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# The resilience to human foraging of intertidal resources on the south Cape coast of South Africa and the implications for pre-historic foragers

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## ABSTRACT

The extent to which modern humans relied upon intertidal resources, and the impact that this food source had on their cognitive and social development, remains contentious. An outstanding question is whether such a resource could have provided a sufficiently reliable and essentially continuous supply of resources to support communities during the Middle Stone Age (MSA). The south Cape coast of South Africa contains abundant evidence dating back to 164 000 years ago (ka) to show that the intertidal zone of this area was highly productive and was intensively used by MSA humans. In this paper we present the results of an experimental approach to answering the question of whether resources could have been sufficiently resilient to support communities similar in size to those of the Middle Stone Age. For a period of 10 months, we monitored the depletion of shellfish in the two dominant types of marine habitat (aeolianite and Table Mountain Sandstone) that occur on the south Cape coast, following intensive harvesting by indigenous foragers every two weeks or every four weeks. We found no evidence of lasting depletion in either type of habitat at either foraging frequency. We also found that replenishment of the foraged areas soon occurred (within two weeks) by repopulation from deeper water rather than by a long-shore movement. The most important prey species in this process was the highly mobile gastropod mollusk *Turbo sarmaticus*, which made up 81.9% of calorific harvest. Overall, mobile species made up 92.2% of the calorific harvest. Another factor that contributed to the resilience of the system is the nature of the coastline of the south Cape. This is characterised by extended shallow bathymetries of hard substrata that provide “pantries” of mobile invertebrates for restocking depleted intertidal habitats. We argue that the presence of such a reliable, easily procured, and nutritionally beneficial source of food may have played an important role in the development of more complex types of social behaviour than previously existed.

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## 1. Introduction

The south coast of South Africa's Cape Floristic Region (south Cape hereinafter) hosts a suite of Middle Stone Age (MSA) sites that bear testament to humans systematically adapting to the use of coastal intertidal resources (Voigt, 1973; Thackeray, 1988;

Henshilwood et al., 2001; Langejans et al., 2012). These include the oldest global record of the use of these resources by humans (Marean et al., 2007; Jerardino and Marean, 2010) and the associated extensive exploitation of the coast. The potential importance of the introduction of marine foods into the human diet is reflected in suggestions that the intensive exploitation of these resources may have been a catalyst for the increased cognitive development of our species (Broadhurst et al., 2002; Parkington, 2010) and/or may have triggered territorial sociality and the evolution of cooperation (Marean, 2014, 2016). The gradual intensification of coastal

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resource-use, commencing around 164 000 years ago (ka) and evolving into a coastal adaptation by 110ka (Marean, 2014), is further evidence that, over time, the foraging potential of this coast remained high. The Later Stone Age (LSA) attests to intensive exploitation of the intertidal zone and to the existence of a possible change in prey choice and size as human populations increased or terrestrial resources became scarce (Klein and Steele, 2013).

The south Cape coast contains many resources that would have been available to MSA hunter-gatherers. The seashore of the region supports a productive and diverse intertidal fauna, a consequence of the mixing of the cold Benguela and warm Agulhas Currents (Branch et al., 1994; Bustamante and Branch, 1996). It was intensively exploited in the MSA (Marean et al., 2007; Marean, 2010, 2011). The terrestrial fauna comprised a diverse array of game, including an extinct megafauna that was largely associated with the exposed Palaeo-Agulhas Plain (Klein, 1974, 1978; 1983; Rector and Reed, 2010; Thompson, 2010) and a browsing and mixed-feeder fauna that was associated with the contemporary, dissected coastal plain (Boshoff et al., 2001). There is good evidence from MSA archaeological sites (Singer and Wymer, 1982; Klein, 1983), and from ethnographic observations, that components of this fauna were exploited by Khoe-San people (Skead et al., 2011). This habitat also supports a diverse and abundant array of terrestrial plant resources (De Vynck et al., 2016a; De Vynck et al., 2016b; Singels et al., 2016). The availability of these carbohydrate-rich resources is highest during winter (De Vynck et al., 2016b; Singels et al., 2016), when intertidal resources tend to be less accessible owing to a seasonal increase in big seas (De Vynck et al., 2016c).

*Homo erectus*, a predecessor of our lineage, once inhabited the Cape; however, there is no evidence that they consumed coastal resources while there. Evidence from further afield indicates that this hominid did eat shellfish but did not systematically exploit it (Colonese et al., 2011). *Homo sapiens neanderthalis* also made use of shellfish, but likewise there is scant evidence that they used it systematically or intensively (Klein et al., 2008; Marean, 2014). True coastal adaptation implies a systematic and intensified use of coastal resources (Snow, 1972; Braun, 1974; Erlandson, 2001; Marean, 2014). This could not be said to be true or typical of what appears to have been little more than the occasional use of intertidal resources by the two aforementioned hominid types, meaning that the archaeological evidence does not show that it was a focal resource to which they had fully adapted. The earliest unequivocal evidence for true coastal adaptation occurs along the Cape south coast and is clearly associated with *Homo sapiens* (Marean, 2014).

Like all tidal coasts, the Cape south coast has distinct, biotic (tidal) zones characterised by distinctive fauna, some of which are sought by human foragers. The lowest tides generally expose “optimal gain” resource species. However, foraging in the intertidal zone near the low-water mark can be dangerous and needs to be timed to coincide with the most favourable part of the daily tidal cycle and the monthly lunar cycle. At 167 ka, people foraged along the higher, less productive mid to upper eulittoral zones (corresponding to the Balanoid Zone in South African terminology), as evidenced by the type of prey species recovered from cave 13B at Pinnacle Point (Marean et al., 2007; Jerardino and Marean, 2010). By 110 ka, prey species from the lowest tidal zone, the lower eulittoral zone (corresponding to the Cochlear Zone), show up in the most prominent MSA sites, signifying an ongoing exploitation (Voigt, 1982; Thackeray, 1988; Klein, 2001; Henshilwood et al., 2001; Marean, 2011). Apart from the shift in prey species corresponding to a deeper penetration of tidal-zone habitats, the remains of shells increase in density, indicating that MSA people increasingly depended on these resources as a component of their diet. This is in contrast to the findings of numerous ethnographic studies, which have shown that intertidal resources in other areas

are unproductive and are only exploited as a fall-back option (Marshall et al., 2009).

The archaeological significance of the sites on the coast of the south Cape is that they reveal a sustained and increased use of intertidal resources over many millennia. Even so, there is disagreement about the effect that access to such a resource might have had on the evolution of early modern humans (Klein and Steele, 2013; Marean, 2014). Some authorities argue that Cape shellfish are a productive and dependable resource (Marean et al., 2010; Marean, 2010; Broadhurst et al., 2002; Parkington, 2010, 2012). Others argue that Cape shellfish are easily depleted and hence could not have supported populations of early *Homo sapiens* (Klein and Steele, 2013). The main reason for this disagreement is that although there is evidence to show that intertidal resources were plentiful and the intertidal zone highly productive (see below), still too little is known about the sustainability of the resource. This central question, “How sustainable is the resource?” is especially relevant in the Cape because of the potential importance of the region to the origin and evolution of modern humans. It is also relevant to an interpretation of shell middens globally.

The productivity of the south Cape intertidal is high and usually equals or exceeds the calorific gain from other extant foraging options observed globally (De Vynck et al., 2016c). Calorific gain is commonly measured by ethnographic observation combined with a quantitative assessment of the associated harvest, the results usually being expressed in terms of hourly benefit ( $\text{kcal/h}^{-1}$ ) from pursuing various resources. Our prior intertidal foraging experiments resulted in an overall energetic return rate of  $1492 \text{ kcal/h}^{-1}$  and showed that foraging can be exceptionally productive under the best sea and tidal conditions ( $\sim 3400 \text{ kcal/h}^{-1}$  for men and  $\sim 1900 \text{ kcal/h}^{-1}$  for women). De Vynck et al. (2016c) compared these results with those from other studies that also used ethnographic observations. The highest return rates reported by these other studies for intertidal foraging was  $1000 \text{ kcal/h}^{-1}$  [Anbarra women, Northern Australia (Jones, 1980; Meehan, 1982)]; hunting for vertebrate game had a rate of return of  $3055 \text{ kcal/h}^{-1}$  [Hiwi men, South American neo-tropics (Hurtado and Hill, 1990)]; and the highest recorded rate of return for edible plant resources was  $1300 \text{ kcal/h}^{-1}$  [!Kung women (Hawkes and O’Connell, 1985)]. The productivity of the south Cape coast therefore is better, to very much better, than the norm. The outstanding question is whether it is sufficiently resilient to be depended upon.

Archaeological interpretations of overharvesting based on variations in shellfish prey choice and size over time must be informed by studies of dependability and resilience. The archaeological record of the MSA of South Africa reveals a low diversity of targeted prey species, the focus having been higher-yield prey (Steele and Klein, 2008; Klein and Steele, 2013). Shell volumes increased whereas prey choice and size showed little variation. During the LSA, foragers broadened their prey choices to include lower-yield options. Also, the volume of shell remains increased from the MSA to the LSA, whereas within-species prey size decreased during the LSA (Jerardino, 1997; Klein and Steele, 2013). The changes in prey choice, volume, and size all point to the possibility that coastal resources had begun to deplete. Ethno-archaeological studies on the variation of prey choice and size elsewhere are informative. Bird et al. (2004) studied coastal foragers in the Meriam Islands and concluded that the under-representation of larger ideal prey at their archaeological sites was due to field processing; the shell was left behind and only the edible portions were transported back home. Also, children were found to target ideal prey, but in addition foraged for smaller, less ideal, prey. Gender, age, climatic variation, lunar phase miscalculation, and other factors can influence the archaeological pattern of shellfish species diversity and size (Lasiak, 1991, 1992; 1993; Jerardino, 1997, 2016; Peacock, 2000; Langejans

et al., 2012; Coddling et al., 2014).

Did MSA people in the Cape deplete coastal resources? It is important to bear in mind that population density during the MSA was likely relatively low (Marean et al., 2014). Modern foragers to the east of the Cape do, indeed, deplete intertidal shellfish stocks (Bigalke, 1973; Lasiak, 1992, 1999; Lasiak and Field, 1995). However, the studies on which such results are based were mainly concerned with sessile, or almost sessile, species (limpets and mussels) rather than with more mobile species such as gastropods, which can migrate from sub-tidal zones and crevices inaccessible to foragers (Yssel, 1989). Furthermore, in some studies, depletion of sessile resources is interpreted as an overall depletion of intertidal resources (Hockey and Bosman, 1986; Lasiak and Field, 1995; Lasiak, 1999). Research on the sub-tropical coast of KwaZulu-Natal, where intertidal resources are relatively limited and there are locally dense human populations, show strong evidence of resource depletion by contemporary foragers (Kyle et al., 1997a, b; Tomalin and Kyle, 1998; De Boer et al., 2002). Although designed depletion experiments have been conducted on the California coast (Jones and Richman, 1995; Kennedy, 2004; Whitaker, 2008), no such research has been undertaken along the south Cape coast. This study aims to fill that gap.

The aim of this study was to test whether sustained foraging of the intertidal shore of the south Cape at a level similar to that estimated to have been used by MSA foragers would have a measurable effect on calorific returns. As part of our experimental design we also compared rates of return from the two major habitat types that made up the rocky intertidal during the Pleistocene glacial and inter-glacial periods, which still occur today, namely aeolianite (more productive) and Table Mountain Sandstones (TMS, less productive: De Vynck et al., 2016c). A secondary aim was to test for possible long-shore (lateral) migration of mobile invertebrates, in order to ensure that the test plots were large enough that return rates were unaffected by target animals moving into the plots from the adjacent intertidal shore, in between harvesting bouts.

Below we provide a brief overview of our experimental design and the thinking behind it. For each type of habitat, we monitored depletion over a 10-month period by harvesting one 300 m long plot every spring tide, i.e. once every two weeks, and one additional plot every second spring tide (once every four weeks). Respectively per habitat, the two plots were in the same broader area, but well removed to ensure that we could test for long-shore migration. We based this design on the following facts. First, prior observation of natural intertidal foraging behaviour had shown that three experienced male foragers could deplete ponds, of a similar size and spatial arrangement, of the preferred prey species in about 45 min when foraged two-weekly or four-weekly at spring low tide. Our experimental design therefore replicates the natural foraging behaviour of indigenous harvesters, which we know immediately depletes the ponds they harvested. If depletion occurs, then harvesting according to this scheme should prove it. Second, aeolianite shores are more productive than TMS shores are (De Vynck et al., 2016c); our design therefore allows us to test whether the former is more resistant to depletion than the latter. Third, we wondered whether a more intensive harvesting cycle, two-weekly compared to four-weekly, would lead to greater depletion. Fourth, an earlier study by De Vynck et al. (2016c) had indicated that the productivity and reliability (calorific potential) of the south Cape coast is strongly affected by tidal levels, conditions of both the sea and the local weather, and individual forager ability. These factors were therefore recorded and included in the analysis. Finally, we subdivided each plot into three sub-plots so that we could test whether the two side sub-plots were differentially repopulated compared to the central sub-plot by long-shore migration, especially by the mobile gastropod species *Turbo sarmaticus*, the main

prey species. This would allow us to determine whether our design approximately replicated the constraints on replenishment that probably were prevalent during the MSA, when all ponds in the vicinity would probably have been harvested to their full potential, and so would not have been available for providing a population of prey species for repopulating depleted ponds by long-shore migration.

## 2. Materials and methods

### 2.1. Study area

The study area comprised a 100 km stretch of coast between Pinnacle Point (just west of Mossel Bay; S34° 12'; E22° 5') and Blombos Cave (about 20 km west of Jongensfontein; S34° 25'; E21° 13'). The intertidal zone of the Cape south coast can be classified into various types of marine habitat (De Vynck et al., 2016c). The shore is dominated by TMS and aeolianite wave-cut platforms, and sandy beaches. The TMS-dominated coast consists of numerous shallow embayments containing a regular sequence of exposed headlands, wave-cut platforms, boulders, and sandy beaches. Aeolianite dominated coasts are mostly linear, backed by beaches, and contain extensive wave-cut platforms. Owing to the low overall productivity of sandy beaches (De Vynck et al., 2016c) this type of habitat was omitted from the study.

The lunar cycle produces two spring tides per month, one every two weeks, coincident with full moons and new moons. Each spring tide period usually allows access to the eulittoral zone for about 1.5 h for about 5 days. Neap tides are caused by waxing and waning moons between spring tides and result in minor tidal fluctuation. Twice annually, in April and September, exceptional tidal fluctuation is caused by equinox spring tides. The lowest daily tidal level is expressed in meters above the lowest reference water level, which corresponds to the Chart Datum or Lowest Astronomical Tide (LAT). Lunar tidal levels are also affected by weather conditions (Mather et al., 2009; Chandler and Merry, 2010), in that atmospheric pressure can change predicted tidal level by one cm per mbar, so that low-pressure cold fronts heighten sea level and high pressure cells lower sea levels. The south coast is also often exposed to strong winds and large swells, which can sometimes render the intertidal zone inaccessible even during spring tides. Cold fronts predominantly occur in winter with winds from the west; high pressure cells mostly occur in summer bringing winds from the east. The weather is generally mild with annual temperature extreme averages ranging from 27 °C in summer to 5 °C in winter. The study area lies between the winter rainfall area in the west and the summer rainfall area in the east and receives year-round rainfall that averages 20–40 mm per month.

#### 2.1.1. Marine intertidal habitat types – Table Mountain Sandstones (TMS)

TMS comprises an erosion-resistant quartzitic sandstone of Palaeozoic origin that was subsequently intensively folded, thereby yielding a habitat that is highly heterogeneous in mesotopography. TMS houses a high diversity of marine fauna and flora. However, the focus here is on species targeted by humans. TMS shores are home to large quantities of bivalve and gastropod molluscs, an ascidian (*Pyura stolonifera*), and octopus (*Octopus vulgaris*). Tidal zones are well defined and the lower-to mid-eulittoral zones (cochlear and lower balanoid zones) house the majority of preferred prey. The mid-to upper eulittoral and supralittoral zones (corresponding to upper balanoid and littorina zones) are unproductive as the species that inhabit these zones have low yields. Few smaller *Cymbula oculus* and *Oxystele sinensis* are found in the mid-to upper eulittoral zones and a very small gastropod,



*Nodilittorina africana knysnaensis* dominates the supralittoral zone. On rare occasions, during equinox spring low tides and other specific climatic conditions, a narrow stretch of the sublittoral fringe (shallow subtidal zone) can also be exposed, revealing some species that inhabit this usually submerged zone.

Three main TMS sub-habitats were distinguished: boulders, wave-cut platforms, and exposed rocky headlands. These sub-habitats constantly occur adjacent to one another, and a short stretch of intertidal coast can typically (due to depositional processes) contain all three. Also, because the depletion study focused on TMS as a whole, and not specifically on the sub-habitats, a study area was selected that contained all three in more or less equal amounts (see Fig. 1 and Table 1). This area, Ystervark Point, west of Gouritz Mouth, lies within one of the most inaccessible stretches of TMS in the whole 100 km coastal stretch. The inaccessible nature of the area meant that any confounding effects of other human foragers would be excluded and a pre-historic hunter-gatherer environment would be closely approximated.

### 2.1.2. Marine intertidal habitat types – aeolianite

Aeolianite is lithified beach sand and is a softer substratum than TMS. This habitat mainly offers the human forager the gastropod mollusc *Turbo sarmaticus* and some Patellidae. On occasion, octopi can be found. Most of these aeolianite shores comprise wide, flat, wave-cut platforms with shallow pools, and they are often strewn with large slabs of loose aeolianite. Tidal zones are often less defined than on TMS and the lower-to mid-euittoral (cochlear to balanoid) zones are wide, with a narrow or no upper littoral zone (highest tidal zone) because of the presence of sandy dunes or aeolianite cliffs. The rarely-exposed sublittoral fringe contains numerous *Turbo sarmaticus*, which are sometimes available to foragers. Because the aeolianite platforms are flatter than TMS environments, they do not offer the same sub-habitats as TMS does and are less heterogenous. Aeolianite platforms extend, almost uninterrupted, for 17 km east of Still Bay. This coast is mostly rimmed by cliffs and access is restricted to only a few points which are not open to the general public; thus, the shoreline is essentially pristine.

## 2.2. Survey methods

### 2.2.1. Foraging experiments

The foraging depletion experiments were undertaken in the intertidal zone of the two basic marine habitat types of the Cape south coast, Table Mountain Sandstones (TMS) and aeolianite. Two 300 m (long-shore width) plots were located in each of the two habitats. The productive and targeted tidal zonations of both habitat types were of similar width approximating 30 m. Plot width did vary over the study period as different low tides exposed either more or less of the intertidal zones. Weather permitting, one plot was harvested with every spring tide (once every two weeks), and one plot was harvested with every second spring tide (once every four weeks). The experiment was run for 10 months (Sept. 2014 to July 2015). Each 300 m plot was divided into three 100 m sub-plots (A, B and C) to test for a possible repopulation effect by the long-shore migration of mobile prey species. Underpinning this design is the conjecture that the outer 100 m sub-plots (A and C) would show higher returns over successive re-harvests if animals were migrating into available or vacated habitats from the sides rather than from deeper water. Each harvest was performed during low-water spring tide, beginning 1 h before peak low tide, and consisted of two passes of each sub-plot, each of which represents a bout. The first pass lasted 30 min, the second pass lasted 15 min. It was carried out on a return-sweep, after first-pass harvesting the other sub-plots (Fig. 2). This gives six bouts per harvest. The tidal height at the start of each harvest was similar to the tidal height at the end of each harvest. The lag between the first and second passes of a sub-plot was therefore either 30 min, 60 min or 90 min according to when in the sequence it was harvested. To offset any bias that this might introduce, the re-harvest start points of all plots were alternated between the side sub-plots A and C. Re-harvests of the different plots were also randomly alternated.

Indigenous foragers with a long history of coastal foraging were recruited from two coastal communities (ethical permission was granted by Arizona State University IRB protocol 1301008742). The experiments were partially supervised, although all foragers had a long history of foraging intertidal areas in search of food for personal consumption. Although foraging times and distances foraged

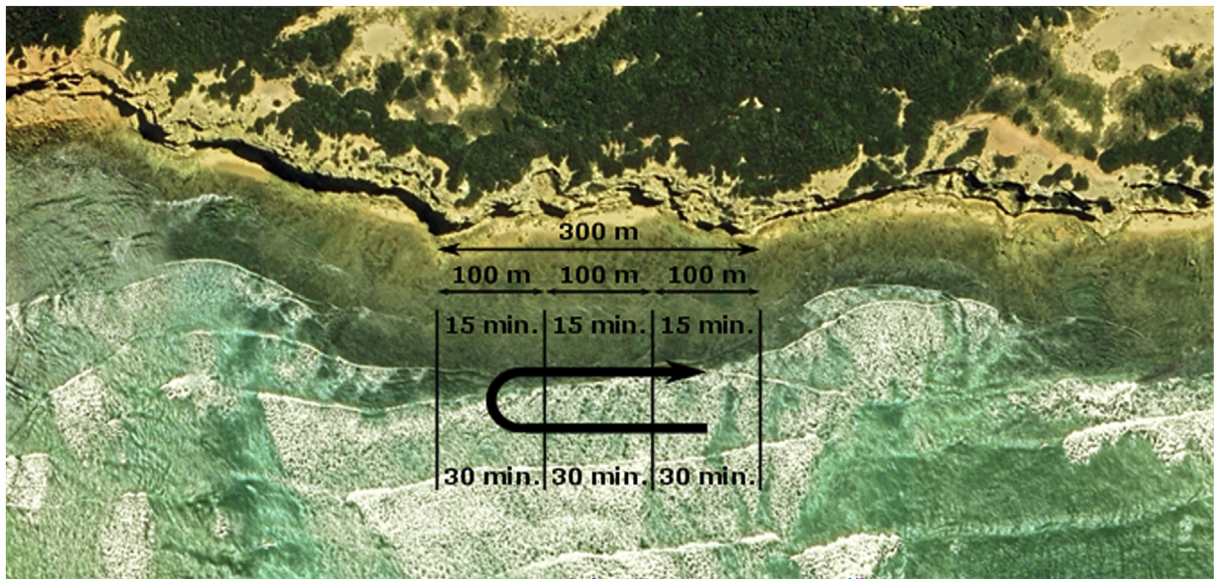


**Fig. 1.** The study area showing the location of the four experimental depletion plots. Plots one and two, Table Mountain Sandstone [harvested once every four weeks (Plot one) and harvested once every two weeks (Plot two)] and plots three and four, Aeolianite reefs [harvested once every four weeks (Plot three) and harvested once every two weeks (Plot four)].

**Table 1**

Descriptive statistics of the plots used for the depletion experiments, showing plot location, harvest frequency, the local community from which foragers were drawn, the number of foragers used (all male), and the age-range of the foragers. The experiment was performed between September 2014 and July 2015.

Survey plot	Coordinates	Harvests	Community	Forager total used	Forager age range
1: TMS four-weekly	S34° 23'35.8"; E21° 43'56.4"	9	Bitouville, Gourits Mouth	8	18 to 63
2: TMS two-weekly	S34° 23'35.5"; E21° 43'18.7"	18	Bitouville, Gourits Mouth	11	12 to 63
3: Aeolianite four-weekly	S34° 21'40.0"; E21° 33'12.5"	9	Melkhoutfontein, Still Bay	9	20 to 63
4: Aeolianite two weekly	S34° 21'33.4"; E21° 32'35.2"	17	Melkhoutfontein, Still Bay	13	17 to 47



**Fig. 2.** Layout of the three sub-plots of a depletion plot, showing bout lengths and the first and second passes of a single harvest (the aerial image was taken at high tide and the foraging patch is therefore submerged).

were restricted by the design of the study, foragers were free to select their own prey and the size of their prey. De Vynck et al. (2016c) have shown that these choices are similar to those that occur in the archaeological record. Foragers harvested with their own procurement tools; these were always metal implements, predominately screwdrivers. Three male foragers were employed per harvest experiment. They foraged together in each of the sub-plots. After each bout, the prey species that each forager had harvested were retrieved so that each forager was free to continue with the next bout. Each forager's harvest was counted and weighed (gross weight or live weight per species) in light mesh bags, using digital hanging scales.

All variables that could possibly affect foraging returns were recorded. These were individual forager ability, low tide level (m), and Cond. The latter is a synthetic controlling variable, which we used in our models to account for factors that affect foraging success, like ocean swell, wind, and rain. Including it is important because this part of the coastline is exposed to frontal systems that often bring wild weather and large swells. In between frontal systems, conditions can be more or less highly favourable. We constructed Cond as follows. Based primarily on estimates of swell height and wind strength assessed on the Beaufort scale, we rated sampling conditions on a scale of 1–4, to give a four-level ordinal variable (Cond). A condition rating of 1 for Cond corresponds to optimal sampling conditions, with small to no swell, sunny, and little wind. A condition rating of 4 for Cond corresponds to highly unfavourable and dangerous conditions with wild winds and wild seas and a risk to life and limb (see De Vynck et al., 2016c for further

details).

### 2.2.2. Data

The data derive from 936 primary records of the calorific content of shellfish harvested from four plots over a ten month period beginning September 2014 and ending July 2015. The total number of foragers used during the duration of the experiments was 27.

This sampling scheme was adhered to for the duration of the study, except for three breaks caused by inclement weather and the unavailability of the lead researcher (JDV). High seas during the last two outings also meant that the second pass of each sub-plot on those outings had to be abandoned. The final version of the dataset contains 477 records. During the first-pass 30 min bout of each sub-plot, foragers followed the lower eulittoral zone (cochlear zone), fringing onto the subtidal area. During the second-pass 15 min return bout they foraged an area slightly higher up the shore (mid eulittoral zone/lower to upper balanoid zones) that had not been foraged during the first pass. They were not instructed to - and in all cases decided not to - retrace the same foraging patch on their return during the 15 min second-pass bout.

### 2.2.3. Variables used and their encodings

Table 2 lists the variables used in the statistical models, the labels that identify them, and their basic parameters.

## 2.3. Statistical analysis

The study was designed to test two hypotheses about shellfish

**Table 2**Descriptive Statistics of the variables used in the statistical models (N = 477).<sup>a</sup>

Variable	Label (units)	Parameters
Rate of return	Rate (kcal/h)	31.1, 394.1, 753.5, 1635.6, 4444.7
Sampling date	DateJ (Julian days)	0, 61, 121, 237, 297
	bs (DateJ)	cubic spline
	DateJ	53 unique values (random effect)
Habitat	Habitat	
Aeolianite	Ael	49%
Table Mountain Sandstone	TMe	51%
Sampling frequency	SFreq	
Two weekly	2W	66%
Four weekly	4W	34%
Sub-plot	SPlot	
	A	33%
	B	33%
	C	33%
Sampling conditions	Cond	
conditions degrade	1	2%
as the level increases	2	40%
	3	40%
	4	19%
Seawater level	CWLev (m)	153 unique values (random effect)
	low	(0.086,0.26]
	medium	(0.26,0.43]
	high	(0.43,0.6]
Forager	Name	27 different foragers (random effect)
Length of bout	Foraging.time (min)	
	30	4%
	45	96%

<sup>a</sup> Continuous variables are summarized using Tukey's five-number summary; for nominal- and ordinal-scale variables (or continuous variables treated as such), the proportion of occurrence of each level is given as a percentage when there are  $\leq 10$  levels, else the number of unique levels/values is given. N is the number of records with non-missing values that were analysed.

foraging returns: (1) whether regular foraging would result in a significant decrease in the amount of shellfish harvested; and (2) whether replenishment, if any, would occur via long-shore drift, in which case returns from lateral sub-plots A and C should be greater than returns from central sub-plot B. To test these hypotheses we fitted a pair of Tweedie mixed models with the following fixed-effects structures (for the notation used, see Section 11 of Venables, Smith, and the R Core Team, 2018)

$$\text{Rate} \sim \text{DateJ} * \text{Habitat} * \text{SFreq} + \text{Cond} \quad (1)$$

and

$$\text{Rate} \sim \text{Habitat} * \text{SFreq} * \text{SPlot} + \text{Cond} \quad (2)$$

Both models used the following common random-effects structure

$$\sim 1 | \text{DateJ} / \text{CWLev} / \text{Name} \quad (3)$$

We call these two models the depletion model (Eq. (1)) and the replenishment model (Eq. (2)), respectively. See Table 2 for a description of the variables used. For the depletion model, we fitted DateJ as a cubic B-spline in one version of the model and as a linear effect in another version of the model. Cond was coded as an ordinal-level variable and fitted using polynomial contrasts; the other variables were fitted using sum-to-zero contrasts. A weights argument was used to adjust for the fact that dangerously high seas cut the foraging time of several bouts short (from 45 min to 30 min).

The response variable (Rate) requires special handling because it cannot be negative, has a minor point mass at zero, and is strongly right-skewed. The Tweedie distribution can cope with all three of these properties. See McElreath and Koster (2014) for a different approach to modelling foraging returns. The default logarithmic link function was used to fit the model; the power parameter of the

Tweedie distribution was estimated using the cpglmm function from the cplm add-on package for R (Zhang, 2013).

Variability in the day-to-day sampling conditions was modelled in two ways. First, variability in the overall sampling conditions was controlled for by using the synthetic variable Cond in the fixed-effects part of each model. Secondly, the random-effects structure, by grouping samples by sampling date (DateJ) at the most general level, accounts for both the correlated nature of the data and variability due to the ability of different foragers at the different tidally-based sea-water levels of each sampling date.

Models were fitted using glmer from the lme4 (Bates et al., 2015) add-on package for R (R Development Core Team, 2016), combined with the Tweedie distribution from the core package mgcv (Wood, 2006, 2011). Type II and Type III omnibus tests were carried out using the car package (Fox et al., 2017); post-hoc analysis was carried out using the effects (Fox, 2003), lsmeans (Lenth, 2016), and multcomp (Hothorn et al., 2008) packages. Partitioning the variance explained into proportions attributable to fixed-effects and to random-effects was carried out using the methods of Nakagawa and Schielzeth (2013) and Nakagawa et al. (2017).

### 3. Results

#### 3.1. Summary of harvested species

Prey species (Table 3) were primarily restricted to molluscs, comprising bivalves (mussels and oysters), gastropods (abalone, limpets, turban shells, whelks and winkles) and cephalopods (octopus). Also included was the ascidian *Pyura stolonifera* (sea squirt/redbait). *Turbo sarmaticus* completely dominated the prey species harvested, followed by *Haliotis spadicea*, *Cymbula oculus*, *Haliotis midae* and *Octopus vulgaris*. Of the total harvest, 88.1% comprised mobile species; the only (almost) sessile species that comprised an appreciable part of the harvest (4%) was the limpet



**Table 3**

Composition of total species harvest during the depletion experiments on all four plots.

Species	Common name	Type	Total Count	Total Calories	Total calorific percentage
<i>Charonia lampas postulata</i>	Pink lady	Sessile	4	746.2	0.2
<i>Cymbula miniata</i>	Pink-rayed limpet	Sessile	90	627.5	0.2
<i>Cymbula oculus</i>	Goat's eye limpet	Sessile	1866	15504.6	4
<i>Haliotis midae</i>	Abalone	Mobile	119	11034.5	2.8
<i>Haliotis spadicea</i>	Venus ear abalone	Mobile	574	22509.6	5.8
<i>Octopus vulgaris</i>	Common octopus	Mobile	40	6276.6	1.6
<i>Oxystele sinensis</i>	Pink-lipped topshell	Sessile	145	92.9	<0.1
<i>Perna perna</i>	Brown mussel	Sessile	106	579.4	0.1
<i>Guinusia chabrus</i>	Cape rock crab	Mobile	37	524.1	0.1
<i>Pyura stolonifera</i>	Redbait	Sessile	63	7148.2	1.8
<i>Scutellastra argenvillei</i>	Argenville's limpet	Sessile	11	167.7	<0.1
<i>Scutellastra barbara</i>	Bearded limpet	Sessile	9	172.1	<0.1
<i>Scutellastra cochlear</i>	Pear limpet	Sessile	34	253.1	0.1
<i>Scutellastra granularis</i>	Granular limpet	Sessile	13	14.4	<0.1
<i>Scutellastra longicosta</i>	Long-spined limpet	Sessile	348	4511.6	1.2
<i>Scutellastra tabularis</i>	Giant limpet	Sessile	18	352.9	0.1
<i>Striostrea margaritacea</i>	Cape rock oyster	Sessile	1	7.7	<0.1
<i>Turbo sarmaticus</i>	Giant turban snail	Mobile	16549	318148.7	81.9
			Total	388671.8	

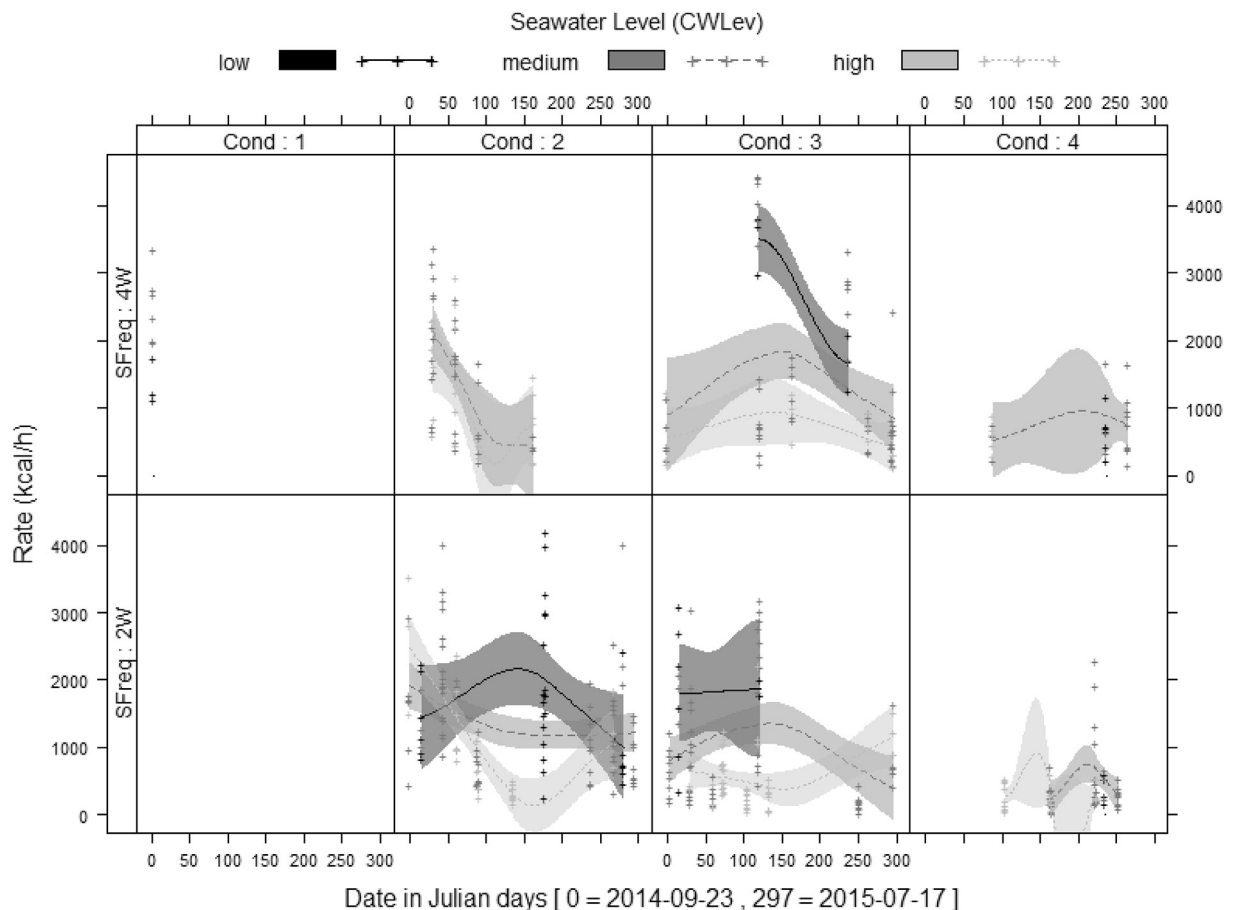
*Cymbula oculus*. The remainder of the harvest consisted almost entirely of various limpet species.

### 3.2. Depletion

Fig. 3 shows the observed rate of return, conditioned on sampling frequency (SFreq) and sampling conditions (Cond). These are

the two most important predictors in the spline-free and the spline-based versions of the depletion model (Table 4). Within-panel loess smooths show the effect of seawater level during sampling (CWLev), after categorization into low, medium, and high tidal levels (Table 2).

The spline-free and spline-based versions of the model (Eq. (1)) explain respectively 87.74% and 88.59% of the variance of the rate of



**Fig. 3.** Trellis plot of the observed data on the rate of return (Rate) versus sampling date (Date), conditioned on sampling frequency (SFreq: 2W = two-weekly; 4W = four-weekly) and sampling conditions (Cond). Loess smooths show the effect of three tidal levels (level-categories determined by cutting the range of CWLev into three equal-length intervals).

**Table 4**

Summaries of the spline-free and spline-based tweedie mixed models of the depletion of the rate of return (Eq. (1)).<sup>a</sup>

	Spline-free	Spline-based
(Intercept)	6.43 (0.27) ***	6.84 (0.28) ***
DateJ	−0.00 (0.00)	
Habitat[S.Ael]	0.33 (0.22)	−0.18 (0.34)
SFreq[S.2W]	−0.19 (0.23)	0.30 (0.30)
Cond.L	−0.93 (0.64)	−1.64 (0.78) *
Cond.Q	−0.42 (0.49)	0.12 (0.56)
Cond.C	0.20 (0.27)	0.10 (0.29)
DateJ:Habitat[S.Ael]	−0.00 (0.00)	
DateJ:SFreq[S.2W]	−0.00 (0.00)	
Habitat[S.Ael]:SFreq[S.2W]	−0.33 (0.22)	−0.03 (0.36)
DateJ:Habitat[S.Ael]:SFreq[S.2W]	0.00 (0.00)	
bs (DateJ)1		−0.95 (0.84)
bs (DateJ)2		0.46 (0.78)
bs (DateJ)3		−0.32 (0.44)
bs (DateJ)1:Habitat[S.Ael]		1.22 (1.00)
bs (DateJ)2:Habitat[S.Ael]		0.14 (0.68)
bs (DateJ)3:Habitat[S.Ael]		0.21 (0.48)
bs (DateJ)1:SFreq[S.2W]		−0.64 (0.80)
bs (DateJ)2:SFreq[S.2W]		−1.46 (0.69) *
bs (DateJ)3:SFreq[S.2W]		−0.22 (0.42)
bs (DateJ)1:Habitat[S.Ael]:SFreq[S.2W]		0.00 (1.02)
bs (DateJ)2:Habitat[S.Ael]:SFreq[S.2W]		−1.42 (0.68) *
bs (DateJ)3:Habitat[S.Ael]:SFreq[S.2W]		0.30 (0.49)
AIC	4836.51	4839.81
BIC	4899.02	4935.66
Log Likelihood	−2403.25	−2396.90
Num. obs.	477	477
Num. groups: Name:(CWLev:DateJ)	474	474
Num. groups: CWLev:DateJ	159	159
Num. groups: DateJ	53	53
Var: Name:(CWLev:DateJ) (Intercept)	0.38	0.38
Var: CWLev:DateJ (Intercept)	0.04	0.04
Var: DateJ (Intercept)	0.11	0.08
Var: Residual	0.12	0.12

\*\*\*p < 0.001, \*\*p < 0.01, \*p < 0.05.

<sup>a</sup> Numbers in parentheses after the estimated regression coefficients ( $\beta$ s) are asymptotic standard errors. Models were fitted using sum-to-zero contrasts for Habitat and SFreq, and polynomial contrasts for Cond. For the spline-based version of the model, DateJ was fitted as a polynomial spline of three degrees. Sum-to-zero coded variables carry a suffix in square brackets giving the treatment-level(s) of the factor. Var gives the variance of intercepts in groups of records identified by the referenced group in the random-effects structure. For instance, the entry DateJ (Intercept) refers to the variance in the 53 intercepts of Date J in the top-level grouping of the random-effects structure (Eq. (3)).

return. We therefore can be reasonably sure that our model includes the main variables that explain the variability of foraging returns. The spline-based version of the model explains a markedly greater proportion of the total variance through its fixed-effects component than the spline-free version of the model does, namely 42.62% compared to 35.69%. Given that the two versions of the model explain approximately the same proportion of the total variance, this difference is reflected in the proportion of that variance that the random-effects component of the model explains: for the spline-free version of the model it is 52.05%, for the spline-based version of the model it is 45.97%.

Estimates of the population-level (or fixed-effects) regression coefficients are reported in Table 5. The complexity of the models means that interpretation of the individual coefficients is not straightforward. However, the spline-based model shows that Cond (sampling conditions) has a statistically significant negative linear effect (Cond.L) on the rate of return; neither the quadratic (Cond.Q) nor the cubic (Cond.C) effects is statistically significant. Sampling conditions affected access to the lower eulittoral (cochlear zone), where the majority of prey species are found. Access to this ideal foraging zone decreased as swell size increased, i.e. as the level of Cond increased, affecting the rates of return of foragers.

**Table 5**

Type II and Type III Wald  $\chi^2$  Tests of the Effect on the Rate of Return of Terms in the Spline-free and Spline-based Versions of the Depletion Model (Eq. (1)).<sup>a</sup>

Model Terms	Spline-free			Spline-based		
	$\chi^2$	Df	p-value	$\chi^2$	Df	p-value
<b>Type II Tests</b>						
DateJ	0.405	1	0.5246	3.695	3	0.2963
Habitat	0.317	1	0.5737	0.423	1	0.5157
SFreq	2.545	1	0.1106	2.931	1	0.0869
Cond	18.677	3	0.0003	23.468	3	0.0000
DateJ:Habitat	0.749	1	0.3868	2.613	3	0.4553
DateJ:SFreq	0.016	1	0.8988	7.184	3	0.0663
Habitat:SFreq	3.956	1	0.0467	4.908	1	0.0267
DateJ:Habitat:SFreq	0.253	1	0.6149	5.845	3	0.1194
<b>Type III Tests</b>						
DateJ	0.371	1	0.5423	1.370	3	0.7126
Habitat	2.219	1	0.1363	0.263	1	0.6078
SFreq	0.669	1	0.4135	1.023	1	0.3119
Cond	18.677	3	0.0003	23.468	3	0.0000
DateJ:Habitat	0.946	1	0.3308	2.660	3	0.4470
DateJ:SFreq	0.010	1	0.9212	6.898	3	0.0752
Habitat:SFreq	2.286	1	0.1305	0.006	1	0.9367
DateJ:Habitat:SFreq	0.253	1	0.6149	5.845	3	0.1194

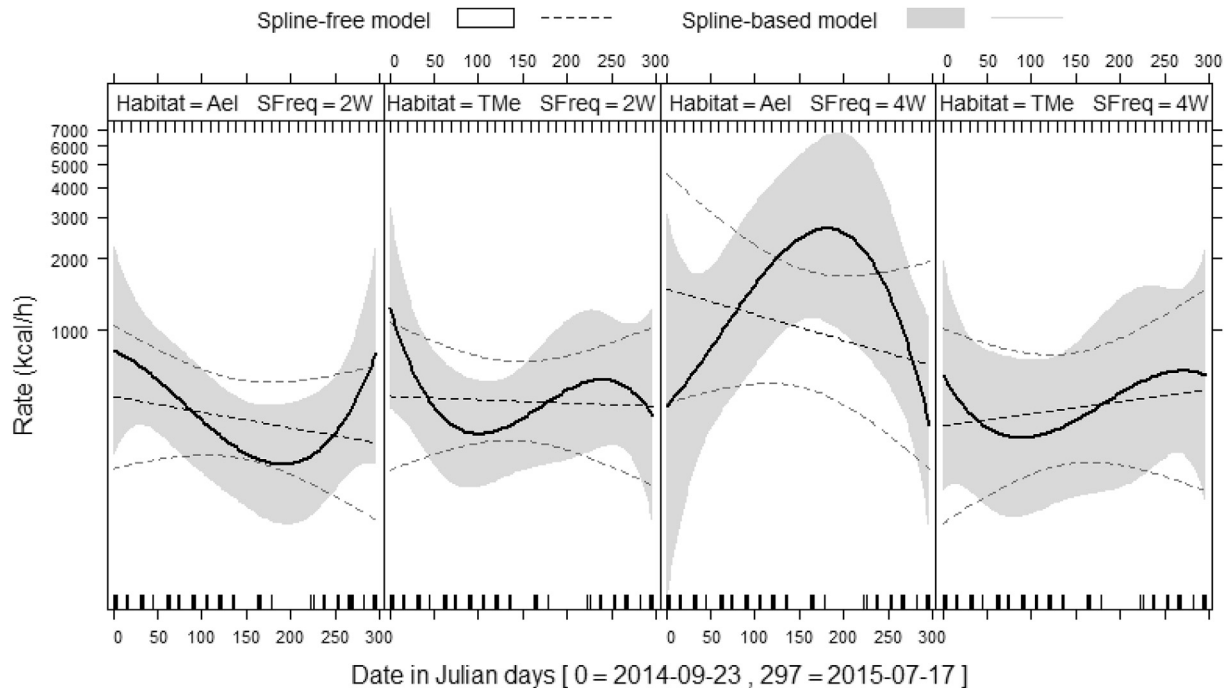
<sup>a</sup> Results of Type II and Type III tests of Cond and the three-way interaction DateJ:Habitat:SFreq are the same.

The entries associated with Var in the bottom part of the table show that most of the variability due to the random-effects grouping structure (between-sample variability) occurs at the innermost level of the structure, and hence is attributable to differences between harvesters in their ability to harvest at different seawater levels on different sampling dates [entry Var: Name: (CWLev: DateJ)]. Individual forager experience resulted in a variation in rates of return. With increasingly risky and challenging sampling conditions (Cond levels 3 and, especially, 4) the more experienced foragers gathered more prey and had higher rates of return than less experienced foragers. Tidal level variation between harvests had a moderate effect on the rates of return of foragers.

Type II tests of model-effects for the spline-based model (Table 5) show that samplingdate (DateJ) had no significant effect on the rate of return ( $\chi^2_{df=3} = 3.70$ ,  $p = 0.2963$ ). The predictor with the greatest effect is sampling conditions (Cond:  $\chi^2_{df=3} = 23.47$ ,  $p < 0.000$ ). The interaction between habitat and sampling frequency (Habitat:SFreq) also had a small effect (based on  $\chi^2_{df=1}$ ) that was statistically significant. Type III tests give broadly similar results to Type II tests, more especially for the terms involving sampling date (DateJ). Fig. 4 (effect plot of the population marginal means) shows that there is no depletionary effect linked to the repeated harvesting of shellfish over a period of 42 weeks, at either the two-weekly or the four-weekly sampling interval, regardless of habitat. Because sampling conditions (Cond) were modelled as an additive effect, changing the level of Cond at which effects were calculated has no effect on the relationships shown. Effects are merely shifted up or down on the y-axis by an amount determined by the level of Cond used.

The trend-tests reported in Table 6, in which the slope of the relationship between the rate of return and sampling date is tested against a slope of zero, i.e. no trend, showed that in all four design-compartment there was no evidence to reject the null hypothesis of no trend between foraging returns and sampling date, for both the spline-free and the spline-based models. In all cases, the 95% confidence interval includes zero. It therefore is not surprising that joint tests of trend are not significant. For the spline-free version of the model the results of the joint test are  $\chi^2_{df=4} = 0.362$ ,  $p = 0.8357$ ; for the spline-based version they are  $\chi^2_{df=4} = 0.607$ ,  $p = 0.6574$ .





**Fig. 4.** Trellis plot of the predicted effect on the rate of return (Rate) of sampling date (DateJ), habitat (Ael = Aeolianite; TMe = Table Mountain Sandstone), sampling frequency (SFreq: 2W = two-weekly; 4W = four-weekly), and sampling conditions (Cond), based on the depletion model (Eq. (1)). Sampling conditions (Cond) was set to its mean value. The y-axis is logarithmic in scale but has been labelled on the response scale. Bands show asymptotic 95% confidence intervals. The rug plot on the inner upper axis shows the prediction grid, that on the inner lower axis the sampling dates.

**Table 6**

Trend Tests of the Rate of Return (Rate) over Sampling Date (DateJ) for the Spline-free and Spline-based Versions of the Depletion Model (Eq. (1)) in the Four Design-compartments of the Study: Two-weekly (2W) and Four-weekly (4W) Harvesting Cycles on Aeolianite (Ael) and Table Mountain Sandstone (TMe). ( $H_0$ : Trend = 0,  $H_A$ : Trend  $\neq$  0).<sup>a</sup>

Habitat:SFreq	Trend	SE	CL <sub>L</sub>	CL <sub>U</sub>	Z-ratio	p-value
<i>Spline-free Model</i>						
Ael:2W	-0.002	0.002	-0.006	0.003	-0.722	0.4706
TMe:2W	0.000	0.002	-0.005	0.004	-0.148	0.8823
Ael:4W	-0.003	0.003	-0.008	0.003	-0.817	0.4137
TMe:4W	0.001	0.003	-0.004	0.007	0.429	0.6680
<i>Spline-based Model</i>						
Ael:2W	0.000	0.004	-0.007	0.008	0.130	0.8964
TMe:2W	-0.006	0.004	-0.014	0.002	-1.524	0.1275
Ael:4W	-0.001	0.006	-0.013	0.010	-0.210	0.8338
TMe:4W	-0.001	0.004	-0.010	0.007	-0.341	0.7332

<sup>a</sup> Trends are based on the log-transformed scale (the scale of the linear predictor of the model). Results were averaged over levels of DateJ (sampling dates) and Cond (sampling conditions). 95% confidence levels (CL) used.

### 3.3. Replenishment

The fitted replenishment model (Eq. (2)) is summarized in Table 7. As for the depletion model, sampling conditions (Cond) have a statistically significant negative linear effect (Cond.L) on the rate of return. The model explains 88.88% of the variance in the rate of return; 38.30% of this variance is explained by the fixed-effects part of the model, 50.57% by the random-effects part of the model. Fig. 5 shows the observed data.

Sub-plot (SPlot) and sampling conditions (Cond) have statistically significant effects on the rate of return, based on Type II and Type III WaldWald<sup>2</sup> tests (Table 8). The results of the two types of test are in good general agreement. Fig. 6 shows predictor effects conditioned on the compartments of the study that were modelled.

Post-hoc analysis using one-tailed tests (Table 9) showed that

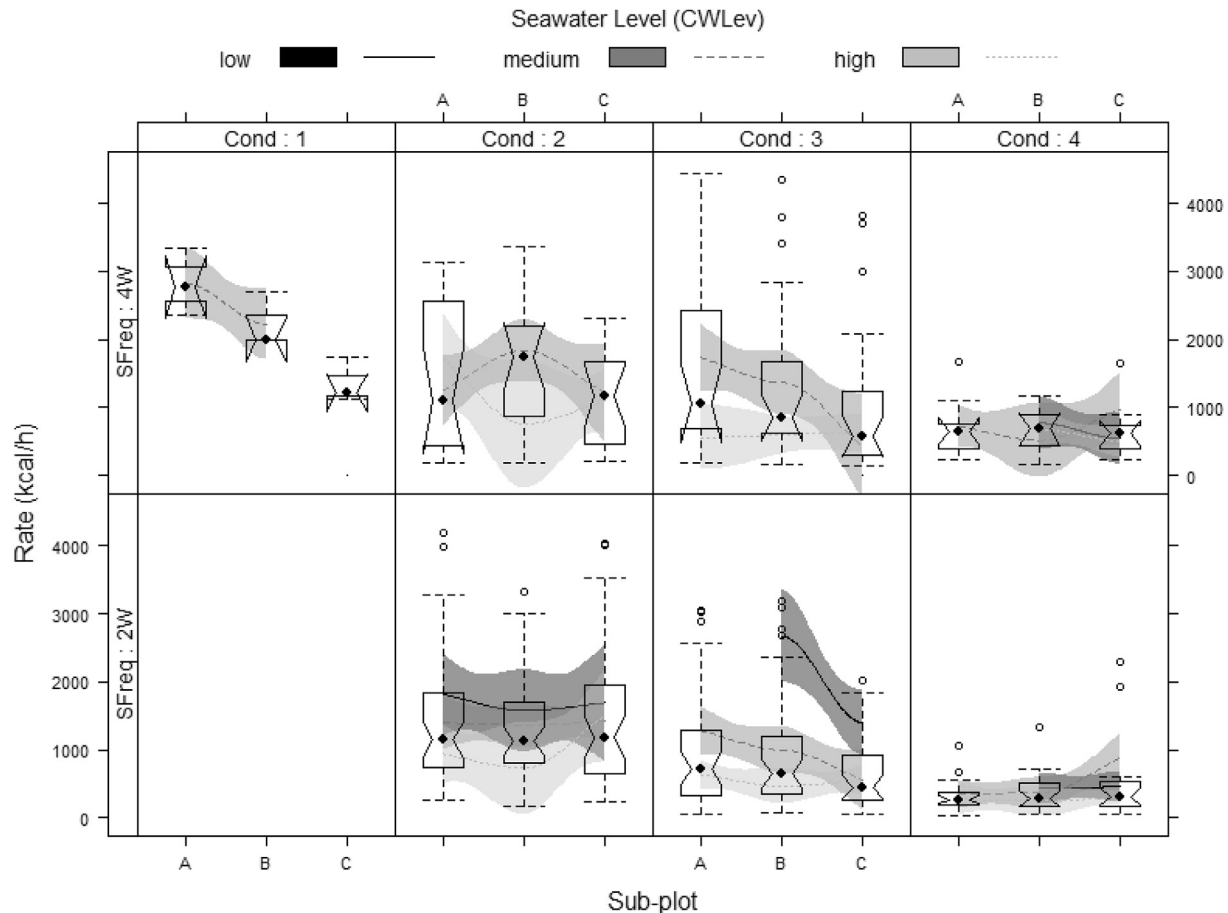
**Table 7**

Summary of the tweedie mixed model of the replenishment of sub-plots (Eq. (2)). Response: Rate of return.<sup>a</sup>

	Replenishment Model
(Intercept)	6.41 (0.22) ***
Habitat[S.Ael]	0.16 (0.12)
SFreq[S.2W]	-0.20 (0.12)
SPlot[S.A]	0.11 (0.06)
SPlot[S.B]	0.05 (0.06)
Cond.L	-1.21 (0.55) *
Cond.Q	-0.25 (0.44)
Cond.C	0.13 (0.26)
Habitat[S.Ael]:SFreq[S.2W]	-0.23 (0.12)
Habitat[S.Ael]:SPlot[S.A]	0.14 (0.06) *
Habitat[S.Ael]:SPlot[S.B]	-0.05 (0.06)
SFreq[S.2W]:SPlot[S.A]	-0.03 (0.06)
SFreq[S.2W]:SPlot[S.B]	-0.06 (0.06)
Habitat[S.Ael]:SFreq[S.2W]:SPlot[S.A]	-0.03 (0.06)
Habitat[S.Ael]:SFreq[S.2W]:SPlot[S.B]	0.12 (0.06) *
AIC	4811.88
BIC	4891.07
Log Likelihood	-2386.94
Num. obs.	477
Num. groups: Name:(CWLev:DateJ)	474
Num. groups: CWLev:DateJ	159
Num. groups: DateJ	53
Var: Name:(CWLev:DateJ) (Intercept)	0.37
Var: CWLev:DateJ (Intercept)	0.02
Var: DateJ (Intercept)	0.12
Var: Residual	0.11

\*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$

<sup>a</sup> Numbers in parentheses after the estimated regression coefficients ( $\beta$ s) are asymptotic standard errors. Models were fitted using sum-to-zero contrasts for Habitat and SFreq, and polynomial contrasts for Cond. Sum-to-zero coded variables carry a suffix in square brackets giving the treatment-level(s) of the factor. Var gives the variance of intercepts in groups of records identified by the referenced group in the random-effects structure. That is, the entry DateJ (Intercept) refers to the variance in the 53 intercepts of DateJ in the top-level grouping of the random-effects structure (Eq. (3)).



**Fig. 5.** Trellis plot of the observed data on the rate of return (Rate) versus sub-plot category, conditioned on sampling frequency (SFreq: 2W = two-weekly; 4W = four-weekly) and sampling conditions (Cond). Box-plots show the distribution of the rate of return in each sub-plot, ignoring seawater level; the solid circle shows the median, open circles show outliers. Loess smooths show the effect of three levels of seawater (level-categories determined by cutting the range of CWLev into three equal-length intervals).

the null hypothesis - that the rate of return from sub-plot B is not significantly less than it is from the other two sub-plots - holds for all but one contrast in the top part of the table (rows 1–8). The exception is the contrast with sub-plot A on Table Mountain Sandstone (TMe) during the two-weekly harvesting cycle (2W).

If we use a contrast matrix that averages over the design-compartments, i.e. over model-covariates and interaction-terms, we get the results shown in the last two rows of Table 9. These provide an overall test of whether replenishment is by long-shore replacement, i.e. migration into the lateral sub-plots from the side. There is no convincing evidence to support such a view; that is, we found no evidence that it is generally true that the rate of return from category B sub-plots is less than it is from either category A or category C sub-plots.

#### 4. Discussion

The results of this study show no significant depletion of prey species, nor long-shore replenishment effect, in either aeolianite or TMS habitats in response to sustained foraging by knowledgeable foragers over a period of 10 months. As was found by a previous study (De Vynck et al., 2016c), the weather and sea conditions (including tidal level) that prevailed during a foraging bout were the strongest predictors of return rates. The presence of a weakly expressed trend for lower return rates towards the end of the study period was a consequence of unfavourable harvesting conditions during that time. Because no significant lateral (long-shore)

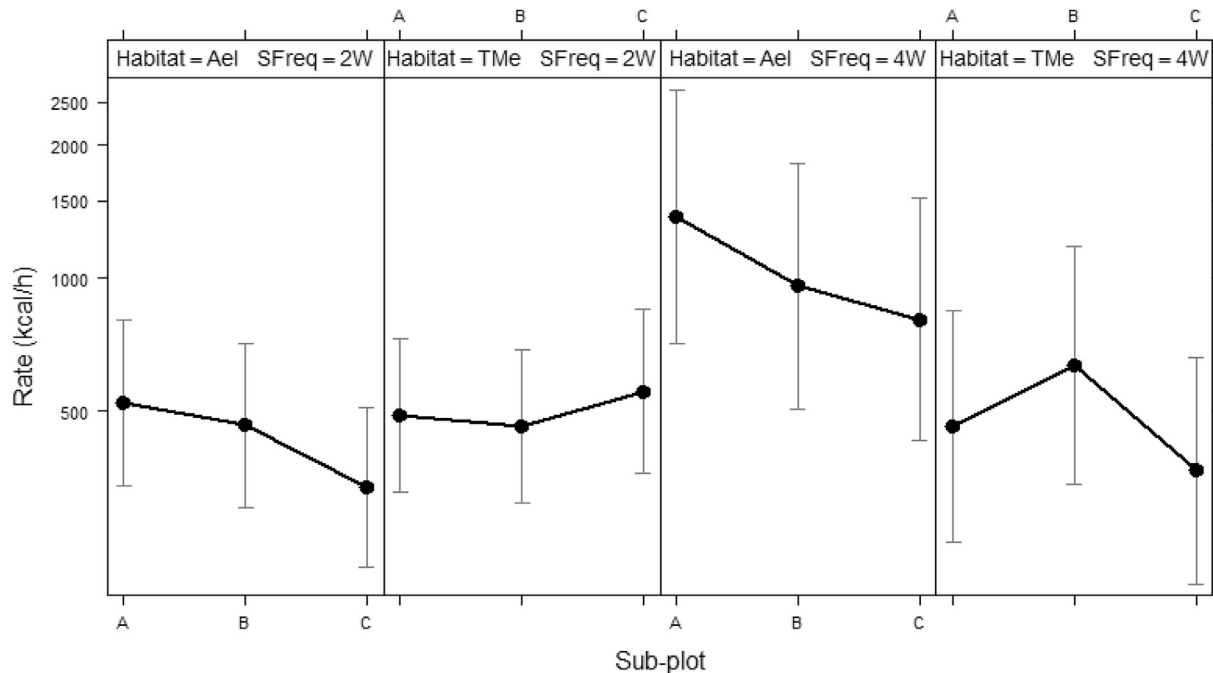
replenishment effect was detected, replenishment occurred by means of the vertical migration of mobile prey species (especially *Turbo sarmaticus*) from the adjacent shallow sublittoral zone. Overall, the intertidal zone showed high resilience to persistent foraging by skilled foragers over the 10 month period of the study. It is important to note that the low foraging intensity of the study was a design-choice, purposefully made in order to simulate the low population densities of humans that occurred during the MSA period of the south Cape coast.

**Table 8**

Type II and Type III Wald  $\chi^2$  Tests of the Effect on the Rate of Return of Terms in the Replenishment Model (Eq. (2)).<sup>a</sup>

Model Terms	Type II Tests			Type III Tests		
	$\chi^2$	Df	p-value	$\chi^2$	Df	p-value
Habitat	0.332	1	0.5642	1.580	1	0.2088
SFreq	2.221	1	0.1362	2.742	1	0.0977
SPlot	17.507	2	0.0002	7.731	2	0.0210
Cond	22.623	3	0.0000	22.623	3	0.0000
Habitat:SFreq	3.632	1	0.0567	3.464	1	0.0627
Habitat:SPlot	5.835	2	0.0541	5.639	2	0.0596
SFreq:SPlot	2.564	2	0.2775	2.199	2	0.3330
Habitat:SFreq:SPlot	5.101	2	0.0780	5.101	2	0.0780

<sup>a</sup> Results of Type II and Type III tests of Cond and the three-way interaction Date  $\times$  Habitat  $\times$  SFreq are the same.



**Fig. 6.** Trellis plot of the predicted effect on the rate of return (Rate) of sub-plot category, habitat (Ael = Aeolianite; TMe = Table Mountain Sandstone), sampling frequency (SFreq: 2W = two-weekly; 4W = four-weekly), and sampling conditions (Cond), based on the replenishment model (Eq. (2)). Sampling conditions (Cond) set to its mean value. The y-axis is logarithmic in scale but has been labelled on the response scale. Bars show asymptotic 95% confidence intervals.

**Table 9**

Simultaneous One-tailed Tests of the General Linear Hypothesis that the Rate of Return from Category B Sub-plots is Greater Than or Equal to that from Either Category A or Category C Sub-plots ( $H_0: B \geq A|C$ ,  $H_A: B < A|C$ ).<sup>a</sup>

Contrast	Habitat	SFreq	Est.	SE	CL <sub>L</sub>	Z-ratio	p-value
<i>Design Compartments</i>							
A–B	Ael	2W	0.119	0.167	–0.201	0.713	0.3630
C–B	Ael	2W	–0.322	0.162	–0.633	–1.989	0.9957
A–B	TMe	2W	0.056	0.017	0.023	3.367	0.0008
C–B	TMe	2W	0.182	0.147	–0.104	1.243	0.2005
A–B	Ael	4W	0.365	0.255	–0.125	1.428	0.1314
C–B	Ael	4W	–0.172	0.246	–0.643	–0.699	0.8858
A–B	TMe	4W	–0.317	0.240	–0.777	–1.320	0.9687
C–B	TMe	4W	–0.547	0.237	–1.000	–2.307	0.9984
<i>Results Averaged</i>							
A–B	.	.	0.039	0.098	–0.147	0.403	0.4829
C–B	.	.	–0.261	0.120	–0.490	–2.170	0.9971

<sup>a</sup> Results are given on the logarithmic scale (the scale of the linear predictor of the model). For the design-compartment tests (top part of the table), population marginal means were averaged over levels of Cond (sampling conditions); for the bottom part of the table (last two rows), they were averaged over levels of covariates Cond, Habitat, and SFreq, and over the interaction terms of the model (Eq. (2)). 95% confidence levels (CL) were used. p-values are right-tailed; they and the stated confidence levels have been adjusted for multiple testing using a method based on the multivariate *t*-distribution that controls the family-wise error rate.

#### 4.1. Species selection

Considered overall, the harvest was mainly comprised of *Turbo sarmaticus* (81.9%). This relatively large snail is abundant, easily harvested by hand, has a high flesh (calorific) yield, and apparently is replenished by migration from the shallow subtidal zone (Pulfrich and Branch, 2002). *Haliotis spadicea*, another mobile species, was the second most preferred prey species (5.8%). Yield per individual was lower than for *T. sarmaticus*. Reasons are that this species inhabits crevices, requires a tool to extract, and replenishment by migration from the shallow subtidal zone is likely to have been poor because of the limited mobility of the species, which amounts to a few metres over a period of months (Muller, 1984).

The third-highest component of the harvest was the limpet *Cymbula oculus* (4%). This species is abundant in the mid eulittoral zone and, on days with unfavourable tide and conditions, was the only foraging option because access to the lower tidal zones was restricted. *Haliotis midae* is a strongly preferred prey species, primarily because of its palatability (pers. obs.). However, its return rates were low because it is essentially a subtidal species, usually only a few smaller individuals occur in the lower eulittoral zone. Foragers only managed to procure this species during ideal tidal and weather conditions and it comprised just 2.8% of the total calorific composition. *Octopus vulgaris* and *Pyura stolonifera* comprised an appreciable part of the harvest (a total of 3.4%). However, neither contain material that would be preserved in the archaeological record. *Scutellastra longicosta*, the second-highest yielding limpet (1.2%), is abundant in the lower eulittoral zone. Foragers harvested this species opportunistically while searching for ideal prey. The remaining 11 species were harvested in very low numbers (a combined calorific yield of 0.9%), indicating either relatively low numbers (e.g. *Scutellastra tabularis*) or low yield per harvesting effort (e.g. *Scutellastra cochlear*, which, although often abundant, grows in wave-exposed areas of the lower eulittoral and is hard to detach from the substrate).

The composition of intertidal prey species that we found differs from that observed in early MSA archaeological records. The earliest known records of intertidal foraging (164 ka; Jerardino and Marean, 2010) indicate that species-choices were restricted to prey typical of the mid-to upper eulittoral zones. In the present study, prey choice corresponds to prey choice typical of the early MSA, with a relatively high yield of *Cymbula oculus* (procured when adverse conditions and high tides restricted access to the lower tidal zones), as found in the fossil record. By 110 ka, all the significant MSA sites in the south Cape (Blombos cave, Pinnacle Point and Klasies River Mouth) reveal that people were exploiting prey found in the lowest tidal zone, and these prey choices are similar to those of the present study. However, species-specific volumes collected during the MSA are moderately different from those recorded in the



present study.

A good example is *Perna perna*, which amounted to just 0.1% of the shellfish collected during our study, yet all MSA sites show significantly higher percentages of this species. A possible explanation for this difference is that *P. perna* was never processed on-site during either the present depletion study or the previous study (De Vynck et al., 2016c;  $n = 53 + 41$  harvests) whereas both *Turbo sarmaticus* and *Haliotis spadicea* usually were. Processing on site results in only edible flesh being transported back home, making an accurate determination of how many individuals of the species were harvested impossible and some species can then be underrepresented at these MSA sites. Also, species are not uniformly distributed along the coast or in different habitat types. *P. perna* is scarce on aeolianite reefs and was not abundant in the TMS plots in the present study, although it can be very abundant on wave-exposed headlands of TMS. Another possible reason relates to prey-choice switching. If the same shore is repeatedly foraged on successive days over a spring low-tide cycle, mobile prey, especially *T. sarmaticus*, are likely to become depleted in the short term. This could result in a change of prey choice to *P. perna* while one spring low period is still in effect. None of the MSA sites (Voigt, 1973; Thackeray, 1988; Henshilwood et al., 2001; Jerardino and Marean, 2010; Langejans et al., 2012) show *T. sarmaticus* in such high volumes as occurred in the present study (where plots were effectively 'rested' for either two weeks or four weeks). It is relevant that TMS sites in the present study consisted mainly of wave-cut platforms, which have higher abundances of *T. sarmaticus* than TMS rocky headlands or boulder shores do; *T. sarmaticus* is also particularly abundant on aeolianite wave-cut platforms. MSA sites today are not necessarily near ideal TMS or aeolianite intertidal habitats for *T. sarmaticus* procurement, and the intertidal structures near these sites would have varied over time because of sea level transgressions and regressions on the Palaeo-Agulhas Plain (Cawthra et al., this issue). Consequently, high numbers of *T. sarmaticus* would not be expected to have occurred at such sites during the MSA.

#### 4.2. Depletion and replenishment in the foraging experiments

The depletion experiments were continued for a period of 42 weeks. They were begun in early spring (September 2014) and ended in winter the following year (July 2015). Towards the end of the experiment, with the onset of winter (May to July), there was a drop-off in yield caused by a deterioration of the sampling conditions. We controlled for this and other weather-related effects by using the variable Cond in our depletion models, and by including forager (Name), and hence forager ability, in the random-effects structure of the models. However, even if we do not control for sampling conditions there is still no statistically significant evidence of depletion [Date] for such a model fitted using a spline has a Wald  $\chi^2_{[df=3]} = 6.768$  ( $p = 0.0797$ ) following a Type II test (see Table 5 for comparison). The fact that we found no evidence of depletion means that the intertidal resources of the south Cape are resistant to depletion if harvested on a two-weekly or four-weekly cycle. It is relevant that our prior observations had established that three foragers foraging around the low-water mark, as in our study, deplete the area foraged of the main prey species. What then underlies this resilience? If target species do not deplete from harvest to harvest, but show a temporary depletion immediately post-harvest, how are they replenished, what is the most likely mechanism?

Prior observation of indigenous foragers on the south Cape showed that foraging at even the low intensity used in the present study results in the immediate depletion of the pond-area foraged. Yet, as the present study shows, two-weeks later the same area was

replete with the preferred prey species. Comparison of the harvests from consecutive bouts showed no depletionary trend, regardless of the type of habitat foraged (aeolianite or Table Mountain Sandstone) or the foraging intensity used (two-weekly or four-weekly). There are several mechanisms (discussed below) that could explain such resilience, the most likely one being that mobile species, which make up the overwhelming proportion of each harvest, are replaced by adults that migrate into the area from somewhere else (Yssel, 1989).

First, replenishment of target species via reproduction (*de novo* recruitment) would in time restore depleted intertidal and subtidal populations; however, rates of recruitment would in general be too slow to replenish most of the species, even after 10 months. The major reproductive period in southern African mollusc species appears to be between September and March, with recruits appearing in the intertidal zone during winter (Lombard, 1977; McQuaid, 1980; Yssel, 1989). However, apart from *Octopus vulgaris* (which can grow to 4 kg within 300 days), "forageable" sizes of the mobile prey species are only attained years after their recruitment into the intertidal zone. *T. sarmaticus* only reaches forageable shell length three to four years after recruitment (Yssel, 1989). *Haliotis spadicea* (5.8%) is relatively slow-growing and takes two years to reach a shell length of about 35 mm (Muller, 1984). Furthermore, it is never very abundant, so *de novo* recruitment would be minimal within a short period and may be excluded as a plausible explanation.

Secondly, sessile (e.g. mussels) or near sessile (e.g. most limpets) species can only replenish the intertidal zone through reproduction. *P. perna* and *C. oculus* have the highest recruitment rates among the targeted sessile species, but both have a lifespan of two to three years and viable shell sizes are only reached after about one year. *De novo* recruitment would therefore have made little contribution to the harvest. Moreover, these are not what would normally be considered to be resilient species. Notably, *P. perna* populations can suffer long-term damage from over-harvesting if whole communities are 'sheeted' from the rocks. Other intertidal invertebrates can then, and do, replace *P. perna* on substrates from which it has been removed, causing delays in recruitment (Dye, 1992). Although *P. perna* comprised only 0.1% of total harvest in the present study, and the mussels were picked individually rather than "sheeted", the MSA record indicates that it was more intensively exploited in the past.

Thirdly, another possible mechanism underlying resistance to depletion is the *in situ* recruitment of smaller individuals into a harvestable size range. That is, for any target species, some smaller individuals may, during the course of the experiment, have grown big enough to become worth harvesting. The effect of such a mechanism is likely to have been small because harvesting took place frequently and the growth rates of most of the animals harvested are relatively slow. *Turbo sarmaticus*, for instance, amounted to 81.9% of the total harvest but has a growth rate that is too slow for this mechanism to have had any appreciable effect on replenishment over the period of the study. *Perna perna* and *Cymbula oculus* have the fastest growth rates of all the targeted sessile species. However, *P. perna* formed a very small proportion of the overall harvest, and although *C. oculus* formed the highest proportion of the harvest of sessile species, its growth rates are not sufficient for it to have had an effect on replenishment (see later). Consequently, recruitment into the target size range is not considered to be an effective replacement mechanism based on the results of the present study.

Finally, for the reasons given above, and because the bulk of the harvested species are mobile species, it is reasonable to conclude that replenishment occurred mainly by means of the migration of adults from elsewhere. Our results show that this "elsewhere" must

be the adjacent deeper water (subtidal fringe/shallow subtidal) and not the lateral adjoining ponds. The key experimental finding here is that the central sub-plots of our study were just as productive, and therefore as resilient to depletion over time, as the lateral sub-plots were. This excludes long-shore migration as a reasonable explanation. Replenishment by migration down the shore may also largely be excluded because the main mobile target species (*Turbo sarmaticus*, *Haliotis spadicea*, *H. midae* and *Octopus vulgaris*) are absent from the upper eulittoral zone and are small and relatively uncommon in the mid-eulittoral zone. They are largest, and occur in the greatest numbers, in the lower tidal and shallow subtidal zones.

Replenishment would therefore have had to occur mainly by the migration of mobile species from the subtidal zone. At the current study-sites (and on much of the associated coastline) the rocky shore recedes gradually from the intertidal zone into the ocean, resulting in extended shallow subtidal areas, 'pantries' of mobile species. It is in this habitat, the lower eulittoral zone and the sub-littoral fringe, that the targeted prey species, especially *T. sarmaticus*, occur in abundance. For this is where wave action keeps the water well oxygenated and provides an abundant source of food in the form a high associated algal biomass (Bustamante and Branch, 1996). At subtidal depths between 2 m and 10 m, *Turbo sarmaticus* can often number  $>2 \text{ m}^{-2}$  (Pulfrich and Branch, 2002). It is likely that mobile species from this rich store would rapidly move up-shore to replace depleted species as niche space became available.

#### 4.3. Depletion on contemporary shores

Studies of the effect of foraging for shellfish in recent times in the east Cape - ca.  $>400 \text{ km}$  to the east of the study area - have demonstrated both the depletion of populations of *Turbo sarmaticus* and a reduction in the mean size of individuals (Foster and Hodgson, 2000; Proudfoot et al., 2006). Comparison of such findings with our results is complicated by several notable differences. First, shores of the south Cape are more productive than those further east because of the enriching effect on the former of the confluence of the warm Agulhas and nutrient-rich cold Benguela Currents (Bustamante et al., 1995). Secondly, and perhaps more importantly, many of the east Cape shores that have been studied (Foster and Hodgson, 2000; Proudfoot et al., 2006) have sandbanks only a few metres below the rocky intertidal platforms and/or rapidly receding bathymetries (Yssel, 1989). Hence there is no, or only a very limited, "pantry" of animals available to replenish a depleted intertidal zone. Finally, the levels of exploitation, in terms of both the duration and the intensity of the exploitation, recorded in these earlier studies were very much higher than they were in our experiments. This, too, was evident in studies conducted further east, on the Wild Coast, where the exploitation of sessile intertidal species caused serious depletion, and where extended exploitation appears to have led to the disappearance of mobile species (Bigalke, 1973; Hockey and Bosman, 1986; Lasiak and Field, 1995; Lasiak, 1999; Proudfoot et al., 2006).

#### 4.4. Depletion signals in the archaeological record

Studies of pre-historic depletion on shores are difficult to compare globally. Some studies focus on the depletion of sessile prey species (Jones and Richman, 1995; Kennedy, 2004; Braje et al., 2007; Whitaker, 2008), others focus on areas with nutrient-poor seas and shores that differ in structure from those of South Africa, especially those of the south Cape (Thomas, 2002; Bird et al., 2002, 2004). In South Africa, archaeological studies on the variation of within-species sizes and species choices over time indicate the

occurrence of depletion on both the west coast and the south coast (Steele and Klein, 2008; Langejans et al., 2012; Klein and Steele, 2013). The west coast is fed by the nutrient-rich cold Benguela Current, resulting in low species diversity but high within-species abundance (Branch et al., 1994). Forageable mobile species are scarce as they predominantly inhabit the subtidal zone. The south coast is influenced by both the Benguela Current and the warm Agulhas Current. Subtropical shores further up the east coast, where there is no influence of the Benguela Current, have high species diversity but low within-species abundance. The confluence of both currents on the south coast causes both high diversity and abundance (Branch and Menge, 2001).

The west coast archaeological record is dominated by sessile species that decline in size from the MSA to the LSA (Parkington, 2008; Steele and Klein, 2008). Indeed, a decrease in the size of sessile species over time is evident everywhere because sessile species show low resilience to human predation. However, Lasiak (1991, 1992, 1993) found that not only humans cause a decrease in population density or shell size. This was especially highlighted by her study of the limpet *Cellana capensis* on exploited and non-exploited shores where there was no evidence for a decline in density on the exploited shore (Lasiak, 1993). In contrast, there was a decline in density on the non-exploited shore resulting from poor recruitment and high mortality of older limpets. Temporal shell size shifts on both shores combined with inter-annual variation in recruitment was not related to human predation. The addition of forageable mobile species to the pre-historic range of prey choices would have increased the resilience of shores where they were found. However, Klein and Steele (2013) showed that *Turbo sarmaticus* sizes on the south Cape also declined with the onset of the LSA. Throughout the MSA, on both the west and south coasts, there is no visible decline in either sessile or mobile species sizes and the suggestion is that, in the LSA, increasing population densities and a resulting higher foraging intensity caused these decreases in size, which are a sign of depletion (Klein and Steele, 2013).

Therefore, the lack of depletion in the MSA implies a light footprint, comparable to the foraging levels of the present study. Larger human populations in the LSA, especially after the arrival on the coast of Khoekhoen pastoralists (Henshilwood, 1996), could well have resulted in significant depletion.

#### 4.5. Implications for human evolution

The present study was done over 10 months and was designed to simulate a level of foraging similar to that used in MSA times, when foraging is thought to have been done by small, mobile groups of foragers providing for small communities (Marean et al., 2014). MSA coastal foraging would have gone on for millennia and specific foraging patches would likely have been revisited periodically. Therefore, the results of the present study are, by design, considered to provide a reasonable estimate of the resilience of these resources under typical MSA conditions covering an unspecified but extended period of time.

The modern south Cape intertidal zone provides insights into shellfish productivity and resilience (the present study and De Vynck et al., 2016c) that shed light on the likely use of this resource during prehistoric times. The extant habitat reflects an inter-glacial period, but when *Homo sapiens* first entered the coastal food niche during Marine Isotope Stage 6 (MIS6) (193ka to 125ka; Middle to Late Pleistocene) the world was going through a glacial period. By  $\sim 110 \text{ ka}$ , the archaeological evidence suggests that early modern humans had fully adapted to using coastal resources. After MIS5e, and throughout MIS5-3, conditions were such that sea levels were always somewhat lower than they had been earlier. The systematic transgression and regression of the coastline during this

time, combined with the gradual disappearance of the Agulhas Bank, rapidly exposed geologically different intertidal zones (Van Andel, 1989; Fisher et al., 2010; Cawthra et al., *this issue*) that would have had a major influence on intertidal productivity. During glacial periods, the south Cape's portion of the Agulhas Bank benefitted from an increase in aeolianite reefs (Cawthra et al., 2016; Cawthra et al., *this issue*), a highly productive type of marine habitat for foragers (De Vynck et al., 2016c). Furthermore, the influence of the nutrient-rich Benguela Current increased during MIS6 as a result of a decrease in the seepage of the Agulhas Current into the Atlantic Ocean (Little et al., 1997; Peeters et al., 2004). Hence, the productivity and resilience of intertidal resources may even have been greater during glacial periods than they are now. But even if it is not true that the pre-historic (MIS6) coast of the south Cape was more productive than it is now, our results clearly show that intertidal shellfish resources likely would have provided a dependable source of food throughout the MSA, and probably at least until the arrival of Khoe-khoen pastoralists on these shores, when increasing human populations would have increased harvesting rates (Henshilwood, 1996; Jerardino, 1997).

Intertidal shellfish are easily procured without complex technology, and during favourable conditions are highly productive (De Vynck et al., 2016c). While some researchers have asserted that shellfish have low return rates because of high processing costs (Clark and Kandel, 2013; De Vynck et al., 2016a,b,c) demonstrate that shellfish return rates can exceed even very productive hunting. Shellfish are nutritionally beneficial (Kyriacou et al., 2014) and fit the category of so-called functional foods, meaning that they have benefits over and above that of providing basic nutrition (Gómez-Pinilla, 2008; Hosomi et al., 2012). However, if they lack resilience in the face of predation then their value as even a primary food resource is minimal. Our study, because it was designed to simulate the level of foraging that would have been required to support populations similar in size to those of the MSA, shows for the first time that intertidal shellfish on the south coast of South Africa are highly resilient to moderately intense foraging by humans. A long-term reliance on this resource is therefore feasible, a fact that lends added credence to the suggestion that intertidal shellfish may have been a key resource for early modern humans, and an important factor in their social (and biological) evolution. It is not unreasonable to suppose that the addition and use of a new and important habitat, and its associated resources, was associated with the development of new and/or modified patterns of behaviour.

It is not clear to what extent these new patterns of behaviour were due to the addition to the diet of a new (functional) food type, one that is known to be associated with cognitive development, and to what extent they were due to the need to work more closely with others to protect the new resource. It is possible that a combination of both factors was involved. Some do argue that the addition of intertidal resources to diet did not influence cognitive development (Klein and Bird, 2016). What is clear from the archaeological record is that the new resource was regularly sought after and used by MSA people in the Cape. The glacial climatological conditions that existed at the time would in all likelihood have reduced the availability of terrestrial resources, but it is unlikely that they greatly affected the productivity of the intertidal zone, which may even have seen an increase. Any reduction of the terrestrial food supply would almost certainly have increased both territoriality and the potential for greater conflict, leading to the selection of more complex social systems and to greater cooperation (Marean, 2016). Interglacial periods likely increased the availability of terrestrial resources, and with the addition of intertidal resources, daily caloric demand would have been satisfied relatively quickly and easily, resulting in more time for social interaction, further aiding in the behavioral development of our species.

## 5. Conclusion

The south coast of South Africa contains MSA settlements that provide the earliest evidence of the intensive use of coastal resources by early modern humans. The available evidence suggests that easy access to such a reliable and easy-to-harvest resource (a sort of marine "bread basket") had a profound effect on the social behaviour of MSA communities and possibly also the adaptation and evolution of *Homo sapiens*. Some researchers have challenged the notion that intertidal shellfish meet the requirements of a primary dietary item (Clark and Kandel, 2013). Depletion experiments performed between Still Bay and Gourits Mouth on the south Cape coast do however show that intertidal resources are highly productive, resilient, and nutritious, and hence have all the characteristics required of a primary food resource. In the present study, mobile species accounted for 92.2% of the caloric harvest composition, with *Turbo sarmaticus*, a very mobile species, dominating the sample with a representation of 81.9%. The results of the study show that mobile intertidal resources are replenished from subtidal 'pantries' in response to ongoing exploitation by foragers, at intensities similar to those expected of populations in the MSA. Not only are the return rates from a mere 2 h of foraging high, but the harvesting process can be repeated with minimal effort in the same areas every two or four weeks for a period of ten months, and perhaps longer. One caveat is that favourable weather conditions and tides are necessary for optimal harvests as these species are found in the more weather- and tidally affected lower tidal zones. De Vynck et al. (2016c) showed that the south Cape intertidal is only productive over spring tides and foragers were not interested in these resources over neap tides as return rates were too low. To an extent, the adverse effects of inclement weather and extreme tides were offset by individual forager ability; for under such conditions the more knowledgeable foragers had higher rates of return than less able foragers did. Sessile species formed a small proportion of the overall harvest, possibly because of the restricted temporal extent of the depletion experiments. Had they been performed for a longer period, replenishment by mobile species would likely have eventually decreased because of the depletion of subtidal mobile species in the vicinity. Foragers would then probably have begun to target sessile species, leading to an overall depletion of the intertidal patch. However, it is likely that MSA coastal foragers alternated foraging activity between different intertidal foraging areas, allowing exploited areas to recover. The dominance of *Turbo sarmaticus*, but more especially its dominance on aeolianite, means that there would have been a greater resilience to over-harvesting during glacial periods because the then exposed Palaeo-Agulhas plain would have provided an increased area of this type of marine habitat (Cawthra et al., *this issue*). At that time, this part of the coastline also had minimal topography, and so provided slowly receding bathymetries, giving ample opportunity for the ongoing replenishment of foraging sites from stocks of subtidal mobile shellfish and other types of marine prey. The existence of such a highly resilient resource in a competitive landscape would have had significant implications for the evolution of social complexity. Finally, ongoing, and arguably increasing, dependence on such shellfish resources would have offered a caloric reprieve during adverse climatic conditions, when terrestrial resources would likely have been subject to periodic declines.

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Mark Difford will be missed and the lead author dedicates this paper in his memory.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106041>.

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