological community. Urchins harbour juvenile abalone, so any diminishment of urchins results in a decline in juvenile abalone, with repercussions for the adult population. Moreover, consumption of grazers such as winkles allows algae to proliferate (Day and Branch 2002; Mayfield and Branch 2000; Mayfield et al. 2000). As a result, reductions in the abundance of rock lobsters have the capacity to completely alter the nature of benthic communities.

Analyses of shellfish samples from Steenbokfontein Cave, Malkoppan, and Grootrif D megamiddens followed the methodology outlined by Jerardino (1997). Size observations on limpet shells were obtained by measuring the total lengths of unbroken shells. Body sizes of black mussels and rock lobsters were derived, respectively, from measurements of prismatic band widths and calcareous mandibles. These initial observations were then transformed to body-size estimates with the use of morphometric equations (Buchanan 1985; Jerardino et al. 2001). The statistical significance of any changes in the mean sizes of these four invertebrate species was tested using one-way analysis of variance (ANOVA; Zar 1984) followed by Tukey-Kramer multiple comparisons (Stoline 1981).

Black mussels were the most heavily collected shellfish between 3,000 and 2,000 years ago, with relative frequencies of 70 to nearly 100 percent of the weight at sampled megamiddens. Black mussels were also abundant in shellfish samples recovered from Steenbokfontein Cave, with frequencies covering 40 to 90 percent. On the other hand, limpets were almost absent from most megamiddens during this millennium, although important exceptions are Malkoppan and Grootrif D megamiddens (Figure 12.1). Limpets were also collected from Steenbokfontein Cave before and during the megamidden period. Limpet frequencies spanned 5 to 30 percent in both of these megamiddens, and 2 to 38 percent in Steenbokfontein Cave. Of the two limpet species, *Cymbula granatina* was collected more regularly

than *S. granularis*, most probably because it produces higher meat yields per individual (Tonner 2005). Rock lobster remains were found in almost all sites that have been systematically excavated (Horwitz 1979; Jerardino 1996, 2000; Jerardino and Navarro 2002). However, large enough samples of mandibles for valid statistical manipulation are present at only two sites where the megamidden period is represented, namely Steenbokfontein Cave and Grootrif D.

In the case of the black mussel, statistically significant changes can be detected through time, particularly reductions in mean shell length during the megamidden period, as illustrated by data for Steenbokfontein Cave (Figure 12.4). Similar changes occurred at Malkoppan as well. Significant reductions in the mean sizes of the granite limpet and the rock lobster were also detected for the megamidden period at Steenbokfontein Cave and Grootrif D megamidden (Figure 12.4). A decreasing trend in shell length during the megamidden period was also detected for *S. granularis* in Steenbokfontein Cave, although this trend was not statistically significant. No significant changes in the mean sizes of *S. granularis* were detected with Grootrif D data either. It is also interesting that the mean sizes of the three quantified mollusk species from Steenbokfontein Cave were smaller around 4000 BP, before the start of the megamidden period (see later).

#### FAUNAL CHANGES IN THE LIGHT OF ENVIRONMENTAL CONDITIONS

There are convincing changes through time in the size composition and the relative proportions of species in middens, and the immediate temptation is to ascribe this to human harvesting. Support for this view comes from declines in the size of harvested species in middens elsewhere in the world (Jerardino et al. 1992). Additional support comes from the documentation of comparable modern faunal changes that can be linked to subsistence harvesting. Declines in the sizes of limpets and mussels in harvested

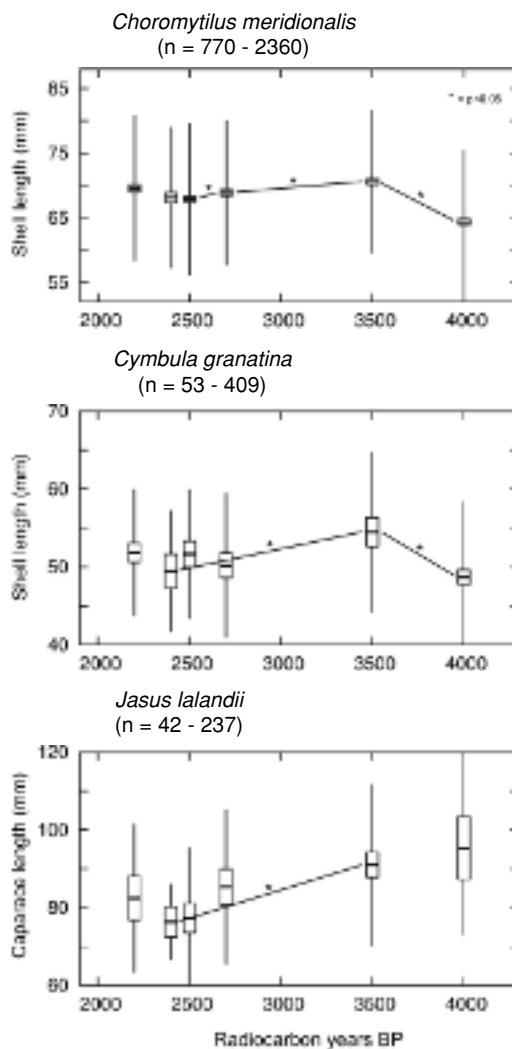


FIGURE 12.4. Changes in mean sizes of black mussels (*Choromytilus meridionalis*), granite limpet (*Cymbula granatina*), and rock lobster (*Jasus lalandii*) at Steenbokfontein Cave (uncalibrated radiocarbon years BP).

areas relative to protected areas testifies to this (Branch 1975; Branch and Odendaal 2003; Kyle et al. 1997; Lasiak 1992; Lasiak and Dye 1989). Changes in modern biological community composition have also been recorded, with convergence on a relatively uniform composition in harvested areas (Hockey and Bosman 1994; Lasiak and Field 1995).

Interpretation of the causes of these modern faunal changes benefits from concurrent observations at harvested and protected areas, thus eliminating or at least reducing possible



confounding factors that may cloud the influence of human harvesting. No such luxury is possible when deducing the effects of human harvesting from archaeological middens. A range of factors other than human harvesting may influence patterns in size composition, including temperatures, productivity, sea level, turbidity, wave action, storms, red tides, and the inherent relative resilience of different species to harvesting. Without at least a consideration of the potential effects of these factors, it is impossible to be confident that harvesting is the factor that drives faunal changes in middens.

Regional differences in temperature serve as a useful proxy for productivity because sea temperatures are inversely related to nutrient levels (Nielsen and Navarrete 2004). Nutrient levels are in turn correlated with growth rates of primary producers, notably phytoplankton and benthic algae, which underpin the growth of secondary consumers such as mussels that feed on particulate matter and limpets that consume algae. Growth rates are positively correlated with maximum sizes that species achieve. Thus, long-term shifts in temperature, or regional differences in temperature, could plausibly be linked to differences in the sizes attained by mussels or limpets in middens. The West Coast of South Africa as a whole is a region of intense upwelling, and limpet biomass and sizes are larger there than on the South and East coasts, where upwelling is infrequent or absent (Bustamante et al. 1995b). However, the West Coast also has focal points of upwelling at particular sites (Shannon 1985), and growth of mussels and maximum sizes of limpets have both been shown to be greater at upwelling centers than downstream, where upwelling is less marked (Menge et al. 2003; Xavier et al. 2007). The relationship between upwelling and growth (or size) is, however, not necessarily a positive one. Upwelling does enhance nutrient levels, but it also translates into advection of surface waters, so the nutrient-rich upwelled waters are shifted offshore, taking with them any phytoplankton growth that has been spurred by

the elevated nutrients. This water is later returned to the shore downstream of the upwelling centers, and particulate food is often more concentrated there than at the upwelling centers (Wieters et al. 2003). Correspondingly, growth of mussels may be expected to be greater downstream than at the focal points of upwelling.

Could temporal differences in productivity have driven the patterns of diminishing sizes recorded in middens over the period 2400–3500 BP, rather than human harvesting? It seems unlikely. First, temperatures were declining over this period (Figure 12.3), indicating elevated rather than diminished productivity; so size should have increased rather than decreased if nutrient-fueled productivity caused the reduction in size. Second, there was a corresponding decrease in temperature during the Little Ice Age (ca. 500 BP), yet mussel sizes *increased* during that period (Jerardino 1997), so opposite responses were recorded during the two periods of temperature decline.

Sea level was at a maximum about 3800 BP, dropped to approximately present levels between 3300 and 2400 BP, and then rose again by about 1 m before declining again (Jerardino 1995b). There is no intrinsic reason why sea level per se would have affected sizes of organisms in middens, but it is possible that associated factors were at work. One option is that turbidity altered with sea level and could have influenced growth rates and size. Patellid limpets are vulnerable to sand cover (Marshall and McQuaid 1989) and are likely to achieve smaller sizes in sand-inundated conditions. Mussels feed less successfully when particulate matter rises above threshold (Stuart et al. 1982) and therefore grow slower and reach smaller sizes. An indirect measure of turbidity can be derived from archaeological middens by quantifying a kind of sediment (water-worn shell and shingle) originally trapped by the byssal threads of mussels and retained later in the middens (see Jerardino 1993: Figure 11.3). The data suggest that turbidity was high around 4000–3000 BP and could explain why sizes of mussels and

limpets were low at that time. This does not explain the decreases in size in the subsequent period, when turbidity seemed to be at a minimum. Again, this allows us to reject turbidity as a cause of size changes between 3300 and 2400 BP (Figures 12.3 and 12.4).

Wave action has profound effects on body sizes, as movements of most limpets are inhibited by wave action, and they achieve smaller sizes on wave-exposed than sheltered shores (e.g., Branch and Odendaal 2003). This is particularly true of both *S. granularis* and *C. granatina*, the two species of greatest interest in West Coast middens. Conversely, mussels, which favor wave-exposed shores because wave action suspends and replenishes greater concentrations of particulate food (Bustamante and Branch 1996a, 1996b), attain greater sizes, growth rates, and cover on exposed shores than in sheltered areas (Branch and Steffani 2004; Steffani and Branch 2003). Two lines of thought argue against wave action as an explanation for diminished sizes of limpets and mussels in middens. First, all middens were associated with relatively short outcrops of rocks where the magnitude of wave action is unlikely to have changed in any systematic manner that can be related to sea-level changes over the period when limpet and mussel sizes were declining. Theoretically, changes in sea level could have altered the coastal topography and thus affected wave action, but rises and falls spanning 3 m would probably have had too small an effect on local topography to bring about significant changes in wave action. Second, and more convincingly, even if wave action was altered, we would have predicted opposite responses from limpets and mussels, yet they both declined in size. In short, alterations of wave action seem an implausible cause of body-size declines in mussels and limpets.

Storms could have had more subtle effects on the size composition of mussels and limpets that would have been available for people to harvest. Periodic storms may eliminate large limpets by physically removing them from rocks (Denny et al. 1985) but are a two-edged

sword when it comes to mussel size. Storms may remove mussels en masse (Branch and Steffani 2004; Steffani and Branch 2003) but sometimes dump huge quantities of large, subtidal mussels in the intertidal zone where they can take hold, increasing both the quantity and sizes of mussels available to intertidal harvesters (G. M. Branch and S. Eekhout, unpublished data). If the frequency or intensity of storms varied systematically over time, they could have influenced body sizes of both limpets and mussels. However, there is no evidence of such systematic changes over the period when sizes of these animals were declining. There is no easy prehistoric measure of storms, but turbidity serves as a proxy, and it shows no variations over time that clearly correlate with limpet and mussel sizes.

Thus far, we have focused on possible environmental effects that could have influenced body sizes of mussels and limpets, but similar questions can be raised about rock lobsters. To what extent is the decline in rock lobster size over the period 3500–2400 BP likely to reflect environmental conditions rather than harvesting? Two important possibilities exist. The first is that rock lobster growth has declined since the late 1980s (Johnston and Butterworth 2005; Pollock et al. 1997). The causes remain unresolved, but reduced food supply or environmental changes have both been invoked as explanations. Reductions in the rate of growth will result in smaller size and lower productivity, so the question that immediately arises is whether any past variations in growth could have influenced the productivity and size composition of rock lobsters found in shell middens. So far, there is no easy way of testing this possibility, although it seems that prehistoric sizes of rock lobsters were often substantially greater than in modern times (A. Jerardino, unpublished data). Secondly, mass “walk-outs” of rock lobsters have been recorded on the West Coast of South Africa, during which (mostly small) lobsters have moved inshore to avoid oxygen-depleted waters and have ended up becoming stranded on the shore in spectacular

quantities—up to 2,000 tons in one episode (Cockcroft 2001). Such events appear to be triggered by upwelling followed by prolonged quiescence, which concentrates phytoplankton inshore in bays, leading to depletion of oxygen as the blooms decay. Ensuing walkouts will influence the availability and size composition of rock lobsters in two ways. They provide a brief bonanza, but they also deplete stocks. There is no way of telling if such walk-outs were more or less frequent in the prehistoric past, but if their frequency has changed it would have powerfully affected the amounts and sizes of lobsters that could have been harvested. In the case of rock lobsters, we are therefore on much less certain ground in attempting to relate declines of size in middens to harvesting pressure. It appears that at least two plausible, but ambiguous, environmental factors may better explain these changes in size.

#### CHARACTERISTICS OF THE SPECIES

In evaluating the potential effects of human harvesting on the abundance and sizes of target species, consideration also needs to be given to both the relative vulnerabilities of different species to harvesting, and human preferences (Lasiak 1991). Not all species are equally vulnerable to harvesting pressure, and their vulnerability depends on a suite of biological properties.

##### *Accessibility*

Species that are confined to the intertidal zone, such as *C. granatina* and *S. granularis*, are readily accessible to harvesters every time the tide recedes sufficiently to expose them. During approximately five days every fortnight the entire shore is exposed during low spring tides, and it is then that human harvesting is most intense. Not all intertidal limpets will, however, be equally vulnerable. *S. granularis* occurs high on the shore and will be most accessible; *C. granatina* occurs lower down but is most abundant on sheltered bays, where it is also easy to harvest; but *S. argenvillei* is characteristically found low on the

shore and on wave-beaten shores, where harvesting is more hazardous (Branch and Marsh 1978; Bustamante et al. 1995a). Mussels also occur in the intertidal zone, but they extend down into the subtidal zone. In the midshore they are small but easy to collect, but at the bottom of the shore they are larger although less accessible. In the subtidal, they cannot be harvested without diving. Rock lobsters are even less vulnerable to subsistence harvesting because they live entirely subtidally and extend offshore for several kilometers, into depths of about 80 m (Griffiths and Branch 1997; Heydorn 1969). There is scant osteological evidence that prehistoric harvesting on the West Coast of South Africa involved diving (A. Morris, personal communication, 2006). Fishers may have used simple gourds and twine but would have been limited to very close to the shore. As far as is known, no watercraft or offshore fishing was developed in the region during prehistoric times. Rock lobsters could have been captured in very shallow water only by wading or by luring individuals with bait. This would have meant that only a tiny proportion of the population would have been exposed to harvesting, making it highly unlikely that harvesting could have dented the size composition of the species, in contrast to the impacts that may have been inflicted on intertidal species.

Two key features emerge. First, the apparent absence of watercraft and means of fishing away from the shore would have curbed the capacity of harvesters to influence the population structure of subtidal species. Second, species that have spatial refugia where they cannot be harvested will be relatively less vulnerable to the effects of fishing.

##### *Mobility*

Capacity for movement will influence the ability of animals to recover after being harvested. Limpets are sedentary and mussels are sessile. Rock lobsters move inshore and offshore in regular annual migrations (Heydorn 1969), however, and can replenish their shallow-water numbers if harvesting takes place there alone. Again, this

points to rock lobsters being relatively immune to the attentions of shore-based harvesters.

#### *Larval Dispersal*

Both the mode and frequency of larval dispersal will also influence the vulnerability of species to harvest pressure. Mussels have a widely dispersed planktonic larval stage but often experience intermittent recruitment. Years may pass with little or no recruitment, interspersed with bouts of intense recruitment. Moreover, settlement takes place mainly into existing beds of adult mussels (Harris et al. 1998). No replenishment can take place in years with no recruitment, and even when settlement does take place, recovery is slow where adult beds have been stripped by overharvesting (Dye et al. 1997), thus increasing the chances that harvesting will influence population structure. Species that are most vulnerable to overharvesting are those that have very limited dispersal. A classic example is the solitary ascidian (*Pyura stolonifera*), colloquially known as "red-bait," which is harvested as a source of food by subsistence fishers on the east coast of South Africa and used as bait for fishing elsewhere. It has a larval stage that lasts only minutes, so its larvae settle within meters of the adults that produce them (Griffiths 1976). As a result, depletion of adults reduces local settlement of larvae, and replenishment by larvae produced afar is impossible. By contrast, the rock lobster has a prolonged larval life lasting 9 to 11 months and is widely dispersed (Silberbauer 1971), so replenishment is possible both by adult movements and by larval settlement.

#### *Growth Rate and Longevity*

Species that are fast growing can recover quickly after being depleted, but they tend to be short-lived so that the size-composition of their populations is made up of a small number of year-groups and is inherently unstable from year to year. From a management perspective, there is thus a trade-off: fast growth translates into rapid recovery but high variability in stocks. Even among groups of

closely related species, wide differences may exist in growth rate. The limpets *Cymbula oculus* and *C. granatina* grow fast, reaching maturity within 2 or 3 years; but other limpets such as *Scutellastra argenvillei* and *S. cochlear* grow agonizingly slowly, maturing after about 6 years and attaining ages of up to 35 years (Branch 1974; Eekhout et al. 1992). Mussels tend to be fast growing, being harvestable after 1 to 2 years and living for about 5 years, but the rock lobster matures only after 7 to 15 years and lives up to 40 years, making it much more prone to the effects of harvesting and slow to recover (Pollock et al. 2000).

#### *Sex Change*

Some species undergo sex change as they age. The result is that older age groups are dominated by one sex. As there are inevitably fewer individuals in these older age groups, this automatically skews the sex ratio. None of the species of central interest here undergoes sex change, but *C. oculus*, a close relative of *C. granatina*, is male during its first 1 to 3 years of life and then becomes female for the rest of its life. Females are consequently not only more rare than males but are prime targets for harvesters because of their larger size. On the east coast of South Africa, where this species is heavily fished by subsistence fishers, it is threatened with extinction because of the depletion of females, which have declined from on average of 36 percent of the sexually mature population in protected areas down to 9 percent in harvested areas (Branch and Odendaal 2003). Clearly, sex change heightens the vulnerability of species to harvesting.

#### HUMAN PREFERENCES

In addition to the characteristics of the species considered above, human preferences will influence the relative impact of harvesting on different species. Particular species may be harvested more intensely than would be predicted based on their abundance. Factors affecting preference include accessibility, ease of procurement, transportability, relative size, yield in relation to effort,

palatability, nutritional value, toxicity, spoilage rate, and desirability. Not all of these aspects can be considered here, but some may have played important roles in determining the rate at which different species were prehistorically harvested on the West Coast of South Africa. For example, the nutritional value of mussels varies on a seasonal basis. Just prior to spawning, mussels are plump and the energy content of the flesh is high due to the buildup of gonads. After spawning, they are scarcely worth collecting. Modern subsistence fishers are well aware of these phenomena and time their harvesting accordingly, often using environmental cues such as the season when particular trees flower as an indication that mussels are "ripe" (Harris et al. 2003).

Another important issue is that periodic blooms of noxious algae on the West Coast of South Africa can result in mussels becoming lethally toxic to humans (Matthews and Pitcher 1996; Pitcher 1999). In Elands Bay Cave, an abrupt hiatus in the harvesting of mussels takes place at about 9500 BP (Parkington 1981), during which harvesting switched for a brief time to focus on much less abundant species, namely, the whelk *Burnupena* and limpets. Although speculative, it is not beyond the bounds of possibility that harvesters were struck by a harmful algal bloom that made mussels toxic, compelling a switch of diet (Parkington 1981; Parkington et al. 1988).

Finally, during the megamidden period of 3000–2000 BP, there is good evidence that mussel were dried and stored for later consumption (Henshilwood et al. 1994). This would have allowed more extended use of mussels, possibly tiding people over periods when the mussels were in poor condition, and overcoming limitations imposed by the greater frequency of toxic algal blooms in summer and storms during winter (Jerardino 1996; Parkington et al. 1988).

#### INTEGRATING THE EVIDENCE AND CONCLUSIONS

Clearly, the potential impacts of human exploitation on marine resources will depend on a blend

of the severity of the impact (e.g., high population pressure), the vulnerability of the species to harvesting, and the extent to which extraneous factors could have influenced the resources. Regarding the first, caution must be exercised when proposing high human population levels in the landscape as the main factor behind declining species' body sizes. Each case needs to be considered and assessed according to its own merits: in some instances population pressure may explain much of the observed variability, but in others, population pressure may be irrelevant. Most important here is the need to present independent evidence for population growth, otherwise, circular logic could feed an argument that ends up presenting population pressure as a self-fulfilling hypothesis.

We have shown that declines in the average sizes of mussels, two species of limpets, and the rock lobster all coincided with a period when human occupation of the study area was intensifying, and when reliance on marine resources was increasing (Sealy and van der Merwe 1988). The coincidence implies that human harvesting was responsible, but this conclusion needs to be evaluated by asking whether these species were sufficiently vulnerable for their populations to have been influenced by harvesting, and whether there were any other factors that could have explained the trends in size.

In the case of both the mussels and the limpets, we could find no convincing evidence that environmental conditions could have caused the declines in size during the megamidden period. Environmental changes did take place over the period when sizes were declining, but none of the factors examined provided a plausible explanation for a diminishment in size in both groups. Limpets and mussels belong to two very different trophic groups, being, respectively, grazers and filter feeders. This alone is significant, because changes in many of the environmental factors examined should yield opposite outcomes for these two trophic groups. Moreover, both mussels and limpets are highly vulnerable to the effects of harvesting because they are accessible, nonmobile as

adults, have intermittent larval recruitment, and to a large extent lack refuges beyond the reach of harvesters. We would expect them to be depleted by intense harvesting. Was harvesting intense enough to accomplish this? Rough calculations based on midden sizes and shell densities leads to the conclusion that about 1,666 kg (wet whole mass) would have been removed per kilometer per year (Griffiths and Branch 1997). This compares with a figure of 5,500 kg km<sup>-1</sup> y<sup>-1</sup> for highly intense modern subsistence fishing on the southeast coast of South Africa, where severe depletion of stocks has been recorded (Hockey et al. 1988). Given the combination of intense harvesting during the megamidden period from limited available rocky shores, high vulnerability of mussels and limpets, and an absence of alternative explanations for declines in mean sizes of these species, harvesting remains the most parsimonious and robust explanation for the declines in their mean sizes over this period.

However, there is a caveat. Over the same time, there was a significant decline in the sizes of rock lobsters. It is extremely unlikely that this decline can be attributed to shore-based harvesting. It is hard to imagine more than a tiny fraction of the rock lobster population being harvested from the shore. The bulk of the population lives in the subtidal zone, where it would have been inaccessible, and even if the shallow-water sector was harvested, it would have been replenished by movement of adults. In short, rock lobsters would not have been sufficiently vulnerable to shore-based fishing for the population to have been dented sufficiently by harvesting to alter the size composition. Additionally, the availability, productivity, and distribution of rock lobsters all depend strongly on environmental conditions, as demonstrated for modern populations. There are thus good reasons for distrusting prehistoric harvesting as a cause of the decline in rock lobster size, even though it too coincides with the period of intensification of harvesting.

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